

The Effect of Sleep on Memory Consolidation of Learning in Infants and Toddlers

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Abstract

Sleep-dependent memory consolidation refers to the process whereby the brain reprocesses and strengthens newly learned information or skills during sleep, thereby rendering memories more stable and durable. Sleep plays a crucial role in consolidating newly acquired information into stable long-term memory. The effects of sleep-dependent memory consolidation vary across different memory types, and different stages and characteristics of sleep exert differential influences on the consolidation of different memory types. Building upon adult research, recent studies on infants and young children have revealed that sleep also serves a vital function in memory consolidation even during early stages of individual development. Compared to control groups that did not experience sleep, infants and young children who slept after learning demonstrated significantly improved learning outcomes and could solve problems better and faster. During sleep in infants and young children, brain regions associated with memory, such as the hippocampus and medial temporal lobe, become significantly activated, and electroencephalographic features like sleep spindles and slow waves correlate with memory consolidation efficacy in this population. This review introduces advances in behavioral and neuroscientific research on sleep-dependent memory consolidation in infants and young children from the perspective of two distinct memory types—declarative memory and procedural memory—thereby facilitating an understanding of how sleep contributes to memory consolidation for learning in early development.

Full Text

The Role of Sleep in Memory Consolidation for Infant and Toddler Learning

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Abstract: Sleep-dependent memory consolidation refers to the process by which the brain reprocesses and strengthens newly learned information or skills during sleep, rendering memories more stable and enduring. Sleep plays a crucial role in transforming newly acquired information into stable long-term memory. The effects of sleep-dependent memory consolidation vary depending on memory type, and different sleep stages and characteristics exert differential influences on the consolidation of different memory types. Building upon adult research, recent studies on infants and toddlers have revealed that sleep serves a vital function in memory consolidation even during early developmental stages. Compared to control groups that remain awake, infants and toddlers who sleep after learning demonstrate significantly improved learning outcomes and can solve problems more effectively and efficiently. During sleep, brain regions associated with memory, such as the hippocampus and medial temporal lobe, show significant activation in infants, and electrophysiological features like sleep spindles and slow waves correlate with memory consolidation efficacy. This review examines the behavioral and neural research progress on sleep-dependent memory consolidation in infants and toddlers from the perspective of two distinct memory systems—declarative and procedural memory—to elucidate how sleep consolidates learning during early development.

Keywords: infants and toddlers, sleep, memory consolidation, sleep slow waves, sleep spindles

Sleep constitutes one of humanity's primary activities, occupying one-third of our lives. Beyond restoring physical energy and stabilizing emotions (Ekinci et al., 2016; Hatzinger et al., 2013, 2014; Przepiórka et al., 2019), sleep consolidates memory and facilitates learning (Stickgold, 2005). Adult studies have demonstrated that post-learning sleep helps solidify newly acquired information into stable, enduring memory representations (Schmid et al., 2020; Stickgold, 2005). Memory formation comprises an initial learning phase followed by two consolidation stages—memory stabilization and memory enhancement (also termed offline learning) (Walker, 2005). While initial learning and stabilization (maintaining post-learning memory representations) do not depend on sleep, the enhancement phase (improving memory without active rehearsal) typically occurs during sleep (Al-Sharman & Siengsukon, 2014; Farhadian et al., 2021; Sugawara et al., 2014; Walker, 2005). Individuals who sleep after learning show significantly superior learning outcomes compared to those who remain awake (Walker, 2005), a phenomenon known as sleep-dependent memory consolidation (Stickgold, 2005).

Adult research confirms that sleep consolidates both declarative and procedural memory (Diekelmann et al., 2009; Schmid et al., 2020). Compared to continuous wakefulness, post-learning sleep enhances declarative memory while also improving procedural memory performance (Wang et al., 2021). However, the

underlying neural mechanisms may differ across memory types (Ackermann & Rasch, 2014). Declarative memory consolidation activates the parahippocampal gyrus, thalamus, medial temporal lobe, prefrontal cortex, and cerebellum (van Dongen et al., 2012), whereas procedural memory consolidation involves the striatum, hippocampus, cerebellum, and motor cortex (Albouy et al., 2008; Cousins et al., 2016). Furthermore, declarative memory consolidation primarily occurs during non-rapid eye movement (NREM) sleep (Rasch et al., 2007), while procedural memory consolidation mainly takes place during rapid eye movement (REM) sleep (Plihal & Born, 1997; Qian et al., 2022). Adult memory consolidation research also identifies sleep spindles as a crucial electrophysiological marker, with their frequency, amplitude, and power closely linked to the consolidation of new information and memory retention (Ulrich, 2016).

Infants are defined as children within the first year of life (including the neonatal period of the first 28 days), while toddlers refer to children aged one to three years (sometimes broadly encompassing one to six years). Research on infants and toddlers similarly indicates that sleep promotes memory consolidation. Behavioral studies show that sleep enhances learning abilities in young children (Berger & Scher, 2017; Seehagen et al., 2015), which primarily involve acquiring new knowledge and skills such as motor skill learning (crawling, sitting, standing, walking) and perceptual learning (color and number recognition) (Veldman et al., 2019). Neuroimaging studies reveal that brain regions activated during initial learning are reactivated during subsequent sleep (Johnson et al., 2020), and EEG research demonstrates connections between specific types of sleep-dependent memory consolidation and sleep architecture features (Friedrich et al., 2019; Satomaa et al., 2020).

However, human sleep undergoes rapid development during the first years of life (Iglowstein et al., 2003; Jenni et al., 2007), with infant sleep patterns differing substantially from those of adults. Early in life, newborns exhibit polyphasic sleep patterns comprising three sleep types: active sleep, quiet sleep, and indeterminate sleep (Ednick et al., 2009). From the second month postpartum, active sleep gradually evolves into REM sleep and quiet sleep into NREM sleep (Jenni et al., 2004; Kurth et al., 2015). While adult NREM and REM sleep alternate throughout the night in approximately 90-minute cycles (McCarley, 2007), three-month-old infants cycle through these stages roughly every 60 minutes (Davis et al., 2004). During the first year of life, sleep spindle density, duration, and frequency in frontal and parietal regions increase continuously, reaching a lifetime peak (D' Atri et al., 2018; Jenni et al., 2004). Sleep spindles emerge at one to two months of age (Grigg-Damberger et al., 2007), then begin declining in power, density, and duration between 12 and 30 months (D' Atri et al., 2018; Page et al., 2018), continuing to decrease across the lifespan (Clawson et al., 2016; Lokhandwala & Spencer, 2022). Sleep slow waves can be observed in infants aged two to four months (Fattinger et al., 2014), gradually increasing during early childhood before decreasing around puberty (Campbell & Feinberg, 2009). These abundant sleep spindles and slow waves during infancy play crucial roles in early memory encoding and consolidation.

Unlike adults, daytime sleep (i.e., napping) constitutes a common component of infant and toddler sleep (Galland et al., 2012; Iglowstein et al., 2003) and proves essential for early memory development (Horváth & Plunkett, 2018). First, daytime sleep helps infants and toddlers consolidate and retrieve new information learned during the day, enhancing memory stability and persistence. Research shows that six- and twelve-month-old infants who nap for over 30 minutes within four hours of learning retain memories longer (Seehagen et al., 2015). Second, daytime sleep strengthens learning outcomes, with studies demonstrating that toddlers who sleep immediately after learning new skills show significant performance improvements (Berger & Scher, 2017), indicating that daytime sleep enhances newly formed memories during learning.

Given these significant differences in sleep structure and physiological mechanisms between infants/toddlers and adults, findings from adult sleep-dependent memory consolidation cannot be directly generalized to young children. Moreover, examining sleep's role in memory consolidation during infancy—characterized by high brain plasticity and unique sleep features—can deepen our understanding of the underlying neural mechanisms. This review synthesizes research on sleep's function in infant and toddler memory consolidation, summarizing its effects on declarative and procedural memory to provide a theoretical foundation for understanding how sleep influences neurodevelopment, cognitive development, and motor development in early childhood.

2. Sleep Consolidation of Declarative Memory in Infants and Toddlers

Throughout infancy and toddlerhood, daytime napping plays an important role in consolidating declarative memory (Mason et al., 2021). Declarative memory includes episodic memory (autobiographical memories associated with temporal or spatial context) and semantic memory (memory for general knowledge). It should be noted that since infants and toddlers have not yet fully developed language abilities such as semantic comprehension and conceptualization, this section will focus on sleep's impact on language and conceptual generalization abilities in the semantic memory domain.

2.1 Sleep Consolidation of Episodic Memory in Infants and Toddlers

In research on episodic memory during infant sleep, Horváth et al. (2018) used a visual paired comparison task to investigate sleep-dependent memory consolidation in three-month-old infants, finding that only infants who napped after learning (1.5 hours) could remember the learned cartoon faces. Moreover, learning speed correlated with sleep EEG measures: the time infants took to habituate to cartoon faces was inversely proportional to frontal sleep spindle density. Spencer's research group in the United States examined sleep's impact on episodic memory in three- to six-year-old toddlers using two different declarative memory tasks. The first study (Kurdziel et al., 2013) employed a

visuospatial learning task and found that toddlers who napped showed higher recall accuracy for cartoon picture locations than those who did not nap, with this difference remaining significant after 24 hours and sleep spindle density positively correlating with recall accuracy. The second study (Lokhandwala & Spencer, 2021) used a cartoon picture sequence memory task and similarly found that toddlers in the post-learning sleep group showed higher recall accuracy in delayed testing than the wake group, with group differences persisting after 24 hours and recall accuracy positively correlating with slow-wave sleep duration. Spencer's two studies indicate that different sleep features make unique contributions to different types of episodic memory during toddlerhood: spatial memory may depend more on sleep spindles, while episodic sequence memory may rely more on sleep slow waves.

Deferred imitation is a widely recognized measure of episodic memory (McDonough et al., 1995), in which participants imitate actions they observed others perform after a time delay. Seehagen's research group in Germany employed this paradigm in three studies, having infants watch and learn from an experimenter's manual toy manipulation (e.g., moving a car, changing a doll's gloves) face-to-face to examine napping's effect on action imitation memory. The first study (Seehagen et al., 2015) found that six- and twelve-month-old infants who napped after action imitation learning showed greater memory quantity and accuracy for learned actions compared to same-age infants who did not nap, with group differences maintained for at least 24 hours. This study provided the first experimental evidence supporting sleep's role in consolidating declarative memory in infants under one year. The second study (Konrad et al., 2016) found that twelve-month-old infants who napped after action imitation learning not only showed significantly better memory quantity for learned actions than non-napping infants but also could extract key learning points from novel stimuli, suggesting that sleep helps infants apply recently acquired knowledge to new contexts. The third study (Konrad et al., 2016) further divided twelve-month-old infants into post-learning sleep, wake, and baseline (no learning) groups, using differently colored toys in learning and test phases (e.g., replacing a learned red mouse doll with a pink one in testing) to examine learning and memory flexibility. Results showed the sleep group demonstrated higher memory quantity for learned actions and executed the first learned action faster than the wake group, indicating that sleep promotes infants' flexible application of learned knowledge to similar retrieval cues. Collectively, Seehagen's three studies demonstrate sleep's important role in memory encoding and consolidation in infants (Seehagen et al., 2019). Additionally, Konrad et al. (2019) investigated selective sleep memory consolidation in toddlers using an action imitation paradigm. During learning, fifteen- and twenty-four-month-old toddlers were shown eight action sequences involving both relevant actions for operating four toys (e.g., removing an obstacle in front of a toy car to let it roll down a ramp) and irrelevant actions (e.g., removing an obstacle behind a stationary toy car). Toddlers who did not sleep after learning retained information about all eight action sequences, whereas those who slept did not show this ordered recall pattern—they only

clearly remembered the four toy-relevant actions. This study provided the first evidence of selective sleep memory consolidation in toddlers, demonstrating that sleep helps children selectively “discard” information they deem useless or irrelevant for future use.

Targeted memory reactivation (TMR) represents an important paradigm for investigating the neural mechanisms of sleep-dependent memory consolidation (Hu et al., 2020). Adult studies show that TMR for declarative memory significantly activates memory-related brain regions including the parahippocampal gyrus, thalamus, and medial temporal lobe (van Dongen et al., 2012). Ghetti’s research group in the United States used the TMR paradigm to examine the neural mechanisms of sleep in consolidating episodic and semantic memory in two-year-old toddlers. In the first episodic memory study (Prabhakar et al., 2018), experimenters had toddlers play with specific dolls in specific rooms while listening to target songs. During natural nighttime sleep one week after learning, functional MRI signals were collected while playing target and novel songs. Results showed that when memory cues associated with episodic memory were played during sleep (target songs, both forward and reversed), toddlers showed increased bilateral hippocampal activation compared to novel songs, with right hippocampal activation positively correlating with memory accuracy for associations between target songs and room locations/dolls. This study highlights the hippocampus’ s important role in episodic memory consolidation during early development. In the second episodic memory study (Mooney et al., 2021), toddlers learned three person-location pairings in sequence (first a doctor went to school, then a firefighter went to the slide, finally an astronaut went to the school bus). Once toddlers could successfully pair the three person-space relationships in chronological order, the program played a reward song (target song). Results showed toddlers could remember spatial location information well after a one-week delay but performed poorly on temporal order memory. Playing the target song during sleep one week after learning revealed that right hippocampal activation levels (compared to novel songs) positively correlated with toddlers’ temporal order memory accuracy but not with spatial location memory performance, revealing a close link between the hippocampus and temporal order memory. The inconsistent hippocampal activation results across these two studies regarding spatial memory conditions may stem from differences in memory tasks: the first used a simple spatial location pairing task, while the second employed a more complex sequence memory task examining both spatial location and temporal order memory. These task differences may lead to different neural mechanisms for memory consolidation. Future TMR studies should further investigate the relationship between the hippocampus and temporal order versus spatial location memory.

In summary, these studies demonstrate that sleep improves memory quantity and accuracy for various types of episodic memory in infants and toddlers, including cartoon faces, toy manipulation, spatial locations, and temporal order, with different sleep features (e.g., spindles and slow waves) making unique contributions to different episodic memories. Furthermore, sleep promotes selective

memory consolidation and knowledge transfer while activating memory-related brain regions such as the hippocampus. These findings provide valuable information for exploring the neural mechanisms of episodic memory during early development.

2.2 Sleep's Impact on Semantic Memory and Generalization Abilities in Infants and Toddlers

Similar to episodic memory, daytime napping plays a crucial role in consolidating semantic memory in young children. In an observational study (Horváth & Plunkett, 2016), researchers collected daytime and nighttime sleep patterns in eight- to thirty-six-month-old toddlers through parental sleep diaries. Results showed that both nap frequency and nighttime sleep efficiency positively correlated with productive vocabulary (words children can actively use in speech or writing) and receptive vocabulary (words children can comprehend) growth four months later, whereas nighttime sleep duration did not predict vocabulary growth.

In laboratory studies of language learning, Nadel's research group in the United States used the habituation-head-turn preference paradigm in two experiments to examine sleep's impact on language learning in fifteen-month-old toddlers. After learning the phonology of 24 artificial "pseudowords" generated by specific spelling rules, toddlers' memory for learned words was tested after napping. The first study (Gómez et al., 2006) found that post-learning naps helped toddlers extract spelling rules from learned word examples and flexibly apply these rules to unlearned words. The second study (Hupbach et al., 2009) found that toddlers only retained memory for spelling rules 24 hours after learning word examples if they had napped after learning. These results demonstrate sleep's important influence on language learning and memory in toddlers. Additionally, Simon et al. (2017) used the habituation-head-turn preference paradigm to examine sleep's effect on statistical word learning in 6.5-month-old infants, finding that only infants who napped after learning could remember linguistic statistical regularities, with consolidation effects positively correlating with alpha and theta power and frontal-central slow wave energy. Beyond habituation paradigms, Williams and Horst (2014) used a story-reading task to investigate sleep's impact on word learning in three-year-old toddlers. One group of toddlers read the same story three times while another group read three different stories to learn new words appearing in the stories, with each reading group then subdivided into nap and wake conditions. Memory tests administered at 2.5 hours, 24 hours, and one week after learning revealed that sleep group toddlers showed significantly higher memory accuracy for new words than wake groups in both reading conditions, demonstrating sleep's memory consolidation effect on word learning. Furthermore, toddlers who read the same story repeatedly showed better word learning and memory than those who read different stories.

The object-category task represents the most commonly used paradigm for investigating semantic learning and generalization in infants and toddlers. Friedrich'

s research group in Germany used this paradigm combined with EEG measures (N400 and spindles) in a series of studies examining sleep' s role in memory reorganization and generalization from language perception to semantic learning. The first study (Friedrich et al., 2015) found that napping (approximately 1.5 hours) in nine- to sixteen-month-old infants could reorganize memory and generate new semantic knowledge, with this semantic generalization effect (applying learned category labels to new objects) positively correlating with sleep spindle amplitude in frontal, parietal, and central regions. The second study (Friedrich et al., 2017) found that six- to eight-month-old infants only showed semantic generalization effects after experiencing NREM sleep following object-category learning, with this effect positively correlating with NREM duration and sleep spindle amplitude; infants in light sleep (without NREM) could only consolidate memory related to phonological perception. Subsequently, this research group used the object-category paradigm combined with the N400 component to examine the relationship between semantic and episodic memory during sleep in fourteen- to seventeen-month-old toddlers (Friedrich et al., 2020). The N400 is a negative waveform over central-parietal regions elicited by semantic expectancy violations. Friedrich et al. (2020) first had toddlers learn object-category label pairings (presenting objects followed by category labels), creating an episodic context. One group of toddlers then napped while another remained awake. During testing, both learned (old) and new objects were presented twice each —once paired with correct category labels and once with incorrect labels. Results showed that new object-incorrect category label pairings elicited N400 in all toddlers (compared to correct pairings), indicating semantic memory formation through learning. Old object-incorrect category labels only elicited N400 in the wake group (not the sleep group). Moreover, old object-correct label pairings elicited a larger negative wave than old object-incorrect label pairings in frontal-temporal regions of sleep group toddlers (reflecting an episodic memory effect), with this component' s amplitude positively correlating with frontal sleep spindle amplitude. These results suggest that after simultaneous episodic and semantic learning, sleep consolidates episodic memory and protects precise episodic memories from temporary interference by semantic memory. Additionally, Spanò et al. (2018) used the object-category paradigm to examine REM sleep' s impact on word semantic learning in typically developing toddlers and children with Down syndrome. Typically developing one- to four-year-old children only showed high accuracy in memory post-tests after napping, with sleep' s memory consolidation effect maintained for at least 24 hours and REM duration positively correlating with word learning accuracy. Conversely, children with Down syndrome showed decreased word semantic learning accuracy after napping compared to wake groups, with learning effects unrelated to REM duration. This represents rare evidence linking REM sleep to declarative memory consolidation, though its reliability requires verification in future studies.

The object naming learning task (also called fast mapping) resembles the object-category task, involving the association of specific objects with new words. Horst' s research groups in the UK and Australia used this task to examine

napping' s effect on semantic learning in 2.5-year-old toddlers. The first study (Axelsson et al., 2018) presented toddlers with novel object pictures and novel word audio to learn word-object pairings, with testing requiring toddlers to point to corresponding object pictures on a screen after hearing object names. Results showed that sleep group toddlers exhibited higher and more stable recall accuracy at 4-hour and 24-hour memory tests, while wake group toddlers showed significantly lower recall accuracy at both tests, with 24-hour performance worse than 4-hour performance. This study demonstrates that napping helps maintain and consolidate memory for object naming learning. The second study (Axelsson et al., 2021) added a memory reinforcement phase during learning, repeating each object-name fast mapping twice. Results mirrored the first study and revealed that toddlers with memory reinforcement showed higher performance at both delayed tests (4 and 24 hours) than at immediate testing, highlighting napping' s memory-enhancing effect on object naming learning.

Another object naming learning task measures cross-modal preferential looking (IPL; Golinkoff et al., 1987), where instead of pointing to objects, toddlers' looking times to target versus distractor objects are measured when hearing names. Horváth' s research group in the UK used this measure in two studies examining sixteen-month-old toddlers' novel word learning. The first study (Horváth et al., 2015) had toddlers learn voice labels for two objects during learning, then randomly assigned them to sleep or wake groups for testing immediately and after a 2-hour delay. No group differences emerged at immediate testing, but after the sleep group napped, they showed longer looking times to target objects upon hearing labels than the wake group at the second test. The second study (Horváth et al., 2016) examined napping' s effect on toddlers' word meaning generalization. After learning object-label pairings and immediate memory testing, toddlers were randomly assigned to sleep or wake groups and retested after 1.5 hours. Both tests presented generalization forms of the two learned objects (same shape but different color from learning) and unlearned new objects. IPL measures revealed an interaction between sleep group and test session: the sleep group showed significantly increased looking times to target objects after napping (compared to immediate testing), while the wake group' s looking times did not differ significantly across tests. This study demonstrates napping' s role in semantic generalization, suggesting that napping is an active language representation enhancement process that extracts and retains key features of semantic concepts.

Targeted memory reactivation (TMR) can also investigate semantic memory consolidation mechanisms. Beyond episodic memory, Ghetti' s research group used TMR to examine how the toddler brain consolidates newly learned words during sleep (Johnson et al., 2021). Toddlers first learned words through an object-label task (object naming learning) and were tested immediately and one week later. Results showed toddlers learned new words and retained memory for them after one week. During natural nighttime sleep one week after learning, playing memory cues (learned words) activated the left hippocampus and left anterior medial temporal lobe (compared to unlearned novel words), with

activation levels in these regions positively correlating with memory accuracy for learned words and vocabulary production at age three. This study confirms the role of the medial temporal lobe, centered on the hippocampus, in semantic memory consolidation.

In summary, existing research demonstrates that timely naps after learning consolidate and enhance declarative memory in infants and toddlers (Mason et al., 2021). Activation of memory-related brain regions during sleep (hippocampus, medial temporal lobe) and sleep EEG measures (spindles, slow wave amplitude) play important positive roles in declarative memory consolidation. A summary of experimental studies on sleep's consolidation of declarative memory in infants and toddlers is presented in Table 1 .

3. Sleep Consolidation of Procedural Memory in Infants and Toddlers

Procedural memory, also called skill memory, refers to our memory for skills, habits, and behaviors that derive from learning and experience and may not be consciously recalled. Studying procedural learning in infancy is challenging because infants' motor abilities are still developing. Currently, few studies examine the relationship between sleep and procedural memory consolidation in infants and toddlers.

The earliest study (Fagen & Rovee-Collier, 1983) trained three-month-old infants to move a mobile above their crib through leg-kicking actions. Two weeks later, kick rate (retention probability of leg-kicking actions) positively correlated with infants' total sleep time during that period. Gibson et al. (2011) examined sleep's impact on motor development in twelve-month-old infants, recording sleep patterns for one week using actigraphy, sleep diaries, and the Brief Infant Sleep Questionnaire, while measuring development using the Ages and Stages Questionnaire (ASQ). Results showed that nighttime sleep efficiency positively correlated with problem-solving skills and fine motor ability scores on the ASQ, indicating that sleep promotes skill and motor development. DeMasi et al. (2023) divided ten- to nineteen-month-old infants into high and low walking experience groups and measured their physical activity during sleep using actigraphy. High walking experience infants showed more irregular movements during sleep, with physical activity increasing hour by hour. This study demonstrates that infants' physical activity during nighttime sleep changes with motor skill learning, with walking experience significantly impacting infant sleep and sleep-related movements. Thus, infant sleep and motor development are mutually influential and facilitative, playing important roles in cognitive development during early development.

Neuroimaging studies on procedural memory in infants and toddlers remain scarce, but preliminary evidence suggests that sleep spindles and slow-wave sleep activity relate to fine motor skill learning and consolidation. For example, Satomaa et al. (2020) found that left frontal and occipital sleep slow waves

in eight-month-old infants positively correlated with fine motor abilities, while Page et al. (2018) found that fine motor abilities in twelve- to thirty-month-old toddlers positively correlated with theta rhythm activity and negatively correlated with delta rhythm during NREM sleep.

The tunnel task provides an excellent paradigm for examining motor problem-solving in infants and toddlers (Brawn et al., 2008). In this task, infants placed before a tunnel must change body posture (from standing to crawling) to enter it. During training, infants learn to crawl through the tunnel via nonverbal cues (toys attracting attention at the tunnel's far end). Motor performance is measured by posture switches, time to pass through the tunnel, and number of cues needed. Berger's research group in the United States used this task in four studies examining sleep's impact on infant motor learning. The first study (Berger & Scher, 2017) had nine- to sixteen-month-old infants learn the tunnel task, comparing motor problem-solving between infants who napped after learning and those who did not, finding that the sleep group required fewer cues to pass through the tunnel. The second study (DeMasi et al., 2021) divided ten- to nineteen-month-old infants into two groups—one napping immediately after learning and another delaying nap by four hours—finding that the immediate nap group required fewer cues and less time to pass through the tunnel at the 6-hour post-learning test, with fewer posture switches before entering, highlighting the importance of timely sleep for procedural memory consolidation in infants. The third study (Horger et al., 2023) randomly assigned ten- to nineteen-month-old infants to three groups: nap between learning and first test, wake between learning and first test, and immediate test after learning, with all groups retested after natural nighttime sleep. While nap and wake groups did not differ significantly in posture switches before the tunnel at first test, the sleep group showed significantly fewer posture switches than the wake group at second test, indicating that only infants who napped immediately after motor learning could further consolidate procedural memory through natural nighttime sleep to improve motor task performance. This study also separately examined the effects of daytime naps and nighttime sleep on infant procedural memory, providing a valuable approach for future research.

The serial reaction time task (SRT) is a classic paradigm for studying motor learning ability, requiring participants to rapidly press buttons in a learned sequence. Wilhelm et al. (2012) used the SRT to examine sleep's consolidation of procedural memory in four- to six-year-old children. Children were divided into high- and low-intensity learning groups (receiving 10 versus 30 training trials), with all children undergoing two tests after learning (30-minute delay, 2-hour delay) and napping or remaining awake between tests. Only children in the high-intensity learning condition showed significantly lower reaction times in the nap group than the wake group at the 2-hour delay test, with no significant sleep effects under low-intensity learning conditions. This study suggests that sleep's consolidation of procedural memory is also influenced by pre-sleep procedural learning levels. Desrochers et al. (2016) used the SRT to examine different sleep types' effects on procedural memory in three- to six-year-old children, with all

children undergoing three tests (immediate, 5-hour delay, 24-hour delay) after learning. At the 5-hour delay test, nap group children's reaction time and accuracy improvements did not differ significantly from immediate post-learning performance, but after 24 hours (following nighttime sleep), behavioral abilities measured by reaction time and accuracy improved significantly. Consistent with Horger et al. (2023), this study suggests that procedural learning requires nighttime sleep to form stable memory representations. Additionally, research using the SRT and its variants has examined sleep disorders' impact on procedural memory consolidation in eight- to eleven-year-old children (Csábi et al., 2016), finding that children with sleep apnea syndrome, like healthy children, showed significantly improved sequence button-pressing reaction times and accuracy after natural nighttime sleep, indicating that sleep also positively affects procedural memory consolidation in children with sleep disorders.

In summary, although research on sleep and procedural memory consolidation in infants and toddlers remains limited, existing studies demonstrate sleep's positive role in consolidating procedural memory. More research is needed on the relationship between sleep and motor skills, particularly regarding REM sleep, which has been extensively linked to procedural memory consolidation in adults (Plihal & Born, 1997; Qian et al., 2022) but remains unexamined in infant studies. A summary of experimental studies on sleep's consolidation of procedural memory in infants and toddlers is presented in Table 2 .

4. Summary and Future Directions

Our review of existing literature reveals that sleep plays an important consolidating role for both declarative and procedural memory in infants and toddlers, with daytime naps significantly facilitating declarative memory consolidation while procedural memory consolidation appears more dependent on nighttime sleep. During sleep, memory-related brain regions (e.g., hippocampus, medial temporal lobe) are activated, and changes in sleep EEG features (spindles, slow wave amplitude) correlate with memory consolidation efficacy. Nevertheless, several issues remain unresolved, and we propose future research address the following questions:

First, does sleep also consolidate memory in newborns? Current sleep memory consolidation research primarily focuses on adults and children/adolescents (Mason et al., 2021; Schmid et al., 2020), with the youngest reported age for sleep-dependent memory consolidation being three months (Horváth et al., 2018; Fagen & Rovee-Collier, 1983). No studies have examined sleep's memory consolidation effects on newborn learning. Younger age is associated with greater brain plasticity. Newborns, having just entered a completely new world, continuously receive environmental information and establish numerous synaptic connections through learning, forming declarative and procedural memory representations. Does sleep play a role in this process, and if so, what role? Although newborns show rudimentary forms of adult sleep cycles, they have not yet developed distinct NREM and REM sleep stages. We recommend future studies use EEG

and near-infrared spectroscopy to monitor newborn sleep states in real time, combined with TMR paradigms, to examine how sleep and associated neural activity consolidate newborn learning.

Second, what are the similarities and differences between infant/toddler and adult sleep-dependent memory consolidation? Sleep can promote new synapse formation to create stable memory representations (Yang et al., 2014). Synaptic number changes represent the brain's process of learning from and adapting to experience and constitute an important memory consolidation mechanism. From birth, human synapse numbers follow a developmental trajectory of initial increase followed by pruning: the first year represents a critical period for synapse development, peaking at age three (approximately twice adult levels), then gradually pruning until stabilizing around adolescence at age 16. Differences in synapse numbers and developmental stages between infants/toddlers and adults may lead to different mechanisms of sleep-dependent memory consolidation, making it inappropriate to simply generalize adult findings to young children. Current adult research explanations for the sleep-memory consolidation relationship primarily include the synaptic homeostasis hypothesis, systems consolidation hypothesis (Squire & Alvarez, 1995), and memory replay overlap theory (Lewis & Durrant, 2011). Studying sleep-memory consolidation relationships in infants and toddlers can not only enhance understanding of cognitive development and learning abilities but also provide new perspectives and evidence for adult theories. For example, does information exchange between hippocampus and neocortex occur during infant sleep? Do infant synapses undergo optimization and pruning during sleep? Does memory replay occur during infant sleep? These questions warrant further exploration. Given that most adult experimental paradigms cannot be used with infant participants, future research should develop new infant-appropriate paradigms to compare sleep-dependent memory consolidation mechanisms across ages. We suggest using simple learning and memory tasks that facilitate behavioral output in infants and toddlers, including but not limited to visual discrimination learning tasks (examining eye movement measures), binaural competitive speech learning tasks (examining head-turn preferences), or oddball paradigms combined with EEG MMR measures to directly assess memory performance using neural indicators.

Third, how does sleep systematically promote social and language learning in infants and toddlers? Unlike children, adolescents, and adults who engage in substantial declarative and procedural learning (e.g., knowledge, skills), the primary tasks during infancy and toddlerhood involve social learning (including secure attachment, social interaction, emotion, theory of mind) and language learning (native language, phonology, vocabulary) (Bremner & Fogel, 2004; Slot et al., 2020; Tomasello, 2001). Although existing research has examined sleep's impact on infant/toddler learning of phonology, semantics, and cartoon faces, many aspects of social and language learning remain unexplored. For example, numerous studies emphasize the importance of early experience in animals and humans, with biologists even proposing imprinting concepts (Robledo et al., 2022). What role does infant sleep play in forming social learning? Which

learning experiences are preferentially consolidated by sleep to form knowledge schemas that subsequently influence cognitive and social development? Furthermore, adult research shows sleep can reduce negative emotional intensity, enhance positive emotional experiences, and improve memory for faces and emotions (Walker & van der Helm, 2009; Tempesta et al., 2018). Does sleep have special effects on emotional and social memory in infants and toddlers (e.g., social smiling, stranger anxiety, separation anxiety)? We recommend future research adopt experimental paradigms suitable for infant/toddler social and language learning to examine sleep's consolidation of social and language memories (e.g., memory for mother's and strangers' faces, vocal tones, and intonation patterns).

Fourth, do different sleep types, durations, and timing contribute differently to memory consolidation? Current research shows daytime naps promote declarative memory in infants and toddlers, while procedural memory consolidation appears more dependent on nighttime sleep. However, direct comparisons of sleep types remain lacking. Do daytime naps and nighttime sleep have specific effects on different memory types? Furthermore, do different effects of daytime versus nighttime sleep on memory stem from differential NREM/REM proportions? Additionally, how do sleep duration (e.g., 2-hour versus 5-hour naps) and sleep onset timing (e.g., immediate sleep versus sleep after a 2-hour delay) affect memory consolidation? These questions merit investigation.

Ackermann, S., & Rasch, B. (2014). Differential effects of non-REM and REM sleep on memory consolidation? *Current Neurology and Neuroscience Reports*, 14(2), 430.

Al-Sharman, A., & Siengsukon, C. F. (2014). Time rather than sleep appears to enhance off-line learning and transfer of learning of an implicit continuous task. *Nature and Science of Sleep*, 6, 27-36.

Albouy, G., Sterpenich, V., Baeteau, E., Vandewalle, G., Desseilles, M., Dang-Vu, T., Darsaud, A., Ruby, P., Luppi, P. H., Degueldre, C., Peigneux, P., Luxen, A., & Maquet, P. (2008). Both the hippocampus and striatum are involved in consolidation of motor sequence memory. *Neuron*, 58(2), 261-272.

Axelsson, E. L., Swinton, J., Winiger, A. I., & Horst, J. S. (2018). Napping and toddlers' memory for fast-mapped words. *First Language*, 38(6), 582-595.

Axelsson, E. L., Swinton, J., Jiang, I. Y., Parker, E. V., & Horst, J. S. (2021). Prior exposure and toddlers' sleep-related memory for novel words. *Brain Sciences*, 11(10), 1366.

Berger, S. E., & Scher, A. (2017). Naps improve new walkers' locomotor problem solving. *Journal of Experimental Child Psychology*, 162, 292-300.

Brawn, T. P., Fenn, K. M., Nusbaum, H. C., & Margoliash, D. (2008). Consolidation of sensorimotor learning during sleep. *Learning & Memory*, 15(11), 815-819.

- Bremner, G., & Fogel, A. (Eds.). (2004). *Blackwell handbook of infant development*. Blackwell Publishing.
- Campbell, I. G., & Feinberg, I. (2009). Longitudinal trajectories of non-rapid eye movement delta and theta EEG as indicators of adolescent brain maturation. *Proceedings of the National Academy of Sciences of the United States of America*, 106(13), 5177-5180.
- Clawson, B. C., Durkin, J., & Aton, S. J. (2016). Form and function of sleep spindles across the lifespan. *Neural Plasticity*, 2016, 6936381.
- Cousins, J. N., El-Deredy, W., Parkes, L. M., Hennies, N., & Lewis, P. A. (2016). Cued reactivation of motor learning during sleep leads to overnight changes in functional brain activity and connectivity. *PLoS Biology*, 14(5), e1002451.
- Csábi, E., Benedek, P., Janacsek, K., Zavecz, Z., Katona, G., & Nemeth, D. (2016). Declarative and non-declarative memory consolidation in children with sleep disorder. *Frontiers in Human Neuroscience*, 9, 709.
- D' Atri, A., Novelli, L., Ferrara, M., Bruni, O., & De Gennaro, L. (2018). Different maturational changes of fast and slow sleep spindles in the first four years of life. *Sleep Medicine*, 42, 73-82.
- Davis, K. F., Parker, K. P., & Montgomery, G. L. (2004). Sleep in infants and young children: Part one: Normal sleep. *Journal of Pediatric Health Care: Official Publication of National Association of Pediatric Nurse Associates & Practitioners*, 18(2), 65-71.
- DeMasi, A., Horger, M. N., Allia, A. M., Scher, A., & Berger, S. E. (2021). Nap timing makes a difference: Sleeping sooner rather than later after learning improves infants' locomotor problem solving. *Infant Behavior & Development*, 65, 101652.
- DeMasi, A., Horger, M. N., Scher, A., & Berger, S. E. (2023). Infant motor development predicts the dynamics of movement during sleep. *Infancy*, 28(2), 367-387.
- Desrochers, P. C., Kurdziel, L. B., & Spencer, R. M. (2016). Delayed benefit of naps on motor learning in preschool children. *Experimental Brain Research*, 234(3), 763-772.
- Diekelmann, S., Wilhelm, I., & Born, J. (2009). The whats and whens of sleep-dependent memory consolidation. *Sleep Medicine Reviews*, 13(5), 309-321.
- Ednick, M., Cohen, A. P., McPhail, G. L., Beebe, D., Simakajornboon, N., & Amin, R. S. (2009). A review of the effects of sleep during the first year of life on cognitive, psychomotor, and temperament development. *Sleep*, 32(11), 1449-1458.
- Eichenlaub, J. B., Jarosiewicz, B., Saab, J., Franco, B., Kelemen, J., Halgren, E., Hochberg, L. R., & Cash, S. S. (2020). Replay of learned neural firing sequences during rest in human motor cortex. *Cell Reports*, 31(5), 107581.

- Ekinci, O., Isik, U., Gunes, S., & Ekinci, N. (2016). Understanding sleep problems in children with epilepsy: Associations with quality of life, Attention-Deficit Hyperactivity Disorder and maternal emotional symptoms. *Seizure*, 40, 108-113.
- Fagen, J. W., & Rovee-Collier, C. (1983). Memory retrieval: A time-locked process in infancy. *Science*, 222(4630), 1349-1351.
- Farhadian, N., Khazaie, H., Nami, M., & Khazaie, S. (2021). The role of daytime napping in declarative memory performance: A systematic review. *Sleep Medicine*, 84, 134-141.
- Fattinger, S., Jenni, O. G., Schmitt, B., Achermann, P., & Huber, R. (2014). Overnight changes in the slope of sleep slow waves during infancy. *Sleep*, 37(2), 245-253.
- Friedrich, M., Mölle, M., Friederici, A. D., & Born, J. (2019). The reciprocal relation between sleep and memory in infancy: Memory-dependent adjustment of sleep spindles and spindle-dependent improvement of memories. *Developmental Science*, 22(2), e12743.
- Friedrich, M., Mölle, M., Friederici, A. D., & Born, J. (2020). Sleep-dependent memory consolidation in infants protects new episodic memories from existing semantic memories. *Nature Communications*, 11(1), 1-11.
- Friedrich, M., Wilhelm, I., Born, J., & Friederici, A. D. (2015). Generalization of word meanings during infant sleep. *Nature Communications*, 6, 6004.
- Friedrich, M., Wilhelm, I., Mölle, M., Born, J., & Friederici, A. D. (2017). The sleeping infant brain anticipates development. *Current Biology*, 27(15), 2374-2380.e2373.
- Galland, B. C., Taylor, B. J., Elder, D. E., & Herbison, P. (2012). Normal sleep patterns in infants and children: A systematic review of observational studies. *Sleep Medicine Reviews*, 16(3), 213-222.
- Gibson, R., Elder, D., & Gander, P. (2011). Actigraphic sleep and developmental progress of one-year-old infants. *Sleep and Biological Rhythms*, 10(2), 77-83.
- Golinkoff, R. M., Hirsh-Pasek, K., Cauley, K. M., & Gordon, L. (1987). The eyes have it: Lexical and syntactic comprehension in a new paradigm. *Journal of Child Language*, 14(1), 23-45.
- Gómez, R. L., Bootzin, R. R., & Nadel, L. (2006). Naps promote abstraction in language-learning infants. *Psychological Science*, 17(8), 670-674.
- Grigg-Damberger, M., Gozal, D., Marcus, C. L., Quan, S. F., Rosen, C. L., Chervin, R. D., Wise, M., Picchietti, D. L., Sheldon, S. H., & Iber, C. (2007). The visual scoring of sleep and arousal in infants and children. *Journal of Clinical Sleep Medicine*, 3(2), 201-240.

Hatzinger, M., Brand, S., Perren, S., Von Wyl, A., Stadelmann, S., von Klitzing, K., & Holsboer-Trachsler, E. (2013). In pre-school children, sleep objectively assessed via sleep-EEGs remains stable over 12 months and is related to psychological functioning, but not to cortisol secretion. *Journal of Psychiatric Research*, 47(11), 1809-1814.

Hatzinger, M., Brand, S., Perren, S., Von Wyl, A., Stadelmann, S., von Klitzing, K., & Holsboer-Trachsler, E. (2014). In pre-school children, sleep objectively assessed via actigraphy remains stable over 12 months and is related to psychological functioning, but not to cortisol secretion. *Journal of Psychiatric Research*, 55, 22-28.

Horger, M. N., DeMasi, A., Allia, A. M., Scher, A., & Berger, S. E. (2023). The unique contributions of day and night sleep to infant motor problem solving. *Journal of Experimental Child Psychology*, 226, 105536.

Horváth, K., Hannon, B., Ujma, P. P., Gombos, F., & Plunkett, K. (2018). Memory in 3-month-old infants benefits from a short nap. *Developmental Science*, 21(3), e12587.

Horváth, K., Liu, S., & Plunkett, K. (2016). A daytime nap facilitates generalization of word meanings in young toddlers. *Sleep*, 39(1), 203-207.

Horváth, K., Myers, K., Foster, R., & Plunkett, K. (2015). Napping facilitates word learning in early lexical development. *Journal of Sleep Research*, 24(5), 503-509.

Horváth, K., & Plunkett, K. (2016). Frequent daytime naps predict vocabulary growth in early childhood. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, 57(9), 1008-1017.

Horváth, K., & Plunkett, K. (2018). Spotlight on daytime napping during early childhood. *Nature and Science of Sleep*, 10, 97-104.

Hu, X., Cheng, L. Y., Chiu, M. H., & Paller, K. A. (2020). Promoting memory consolidation during sleep: A meta-analysis of targeted memory reactivation. *Psychological Bulletin*, 146(3), 218-244.

Hupbach, A., Gomez, R. L., Bootzin, R. R., & Nadel, L. (2009). Nap-dependent learning in infants. *Developmental Science*, 12(6), 1007-1012.

Iglowstein, I., Jenni, O. G., Molinari, L., & Largo, R. H. (2003). Sleep duration from infancy to adolescence: Reference values and generational trends. *Pediatrics*, 111(2), 302-307.

Jenni, O. G., Borbély, A. A., & Achermann, P. (2004). Development of the nocturnal sleep electroencephalogram in human infants. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology*, 286(3), R528-538.

Jenni, O. G., Molinari, L., Caffisch, J. A., & Largo, R. H. (2007). Sleep duration from ages 1 to 10 years: Variability and stability in comparison with growth.

Pediatrics, 120(4), e769-776.

Johnson, E. G., Mooney, L., Graf Estes, K., Nordahl, C. W., & Ghetti, S. (2021). Activation for newly learned words in left medial-temporal lobe during toddlers' sleep is associated with memory for words. *Current Biology*, 31(24), 5429-5438.e5425.

Johnson, E. G., Prabhakar, J., Mooney, L. N., & Ghetti, S. (2020). Neuroimaging the sleeping brain: Insight on memory functioning in infants and toddlers. *Infant Behavior & Development*, 58, 101427.

Konrad, C., Dirks, N. D., Warmuth, A., Herbert, J. S., Schneider, S., & Seehagen, S. (2019). Sleep-dependent selective imitation in infants. *Journal of Sleep Research*, 28(1), e12777.

Konrad, C., Herbert, J. S., Schneider, S., & Seehagen, S. (2016). Gist extraction and sleep in 12-month-old infants. *Neurobiology of Learning and Memory*, 134 Pt B, 216-220.

Konrad, C., Seehagen, S., Schneider, S., & Herbert, J. S. (2016). Naps promote flexible memory retrieval in 12-month-old infants. *Developmental Psychobiology*, 58(7), 866-874.

Kurdziel, L., Duclos, K., & Spencer, R. M. (2013). Sleep spindles in midday naps enhance learning in preschool children. *Proceedings of the National Academy of Sciences of the United States of America*, 110(43), 17267-17271.

Kurth, S., Olini, N., Huber, R., & LeBourgeois, M. (2015). Sleep and early cortical development. *Current Sleep Medicine Reports*, 1(1), 64-73.

Lewis, P. A., & Durrant, S. J. (2011). Overlapping memory replay during sleep builds cognitive schemata. *Trends in cognitive sciences*, 15(8), 343-351.

Lokhandwala, S., & Spencer, R. M. C. (2021). Slow wave sleep in naps supports episodic memories in early childhood. *Developmental Science*, 24(2), e13035.

Lokhandwala, S., & Spencer, R. M. C. (2022). Relations between sleep patterns early in life and brain development: A review. *Developmental Cognitive Neuroscience*, 56, 101130.

Mason, G. M., Lokhandwala, S., Riggins, T., & Spencer, R. M. C. (2021). Sleep and human cognitive development. *Sleep Medicine Reviews*, 57, 101472.

McCarley, R. W. (2007). Neurobiology of REM and NREM sleep. *Sleep Medicine*, 8(4), 302-330.

McDonough, L., Mandler, J. M., McKee, R. D., & Squire, L. R. (1995). The deferred imitation task as a nonverbal measure of declarative memory. *Proceedings of the National Academy of Sciences of the United States of America*, 92(16), 7580-7584.

Mooney, L. N., Johnson, E. G., Prabhakar, J., & Ghetti, S. (2021). Memory-related hippocampal activation during sleep and temporal memory in toddlers.

Developmental Cognitive Neuroscience, 47, 100908.

Page, J., Lustenberger, C., & Fr hlich, F. (2018). Social, motor, and cognitive development through the lens of sleep network dynamics in infants and toddlers between 12 and 30 months of age. *Sleep*, 41(4).

Plihal, W., & Born, J. (1997). Effects of early and late nocturnal sleep on declarative and procedural memory. *Journal of Cognitive Neuroscience*, 9(4), 534-547.

Prabhakar, J., Johnson, E. G., Nordahl, C. W., & Ghetti, S. (2018). Memory-related hippocampal activation in the sleeping toddler. *Proceedings of the National Academy of Sciences of the United States of America*, 115(25), 6500-6505.

Przepiórka, A., Błachnio, A., & Siu, N. Y. (2019). The relationships between self-efficacy, self-control, chronotype, procrastination and sleep problems in young adults. *Chronobiology International*, 36(8), 1137-1145.

Qian, L., Ru, T., He, M., Li, S., & Zhou, G. (2022). Effects of a brief afternoon nap on declarative and procedural memory. *Neurobiology of Learning and Memory*, 194, 107662.

Rasch, B., Büchel, C., Gais, S., & Born, J. (2007). Odor cues during slow-wave sleep prompt declarative memory consolidation. *Science*, 315(5817), 1426-1429.

Robledo, J. P., Cross, I., Boada-Bayona, L., & Demogeot, N. (2022). Back to basics: A re-evaluation of the relevance of imprinting in the genesis of Bowlby's attachment theory. *Frontiers in Psychology*, 13, 1042920.

Satomaa, A. L., Mäkelä, T., Saarenpää-Heikkilä, O., Kylliäinen, A., Huupponen, E., & Himanen, S. L. (2020). Slow-wave activity and sigma activities are associated with psychomotor development at 8 months of age. *Sleep*, 43(9).

Schmid, D., Erlacher, D., Klostermann, A., Kredel, R., & Hossner, E. J. (2020). Sleep-dependent motor memory consolidation in healthy adults: A meta-analysis. *Neuroscience and Biobehavioral Reviews*, 118, 270-281.

Seehagen, S., Konrad, C., Herbert, J. S., & Schneider, S. (2015). Timely sleep facilitates declarative memory consolidation in infants. *Proceedings of the National Academy of Sciences of the United States of America*, 112(5), 1625-1629.

Seehagen, S., Zmyj, N., & Herbert, J. S. (2019). Remembering in the context of internal states: The role of sleep for infant memory. *Child Development Perspectives*, 13(2), 110-115.

Simon, K. N. S., Werchan, D., Goldstein, M. R., Sweeney, L., Bootzin, R. R., Nadel, L., & Gómez, R. L. (2017). Sleep confers a benefit for retention of statistical language learning in 6.5-month old infants. *Brain and Language*, 167, 3-12.

Slot, P. L., Bleses, D., & Jensen, P. (2020). Infants' and toddlers' language, math and socio-emotional development: Evidence for reciprocal relations and

differential gender and age effects. *Frontiers in psychology*, 11, 580297.

Spanò, G., Gómez, R. L., Demara, B. I., Alt, M., Cowen, S. L., & Edgin, J. O. (2018). REM sleep in naps differentially relates to memory consolidation in typical preschoolers and children with Down syndrome. *Proceedings of the National Academy of Sciences of the United States of America*, 115(46), 11844-11849.

Squire, L. R., & Alvarez, P. (1995). Retrograde amnesia and memory consolidation: A neurobiological perspective. *Current opinion in neurobiology*, 5(2), 169-177.

Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature*, 437(7063), 1272-1278.

Sugawara, S. K., Tanaka, S., Tanaka, D., Seki, A., Uchiyama, H. T., Okazaki, S., Koeda, T., & Sadato, N. (2014). Sleep is associated with offline improvement of motor sequence skill in children. *PLoS One*, 9(11), e111635.

Tempesta, D., Socci, V., De Gennaro, L., & Ferrara, M. (2018). Sleep and emotional processing. *Sleep Medicine Reviews*, 40, 183-195.

Tomasello, M. (2001). Cultural transmission: A view from chimpanzees and human infants. *Journal of Cross-Cultural Psychology*, 32(2), 135-146.

Ulrich D. (2016). Sleep spindles as facilitators of memory formation and learning. *Neural plasticity*, 2016, 1796715.

van Dongen, E. V., Takashima, A., Barth, M., Zapp, J., Schad, L. R., Paller, K. A., & Fernández, G. (2012). Memory stabilization with targeted reactivation during human slow-wave sleep. *Proceedings of the National Academy of Sciences of the United States of America*, 109(26), 10575-10580.

Veldman, S. L. C., Santos, R., Jones, R. A., Sousa-Sá, E., & Okely, A. D. (2019). Associations between gross motor skills and cognitive development in toddlers. *Early human development*, 132, 39-44.

Walker, M. P. (2005). A refined model of sleep and the time course of memory formation. *The Behavioral and Brain Sciences*, 28(1), 51-64; discussion 64-104.

Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002). Practice with sleep makes perfect: Sleep-dependent motor skill learning. *Neuron*, 35(1), 205-211.

Walker, M. P., & van der Helm, E. (2009). Overnight therapy? The role of sleep in emotional brain processing. *Psychological Bulletin*, 135(5), 731-748.

Wang, S. Y., Baker, K. C., Culbreth, J. L., Tracy, O., Arora, M., Liu, T., Morris, S., Collins, M. B., & Wamsley, E. J. (2021). 'Sleep-dependent' memory consolidation? Brief periods of post-training rest and sleep provide an equivalent benefit for both declarative and procedural memory. *Learning & Memory*, 28(6), 201-208.

Wilhelm, I., Metzkw-Mészáros, M., Knapp, S., & Born, J. (2012). Sleep-dependent consolidation of procedural motor memories in children and adults: The pre-sleep level of performance matters. *Developmental Science*, 15(4), 506-515.

Williams, S. E., & Horst, J. S. (2014). Goodnight book: Sleep consolidation improves word learning via storybooks. *Frontiers in Psychology*, 5, 184.

Yang, G., Lai, C. S., Cichon, J., Ma, L., Li, W., & Gan, W. B. (2014). Sleep promotes branch-specific formation of dendritic spines after learning. *Science*, 344(6188), 1173-1178.

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