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CLINICAL REVIEW

Sleep and human cognitive development

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SUMMARY

Emerging studies across learning domains have shed light on mechanisms underlying sleep's benefits during numerous developmental periods. In this conceptual review, we survey recent studies of sleep and cognition across infancy, childhood, and adolescence. By summarizing recent findings and integrating across studies with disparate approaches, we provide a novel understanding of sleep's role in human cognitive function. Collectively, these studies point to an interrelation between brain development, sleep, and cognition. Moreover, we point to gaps in our understanding, which inform the agenda for future research in developmental and sleep science.

Introduction

Sleep changes dramatically across human development. Infants' 14–20 h of daily sleep are halved before adolescence [1]. Additionally, while infants' sleep is distributed across multiple bouts, sleep is consolidated to a single bout by 5–7 years [2]. Circadian rhythms also change across development, from early bedtimes in childhood to late nights in adolescence. However, sleep and sleep timing are also marked by individual differences. Confidence intervals mark a 10 h range in sleep time for young infants [3]. Likewise, late sleep onset may reflect only ~20% of adolescents' circadian rhythms [4].

Importantly, sleep supports cognitive performance. As such, it is important to consider individual differences in sleep as a factor underlying individual differences in cognitive and brain development [5]. Here, we review evidence that individual variability in sleep physiology and timing across childhood may influence the benefits of sleep on cognition. Moreover, we propose that differences in sleep and differences in brain development may bidirectionally reflect one another, and jointly impact cognition.

Relations between sleep changes and brain development

Developmental changes in sleep, such as cessation of napping, are posited to reflect brain development. In preschool-aged children, decreases in napping have been associated with higher vocabulary and enhanced memory after intervals awake, even when controlling for age [6,7]. These cognitive improvements are thought to indicate development of memory-related brain regions. Indeed, hippocampal subfield volumes vary between 4 and 6 year-old nappers compared to non-habitual nappers after controlling for variables such as age, gender, and intracranial volume [8]. This difference suggests increasing efficiency of memory storage in non-habitual nappers. Thus, natural cessation of napping may be a marker of brain maturation.

Recent studies also report associations between sleep microstructure and brain maturation. Specifically, maximal slow-wave activity (SWA) shifts from posterior to anterior areas, paralleling cortical maturation [9]. In a cross-sectional sample ranging from 2 to 26 years, the topography of maximal SWA predicted cognitive

Abbreviations: EEG, electroencephalography; SWA, slow-wave activity; fMRI, functional magnetic resonance imaging; SWS, slow-wave sleep; nREM, non-rapid-eye-movement sleep; REM, rapid-eye-movement sleep; PSG, polysomnography; ADHD, Attention-deficit hyperactivity disorder.

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performance and gray matter maturation. Moreover, among children 2–13 years, SWA propagation distance positively correlated with whole-brain and inter-hemispheric myelin content, while propagation speed and cortical involvement correlated with myelin content in the superior longitudinal fascicle [10]. Such patterns suggest that SWA topography and dynamics may track early brain development.

Sleep has also been associated with developments in functional brain connectivity. In a longitudinal analysis of children at 2, 3, and 5 years, overnight changes in EEG coherence (a proxy for white matter connectivity) varied with age [11]. EEG coherence in the sleep spindle range overnight was minimal at 2 years, yet it increased by ~10% at 5 years. At all ages, overnight sleep promoted inter-hemispheric coherence across most sleep frequencies, while intra-hemispheric coherence tended to decrease, suggesting that sleep may modulate neural connectivity in early childhood.

Effects of sleep differences on cognition across development

Given sleep's relations to brain development, it may be expected that the cognitive function of sleep changes across this period as well. Studies from infancy through adolescence support sleep's role across cognitive domains (Table 1). However, developmental studies have minimally explored how sleep physiology (Table 2) and timing moderate this benefit. Below, we review developmental changes in sleep's effects within the most studied domains.

Declarative memory

Declarative memory denotes explicit memory for events or facts. We discuss this domain broadly as examination of subdivisions of declarative memory are limited.

Behavioral findings

Declarative memory studies in infants and young children mainly focus on napping. Napping benefits memory [12–16] in infants as young as 3 months, with such benefits observable both shortly after napping and on more delayed timescales. In one study of deferred imitation [13], infants, 6–12 months, who napped for ≥30 min reproduced more previously demonstrated actions after 4 h than a control group who did not observe the actions. In contrast, infants who remained awake or took brief naps showed no performance differences compared to the control group. Furthermore, following overnight sleep, infants in the nap group showed better action performance than infants in both the control and wake/short nap groups. These results suggest that napping shortly after learning may strengthen infants' declarative memory, with benefits apparent even after overnight sleep.

Such declarative nap benefits may differ between episodic and semantic memory types [17]. For example, in one study, 14-17-month-old toddlers were shown objects paired with correct category labels and subsequently napped or remained awake (between subjects). Afterward, toddlers were shown both the same ("old") and new objects belonging to the same categories. Event-related potential (ERP) measures suggested that toddlers who napped formed distinct episodic memories of the old objects, and a separable semantic response for new objects. In contrast, toddlers who remained awake did not exhibit episodic memory, showing semantic responses to old and new objects. These findings suggest that napping may allow toddlers to better consolidate episodic details.

Napping continues to support declarative memory across early childhood. Among children 3–5 years, napping between learning and test has been shown to benefit storybook memory [18] and visuospatial learning [7], with effects observable immediately after napping as well as the day following. In another study [19], declarative word learning was assessed among 3.5-year-olds exposed either to one story three times or to three different stories. Children who napped retained more words and maintained superior performance after 7 days than children kept awake. Notably, children in the nap group were habitual nappers while those assigned to the wake group were infrequent nappers. As such, it is intriguing that children in the wake group experienced a memory disadvantage, given work suggesting that nonhabitual nappers can retain declarative memories more proficiently than habitual nappers when daytime wake follows learning [7]. However, criteria for nap habituality were not defined, and differences may speak to the interval at which memory was tested, as prior work [7] had short-term and not 7-day follow-up. Additionally, children in [19] were younger and spanned a smaller age range than children in [7]. Although nap habituality has been shown to predict cognitive performance independent of age [6], the fact that children in [19] were all relatively young may suggest that nap frequency differences in this study (along with possibly being less distinctive) could have been more driven by extrinsic influences than by children's own brain maturation or readiness to give up napping. Together, these findings suggest that napping shortly after learning can aid declarative memory in early childhood, and that perhaps in the long term, delayed sleep may not allow children to recover memories lost by staying awake.

Studies of children >5 years have focused on overnight sleep, generally finding sleep advantageous for declarative memory [20–22]. Furthermore, these benefits occur even with a long delay between initial encoding and sleep. In one study [21], 7-12-year-olds learned novel words, followed by overnight sleep or daytime wake. Word recognition improved following sleep, but not after equivalent time awake. However, after delayed overnight sleep, the wake group's recall also improved. Likewise, 9-12-year-olds' memory in a word-matching task improved following overnight sleep, regardless of whether learning occurred in the morning or evening [20]. These studies indicate that overnight sleep can benefit declarative memory consolidation in children, even with delays between encoding and sleep. Importantly however, sleep timing effects on declarative memory may emerge in the longer term, as one recent study in 8–12-year-olds showed enhanced declarative memory retention after 4–10 weeks when sleep followed initial learning [23].

Sleeping shortly after learning may likewise be optimal at later ages ([24–26], but see [27]). For example, high school students who learned words from an unfamiliar language showed greater forgetting when they learned ≥12 h before sleep compared to when they learned within a few hours of sleep [24]. Performance differences remained 48 h later, suggesting that additional overnight sleep did not recover memories.

Aside from comparing sleep to wake, many adolescent studies assess how sleep *duration* affects declarative memory. Intriguingly, neither natural nor experimental differences in sleep duration seem to impact adolescent memory consolidation. Memory retention was similar among adolescents who slept 4–5 h compared to 9 h [28,29], and it is speculated that as little as 1–2 h of sleep may be sufficient for declarative consolidation at this age [29]. Nonetheless, sleep restriction may adversely affect adolescents' *encoding* of declarative information [30,31].

Physiological mechanisms

In adults, SWS and sleep spindles are suggested to support declarative memory consolidation [32]. Specifically, one of the most established theories is the *active systems consolidation theory*, which posits that hippocampal sharp-wave ripples reactivate declarative memories in co-occurrence with sleep spindles and slow oscillations

Table 1
Developmental studies assessing relations between sleep and cognition (ordered by age tested).

Cognitive Domain	Author/Ref	Age(s) Tested	Task Description	Sleep bout(s) considered	Experimental Manipulation?	Immediate[a] Post-Sleep Benefit?	Next-Day Benefit?	Extended (>24 h) Benefit?
Declarative Memory	Seehagen et al. [13]	6 & 12mo	Deferred imitation	Nap & Overnight	Nap vs. No Nap vs. Baseline	Yes	Yes	
	Friedrich et al. [14]	9–16mo	New word learning (specific exemplars)	Nap	Nap vs. No Nap	Yes		
	Friedrich et al. [17]	14–17mo	Episodic memory (old vs. new objects)	Nap	Nap vs. No Nap	Yes		
	Horváth et al. [15]	16mo	Object-word pair associations	Nap	Nap vs. No Nap	Yes		
	Kurdziel et al. [7]	36–67mo	Visuospatial recall	Nap & Overnight	Nap vs. No Nap	Yes	Yes	
	Lokhandwala et al. [18]	36–71mo	Episodic recall (storybook paradigm)	Nap & Overnight	Nap vs. No Nap	Yes	Yes	
	Williams & Horst [19]	3.5y	New word learning (storybook paradigm)	Nap, Overnight, 1wk later	Nap vs. No Nap	Yes	Yes	Yes
	Spanò et al. [39]	41–84mo	Word learning	Nap & Overnight	Nap vs. No Nap	Yes	Yes	
	Henderson et al. [21]	7–12y	Word learning, visuospatial recall	Overnight, 1wk later	AM vs. PM learning	Yes[b], but no comparison after sleep across groups	Yes (relative to own prior timepoint)	Yes (relative to own prior timepoint)
	Peiffer et al. [42]	7–12y, adults	Definition learning	Overnight	AM vs. PM learning groups	Yes, for children only		
	Wilhelm et al. [41]	8–11y, adults	Declarative recall of motor sequences	Overnight	Nocturnal sleep vs. Daytime wake	Yes		
	James et al. [23]	8–12y	New word learning (picture-naming, stem-completion, object-location)	Overnight	Nocturnal sleep vs. Daytime wake	Yes (night condition improved > day from 0 to 12hr)	Yes[c] (day condition improved > night from 12 to 24hr)	Yes (night condition improved > day relative to own baselines)
	Backhaus et al. [20]	9–12y	Word pair associations	Overnight	AM vs. PM learning	Yes, but no comparison after sleep across conditions	Yes[d] (relative to own baseline)	
	Voderholzer et al. [29]	13–17y	Word pair associations	Overnight (multiple days)	Sleep restriction (5,6,7,8,9 h)			No differences
	Kopasz et al. [28]	14–16y	Word pair associations	Overnight (multiple days)	Sleep restriction (4 h vs. 9 h)		No differences	
	Hahn et al. [43]	14–18y	Word pair associations	Overnight	Wake (AM learning) vs. Sleep (PM learning)	Yes		
	Cousins et al. [30]	15–18y	Picture Encoding	Overnight (multiple days)	Sleep restriction (5 h vs. 9 h)	Yes		
	Lau et al. [25]	15–18y	Word pair associations, story recall, list learning	Nap	Nap vs. No Nap	Yes[e]		
	Holz et al. [27]	16–17y	Word pair associations	Overnight	Afternoon vs. Evening Learning		No	No differences
	Gais et al. [24]	17y	Novel word learning	Overnight	Multiple sleep-delay	Yes	Yes	Yes
	Leong et al. [26]	17y	Semantic categorization	Overnight	Wake vs. Sleep	Yes		
Procedural Memory	Fagen & Rovee-Collier [46]	3mo	Operant foot kicking	Not specified (total sleep time across 8 h interval)	Observational (correlation btwn sleep duration and recall)	Yes		
	Berger & Scher [47]	9–16mo	Tunnel task	Nap	Nap vs. No Nap	Yes		
	Desrochers et al. [48]	33–71mo	Serial reaction time	Nap & Overnight	Nap vs. No Nap	No differences	Yes	
	Wilhelm et al. [49]	4–6y	Motor sequence learning	Nap	Nap vs. No Nap X Standard vs. Extended training	Yes[f]		
	Wilhelm et al. [22]	6–8y	Finger sequence tapping	Overnight	Nocturnal sleep vs. Daytime wake	No		

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Table 1 (*continued*)

Cognitive Domain	Author/Ref	Age(s) Tested	Task Description	Sleep bout(s) considered	Experimental Manipulation?	Immediate[a] Post-Sleep Benefit?	Next-Day Benefit?	Extended (>24 h) Benefit?
	Fischer et al. [51]	7-11y	Serial reaction time	Overnight	Nocturnal sleep vs. Daytime wake	No		
	Henderson et al. [21]	7–12y	Serial reaction time	Overnight, 1wk later	AM vs. PM Learning	No differences	No differences	No differences
	Prehn-Kristensen et al. [50]	10–13y	Mirror tracing	Overnight	Nocturnal sleep vs. Daytime wake	No differences		
	Holz et al. [27]	16–17y	Finger sequence tapping	Overnight	Afternoon vs. Evening Learning		Yes	Yes
Generalization	Friedrich et al. [96]	6–8mo	Object-label generalization	Nap	Short vs. Long nap	Yes[g]		
	Simon et al. [97]	6.5mo	Declarative retention of statistical learning	Nap	Nap vs. No Nap	Yes (block-specific)		
	Friedrich et al. [14]	9–16mo	Object-label generalization	Nap	Nap vs. No Nap	Yes		
	Konrad et al. [66],	12mo	Generalization of deferred imitation	Nap	Nap vs. No Nap	Yes		
	Gómez et al. [64]	15mo	Artificial language	Nap	Nap vs. No Nap	Yes		
	Hupbach et al. [65]	15mo	Artificial language	Nap & Overnight	Nap vs. No Nap		Yes	
	Horváth et al. [98]	16mo	Object-label generalization	Nap	Nap vs. No Nap	Yes		
	Werchan & Gomez [69]	2.5y	Noun learning	Nap	Nap vs. No Nap	No		
	Werchan et al. [71]	29–36mo	Noun learning	Nap & Overnight	Nap/Overnight vs. No-Nap/ Overnight vs. Nap Only	Unclear (no No-Nap Only group)	Yes	
	Sandoval et al. [70]	3y	Verb learning	Nap & Overnight	Nap vs. No Nap		Yes	
Emotional Cognition	Mindell et al. [77]	3–18mo	Social Emotional Assessment	Overall sleep patterns	Observational: Assessments at 6, 12, and 18mo			Yes
	Berger et al. [80]	2.5–3y	Emotion-eliciting task	Nap	Nap vs. No Nap	Yes		
	Kurdziel et al. [78]	34–64mo	Emotional memory	Nap & Overnight	Nap vs. No Nap	No differences	Yes	
	Cremone et al. [79]	3-5y	Dot Probe (Emotional Attention Bias)	Nap	Nap vs. No Nap	Yes		
	Bolinger et al. [81]	8–11y	Emotional/Neutral pictures	Overnight	Nocturnal sleep vs. Daytime wake	Yes		
	Vriend et al. [84]	8–12y	Affective response task (ART)	Overnight	Sleep restriction and extension	Yes		
	Prehn-Kristensen et al. [89]	9–12y	Emotional picture recognition	Overnight	Nocturnal sleep vs. Daytime wake	Yes[h]		
	Prehn-Kristensen et al. [50]	10–13y	Emotional recognition task	Overnight	Nocturnal sleep vs. Daytime wake	Yes		
	Baum et al. [85]	14–17y	Mood and emotion regulation assessments	Overnight	Sleep restriction	Yes		
	Short & Louca [86]	14–18y	Profile of Mood States	Overnight	Baseline vs. total sleep deprivation	Yes		

For the rightmost three columns, 'No' is indicative of a sleep detriment.

[a] "Immediate" refers to recall ≤4 h after the *first sleep bout*. i.e., following a nap in nap + overnight protocols, in the morning following overnight protocols.

[b] A group effect was observed for the explicit word learning task, and group × timepoint interactions for both declarative tasks.

[c] Only for picture-naming reaction time; no differences for picture-naming accuracy, stem-completion, or object-location tasks.

[d] While memory did not increase further after the wake interval, the boost resulting from overnight sleep remained.

[e] Nap benefited story word-pair recall, but not for list learning.

[f] With extended training.

[g] Short naps promoted surface–level associations; long nap promoted more semantically-based associations.

[h] Typically developing children benefited from sleep, while those with ADHD did not.

Table 2
Developmental studies assessing relations between sleep *physiology* and cognition (ordered by age tested).

Cognitive Domain	Author/Ref	Age(s) Tested	Sleep bout(s) examined	Memory associated w/PSG?	Physiology Associated with Cognitive Performance			
					Sleep Spindles or σ Power (any sleep stage)	SWS or SWA/slow oscillation power	REM (time, % time, REM theta power)	Other/ additional stages or microstructure (description)
Declarative Memory	Horváth et al. [12]	3mo	Nap	No				
	Friedrich et al. [14]	9–16mo	Nap	No				
	Friedrich et al. [17]	14–17mo	Nap	Yes	X			
	Spanò et al. [39]	2:2–4:2y	Midday nap	Yes[a]			X[a]	
	Kurdziel et al. [7]	2:9–5:6y	Midday nap	Yes	X			
	Lokhandwala et al. [18]	2:9–5:11y	Midday nap	Yes		X		
	Wilhelm et al. [41]	8–11y	Overnight sleep	Yes		X		
	Hahn et al. [43]	8–11y; 14–18y	Overnight sleep	Yes	X			
	Zinke et al. [62]	8–12y	Overnight sleep	Yes	X			
	Backhaus et al. [20]	9–12y	Overnight sleep	Yes				% nREM (summed across nREM 2,3/4)
	Piosczyk et al. [45]	16y	Afternoon nap	Yes	X			
	Holz et al. [27]	16–17y	Overnight sleep	No				
Procedural Memory	Wilhelm et al. [49]	4–6y	Midday nap	No				
	Wilhelm et al. [22]	6–8y	Overnight sleep	No				
	Fischer et al. [51]	7–11y	Overnight sleep	No				
	Wilhelm et al. [41]	8–11y	Overnight sleep	Unknown				
	Zinke et al. [62]	8–12y	Overnight sleep	Yes	X	X		
	Saletin et al. [57]	10–12.9y	Overnight sleep	No[b]				
	Holz et al. [27]	16–17y	Overnight sleep	No				
Generalization	Friedrich et al. [96]	6–8mo	Nap	Yes	X			
	Simon et al. [97]	6.5mo	1st Nap of day	Yes		X		Absolute alpha and theta across brain
	Friedrich et al. [14]	9–16mo	Nap	Yes	X			
	Friedrich et al. [99]	14–16mo	Nap, but memory assessed next day	Yes	X			
Emotional Cognition	Kurdziel et al. [78]	34–64mo	Nap & Overnight sleep	Yes		X		
	Cremone et al. [79]	37–69mo	Nap	Yes[c]		X		
	Bolinger et al. [81]	8–11y	Overnight sleep	No				
	Prehn-Kristensen et al. [89]	9–12y	Overnight sleep	Yes[d]		X	X	
	Prehn-Kristensen et al. [90]	11–14y (typical group)	Overnight sleep	Yes		X		nREM duration

[a] In typically-developing children, not children with Down syndrome.
[b] Physiology/memory association only seen in ADHD.
[c] SWA correlated with faster response times overall, not specifically to emotionally "congruent" trials.
[d] Physiological/behavior association only in typically developing children when combined with adults.

to promote information transfer from hippocampus to neocortex [32]. However, it has been suggested that in infancy, SWS aids memory through *cortical synaptic downscaling* (i.e., weakening global synaptic potentiation, and increasing signal-to-noise for connections increased during learning) rather than active systems consolidation [33]. Supporting this perspective, younger infants often require multiple exposures to retain declarative information [12], which is arguably characteristic of cortically-mediated learning rather than rapid hippocampal learning [33].

Synaptic downscaling has been associated with SWA [34]. Yet, the only study to find associations between infant sleep physiology and consolidation reported a correlation between frontal *fast spindle* (13–15 Hz frequency) amplitude and episodic memory in 14–17-month-olds [17]. This result instead supports that active systems consolidation may be present in infants as fast spindles have specifically been associated with hippocampal-cortical functional connectivity and active memory restructuring [35]. Additionally, intracranial recordings and experimental manipulations have linked spindles with enhanced hippocampal-neocortical coupling [36] and declarative memory performance [37]. Although [35–37] focused on adults, behavioral findings in infants further support early active systems consolidation, as 12-month-olds can retain some declarative information after just three brief demonstrations within the same learning session [13], and 14-17-month-olds can retain episodic details over just two demonstrations [17]. However, given that these studies were done in older infants ($\geq$12 months), it is possible that infants <12 months may benefit from synaptic downscaling while older infants benefit from active systems consolidation.

Though associations between spindles and sleep-dependent declarative gains have only been found in older infants thus far, nap spindles have also been associated with *pre*-sleep declarative learning in younger infants (3 months) [12]. No other studies have found relations between declarative retention in infants and either SWS or sleep spindles (however, see [14]). Such null SWS findings may be attributable to ceiling effects (infant naps generally have high SWS), or perhaps SWS serves different functions in infancy compared to adulthood.

More studies have addressed mechanisms underlying nap benefits in early childhood, but these results are discrepant. One

study found relations between preschool-aged children's nap spindle density and post-nap visuospatial memory [7]. However, a more recent study found that SWS duration, but not spindles, correlated with post-nap memory for story sequences [18]. These contrasting findings may suggest that relevant sleep physiology is task-dependent. The visuospatial task [7] may particularly depend on spatial-coding place cells whereas the story task may rely on mechanisms such as SWS-dependent downscaling. Alternatively, both spindles and SWS may aid memory in these tasks [38], but different associations may emerge due to other paradigmatic differences or sample characteristics (for example, spindle density ranges in [7] were wider than in [18]).

REM has also been implicated in early learning. Typically-developing preschool-age children with more REM retained more learned items than those with less REM [39]. Moreover, children with Down syndrome who exhibited minimal REM showed no nap-dependent benefits. Importantly, this REM role may emerge with longer or more ecologically typical naps, as REM and overall nap durations were longer in this in–home study than in other laboratory-based nap paradigms ([39]: 13.97 min REM/104.09 min sleep; [7]: 1.32 min REM/73.83 min sleep; [18]: .39 min REM/94.18 min sleep). Nonetheless, a specific role for REM in declarative memory consolidation among preschoolers stands in contrast with adult studies which infrequently find REM-related declarative memory benefits [40].

In middle childhood, declarative memory has been associated with overnight nREM sleep [20]. For example, 8-11-year-old children's recall was associated with higher overnight SWA and increased hippocampal activation [41]. These children also experienced greater sleep-dependent explicit memory gains when compared to a group of adults, attributed to greater SWS and SWA in children. Another study [42] corroborated the superior sleep-dependent declarative benefits experienced by children (7–12 years) compared to adults, though the authors did not measure sleep physiology. Intriguingly, a recent longitudinal study starting at ages 8–11 years suggested that slow spindle densities positively predicted absolute declarative performance, but that overnight increases in slow spindles negatively predicted overnight memory consolidation [43]. In contrast, fast spindle densities in adolescence (14–18 years) positively predicted overnight consolidation, and changes in sleep-dependent memory benefits across the two timepoints were related to developmental changes in fast spindles. Overall, these studies suggest that different features of nREM in middle childhood may have contrasting impacts on declarative memory.

In adolescent sleep restriction studies [28,29,44], SWS duration was largely preserved at the expense of other sleep stages. Preservation of SWS might explain why declarative memory consolidation is relatively maintained [29]. Additionally, EEG sigma power in naps predicted declarative memory consolidation apart from IQ or encoding differences [45]. These data indicate that the mechanisms implicated in adolescent declarative memory consolidation parallel findings in adults.

Procedural memory

Procedural memories are memories for skills and motor sequences, relying on distinct neural circuitry (e.g., basal ganglia, cerebellum) in adults. Although adult studies have considered forms of non-motor procedural learning, studies in development have been limited to the motor domain.

Behavioral findings

Although research exploring sleep and “procedural memory” is scarce in infants, two studies suggest that sleep may be beneficial. In one [46], 3-month-olds were trained to move a mobile above their crib via kicking. Two weeks later, the mobile was again presented, and memory was assessed via kick rate. Retention positively correlated with the percentage of time infants slept during the delay. Napping likewise benefited locomotor learning in 9–16-month-olds. Infants were placed in front of a tunnel that required them to switch from walking to crawling [47]. Following a delay including napping or wake, infants completed the tunnel task again. Infants who napped were quicker, required fewer chances to traverse the tunnel, and had fewer “body-tunnel mismatches” at test compared to infants who stayed awake. Together these findings support a beneficial role of sleep in early procedural learning.

Whether naps benefit procedural learning in early childhood is ambiguous. One study using a sequential learning task in children 2.9–6 years did not find an immediate nap benefit, but found a nap benefit after overnight sleep [48]. In contrast, another report in 4-6-year-olds [49] showed an immediate nap benefit but only with additional training, suggesting that weak initial learning may not benefit from sleep. Thus, while napping may benefit procedural memory in young children, augmentation (additional sleep, training) may be necessary for such benefits to be realized.

Procedural studies in middle childhood show either no sleep benefits compared to wake [21,50] or, surprisingly, a negative effect of sleep [22,51]. Notably, studies reporting negative results examined only short-term performance effects and not possible delayed benefits. The need to examine longer-term sleep effects is exemplified by work in juvenile songbirds, which shows that the magnitude of overnight performance deterioration following early motor learning positively predicts long-term performance gains (>30 days later) [52]. Initial sleep-related impairments are thought to reflect short-term memory destabilization due to sleep-related reactivation, which predicts long-term stabilization. Thus, it is possible that negative sleep effects in middle childhood may yield delayed advantages.

On the other hand, the distinction between sleep's effects on procedural versus declarative memories has led to speculation that, in early childhood, sleep may preferentially consolidate declarative memory at the expense of procedural memory [22,51,53]. Studies of children with ADHD may lend credence to this hypothesis, as sleep supports their motor learning [54] while their sleep architecture differs from that of typically-developing same-aged children [55]. ADHD also often entails atypical connectivity of brain networks important for explicit learning and attention [56]. Network reductions combined with sleep differences may attenuate the neural competition between declarative and procedural memories observed in typically-developing children [54,57], allowing children with ADHD to experience a sleep benefit in both domains.

No studies have directly contrasted sleep and wake-related procedural memory changes in adolescents. However, one study in 16–17-year-olds considered the timing of procedural learning relative to sleep [27]. Adolescents who learned a finger-tapping task immediately prior to sleep showed greater next-day improvements compared to those who learned 7.5 h before sleep. These differences remained 7 days after training, suggesting that, similar to declarative memory, shorter intervals between learning and sleep may produce long-lasting procedural memory benefits during adolescence.

Physiological mechanisms

In adults, both REM and nREM2 sleep characteristics are implicated in procedural memory, possibly interacting to aid learning and consolidation [58]. How sleep facilitates infants'

procedural memory is poorly understood. However, if we expand early procedural learning to include common motor milestones such as crawling and coordinated reaching, recent perspectives on sensorimotor development provide insights. For instance, Blumberg and colleagues [59] posit that during fetal development and early infancy, myoclonic twitches during active sleep (the precursor to REM) may aid sensorimotor organization via sensory feedback, allowing young infants to build "topographic maps" that enhance limb and behavioral coordination and promote cortical development [60]. Supporting this notion, a study in premature human infants found that sleep twitches produced oscillatory activity in somatotopically related cortical areas [61]. Thus, it is possible that active/REM sleep and its associated neural and movement patterns may play a functional role in infants' motor learning.

Of six PSG studies of childhood and adolescence, only one found associations between procedural memory and sleep, specifically spindles and SWA [62]. Given that children's procedural learning often does not show sleep-dependent improvements, this paucity of associations is perhaps not surprising. However, in adults, procedural consolidation is often linked to sleep microstructure, such as number of sleep spindles or rapid eye movements. Few child studies consider sleep microstructure; thus, discrepant results may reflect analytical differences. Alternatively, sleep differences between children and adults may underlie a shift in sleep's function with age. In a study comparing 7-11-year-olds and adults, children's sequence learning suffered following overnight sleep while adults' performance improved [51]. Children also spent more time in SWS compared to adults, corroborating the suggestion that because children have more SWS and greater SWA, procedural memory may be less prioritized for processing than declarative learning at this age [53]. However, more research is needed to directly test this possibility.

Generalization

Generalization involves abstracting broad rules, representations, or concepts from specific examples that share similar features. Whether sleep supports generalization in early development is of particular interest, as the ability to generalize is critical for semantic category learning (i.e., identifying similarities between related but non-identical items or examples), language learning, and flexibility in new contexts [63,64].

Behavioral findings

Sleep benefits generalization from a young age. When 9-16-month-olds were randomly assigned to nap or wake groups, only infants who napped showed ERP evidence of generalizing recently learned object labels to new examples [14]. Likewise, Gómez et al. [64] demonstrated that after hearing syllable sequences with a specific grammar, only 15-month-olds who napped recognized the underlying grammar. This nap benefit persisted 24 h after encoding [65].

These effects extend to non-linguistic learning as well. Infants who napped after viewing an experimenter perform target actions on different hand puppets performed more target actions with a novel puppet compared to infants kept awake [66]. One possible explanation for this result is that naps promoted generalization to the new puppet via forgetting of less frequent or non-overlapping aspects of the training puppets [33]. However, forgetting alone would not explain differences in performance from the wake group, who would also theoretically forget due to interference from waking sensory input [67]. Thus, perhaps a more nuanced explanation is that napping adaptively increased the signal-to-noise ratio of overlapping commonalities across stimuli [68]. Mechanism aside, these results suggest that napping supported infants' abstraction and generalization of actions performed on similar items.

Findings regarding naps and generalization in early childhood (2.5−3.5 years) are mixed. One study suggested that children better generalize newly-learned nouns to novel examples when kept *awake* following learning [69]. However, another study found children more adeptly generalized novel verbs to new agents 24 h later if they napped within 5 h of learning [70]. Aside from targeting different parts of speech (noun vs. verb), one distinction between these studies is the timing at which generalization was probed (4 vs. 24-hrs later). A follow-up experiment using the noun learning task from [69] confirmed the importance of additional sleep for nap-dependent generalization effects. After overnight sleep, children who napped after learning the prior day more accurately generalized noun labels to new exemplars than children who stayed awake for at least 4 h following learning [71]. Why generalization might depend on multiple sleep bouts at this age is unclear, though it may be that additional sleep cycles including longer REM sleep intervals are needed. Such REM intervals could promote reorganization and integration of related memories strengthened during nap nREM by increasing cortical plasticity, a function attributed to REM [72−74]. Still, given the lack of PSG studies for generalization tasks in this age range, the role of REM for generalization in early childhood is only speculative.

No studies to our knowledge have assessed the role of sleep on generalization in middle childhood or adolescence. Further work must address the conditions under which sleep benefits generalization during these periods of development.

Physiological mechanisms

Infants' generalization has largely been associated with sleep spindles, but there is speculation regarding mechanism. Friedrich et al. [14] argue that infants' spindles assist with active memory reorganization, increasing synaptic plasticity by driving neocortical short- and long-term potentiation. This plasticity is thought to allow for active strengthening of overlapping elements across experiences. However, Gómez and Edgin [33] maintain that infants' sleep-dependent generalization is due synaptic downscaling during sleep, whereby only connections strengthened during learning survive in memory. Though they concede that associations between spindles and generalization may reflect more active cortical synaptic strengthening, they distinguish between active spindle-related enhancement of cortical memory and active systems consolidation involving the hippocampus, which they argue is not sufficiently mature in infancy. Resolving these speculations requires future work with brain-based measures.

There is a gap in both behavioral and physiological studies of sleep-dependent generalization in childhood and adolescence. However, given the role of overnight sleep in nap-dependent generalization in young children, it is possible that overnight REM enhances generalization in correspondence with nREM shortly after learning. Further behavioral and physiological studies beyond infancy may elucidate the requisites for sleep-dependent generalization across development.

Emotional cognition

Sleep contributes to emotion processing in adults. In developmental studies, although the domains and paradigms vary, these studies collectively support a role of sleep on emotion processing.

Behavioral findings

No studies have examined the direct effects of sleep compared to wake on emotional memory in infancy. However, a pair of studies used MRI while infants slept to evaluate emotion processing. This work found that infants 3–12 months can process and differentiate emotional content while asleep [75,76], though whether such processing is enhanced relative to wake is unclear. However, consistent with this, more sleep at 6 months predicted fewer parent-reported emotional difficulties at 12 months [77]. Although correlational (and limited to parent sleep reports), these studies suggest that differences in sleep during infancy may affect emotional development.

Likewise, sleep in early childhood benefits emotion processing. One study [78] experimentally manipulated sleep to understand how naps influence preschoolers' memory for faces encoded in an emotional context. Although no immediate nap benefit was found, memory for both "mean" and "nice" faces was greater the following day if a nap followed learning. It is possible that the next-day nap benefit reflects nap-specific memory reactivation that left memory unstable initially but primed it for overnight consolidation. In contrast, other work has shown an immediate nap benefit for tasks probing emotional attention and regulation. For example, 3-5-year-olds showed an emotional attention bias when kept awake during naptime compared to when they napped [79]. Likewise, nap-deprived 2.5-3-year-old children responded more negatively towards neutral and negative stimuli and less positively to positive stimuli in an emotion-eliciting task compared to when they were well-rested [80]. Nap-deprived children also spent less time conveying positive affect when completing a solvable puzzle and more time expressing negative affect toward an unsolvable puzzle. Such findings indicate that early childhood naps may facilitate adaptive emotional responses in various contexts, though expression of emotional memory consolidation per se may depend on additional nighttime sleep [78].

A few studies have explored the effects of overnight sleep and sleep restriction on emotion in later childhood and adolescence. For example, overnight sleep (relative to daytime wake) generally improved 8-11-year-olds' image recall, regardless of emotional valence [81]. Intriguingly, sleep also attenuated children's EEG reactivity and subjective emotional valence ratings, while increasing automatic emotional responses (heart rate deceleration). Thus, sleep may have paradoxical effects on children's emotional reactivity, attenuating more cognitively-mediated reactions while increasing the automatic physiological impact of emotional content. Studies in adults [82,83] have shown that a SWS-associated mechanism supports protection of emotional valence while a REM-dependent mechanism protects emotional physiological reactivity. It is possible the former is underdeveloped in this age group. However, this seems unlikely given that declarative memories, thought to rely on the same mechanism, are consolidated with SWS at this age [41].

In other work [84], 8-12-year-olds exhibited less positive affect on a laboratory task and had poorer emotional regulation when experimentally sleep-restricted by 1 h across 4 days. When 14-17-year-olds' sleep was restricted to 6.5 h for five nights, adolescents rated themselves higher in emotional dysregulation, confirmed also by parents [85]. Additionally, a study in 14–18-year-olds [86] reported significantly depressed mood after one night of total sleep deprivation, but only in female participants. Collectively, these findings indicate that the effects of sleep restriction or deprivation on adolescent emotion are generally deleterious, but may be moderated by demographic factors.

Physiological findings

In adults, emotional processing is frequently attributed to REM sleep, though recent studies support a role for SWS [87]. During REM, theta oscillations from the amygdala synchronize with hippocampal and cortical activity, corresponding to emotional memory enhancement [88]. When emotional memory involves declarative aspects, SWS likely also supports such aspects as previously described.

In studies of early childhood, SWS is most often implicated in emotion processing. For instance, the next-day nap benefit for emotional face memory [78] was associated with nap SWA, suggesting a possible interaction between nap SWA and overnight sleep. Additionally, SWA in preschool children's naps predicted faster post-nap response times in an emotional attention task [79].

Among 9-12-year-old children and adults, both REM theta and SWS positively predicted emotional picture memory [89]. SWS was also found to correlate with 11–14-year-olds' emotional memory consolidation, though this association was not specific to emotional items [90]. Considering this study and others [79], future work should focus on whether sleep physiology in childhood and adolescence specifically supports emotional over neutral memory consolidation.

Interrelations between brain development, sleep, and cognition

In the present review, we have outlined how sleep changes developmentally in tandem with early brain development, and how sleep may support early cognition. Broadly speaking, studies support either a facilitative or direct physiological role for sleep across multiple cognitive domains. However, these domains differ in the conditions under which sleep supports them, and age differences may also influence the conditions necessary for sleep-dependent benefits. Additionally, though progress has been made in investigating the sleep correlates of memory and cognitive development, physiological data remain sparse within most developmental age ranges and cognitive domains. Thus, while we discuss the implications of the available literature, conclusions are preliminary, and replication and expansion is needed.

Physiologically, sleep spindles and slow waves appear to be the most prominent facilitators of cognitive processing across development thus far (see Table 2). While this may reflect limitations in paradigms (e.g., nap studies in infants and early childhood), it may also point to a distinct function of REM unrelated to localized cognitive processing. A recent mathematical model of sleep physiology, sleep time, and brain weight concluded that the function of sleep, and particularly REM sleep, shifts abruptly between two and three years. In infancy, REM may support neural reorganization while, at later ages, REM function may shift to neural repair [91]. Consistent with this, REM sleep supports new dendritic spine formation during early development [92] and synaptic pruning begins around 2 years [93]. Thus, there may be a role of nREM in local memory networks while REM supports more global reorganization that might be more evident in longer-term follow-up studies. Note that, in addition to REM supporting spine formation in

development, REM was also found to stabilize new spines immediately post-learning in adult animals [92].

Additionally, our review indicates that sleep timing may affect early sleep-dependent cognitive benefits. Infants and children who do not nap shortly after declarative learning show reduced consolidation even after one or multiple days of unrestricted follow-up sleep, and even if initial learning occurs during an interval in which they would not normally nap (in contrast to nap deprivation; i.e., [13,19]). Intriguingly however, older children benefit from sleep in some tasks even when the interval between learning and sleep is extended [20,21]. This may suggest that the increased development of memory-related brain areas in older children allows memories to be held longer without interference. However, older adolescents' performance shows varying dependence on the temporal proximity of sleep relative to learning, depending on the task [24,27]. These differences in reliance on sleep timing between children and older adolescents require further investigation.

We have described general trends regarding sleep's influence on cognition, yet individual differences also impact sleep's effects. Specifically, nap habituality may predict the effects of wakefulness on memory in infants and young children ([7], but see [19]), and differences in spindle densities and SWA predict learning differences across same-age children [7,78]. Neurodevelopmental conditions (ADHD, Down syndrome) may also alter sleep's effects, either by affecting sleep directly or through other indirect neural processes [39,54,90]. Furthermore, sleep may be influenced by cultural and socioeconomic variables [94], indicating that sleep could moderate or mediate associations found between cognition and sociodemographic factors. Finally, sleep's benefits may also depend on individuals' relative skill level and depth of initial encoding, as indicated in some of the child studies reviewed here [23,49] and noted in adults [95].

Given recent studies connecting sleep microstructure changes with early brain development [8,9], future work should tease apart whether such changes, including topographical shifts in maximal SWA, also predict developmental shifts in sleep's benefits for cognitive abilities that rely on different neural networks (i.e., declarative vs. procedural memory). If relations are found, further analyses should tease apart whether these relations are accounted for solely by brain development, or if brain development leads to specific sleep changes that directly alter sleep's influence on cognition. Overall, the current data imply not only that developmental differences in sleep may impact cognition, but reciprocally that sleep itself—and its relative benefits—may be affected by brain development.

Concluding remarks

Our review highlights a growing interest in understanding how the timing, physiology, and developmental characteristics of sleep support cognition in human development. Although much has been done to elucidate sleep's short-term role in early memory and learning, further work must clarify how early sleep bouts interact over hours and days to support cognitive development. By assessing the impact of sleep at multiple timepoints and across domains, we will understand not only how different cognitive abilities change developmentally, but also how the neural systems and physiology supporting cognition emerge to influence individual developmental trajectories.

Practice points

1. Sleep timing and structure changes significantly across development. Additionally, individual differences in sleep within the same developmental period are common.
2. For infants and children, sleep *immediately following learning* may maximize sleep's benefits on memory.
3. Current sleep physiology studies underscore the interactive role of sleep spindles and SWS in sleep-dependent memory consolidation, particularly for declarative memory. SWS is also implicated in emotional memory, and spindles in generalization.
4. Differences in relations between sleep physiology and memory across studies likely result from differences in sample characteristics and behavioral task(s) employed.
5. In contrast to earlier reviews that did not find a sleep benefit for procedural learning in children, recent studies have found this association under specific study paradigms (e.g., extended training), and when considering multiple sleep bouts.

Research agenda

1. Investigate the interactive effects of multiple sleep bouts on early cognition, and assess sleep effects over multiple days to identify extended sleep benefits.
2. Longitudinally examine interrelations between brain structural/functional development, sleep characteristics, and cognition.
3. Consider how paradigms employed might affect study outcomes. Determine whether outcomes are task-specific by including more tasks within a single paradigmatic framework.
4. Examine whether eliminating naps (as is sometimes done to promote overnight sleep in young children) is detrimental to cognitive development.

Conflicts of interest

The authors do not have any conflicts of interest to disclose.

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