

Selectivity in Sleep-dependent Memory Consolidation

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ABSTRACT

Memory is not uniformly stored in the brain. There are various types of memories and only some are retained over time. Much is forgotten, and of those memories retained, their representations are transferred into long-term stores, a process called consolidation, which occurs predominantly during sleep. Sorting out how sleep contributes to memory has not been straightforward, but nonetheless, emerging data suggest that sleep plays a causal role in how our memories are formed and ultimately stored. One of the intriguing aspects of sleep-dependent memory consolidation is its selectivity. Memories of future relevance are tagged during encoding and prioritized for consolidation during subsequent sleep, leading to the discriminatory selection for memories that are emotional, show difficulty during learning, have high retrieval expectancy, or are associated with rewards. Several brain regions, electrophysiological oscillations and neurotransmitters are at the heart of this process, guiding each organism through its unique life.

Introduction

The ability to form and store memories enables organisms to acquire new information and retain that knowledge over time. As a result of this knowledge build over a lifetime, we are in good measure of who we are of what we have learnt and what we remember. There is, however, more than one type of memory. Memory is most commonly divided into declarative memory and non-declarative memory (Fig. 1). Declarative memory is conscious memories including facts and events, and non-declarative memory can be further divided into categories like procedural skills and conditioning. Regardless of the type of memory, the two-stage model of memory proposes that memory is first encoded in a temporary store, and through reactivation and redistribution process that takes place during offline periods (sleep), it is gradually reorganized into long-term stores. Memory consolidation is the term that describes this system-level reorganization and the local synaptic level changes that occur in individual neurons, stabilizing memory to become more resistant to interference. I begin this review by providing evidence for the active role that sleep plays in memory consolidation for memories such as declarative memory and motor tasks. I follow this by outlining studies that show selectivity of memory consolidation during sleep. Based on peer review research, sleep has been shown to facilitate the discriminatory consolidation of encoded memories through altered functional connectivity between brain regions and cycles of different sleep stages, which provide organisms with the ability to adapt to changes and act with the most relevant information. The process of memory consolidation is future-oriented, focusing on information that will be useful for predicting and surviving the next day.

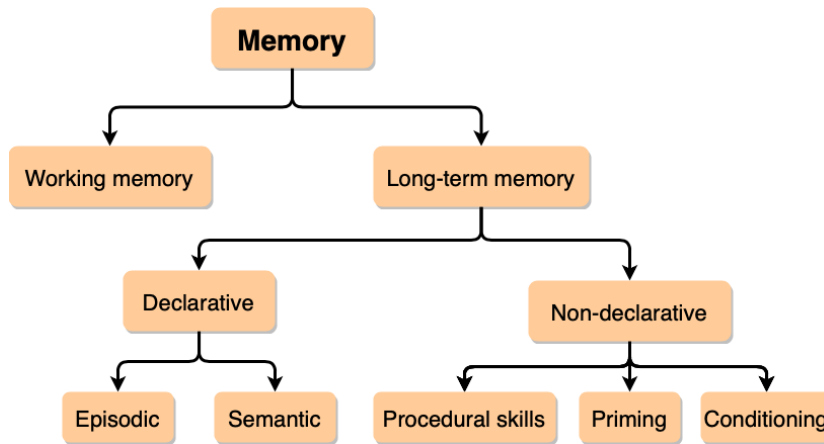


Figure 1. Categorization of memory systems.

The role of sleep in active memory consolidation

Long term memory is formed and stored in the neocortex, initially with the critical help of the hippocampus. Through consolidation, those memories can be reactivated independent of the hippocampus. Consolidation processes are often referred to as “sleep-dependent” because of the unique conditions during sleep. It does not imply that all memory processing is sleep-dependent, but rather that some consolidations only occur during sleep. For instance, some forms of non-declarative motor skill learning and emotional learning can be enhanced during wakefulness, but these memories also show additional improvements during sleep (Dunsmoor et al., 2015; Walker et al., 2003).

Sleep is a natural and reversible state composed of 90 minutes cycles divided into rapid-eye-movement sleep (REM) and non-REM sleep (NREM), which is then further divided into stages 1 to 4 (Rasch & Born, 2013) (Fig. 2). Sleep stages differ in depth, frequency of dreaming, EEG oscillations, eye movements, regional brain activation, and dialogue between memory systems (Stickgold, 2005). Sleep has always been known for its passive protection of memories, meaning that sleep is a guarded period of time when the animal does not take in new information to interfere with old learnings, but it does much more than that. Research has shown that sleep plays an active role in memory consolidation. The term “active” refers to electrophysiological events that directly contribute to memory consolidation, such as slow oscillations, spindle activity, and hippocampal ripples (Born & Wilhelm, 2012). Instead of one specific aspect of sleep leading to sleep-dependent memory consolidation, each stage of sleep contributes differently. Driven by slow-oscillations during SWS, memories are repeatedly reactivated in the presence of sharp-wave ripples and thalamo-cortical spindles, which are involved in cortical plasticity (Rasch & Born, 2013). Subsequent REM stabilizes the reactivated memories and contributes to the synaptic consolidation process. For example, hippocampus-dependent declarative memories are reactivated during SWS and their representations are redistributed from hippocampal to neocortical sites for long-term storage (Wilhelm et al., 2011).

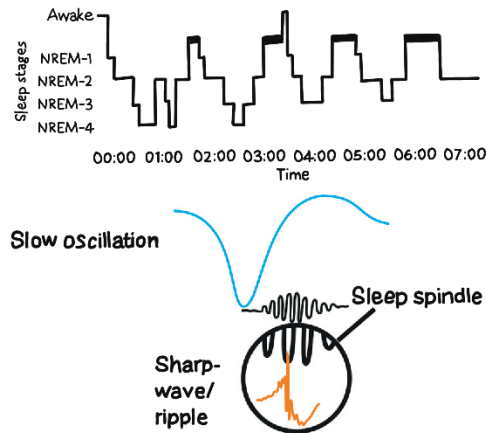


Figure 2. Categorization of sleep stages and electrophysiological events. (Reproduced from Feld and Born, 2017)

There appears to be a causal role between off-line reactivation of memory representations and consolidation of memories. In an odour experiment, re-exposure to the odour present at encoding during sleep effectively enhanced memory, but only when it is presented during SWS and not during wakefulness (Born & Wilhelm, 2012). Human memories that have been shown to be improved after a night of sleep include motor sequence tasks, motor adaption tasks, declarative learning, and complex cognitive procedural learning (Stickgold, 2005). In all of these memory tasks, a night of sleep or specific stages of sleep improves performance, but not during equivalent periods of day or night wakefulness. Interestingly, multiple nights of sleep after learning induces better retrieval than one night of sleep, and sleep during the day triggers similar results to sleep at night (Kuriyama et al., 2004; Walker et al., 2003). When taken as a whole, evidence from human studies (e.g., nap studies and sleep physiology studies) and animal experiments (e.g., sleep deprivation studies and firing patterns in animals during sleep) offer converging evidence for sleep-dependent memory consolidation (Graves et al., 2003; Hasselmo & Bower, 1993; Lahl et al., 2008; Stickgold, 2005).

Discriminatory selection of sleep-dependent consolidation

Not all memories are stored with equal probability. Contrary to earlier assumptions that sleep-dependent memory consolidation preserves all encoded events equally, the active consolidation concept implies that the process is selective. A global strengthening of synaptic connections and reorganization of memories is likely to result in a system overflow (Rasch & Born, 2013). Instead, a growing body of experiments favours a more discerning view of memory processing. High-value information is prioritized and strengthened during sleep, while low-value information shows trivial improvements regardless of brain state. This selection process is achieved by “tagging” high-value information that has relevance for future behaviour during encoding to be selectively consolidated during subsequent sleep (Dunsmoor et al., 2015). This includes memories that are emotionally salient, show difficulties at encoding, have high retrieval expectancy and are associated with rewards. In other words, discrimination of consolidation is driven by a motivation to better adapt to future circumstances.

Experiments designed to test this model sometimes fall into the trap of equating encoding with consolidation. If future expectancy is presented during learning, the effects of consolidation will be indistinguishable from those of encoding (Wilhelm et al., 2011). This is especially prominent in emotional memories where salient information is often more strongly encoded due to focused attention on the emotional aspects of the scene. In the studies I will present below, various procedures have been taken to ensure the encoding depths are comparable in all groups and that consolidation occurs during sleep, not due to deliberate practice after the learning phase. Some steps taken include

introducing the expectancy of retrieval after the learning phase, including an additional surprise test after sleep, presenting emotional importance for neutral objects after learning, removing subjects who report having been engaged in any rehearsal, playing computer games or watching movies until being put to bed, and picking tasks that are innately hard to be rehearsed mentally (e.g., 2D object location task compared to a verbal word pair task) (Dunsmoor et al., 2015; Murty et al., 2017; Saletin et al., 2011; Wilhelm et al., 2011). Together, these procedures ensure that the benefit seen during recall tests is solely based on the time spent sleeping or staying awake, not on other factors like discrepancies during encoding and mental rehearsals.

Emotional memory

One form of selectivity in memories is determined by the emotionality of stimuli. Emotional arousing events are better remembered because it is essential for survival of a threat or other external stimuli, while insignificant details are not associated with anything meaningful. There is evidence suggesting that emotionally arousing images are preferentially conserved during sleep and have better recall rates compared to neutral images (Atienza & Cantero, 2008; Hu et al., 2006; Payne et al., 2015) (Fig. 3). Moreover, emotional objects are selectively retained compared to neutral objects or neutral backgrounds. By varying the foreground and background, emotional objects in the foreground are better remembered compared to non-emotional foreground or peripheral background (Payne et al., 2008; Payne et al., 2015). The effects of emotion on memory formations have also been studied using remember-know (R-K) procedures. Remember judgements refer to recollection or the slow and conscious process that are involved with retrieving specific information, whereas know judgements are a measure of familiarity and are automatic processes (Atienza & Cantero, 2008). Evidence have shown that recognition accuracy for remember judgements of emotional stimuli increased significantly after sleep, compared to neutral images (Atienza & Cantero, 2008; Hu et al., 2006). By contrast, know judgements increase with the degree of arousal, but are not related to sleep. This suggests that emotional memory based on specific details of the encoding process is preferably enhanced after sleep, but this benefit is not extended to familiarity.

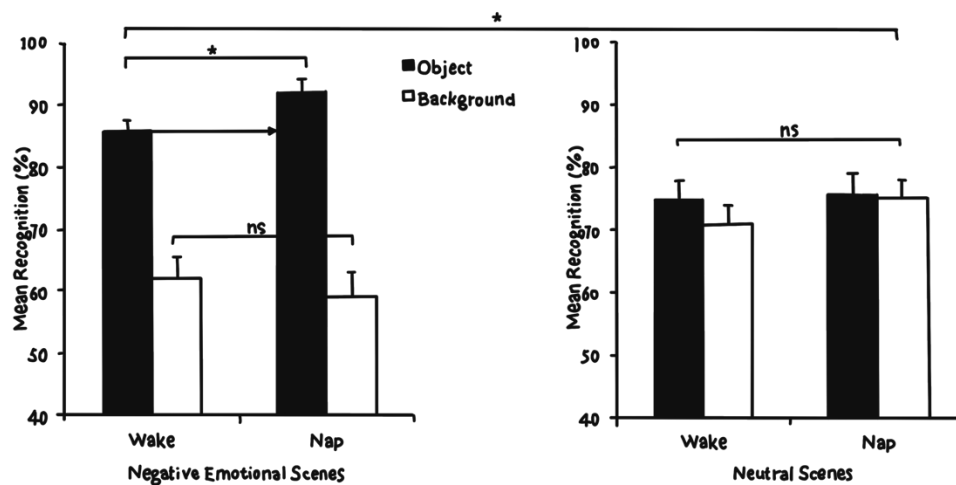


Figure 3. Napping selectively benefits memory for emotional components of scenes. (Reproduced from Payne et al., 2015)

Another form of emotional memory is fear conditioning. This is a type of associative learning task in which subjects learn to fear a new environment, because of the association between the context and an aversive unconditioned stimulus (e.g., electric shock) in that environment. When exposed to the same stimulus or environment, humans and other animals exhibit a range of fear responses, including freezing for animals and high skin conductance response for

humans. Context fear conditioning is a form of declarative memory that is impaired by sleep deprivation and, therefore, may benefit from sleep. Graves and colleagues (2003) found that sleep deprivation 0 – 5 hours after fear conditioning impairs freezing in response to the same shocked context, whereas sleep deprivation 5 – 10 hours after has no effect. This result indicates that sleep deprivation immediately after training selectively affects hippocampus-dependent contextual fear conditioning and that sleep is necessary for the consolidation of conditioned fear memory. By contrast, Dunsmoor et al. (2015) observed that enhancement of emotional learning is dependent on duration of time since learning, but not sleep. Dunsmoor and colleagues (2015) compared effects of emotional learning immediately after learning, after 6 hours, and after 24 hours, and concluded that it was only dependent on time because memory enhancements became evident after 6 hours. However, these two studies (Dunsmoor et al., 2015; Graves et al., 2003) are based on mice and humans respectively. One possibility might be that mice and humans display different subtypes of fear conditioning since human participants are aware that their experience is in a laboratory setting. An alternative explanation is that the first study tests fear conditioning based on the same context, while the second is on a set of novel images in the same category. The former study was testing direct memory recall of past emotional experience whereas the latter examined retrospective memory. For the purpose of this review, memory refers to direct recollection of the past, not inferences of new information based on the past. Both studies demonstrate that fear conditioning becomes apparent after a time delay, but not immediately afterwards, and the first study suggests that sleep is important for fear-conditioned memories. Thus, sleep can separate fear conditioning from irrelevant contexts for selective consolidation.

Although some argue that emotional selectivity is a direct result of attentional factors during encoding, evidence suggests that the time spent looking at the emotional component is not associated with selectivity (Steinmetz & Kensinger, 2013). Furthermore, the degree of selectivity differs with the delay of the interval, suggesting that selective memory consolidation requires factors other than the initial encoding of memory, like the subsequent consolidation during sleep.

Difficulty level

Beyond emotional memories, sleep can selectively enhance memories based on the difficulty level during encoding. In addition to sleep-dependent improvements of simple motor skills (Stickgold, 2005), sleep-dependent gains increase as the task becomes more complex. In one of these insightful experiments, Kuriyama and others (2004) varied limb complexity and sequence length in a series of motor-sequence tests and found that sleep provided the maximum benefit to motor skill procedures that were the most difficult during the learning phase (Fig. 4). Following a period of sleep but not after an equivalent period of wakefulness, the more difficult sequences showed the greatest improvement, once again demonstrating the selectivity in sleep-dependent memory consolidation.

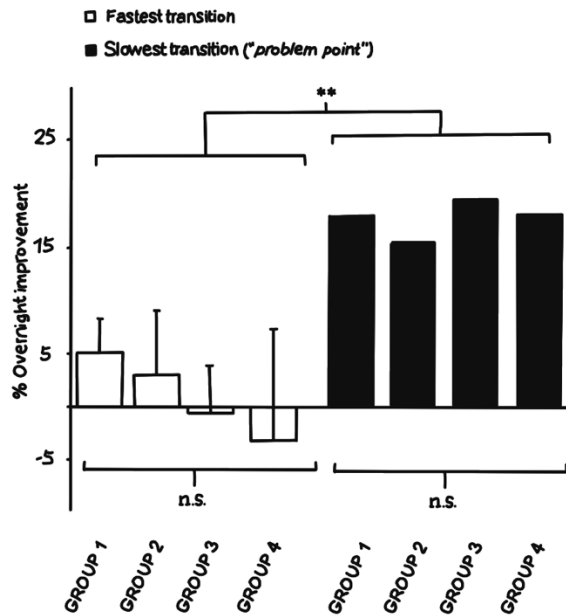


Figure 4. The slowest transitions before sleep experience greater overnight improvement than the fastest transitions. (Reproduced from Kuriyama et al., 2004)

Retrieval expectancy

Merely being told of a future test after the learning phase enhances sleep-dependent consolidation of that information. This effect is observed in tests of declarative memory (Born & Wilhelm, 2012), episodic memory (Stickgold & Walker, 2013), visuospatial memory, and procedural motor memory (Wilhelm et al., 2011). In one of these studies (Wilhelm et al., 2011), subjects learnt declarative memories (2-D object location task) before periods of sleep or wakefulness and were informed or not informed about a future test after the encoding period. Compared to wakefulness, post-learning sleep produced a significant improvement at delayed retrieval, but only if subjects were informed about the test after learning. Curiously, a sleep-associated memory improvement can also be seen in subjects who were not informed but nevertheless suspected a test, suggesting that the mere expectancy induces a selective effect regardless if it is explicitly stated or just self-guesswork.

Retrieval expectancy can also be achieved through explicit instructions to either “remember” or “forget” individual items after encoding (Saletin et al., 2011). Studies suggest that sleep differentiates information based on future relevance and can perhaps control remembering as well as forgetting. Both in day-to-day lives (e.g., forgetting yesterday’s path in preference to today’s) and clinically (e.g., PTSD), the capacity to forget is as important as remembering. The inability to do so will lead to a decrease in both neural resources required for remembering and the efficiency of recall. Saletin and colleagues (2011) examined online influences on words cued as “remember” and “forget” items. At immediate testing, performance for “remember” words was significantly greater than “forget” words. When recall was again measured after sleep, subjects showed additional preferential recall of “remember” words, yet this benefit was not extended to “forget” words (Fig. 5). Importantly, sleep and no-sleep groups expressed equivalent portions of both types of words during immediate testing, indicating that there is no difference in the strength of encoding between conditions. Only after a period of sleep or wakefulness did the difference in performance emerge. Thus, sleep, relative to wakefulness, can selectively ignore items cued to be forgotten, yet preferentially improve recall for items cued to be remembered.

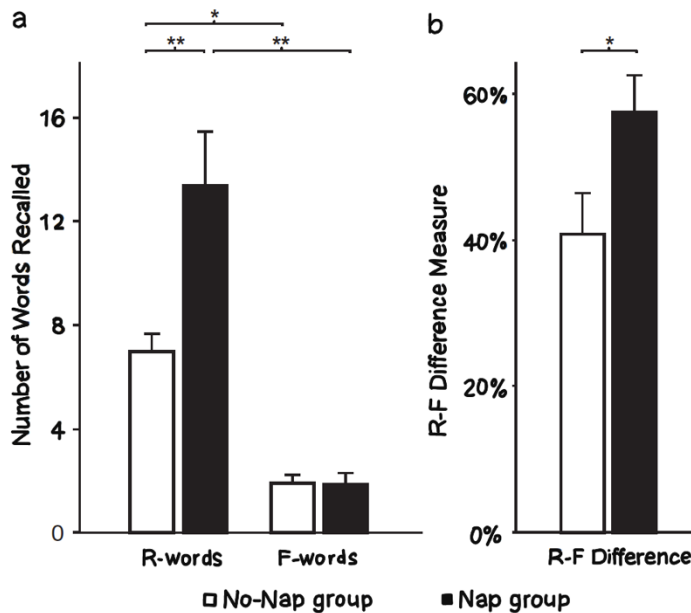


Figure 5. Selectivity resulting from retrieval expectancy. Figure 5a shows the number of words recalled based on prior cue instruction (Remember, R-words; Forget, F-words) in the Nap and No-Nap groups. Figure 5b shows the efficiency measure of directed forgetting, calculated as the subtraction of R-words and F-words. (Reproduced from Saletin et al., 2011)

Reward

Waking knowledge of potential monetary reward further contributes to selective memory consolidation during sleep. By varying the amount of reward, the degree of memory consolidation also varies. In one such study (Fischer & Born, 2009), subjects were trained 2 different motor sequence tasks before 12 hours of nocturnal sleep or daytime wakefulness. A momentary reward was then associated with both tasks after learning. Performance was significantly improved for the sequence deemed with high reward, while no or minor gains were observed after wakefulness. This result is echoed by Igloi et al. (2015)'s and Murty et al. (2017)'s experiments where researchers found that sleep not only favoured the selective consolidation of high reward memory (Fig. 6), but memories were also remembered with greater subjective confidence (Igloi et al., 2015). Notably, consolidation of morphine reward memory was disrupted after sleep deprivation in rats, suggesting that sleep played a critical role in this type of memory, and that sleep deprivation may be a potential non-pharmacotherapy for the management of relapse associated with drug-related reward memory (Shi et al., 2011). In combination, this series of studies implicate that sleep-dependent selectivity of memory consolidation is motivationally driven, giving preference to memories that are most relevant for future behaviours.

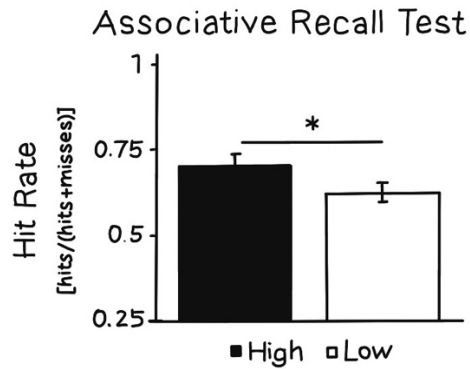


Figure 6. Rewards influence 24h associative memory. At a 24h test, associative cued recall was greater for pairs encoded under high- versus low-reward motivation. (Reproduced from Murty et al., 2017)

Underlying mechanisms for selective consolidation during sleep

Prefrontal cortex and functional connectivity

The precise neural mechanisms of this selection process remain largely uncharacterized. Learning is associated with long-term potentiation (LTP), but its relevance to selective consolidation is unknown. Nevertheless, early evidence offers some insights. The processing of anticipatory aspects of behaviour is linked to prefrontal cortex functions (Miller & Cohen, 2001). The executive function of the prefrontal cortex regulates activation of memory representations during retrieval of future-oriented memories (Polyn & Kahana 2008). At a neuronal level, the prospective aspects of memory may become manifested in the tagging of newly encoded memories that have characteristics described above (emotional, difficult, high retrieval expectancy, and high reward) (Born & Wilhelm, 2012). During sleep, neural patterns reflecting previously acquired information are replayed. Consistent with this view, memory representations are not only replayed in the hippocampus but also the prefrontal cortex during SWS for both rats (Peyrache et al., 2009) and humans (Wilhelm et al., 2011). Moreover, in rat experiments, cortical replay onset times precede hippocampal ones, implying an initial feed-forward interaction from the cortex to the hippocampus (Ji & Wilson, 2007). Thus, prefrontal tagging of selective memories and replay during subsequent sleep could in fact be decisive for selectivity in memory consolidation.

Parallel replay in the cortex and the hippocampus also suggests functional connectivity. Functional connectivity is defined as “the temporal coincidence of spatially distant neurophysiological events” (Friston, 1994). That is, functional connectivity exists when there is a statistical relationship between the activity of two regions, not when anatomical connection between structures is changing. There is evidence suggesting that changes in connectivity predict memory for high and low valued information. For instance, the strengthening of connectivity with sensory regions associated with reward leads to the selective enhancement of valuable information. Specifically, the increased connectivity of the category-selective cortex (CSC) with the anterior hippocampus predicted associated memory for high reward memories, whereas connectivity of the posterior hippocampus with CSC positively correlated with low reward memory (Murty et al., 2017) (Fig 7). Such connections hint at differential memory consolidation and their integration within associated cortices.

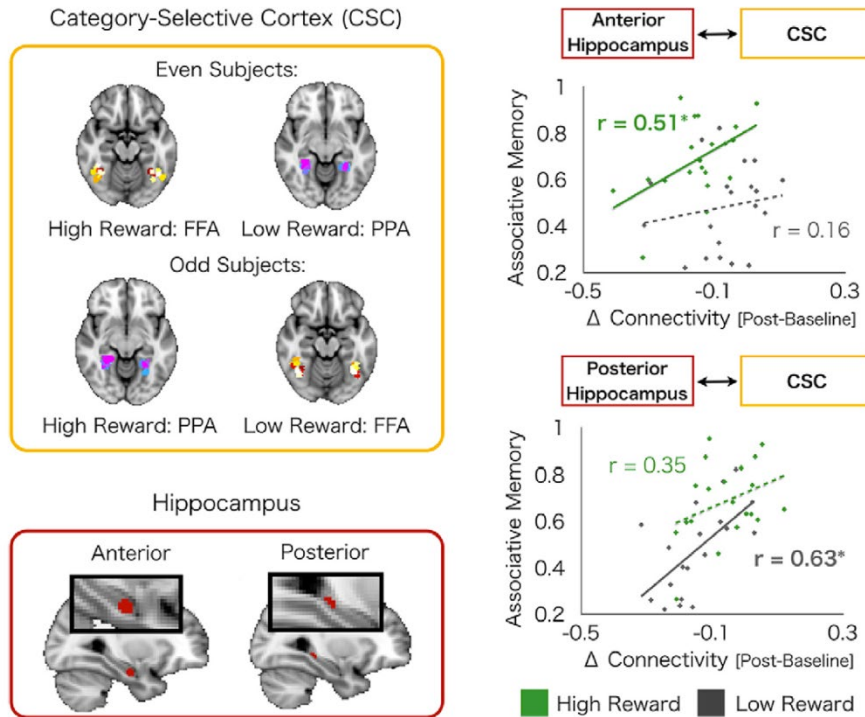


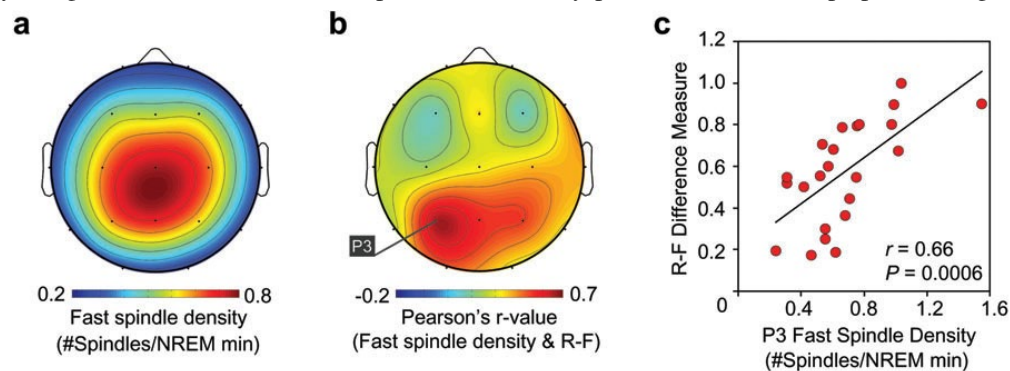
Figure 7. Postencoding interactions between the hippocampus and CSC predict high- and low-reward memory. High-reward CSC refers to the regions of CSC associated with high-rewards during encoding, vice versa for low-rewards CSC. Solid lines in the graphs on the right indicate significant correlations. Interactions between anterior hippocampus with high-reward CSC predict high-reward memory (top right). Conversely, interactions between posterior hippocampus with low-reward CSC predict low-reward memory (bottom right). (Reproduced from Murty et al., 2017)

Sleep specific electrical oscillations and neurochemical signaling

Interestingly, the prefrontal cortex is also strongly involved in the generation of slow wave oscillations (Murphy et al., 2009). Electrophysiological oscillations like slow oscillations during sleep may provide further insight into the mechanisms governing selective consolidation of tagged memories. Unique electrophysiological properties in REM and non-REM may interact to contribute to regional connectivity and memory consolidation. Sleep's active role emerges in electrophysiological events such as theta waves, slow oscillations, sleep spindles, and cholinergic neurotransmitters seen across sleep cycles (Payne et al., 2008). It has been hypothesized that memories are selectively replayed and restabilized during REM sleep and reactivated and integrated into cortical networks during the following cycles of SWS (slow oscillations and sleep spindles) phases (Kim & Payne, 2020).

Specifically for emotional memory, the selective benefit of sleep for performance is predicted by theta oscillations during REM, which is also a stage that shows increased activity in the amygdala-hippocampus-mPFC network (Kim & Payne, 2020). Cortical slow oscillations during SWS facilitate sleep-dependent memory reactivation and hippocampal-neocortical dialogue, which contributes to functional connectivity of brain regions. In a future relevance task mentioned above, subjects expecting a retrieval test showed enhanced overnight consolidation. They also displayed a robust increase in slow oscillation activity and sleep spindle count during post-learning SWS, but this did not hold true for uninformed subjects (Wilhelm et al., 2011). Similar sleep-oscillation relationships have been reported for other forms of selective consolidation. The sleep benefit for recall of items cued to be remembered over items cued to be forgotten is predicted by sleep spindles (Saletin et al., 2011) (Fig. 8). Sleep spindles are short synchronous bursts of activity between 12 and 15 Hz and have been related to offline declarative memory processing. Spindle activity is associated with changes in memory performance, but not absolute performance (Schabus et al., 2004). This conclusion is consistent with the hypothesis that sleep spindles are related to memory consolidation. The differentiated remember/forget effect is strongly correlated with sleep spindles in the left parietal cortex. Importantly, subjects with more spindles not only recalled more items that were previously cued for remembering but also recalled fewer items cued for forgetting, suggesting that sleep-dependent mechanisms may actively promote remembering as well as forgetting.

Figure 8. Physiological data for the relationship between memory performance and sleep spindles. Figure 8a is a



topographic plot for fast sleep spindle density in the nap-group. Figure 8b shows a correlation topographical plot demonstrating the strength of relationship between fast sleep spindle density and R—F score. This relationship is strongest at P3 (left parietal) electrode site. Figure 8c shows a linear relationship between fast sleep-spindle density at P3 and the R--F score across participants in the nap-group. (Reproduced from Saletin et al., 2011)

Acetylcholine is a neurotransmitter associated with the consolidation of memory and the learning of new information (Graves et al., 2003). Reduction in cholinergic neurotransmission like in Alzheimer's disease or experimentally induced by an antagonist distinctly impairs memory function (Coyle, 1983). For example, the administration of scopolamine, an acetylcholine antagonist, to rats after fear conditioning impairs memory (Rudy 1996). A striking paradox derives from the fact that during SWS, declarative memory consolidation is particularly strong, while it is also characterized by the suppression of cholinergic activity in the hippocampus, compared to high cholinergic tone during wakefulness and REM sleep (Gais & Born, 2003). Gais and Born (2003) found that acetylcholine is an important modulator of the direction of information flow between hippocampus and neocortex, and proposes that this process underlies the integration of new memories into existing neocortical networks. Therefore, a high acetylcholine level is critical for learning new information, while decreased cholinergic modulation may set the appropriate dynamics for consolidation during SWS (Hasselmo & Bower, 1993).

Although research has yet to identify a specific tagging system, there is correlational evidence that the neurobiology of stress response (e.g., the release of norepinephrine and cortisol) modulates activity in the amygdala and hippocampus. When a stress response is activated in emotional learning or fear conditioning, it alters neural networks in ways that have downstream effects on the selective consolidation of emotional memories. Arousal-related

neuromodulators present during and after learning help set molecular ‘tags’ that designate specific traces of emotion to be prioritized for consolidation (Kim & Payne, 2019; Payne & Kensinger, 2017).

While a full behaviour and neurophysiological explanation of selective sleep-dependent memory processing remain to be established, mounting evidence encourages a view that sleep may be the ideal brain state for selective memory processing to occur not only because it is a protected time, but also because it consists of several unique electrophysiological events and involves neurotransmitters like acetylcholine.

Summary

For more than a century it has been known that sleep benefits memory, and research in this field has put forward different explanations for this phenomenon and the specifics of that benefit. Whereas initial research largely concentrated on sleep’s passive protection of memory, recent research has begun systemically examining the qualitative changes that memory undergoes during sleep-dependent consolidation. The encoding of memory is just the first step in a cascade of events that includes reactivation and reorganization on a synaptic and system level. Such processing is neither global nor uniform but appears to be selectively dependent on sleep and the future value that information holds. This offline discriminatory selection of memories is based on prior tags during encoding. Memories that are emotional, show difficulty during learning, have high retrieval expectancy, and are associated with reward are tagged during the encoding phase and are prioritized in their consolidation in subsequent sleep. The underlying neurophysiological mechanisms governing these memory selection processes are beginning to be uncovered. Hypothesis includes the prefrontal cortex’s role in tagging specific information, connectivity between memory regions and cortical areas, and various electrophysiological oscillations and neurotransmitters. More work is needed to reveal the rich collection of mechanisms occurring during selective sleep-dependent memory processing to gain a better understanding of the reciprocity between wake-dependent learning and sleep-dependent consolidation.

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