

Review Article

Sleep and memory consolidation in healthy, neurotypical children, and adults: a summary of systematic reviews and meta-analyses

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This review systematically assesses the impact of sleep on memory and cognition in healthy individuals across different life stages. It specifically examines how sleep affects memory processes in children, adults, and older adults. The methodology involved a comprehensive literature search, starting with 46 known papers. Keywords and Mesh terms related to sleep and memory consolidation were derived using the Word Frequency Analysis tool in SR Accelerator and Mesh on Demand. A detailed search on PubMed yielded a large set of records. Classifier training on 4854 decisions, these were narrowed down to 1437 papers for full-text screening, culminating in 19 systematic reviews and meta-analyses. Sleep enhances memory consolidation, especially for complex declarative information. While the role of sleep in procedural memory consolidation in children remains less robust compared to declarative memory, findings suggest potential but inconsistent benefits. Sleep improves prospective memory consolidation and aids in complex associative memory tasks. Memory reactivation during sleep, specifically slow-wave sleep, and spindles are implicated in memory consolidation. Meta-analytic evidence suggests that while sleep benefits both emotional and neutral memory consolidation, there is no strong preferential effect of sleep on emotional memory in comparison to neutral memory. In older adults, there is a noticeable reduction in sleep-dependent memory consolidation, particularly for declarative memory, likely linked to a decline in slow-wave sleep. This suggests a decrease in the benefits of sleep for memory consolidation with aging. Overall, the review underscores the importance of sleep in memory processes across all ages, highlighting variations in its impact on different types of memory and across age groups. It points to future research directions for enhancing understanding and practical applications in clinical and educational settings.

Introduction

This article is a review of existing systematic reviews and meta-analyses, representing a rigorous compilation of the highest quality evidence on the role of sleep in memory consolidation. Our aim is to summarise and evaluate the findings from these comprehensive reviews to provide a clear and authoritative perspective on how sleep facilitates the transformation of experiences into lasting memories. This approach ensures that we base our conclusions on the most robust data available, offering a critical overview of the current state of research in this field for academics and practitioners alike.

Sleep and memory consolidation: a brief history

The relationship between sleep and memory was first noted by Ebbinghaus in 1885, who found that there was less forgetting of newly learned information after sleep than during wake. He ascribed this to a reduction in interference during sleep compared with wake. Sleep was thought to be passively protective of memories. However, there is now a wealth of evidence that sleep has an active role to play in

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supporting the development of robust memories, this is known as sleep-associated memory consolidation. Put simply, sleep has been shown to have a role in transforming newly learned information which is weakly and sparsely encoded into robust and stable memories integrated with existing knowledge in long-term memory (LTM). Memory is not a unitary concept, and sleep's impact on consolidation differs by memory type (see Box 1).

Müller and Pilzecker [1] suggested the consolidation hypothesis as a result of their empirical observations on retroactive interference, where they noticed that newly acquired information (in their case, lists of syllables) was susceptible to being disrupted by subsequent learning. They inferred that after the initial learning event, the memory traces of the syllables needed time to stabilise. The hypothesis was that during this stabilisation period, known as consolidation, the memory traces would become less vulnerable to interference from additional information. The suggestion was that this post-learning period was critical for the memory traces to become more permanent, a process they believed to be underpinned by physiological changes in the brain. However, under this view, the role of sleep is seen as protective and relatively passive.

During the 1920s the foundational work of Jenkins and Dallenbach [2] set the precedent for understanding the beneficial role of sleep on memory retention. They demonstrated empirically that sleep served to preserve memory from the gradual decay that occurs over time. This work was pivotal in shaping the hypothesis that sleep contributes to memory consolidation, which has been a subject of robust scientific inquiry over the last century.

Research on sleep and memory gained momentum in the mid-1990s through key papers that began to differentiate the effects of sleep on various types of learning (e.g. declarative vs. procedural [3]). Concurrently, significant contributions from the fields of neurophysiology and neuroanatomy focused on synaptic plasticity mechanisms, the reactivation of neural networks during sleep that had been active during learning, and the identification of the central nervous system structures involved [4].

According to Stickgold [5] the first study to report a clear role for sleep in human memory consolidation was reported in a seminal paper by Karni, Sagi, and colleagues in 1994. They found that performance on a simple visual discrimination task improved after a night of normal sleep, but that this improvement was diminished by selective disruption of REM sleep. Around the same time, Plihal and Born [3] found that sleep generally enhanced recall compared with wakefulness and that the benefit depended on the type of memory and the phase of sleep. The recall of paired-associate lists (declarative memory) improved more during early sleep, and mirror-tracing skills (procedural memory) improved more during late sleep. Their study was significant in demonstrating the specific effects of early and late sleep in humans for the first time. The rate of publication of research papers on sleep-dependent learning and memory consolidation burgeoned throughout the following decade and has continued to grow exponentially.

Systems consolidation and neural underpinnings

The Complementary Learning Systems Theory, proposed by McClelland et al. [6], laid the groundwork for understanding the balance between rapid learning of specific experiences and gradual integration into existing knowledge networks. More recent research has built on this by examining neural reactivation during sleep. The theory posits that the brain achieves this balance through two specialised learning systems, each with distinct roles.

The first system, centred in the hippocampus, is responsible for the rapid learning of the specifics of individual items and experiences. This system is characterised by its ability to form new memories quickly without disturbing older memories, a process known as pattern separation. The second system, located in the neocortex, supports the gradual acquisition of structured knowledge about the environment. It integrates new information over time into the existing network of knowledge, helping to stabilise, and consolidate memories. This dual-memory system helps to prevent what is known as catastrophic interference, which can occur when new learning disrupts previously established knowledge (McClelland et al. [6] see [7] for a recent review).

Furthermore, the CLS theory suggests that multi-layer neural networks, akin to the neocortex in the brain, should work in tandem with fast-learning systems like the hippocampus. This partnership allows for both the rapid assimilation of new, detailed information and the slow, integrative learning that underpins the development of semantic networks and schemas [6].

This dual-system framework, with the complementary roles of the hippocampus and neocortex, provides a robust explanation for how the brain can manage the delicate balance of learning and memory, ensuring both flexibility and stability in cognitive function.

Sleep has been demonstrated to facilitate the transformation of new information, which is initially encoded in a fragile and dispersed manner in the hippocampus, into strong, stable memories that are integrated with pre-existing knowledge in LTM. This encapsulation of sleep's role in memory processing reflects a shift of information

within the brain from an initial, vulnerable state to a more consolidated and integrated one, suggesting a systemic reorganisation of memory traces from the hippocampal region to neocortical structures over time [5].

During sleep, the hippocampus is particularly active in aiding the construction of semantic representations of information in the neocortex, which effectively transforms the nature of the memories from a transient to a more stable state. This interplay between the hippocampus and neocortex during sleep is crucial for the consolidation of new memories (Box 1).

Box 1. The different facets of memory and how they are measured

Memory is not a unitary construct and specific tasks used in sleep and memory research aim to examine how sleep affects the consolidation process of different types of memory. For example, declarative memories may benefit from SWS, which is proposed to help integrate recently learned material. In contrast, REM sleep might be particularly important for complex and emotionally charged declarative memories. However, these findings can be inconsistent and are a topic of ongoing research.

- *Procedural Memory*: This is a part of long-term memory responsible for knowing how to do things, also known as motor skills. It stores information on how to perform certain procedures, such as walking, talking, or riding a bike. The serial reaction time task or a finger-tapping task, is often used, where participants learn a sequence of movements.
- *Declarative Memory*: Declarative memory stores facts and events. It's what people typically think of as memory—the conscious recollection of information like dates or words. It can be divided into *episodic memory* which is autobiographical in nature and includes details of the context in which the memory was formed, such as the time, place, associated emotions, and other environmental details, and *semantic memory* which encompasses knowledge that is not tied to specific personal experiences. Studies often use word-pair association or list-learning tasks before and after sleep to evaluate how well factual information is retained.
- *Associative Memory*: This is the ability to learn and remember the relationship between unrelated items, such as the name of a person we just met or the aroma of a particular food. Pairing tasks where two items (like a face and a name) are associated with each other; recall is then tested after a period of sleep.
- *Prospective Memory*: This refers to our ability to remember to perform a planned action or recall a planned intention at some future point in time. Participants may be asked to remember to perform a task at a certain time during a session after sleeping, to test how well sleep has consolidated their intention.
- *False Memory*: This involves recalling something that did not happen or remembering it differently from the way it actually happened. It can be influenced by various factors, including suggestions from other people. The Deese–Roediger–McDermott (DRM) paradigm can be used, where sleep is tested for its role in the creation or prevention of false memories by assessing recall of lists of semantically related words, where a critical lure word is often falsely remembered (e.g. bed is falsely recalled following a list of sleep-related words such as pillow, dark, tired).

Assessing the state of the art: a brief review of reviews

Rationale

Thirty years on from Karni et al. [8], we know so much more about the active role that sleep plays, the many different facets of memory, and the complex interplay of the different stages of sleep in memory consolidation. This review seeks to provide an overview of what we know now, and where we need to go next. We have reviewed existing systematic reviews and meta-analyses to provide an overview of the most rigorous reviews of the relevant literature. However, we acknowledge that this necessarily narrows the scope given that we did not include narrative reviews. Additionally, we acknowledge that we lacked the resources to undertake double screening throughout the screening process, and similarly, lacked the resources to undertake a formal critical

appraisal (e.g. AMSTAR2) of the included reviews. As such, whilst we have sought to be transparent in our methods, this is not an umbrella review of the literature.

Methods

The inclusion criteria for our systematic review and meta-analysis were specifically designed to ensure a focus on relevant and high-quality reviews. We included only systematic reviews and meta-analyses, emphasising studies that provided a comprehensive synthesis of existing research. The population of interest comprised healthy neurotypical children and adults, allowing us to understand the effects of sleep on memory consolidation across a broad age range. Our review concentrated on studies examining the relationship between sleep and memory consolidation. Additionally, we restricted our review to studies published in English, due to resource limitations.

From an initial seed of 46 relevant studies known by the first author (ARW) to support the development of a search strategy, we identified keywords related to sleep and memory consolidation using the word frequency analyser (WFA) tool in SR Accelerator [9]. Additionally, Mesh terms were identified using Mesh on Demand [10], using the same seed set of relevant papers. These were then developed into a search for PubMed. Appendix 1 contains the list of words identified for use using WFA and the full PubMed search. Resources precluded a broader set of search databases. This retrieved 31 273 records, from which a deduplicated set of 30 678 was identified using Rayyan [11]. We employed the classifier within Rayyan, where we screened 4854 abstracts (single screened by ARW) until no abstracts with a probability of inclusion of >50% remained. Of those, 1437 were marked for full-text screening. Within these, 88 were identified as reviews, with 19 identified as systematic reviews and/or meta-analyses. The search was limited to PubMed due to resource constraints. Future work should conduct a broader database search for a more thorough review.

Overview

Table 1 summarises the included systematic reviews. Looking across the systematic reviews identified it is clear that sleep facilitates memory encoding, consolidation, and associative processing, with slow-wave sleep (SWS) and spindles playing critical roles [13, 23]. However, sleep-dependent memory benefits are reduced in older adults [19, 20] and may vary for procedural versus declarative memory in children [22], and as a result of transcranial electric stimulation [12] or closed-loop stimulation [16]. In healthy younger adults, sleep compared with wakefulness consistently improves declarative [14], episodic [14], emotional [26], prospective [24], and motor memory consolidation [28]. Sleep also aids complex associative memory processing like gist extraction, integration, and rule learning [15]. Memory reactivation via cues during sleep enhances consolidation [21], implicating sleep as a period when memories remain receptive to modification. Analyses indicate SWS [23] and sleep spindles [23] facilitate declarative memory consolidation, which correlates with hippocampal activation patterns [14]. However, sleep does not appear to preferentially consolidate emotional over neutral memories based on a comprehensive meta-analysis [26]. In healthy older adults, sleep-dependent memory consolidation is reduced compared with younger adults, particularly for declarative/hippocampal-dependent memory [19]. SWS decline may contribute to this effect, as SWS is critical for declarative memory and diminishes with aging [19, 29]. While overall sleep-memory association strength is similar across age groups [20], specific sleep parameters like SWS and wake after sleep onset show differential relationships with memory performance between young and old [20]. Acoustic stimulation during sleep improves declarative but not non-declarative memory in young but not older adults [29]. Overall, normal aging is associated with decreased sleep-based memory consolidation [19].

Children and young adults

In the context of cognitive development during childhood and adolescence, sleep has been identified as a pivotal factor for memory consolidation. Kopasz et al. [22] systematically reviewed the literature, revealing that sleep is beneficial for encoding and working memory tasks, particularly those requiring complex declarative processing. This is consistent with the known involvement of the hippocampus in declarative memory during sleep [4, 27]. However, procedural memory consolidation in children shows less consistent improvements compared to declarative memory, suggesting a need for further investigation into the developmental processes at play [31].

Furthermore, Kopasz et al. [22] found that the impacts of sleep on memory are moderated by factors such as sleep duration and restriction. Prolonged sleep restriction has been linked to cognitive impairments [17] while

Table 1. Summary of included studies

Part 1 of 3

Reference	Question	Methods	Results	Conclusion
Barham et al. [12]	Does transcranial electrical stimulation (TES) administered during sleep modulate declarative and procedural memory consolidation?	Systematic review and meta-analysis of 13 experiments involving 179 participants. TES was applied during sleep, measuring effects on consolidation of declarative (hippocampus-dependent) and procedural (cortico-striatal dependent) memories.	TES significantly enhanced declarative memory consolidation (average effect size 0.447), but did not significantly enhance or disrupt procedural memory consolidation (average effect sizes 0.154 and 0.076, respectively).	TES applied during sleep can reliably modulate the consolidation of declarative but not procedural memories. This finding supports the role of sleep in hippocampal-dependent memory consolidation.
Belia et al. [13]	What role does sleep play in supporting word learning processes, such as stabilising and generalising new word meanings, in infancy?	Review of 16 studies examining sleep's effects on infant word learning. Methods included comparing performance post-naps vs. wake periods, measuring brain responses, tracking longitudinal vocabulary development, and analysing sleep physiology.	Naps were found to help stabilise memory for new word forms and meanings in the short term and support generalisation of words to new category members. Brain responses and sleep spindles were linked to better post-nap retention and generalisation. Longer nighttime sleep was associated with larger vocabularies later on.	Sleep facilitates multiple aspects of word learning in infancy through memory consolidation, akin to findings in adults and older children. Further research is needed on the interaction of existing knowledge and sleep in strengthening new word memories, the distinct roles of naps versus overnight sleep, and neural correlates of consolidation.
Berres and Erdfelder [14]	Does sleep improve episodic memory compared with wakefulness, and what are the underlying processes and moderators?	Systematic review and meta-analysis with a comprehensive literature search. Inclusion criteria focused on studies assessing episodic memory after sleep versus wakefulness. Moderator variables were coded. Statistical analysis involved multilevel meta-regression models with robust variance estimation (RVE).	Analysis of 823 effect sizes from 271 samples showed a moderate effect of sleep-improving episodic memory (Hedges' $g = 0.44$). Larger effects were noted with multiple study repetitions, free recall tests with words, and difference scores between immediate and delayed tests. Effects were stronger for natural nighttime sleep and naps. Emotional valence, age, total sleep time, slow-wave sleep, and REM sleep duration did not significantly moderate effects.	The findings support the theory that sleep improves episodic memory through both strengthening memory storage via consolidation and enhancing retrieval by reducing interference. These results have implications for memory theory and provide methodological guidance for future research. Limitations include a lack of unpublished data and insufficient samples for some moderators.
Chatburn et al. [15]	Does sleep facilitate complex associative memory processing, such as extracting general meaning or rules from stimuli sets, relative to wakefulness?	Systematic review and meta-analysis of 27 studies on sleep and associative memory in healthy adults. Experimental paradigms assessed false memories/gist extraction, item integration, and rule extrapolation.	The meta-analysis revealed a moderate overall effect of sleep on associative memory compared with wakefulness. Sleep increased false memories in recall tasks, integrated new words into lexical networks, and improved rule extraction from stimulus sets.	The findings suggest that sleep assists in assimilating new memories into existing knowledge networks and extracting commonalities between memories. The relationship between sleep physiology and outcomes was mixed, indicating varying benefits depending on the specific task and sleep stage.
Choi et al. [16]	How do closed-loop feedback systems enhance sleep-related outcomes?	Review of 20 articles using PRISMA protocol from databases like IEEE Xplore, PubMed. Focus on closed-loop feedback in human sleep studies.	Closed-loop systems shown to improve memory consolidation by modulating SO and sleep spindle activities. Limitations in modulating all sleep-dependent brain activities.	Closed-loop feedback systems are promising in sleep research, particularly for memory consolidation. Future advancements in automation and machine learning expected to enhance effectiveness.
Dutheil et al. [17]	What are the effects of a short daytime nap on	Systematic review and meta-analysis of 11 controlled studies (381	No difference in baseline cognitive performance	Daytime napping enhances cognitive performance, particularly

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Table 1. Summary of included studies

Part 2 of 3

Reference	Question	Methods	Results	Conclusion
	cognitive performance in working-aged adults?	participants) comparing cognitive performance pre- and post-nap versus rest without napping. Databases such as PubMed, Cochrane Library, ScienceDirect, and PsycInfo were used. Study quality was assessed using CONSORT, STROBE, and SIGN criteria.	between nap and control groups. Post-nap cognitive performance improved, especially in alertness, lasting up to 2 h. Benefits varied depending on the time of nap, with earlier naps showing greater benefits. Mixed results were observed during the sleep inertia period.	alertness, for up to 2 h post-nap. Most studies were laboratory-based, indicating a need for further research in real workplace settings. Benefits may vary based on individual circadian rhythms and nap timing, preferably in the early afternoon.
Farhadian et al. [18]	Does daytime napping improve declarative memory performance in healthy adults compared with wakefulness, and what mechanisms are involved?	Systematic review of 22 studies. Methods included various declarative memory tasks, polysomnography, fMRI, and actigraphy to correlate memory changes with nap physiology.	Enhanced declarative memory after napping compared with wakefulness was consistently found. Memory benefits were linked to specific sleep stages (slow-wave sleep, stage 2 sleep) and neural oscillations during nap. Sleep spindles, slow oscillations, and delta waves were associated with improved post-nap recall.	Daytime naps improve declarative memory consolidation in healthy adults, with slow-wave sleep and sleep spindles playing a critical role in hippocampal-dependent memory processing. Naps, even as brief as 6 min, can stabilise weakly encoded declarative memories.
Gui et al. [19]	Does sleep-based memory consolidation change as a function of age?	Meta-analysis of 22 comparisons between young adults (18–35 years) and older adults (60–85 years) using behavioural tasks measuring sleep-based memory consolidation. Tasks assessed declarative and procedural memory. Effect sizes were calculated for memory retention differences between sleep and wake conditions in each age group.	Sleep significantly benefited memory retention in young adults but not in older adults. Older adults showed reduced sleep-based consolidation for declarative memory but relatively preserved consolidation for procedural memory compared with young adults. The decline in older adults was more pronounced after sleep than after wakefulness.	Healthy ageing is associated with a decline in sleep-based memory consolidation, particularly for declarative memory, while procedural memory consolidation is relatively preserved. The decline seems to stem from deficient memory processing during sleep.
Hokett et al. [20]	Do sleep-memory associations differ between young and older adults? Do study characteristics like sleep measurement method or memory task moderate these associations?	Systematic literature search identifying 54 studies with 1840 participants. Sleep quality measured using PSG, actigraphy, or self-report; episodic memory assessed with behavioural tasks (recall, recognition). Meta-analyses used 3-level random effects models.	Positive sleep-memory associations ($r = 0.20$) with no age differences. Age differences in specific sleep parameters: slow-wave sleep more associated with memory in young adults, wake after sleep onset more negatively associated in older adults.	Certain sleep parameters can be indicative of early memory decline in ageing, as age influences the sleep correlates of memory.
Hu et al. [21]	Can targeted memory reactivation (TMR) during sleep enhance memory consolidation?	Meta-analysis of 82 published and unpublished human TMR studies. Sensory cues (auditory or olfactory) were used during sleep to reactivate memories. Memory performance of reactivated memories was compared with non-reactivated controls post-sleep.	TMR during sleep significantly improved memory performance (Hedges' $g = 0.29$), particularly during NREM sleep stages N2 and SWS. TMR was effective across various memory types, including declarative, skill, and emotional memories.	Sensory cues delivered during NREM sleep can reactivate and causally enhance memory consolidation across different learning tasks. This evidence highlights that sleep, especially NREM sleep, is a crucial period for memory receptivity to external influences.
Kopasz et al. [22]	What is the role of sleep in learning, memory, and neural plasticity in healthy children and adolescents?	Literature search for studies published between 1966 and March 2008 on sleep, memory, and learning in children and adolescents. Fifteen	Evidence indicates that sleep facilitates memory encoding, working memory, and long-term memory consolidation, particularly for	Most studies support the hypothesis that sleep facilitates working memory and memory consolidation in children and adolescents. Significant questions remain about

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Table 1. Summary of included studies

Part 3 of 3

Reference	Question	Methods	Results	Conclusion
		studies meeting inclusion criteria were reviewed.	complex cognitive tasks in children and adolescents. Sleep restriction impacts emerge after prolonged periods. Declarative memory benefits from sleep, but procedural memory may not to the same extent. Factors like age, socioeconomic status, and pre-sleep media modulate sleep's effects on memory.	the impact of developmental stage, memory types, and sleep restriction tolerance. More research with age-appropriate tasks and consideration of circadian factors is needed to optimise learning and memory through sleep in educational settings.
Kumral et al. [23]	Do sleep spindles facilitate memory consolidation and how do factors like memory type, spindle characteristics, and EEG topography impact this?	Systematic literature search identifying studies on sleep spindles and memory consolidation in healthy adults. Analysis of 53 studies reporting 1427 effect sizes using multilevel models. Moderator analyses for memory type, spindle type/measures, and EEG topography. Publication bias assessed using modified Egger's test.	Small-to-moderate overall association between sleep spindles and memory measures. Stronger association for procedural memory than declarative memory. Spindle power and frequency had the strongest correlations with memory. Publication bias detected, suggesting possible overestimation of effects.	Sleep spindles facilitate memory consolidation, particularly for procedural memory. The results support theories of sleep spindles aiding systems-level memory consolidation and indicate the role of spindle oscillations in promoting synaptic plasticity. Highlighting the importance of considering publication bias in this research field.
Leong et al. [24]	Does sleep benefit prospective memory (PM), and through which retrieval processes - strategic monitoring or spontaneous retrieval?	Systematic review and meta-analysis of 24 independent samples ($N = 165\ 432$) examining sleep's effects on PM. Studies included manipulated sleep/wake intervals, contrasted sleep disorder groups with controls, or correlated PM performance with sleep measures.	Overall, sleep had a significant small-to-medium benefit on PM performance ($d = 0.41$). No increase in strategic monitoring ($d = -0.11$), but a greater benefit in conditions favouring spontaneous retrieval ($d = 0.94$ vs. $d = 0.45$).	Sleep facilitates PM by enhancing spontaneous retrieval processes rather than strategic monitoring. Sleep may strengthen cue-action associations, allowing intentions to be reflexively triggered by cues.
Newbury and Monaghan [25]	When does sleep affect veridical (accurate) and false memory consolidation in the Deese-Roediger-McDermott (DRM) paradigm?	Meta-analysis of 13 experiments (596 participants) using the DRM paradigm to examine the effects of sleep vs. wakefulness on memory consolidation. Experiments included tests of free recall and recognition. Moderators like test type, words per list, and sleep type (overnight vs nap) were examined.	No overall effect of sleep on accurate or false memories. Sleep's effect varied by test type and list length: increased false memories in recall tests; mixed effects in recognition based on list length; improved accuracy for old words and rejection of new words in specific conditions.	Sleep's impact on veridical and false memories depends on memory task specifics. Sleep may enhance spreading activation in sparse networks (shorter lists) but reduce false memories in denser networks (longer lists). Sleep aids consolidation in a targeted manner based on network density and test constraints.
Schäfer et al. [26]	Does sleep selectively enhance memory for emotions compared with neutral stimuli?	Meta-analysis of 34 samples ($N = 1382$) from studies on the effects of post-learning sleep vs. wakefulness on emotional and neutral recognition memory. Used nap or whole-night sleep manipulations. Effect sizes calculated accounting for within-subject correlation between emotional and neutral memory scores. Separate meta-analyses for studies without a wake group to estimate wake effects.	No significant difference between sleep and wake in relative benefit for emotional over neutral memory. Estimating missing wake effects showed a larger emotional-memory benefit after wakefulness. REM-rich sleep showed a larger emotional-memory benefit than SWS-rich sleep.	Sleep does not selectively enhance emotional over neutral memory. The emotional-memory benefit is not larger after sleep compared with wakefulness, but REM sleep might selectively boost emotional memory compared with SWS, without increasing the emotional benefit after full nights of sleep versus wake.
Schimke et al. [27]	What is the effect of sleep compared with wakefulness on the acquisition and	Systematic review and meta-analysis of 25 studies with a between-group design comparing sleep and wake conditions in novel word learning.	Significant moderate effect size overall, indicating sleep benefits novel word learning. Variations in effect size across	Sleep facilitates the acquisition and consolidation of novel words in healthy adults, supporting sleep-based language learning

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Table 1. Summary of included studies

Part 3 of 3

Reference	Question	Methods	Results	Conclusion
	consolidation of novel words in healthy adults?	Data extracted on sample characteristics, design, vigilance measures, stimuli, tasks, and outcomes. Meta-analyses conducted for overall effect and specific retrieval domains (recall, recognition, lexical integration), with moderator analyses for variables influencing sleep's effect.	recall, recognition, and lexical integration domains. Type of word stimuli (native vs foreign) impacted effect size.	models. Effect sizes vary depending on retrieval test type and word stimuli, impacting study consistencies. Findings are relevant for second language learning enhancement strategies. Sleep benefits word learning through consolidation, with factors like age, word type, and task moderating effects.
Schmid et al. [28]	Does sleep enhance the consolidation of motor memories compared with wakefulness, and do certain motor tasks or experimental designs show greater sleep-dependent gains?	Meta-analysis of 48 studies examining sleep's effect on motor memory consolidation. Studies compared motor memory performance post-sleep versus post-wakefulness. The relative sleep gain (RSG) was calculated for overall effects and specific tasks like finger tapping and mirror tracing. Subgroup analyses for experimental design impacts.	Significant small-to-medium overall RSG effect, indicating superior motor memory after sleep. No differences based on experimental design. Specific tasks showed a small effect for finger tapping and medium for mirror tracing.	Sleep benefits motor memory consolidation compared with wakefulness. Task-specific analyses did not reveal substantial performance differences, suggesting the need for future research to examine distinct task dimensions rather than tasks themselves for understanding the consolidation mechanisms.
Stanyer et al. [29]	What is the impact of acoustic stimulation during sleep on memory and sleep architecture in young and older adults?	Systematic review and meta-analysis of studies on acoustic stimulation during slow-wave sleep and its effects on memory performance and sleep architecture in young (<35 years) and older adults (>35 years). Studies used acoustic stimulation and sham control conditions.	Significant medium-sized effect on memory performance in young adults, with a large effect for declarative memory tasks. No significant effect in older adults. No significant differences in sleep architecture parameters between stimulation and sham conditions in either age group.	Acoustic stimulation during sleep enhances declarative memory consolidation in young adults but not in older adults, supporting the role of slow-wave sleep in memory consolidation. Limited study numbers and varying methodologies indicate a need for more research to understand acoustic stimulation's impact on various memory types and cognitive processes.
Zhang and Gruber [30]	Does enhancing slow-wave sleep (SWS) improve memory consolidation?	Systematic review of studies using auditory stimulation, electrical stimulation (tDCS), or pharmacological agents to enhance SWS. Literature searches were conducted in databases for studies measuring cognitive outcomes, particularly memory.	All three methods enhanced SWS, indicated by increased slow-wave activity (SWA) power and/or SWS duration. Auditory stimulation improved verbal declarative memory; electrical tDCS showed mixed results; pharmacological enhancement had limited cognitive benefits.	Enhancing SWA power through auditory or electrical stimulation shows efficacy in improving memory consolidation. Pharmacological enhancement of SWS increases its duration but offers limited cognitive benefits. Enhancement of sleep spindles alongside SWS may be necessary for cognitive improvements. More extensive studies in clinical populations are needed to evaluate these techniques' efficacy.

acute sleep deprivation can have varying effects on memory functions, potentially dependent on the cognitive load of tasks [18]. Socioeconomic status and pre-sleep media consumption are additional variables influencing the quality of sleep and subsequent memory performance [21].

In healthy younger adults, sleep compared with wakefulness consistently improves declarative memory, as evidenced by a meta-analysis of 271 independent samples which found a moderate effect of sleep on episodic memory enhancement [14]. This review utilised multilevel meta-regression models to analyse a broad range of studies, revealing larger effects for emotional stimuli and direct retention measures. Although some studies suggest larger effects for emotional stimuli, comprehensive meta-analyses have found no consistent preferential effect of sleep on emotional over neutral memories, although REM-Rich sleep showed some specificity for emotional memory enhancement (Schäfer et al. [26]).

Although some studies suggest larger effects for emotional stimuli, comprehensive meta-analyses have found no consistent preferential effect of sleep on emotional over neutral memories. REM-rich sleep showed some specificity for emotional memory enhancement.

Prospective memory enhancement through sleep was demonstrated by Leong et al. [24], while motor memory consolidation was similarly supported by a systematic review and meta-analysis of 48 experiments indicating a small-to-medium-sized benefit of sleep across various tasks [28].

Complex associative memory processing, essential for gist extraction and rule learning, was shown to be facilitated by sleep, with Chatburn et al. [15] presenting a moderate effect size for such cognitive processes across 27 studies, indicating sleep's role in integrating new information into established schemas.

Furthermore, sleep has been shown to improve the integration of new information into existing neocortical knowledge networks and the extraction of common themes between discrete memories, promoting generalisation, and adaptation [15]. Veridical consolidation during sleep also appears to be influenced by semantic network density and the demands of memory tests, although no greater relative benefit for emotional memory was observed [25]. For associative memory, sleep increases gist extraction and false recall but decreases false recognition for longer study lists [25], delineating effects based on semantic network density and memory test demands. Sleep promotes spreading activation when fewer related 'lure' words are presented, enhancing true and false recall. But for longer lists with greater overlap, sleep-dependent consolidation is reduced, decreasing false recognition [25]. However, the specific neurocognitive mechanisms by which sleep shapes veridical and false memory formation across declarative retrieval modalities remain to be further elucidated through research controlling stimuli characteristics and using consistent paradigms.

Likewise, in adults sleep enhances the integration of phonologically similar novel words into lexical networks [27] but differentially benefits native language vocabulary learning over foreign words [27]. Sleep appears to aid the assimilation of new linguistic information in a targeted way based on network density and prior lexical knowledge. Similar findings are observed with school-aged children [31] but a comprehensive systematic review is required.

A review of 16 studies with infants and young children (<3 years old) found that sleep facilitates multiple aspects of word learning in infancy through memory consolidation, similar to findings in adults and older children. However, more research is needed on how existing knowledge interacts with sleep to strengthen new word memories, the respective roles of naps versus overnight sleep, and neural correlates of consolidation.

Despite the broad enhancement of memory across domains by sleep, the specific neurobiological mechanisms underlying these effects remain an area of active investigation.

Kumral et al. [23] conducted a meta-analysis to explore the contribution of sleep spindles to memory consolidation, reviewing 53 studies. They found a small-to-moderate correlation between spindle activity and memory, especially procedural memory, using multilevel meta-analytic models. Various spindle characteristics and EEG topography were examined, with oscillatory power and peak frequency showing the most substantial associations with memory performance. These findings support theories that spindles are involved in memory consolidation processes during sleep by promoting memory reactivation and synaptic plasticity. This evidence reinforces the role of sleep spindles in offline memory processing. While these effects are statistically significant, the practical or clinical impact of such improvements on day-to-day functioning requires further exploration.

Older adults

In healthy older adults, sleep-dependent memory consolidation exhibits decline compared with younger counterparts, especially for declarative memory reliant on hippocampal function, as reported in a meta-analysis of 22 comparisons by Gui et al. [19]. This study found sleep improved next-day memory retention in young adults but not older ones, with the age-related decline being particularly pronounced for declarative memory tasks. The research points to a reduction in SWS as a contributing factor, which is critical for declarative memory and known to diminish with age.

Hokett et al. [20] conducted a systematic review and meta-analysis of 54 studies to assess the relationship between sleep quality and episodic memory performance across age groups. The findings indicated a significant positive association between sleep quality and episodic memory performance, with no overall age differences in sleep-memory association strength. Yet, age-specific variations were evident in the relationship between particular sleep parameters and memory performance, suggesting that SWS had stronger memory associations in young adults, whereas disruptions such as increased wake after sleep onset correlated with poorer memory in older adults [19].

These findings collectively highlight the complexity of sleep-dependent memory consolidation and its modulation by age. While normal ageing correlates with reduced memory consolidation, young and older adults display differences in how specific sleep parameters interact with memory performance. Further understanding the role of sleep in memory and ageing could enable the development of sleep-based interventions to mitigate memory decline in older populations.

Future directions

The crucial role of overnight sleep for memory consolidation is clear but there is a limit to the extent to which overnight sleep can be modified, particularly in a naturalistic environment.

However, daytime napping has been documented to provide cognitive benefits, enhancing alertness, reaction time, and memory retrieval, as evidenced by a synthesis of findings from experimental studies [17, 18]. These benefits are particularly pronounced for naps taken earlier in the afternoon, with even brief naps of ~6 min shown to bolster declarative memory consolidation through sleep-specific mechanisms such as sleep spindles and slow-wave activity [18]. It is possible that naps could prove a useful way of boosting memory during the day.

Memory reactivation via cues during sleep has been shown to enhance consolidation, suggesting a receptive state for memory modification during this period [21]. This is complemented by findings indicating that SWS and sleep spindles, particularly their power and density, are conducive to declarative memory consolidation, correlating with hippocampal activation patterns [23].

Recent research has highlighted the potential of modulating sleep to enhance memory through external stimulation [30]. Two primary techniques, targeted memory reactivation (TMR) and closed-loop auditory stimulation, have been central to these findings [30]. TMR involves reintroducing sensory cues linked to previous learning during sleep, specifically during NREM sleep phases N2 and SWS, but not during REM sleep. This technique has been shown to significantly improve memory retention across various learning tasks, as evidenced by a meta-analysis of 82 human TMR studies [15]. Closed-loop auditory stimulation, a subset of TMR, utilises real-time EEG to deliver auditory cues in sync with sleep-slow oscillations or spindle events. This method has been particularly effective in enhancing declarative memory consolidation in young adults, though its impact on older adults and non-declarative memory tasks is less pronounced. A systematic review of 16 studies supports the efficacy of this technique in augmenting memory processes associated with SWS in younger individuals [28]. While closed-loop TMR offers greater experimental control and the potential to influence sleep physiology, its effectiveness in real-world settings outside of controlled laboratory environments remains to be fully explored.

The development of TMR is particularly exciting when considering populations with memory and/or sleep difficulties. For example, closed-loop auditory stimulation has shown promise with clinical populations including people with schizophrenia [32] older adults [33], and children with ADHD [34]. This is undoubtedly an exciting development. Although promising, these techniques remain experimental. Further research is needed to optimise parameters and assess feasibility in real-world settings before clinical applications can be recommended.

Summary and discussion

Overall, while there is evidence that sleep promotes memory consolidation across domains including declarative, episodic, emotional, prospective, and motor memory [14], effects are nuanced, relying on interactions between specific sleep stages like SWS and spindles [23], task characteristics and participant age across the lifespan from children to older adults [19, 22].

The conclusions drawn from the synthesis of systematic reviews and meta-analyses affirm that sleep plays a significant and active role in memory consolidation. The evidence points to the critical functions of SWS and sleep spindles in supporting this process. The benefits of sleep on memory are broad, yet not uniform across age groups or memory types. In younger adults, sleep shows a consistent positive impact on declarative, episodic, and emotional memory consolidation. While there is a theoretical basis for REM sleep preferentially consolidating emotional memories, empirical evidence remains mixed. Some studies demonstrate emotional memory benefits, but meta-analyses, such as Schäfer et al. [18], do not consistently support preferential consolidation of emotional over neutral memories. Conversely, in older adults, a decline in sleep-dependent memory consolidation is evident, possibly due to reduced SWS. For children, sleep's role is pivotal for complex declarative tasks, including language learning, yet the benefit of procedural memory is less pronounced compared with adults. Innovations like TMR and closed-loop auditory stimulation present promising avenues for enhancing memory consolidation during sleep. The review underscores the need for further research, especially in clinical

and educational contexts, to further our understanding of neurocognitive mechanisms and harness the potential to enhance sleep and memory.

Summary

- Sleep plays a significant and active role in memory consolidation, across a range of tasks and stages of development.
- The literature is fast growing, and more evidence synthesis is required, especially in relation to the role of sleep in memory consolidation in childhood, especially vocabulary learning.
- Further research should focus the application of findings in clinical and educational settings and in the understanding of the neurocognitive mechanisms at play.
- TMR and closed-loop auditory stimulation offer the potential to modulate the sleep architecture and boost memory with the potential for clinical benefit.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Abbreviations

LTM, long-term memory; CLS, complementary learning systems; WFA, word frequency analyser; TMR, targeted memory reactivation; DRM, Deese–Roediger–McDermott; SWS, slow-wave sleep.

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