

A Study on the Consolidation Characteristics of Sleep on Memory of Different Intensity

Bingqin Ma^a, Lianyou Li^b

Qufu Normal University, Qufu, Jining, Shandong, 273165, China
^a641760660@qq.com, ^b188247838@qq.com

Keywords: Sleep; Memory consolidation; Memory intensity

Abstract: Sleep and learning memory belong to the most important basic functions of the brain, and sleep plays an important role in the cognitive function of individuals, and a large number of studies have proved that there is a close relationship between the two, and good sleep can help people consolidate memory. With the deepening of research, according to memory type, memory can be divided into strong memory and weak memory, and many studies have tried to explore the effect of strong and weak memory in sleep-dependent memory consolidation, but a unified theoretical model has not yet been formed. Synthesizing the research results in this field in recent years, we focus on the process of memory consolidation in sleep for strong and weak memories, and briefly introduce the related studies involved. In the future, there is still a need to explore and validate the operation mechanism and application model, so as to provide more theoretical support for the field of memory efficacy and sleep.

1. Introduction

Sleep is an innate physiological phenomenon, and according to statistics, human individuals spend about one-third of their lives in sleep activities. As a state of reduced responsiveness of the organism, sleep is characterized by spontaneity and periodicity, and plays an important role in the performance of cognitive functions, which is closely related to learning ability and memory system^[1]. Its physiological characteristics are mainly characterized by the temporary failure of active consciousness, the interruption of the interval of external awareness and the decrease of responsiveness to environmental stimuli. Good sleep habits are indispensable to maintain the health of the organism, and whether they are good or not depends not only on the length of sleep, but also on the quality of sleep, such as the quietness of the sleep environment and the stability of circadian rhythms. However, with the accelerated pace of society, more and more modern workers are unable to have a good sleep habit due to the influence of work cycle and intensity, which largely affects the health of the organism, and then makes the overall health level of the whole society drop significantly, so the sleep-related problems have gradually risen to become a social problem that needs to be solved urgently, which has attracted widespread attention from all walks of life. Many studies in humans, birds, and rodents have shown that sleep greatly affects memory acquisition and retention^[2-3].

2. Sleep and memory consolidation

2.1 Sleep

Based on the brain physiological indicators observed by EEG technology, coupled with the synergistic study of eye movements and muscle tension changes, the sleep cycle can be categorized into Rapid Eye Movement (REM) sleep stages and non-REM sleep stages. Among them, the non-REM sleep stage can be subdivided into three periods, i.e., light sleep (sleep I), light sleep (sleep II), and deep sleep (sleep III), and the brain wave imaging in the deep sleep period is characterized by slow-wave oscillations, so that the deep sleep period is also referred to as slow-wave sleep. The transition from one period to the next is accompanied by changes in the level of information processing and the state of consciousness^[4]. Generally, when individuals enter the sleep state, they will first experience the non-REM sleep stage before adjusting to the REM sleep stage. Different stages of sleep are accompanied by different physiological responses. Non-REM sleep is associated with the promotion of metabolic functions, during which the heart rate slows down, blood flow slows down, respiratory rate decreases, and the pituitary gland pulsates to secrete growth hormone; whereas, during REM sleep, the heart rate, respiratory rate, and blood pressure become irregular, and the autonomic nervous system tends to be active, which may produce rich dreaming accompanied by rapid eye-sweeping activity^[5].

2.2 Memory consolidation

After the acquisition of specific knowledge or skills, the next stage in the complete process of memory formation is consolidation.

Memory consolidation is the process of transforming newly learned knowledge, experience and other information into new memories that are stored in the brain and form long-term memory^[6]. The transformation of newly acquired information into long term memory does not happen overnight, but requires a certain time process for the information to be incorporated into long term memory, which means that there is a time dependency in memory consolidation. Over time (hours to days), the consolidated memory becomes more resistant to interference and competition, and tends to stabilize^[7]. Duncan conducted electroshock experiments on rats, in which he found that electroshock immediately after a behavioral learning operation significantly impaired memory^[8], while electroshock a few hours after learning was completed significantly impaired memory, while electroshock several hours after learning was completed significantly impaired memory. In this study, it was found that electroshock immediately after a behavioral learning procedure was performed on rats significantly impaired their memory, whereas electroshock several hours after the learning procedure was completed did not have a significant negative effect on the memory associated with previous learning. The above study reveals the time dependence of memory consolidation^[9].

Memory consolidation is a very important part of the process of information storage in the human brain, which can transform the primary representations formed in the brain by external input or internally generated stimuli into a more stable form for storage in the cerebral cortex and for later retrieval when needed. The process of memory consolidation is spontaneous and does not require active or deliberate control, nor does it require repeated associations with learned material, so memory consolidation is also regarded as an "offline" activity. The internal operation mechanism of this activity is also more complex, including multiple stages of action, such as stabilization and reinforcement. This leads to two forms of memory consolidation: offline stabilization and offline reinforcement. Offline stabilization refers to the stabilization and maintenance of an individual's memory level, i.e., the resistance of a specific part of memory to interference is increased^[10]; offline

reinforcement refers to the enhancement of an individual's memory level, i.e., the specific memory traces are more robust^[11]. In addition, a study by Genzel et al demonstrated that neurophysiological structures during memory consolidation change over time and are not static^[12].

2.3 Relationship between sleep-dependent memory consolidation

Research has shown that the performance effects of the memory consolidation effect are largely influenced by the temporal phases that memories undergo in specific brain states, such as sleep and different phases during sleep. In addition, it has been demonstrated that the memory consolidation effect not only has the basic property of stabilizing memory, but also shows the property of enhancing memory during sleep^[11]. These results suggest that sleep plays an important role in memory consolidation, especially during slow-wave sleep^[13]. Experiencing sleep after a learned behavior stabilizes the newly acquired memory in the mind, a process known as sleep-dependent memory consolidation. Sleep-dependent memory consolidation has been found in many species and across a range of memory systems^[11]. There have also been many subsequent studies in humans utilizing functional magnetic resonance imaging (fMRI) techniques and have shown that the individual brain automatically reactivates content experienced prior to rest during subsequent periods of rest and influences subsequent memory performance in relation to it^[14-16].

Maquet et al discovered the plasticity that sleep-dependent memory consolidation possesses when they studied it using functional magnetic resonance imaging (fMRI) techniques^[17]. Subjects were administered a series of procedural skill training tasks and were tested three days after the end of the training. Half of the subjects were subjected to deprivation control during the first night of sleep, while the other half had three full nights of sleep. Subjects who experienced 3 full nights of sleep were found to show enhanced behavioral performance and increased activation of alternatives in the superior temporal sulcus region of the brain on retesting than subjects who were deprived of 1 night of sleep^[17]. The finding of plasticity in sleep-dependent memory consolidation provides solid evidence that sleep is a key mediator of memory consolidation^[18], and similar experiments were conducted in a study by Fischer et al, which also confirmed that sleep on the first night of learning has a critical effect on the consolidation of relevant memories^[19]. It follows that the initial sleep deficit cannot be repaid by subsequent nights of sleep, and Walker and Stickgold argued that the effect of sleep-dependent memory consolidation is very much dependent on the sleep activity that takes place in the 24 hours after learning^[11]. Earlier in their work, Maquet et al found in subjects using brain imaging that signals of brain activity that were apparent during daytime when they received specific training reappeared during REM sleep that night^[20], while those subjects who did not receive daytime-specific training showed no relevant changes in brain activity during REM sleep that night. In addition, Peigneux et al further demonstrated a positive correlation between the degree of learning during training performed during the daytime and the amount of reactivation of brain signals during REM sleep^[21]. There are also studies in which experiments were conducted using semantically related word pairs and semantically unrelated word pairs as materials, and the results showed that the quality of recall for both semantically related word pairs was better after experiencing sleep than remaining awake^[22].

A growing body of literature supports the memory-improving effects of sleep, which not only stabilizes memory performance but also promotes memory enhancement. The combination of practice and sleep can increase the efficiency of memory consolidation compared to full-day practice activities. Based on current evidence, prolonged 24/7 practice is detrimental to memory consolidation, and shortened sleep duration can lead to negative performance of sleep-dependent memory consolidation plasticity. Ensuring adequate sleep time during the practice process may help maximize learning efficiency and individual learning potential^[18]. So, will sleep after learning have

the same beneficial effect on all memories? Or does it prioritize the consolidation of specific memories differently? A large body of research evidence has accumulated in the past suggesting that there is indeed clearly observable selectivity in sleep-dependent memory consolidation, and many scholars have attempted to corroborate the selective prioritization properties of this process across different memory types.

3. Memory strength and sleep-dependent memory consolidation

3.1 Memory strength

The problem of controlling memory strength has been addressed by many researchers in the past, who have provided a variety of manipulation methods. For example, Sio achieved control of memory strength by varying the difficulty of the task (solving a specific problem) in an experiment^[23], while Kuriyama used control of the difficulty of a motor sequence to achieve the effect of controlling memory strength^[24], with a low difficulty of the motor sequence leading to relatively strong procedural memory and a high difficulty of the motor sequence leading to relatively weak procedural memory. The effect of the control on memory strength is realized by controlling the difficulty of the motor sequences. Not only that, there are other manipulations used to achieve the purpose of controlling memory strength, and it is worth mentioning that the manipulations mentioned above are relatively indirect, while some researchers have used relatively more direct manipulations of controlling memory strength, such as controlling the number of times a particular material is presented or learned^[25-27], etc. In this regard, some researchers also mentioned that the strength of training can represent the strength of memory, which to some extent predicts that the enhancement of training strength will prompt the enhancement of memory traces, and thus, the strength of memory traces can be the performance prompted by the strength of training strength. In addition, McDevitt reduced memory strength by implementing a retrospective interference manipulation immediately after subjects performed an encoding activity^[28].

3.2 Evidence that "strong memories" are prioritized for consolidation

Memory consolidation that occurs during sleep does not exert an equally beneficial effect on all memories^[25]. Recent research suggests that the memory consolidation process of sleep may exert different degrees of effect on different types of memories, and that different types of memories benefit differently from sleep. Wilhelm, after administering a word-matching task and a finger-tapping task to subjects targeting the two main memory systems (declarative and procedural)^[29], found a significant effect on sleep-dependent memory consolidation in a subsequent retrieval test. The significant facilitation of retrieval anticipation on sleep-dependent memory consolidation suggests that although sleep exerts consolidation effects on both memory systems, it prioritizes the consolidation of memories that will be used in the future. In other words, sleep prioritizes the consolidation of relevant information conducive to future behaviors. This suggests that the prefrontal hippocampal system may be critical for the selectivity of memory consolidation. In addition, Payne explored the evolution of memories about scenes that elicit negative emotions under conditions of 30-minute intervals^[30], 12 daytime hours (staying awake without experiencing sleep) and 12 nighttime hours (experiencing sleep), and found that sleep showed a more significant memory consolidation of objects and their contexts with elements of negative emotions compared to neutral scenes. There is also evidence that memories of reward-related experiences are preferentially replayed during sleep because of their ability to modulate their own behavioral performance and thus enhance the individual's survival adaptations^[31]. These types of memories mentioned above are to some extent processed more deeply during encoding^[32], and based on these

results it can be seen that sleep-dependent memory consolidation may prioritize the consolidation of stronger memories^[33]. However, one view that exists in response to the explanation for the lower consolidation priority of strong memories over weak memories during sleep memory consolidation is that it is limited by ceiling effects. Artificially manipulating the memory content into the weak memory category during the experiment sometimes does not allow for a precise cut, i.e., the variable control is not optimal, resulting in a lower reliability of the test results.

Conversely, it is also currently argued that weaker memories may benefit more from sleep memory consolidation after learning than stronger memories^[33]. That is, the brain processes weaker memories with an emphasis on recurrence during sleep to deepen the retention traces of the weaker memories.

3.3 Evidence that "weak memories" are prioritized for consolidation

In a study by Schapiro^[34], subjects were divided into two groups: a wakeful group (who studied at 9 a.m. and were tested at 9 p.m. on the same day) and a sleep group (who studied at 9 p.m. and were tested at 9 a.m. on the following day). After learning the features of images belonging to three categories, they underwent a memory test. Their brain activity was tracked in the hippocampus during resting periods using functional magnetic resonance imaging (fMRI) techniques. The study found that information items with weaker initial memory strength before rest showed a higher number of replays during sleep compared to the wakeful period. This suggests a prioritization of memory strength in sleep-dependent memory consolidation. The researchers also found that replay of specific memory objects predicted subsequent related memory performance, and that replay predicted memory improvement during the delay only if the delayed test period included sleep. The results suggest that the replay function in the hippocampus is automatically skewed toward memories that need more help (i.e., weak memories), and that related memories benefit (are consolidated) during replay. And there have been many studies demonstrating this functional role of the hippocampus in the consolidation and enhancement of memories^[14-16,35].

In Denis's study^[36], a sleep and wakefulness group were set up for comparative analysis and two pathways were manipulated to control encoding intensity: the number of learning items presented and the success rate of visualizing the learning items. Visualizing interconnected words promotes memory enhancement, and an associative link between two objects can be facilitated through successful visualization, resulting in deeper memory formation^[37]. And previous research has demonstrated the extent to which associative memory can benefit sleep^[38]. It was found that for information with a weaker encoding strength, the largest difference in data results was found between the sleep and wakefulness groups, suggesting that learning items with a lower initial encoding strength benefit most significantly during sleep.

In terms of measuring the sleep status of individuals, the researcher used sleep logs, the Pittsburgh Sleep Quality Index (PSQI), and the Stanford Sleepiness Scale (SSS) for pre-assessment. The sleep log was used to ask and record the subjects' sleep during the three nights prior to the start of the experiment; the Pittsburgh Sleep Quality Index (PSQI) was used to measure the sleep quality of the subjects one month prior to the start of the experiment; and the Stanford Sleepiness Scale (SSS) was used to measure sleepiness and alertness before the experiment was formally conducted^[39].

The hippocampus has a key role in the encoding and consolidation of memories^[40-41]. Recent studies have shown that the consolidation of weak memories is very specifically associated with sleep spindle waves^[25,42]. A number of studies have been conducted to provide additional reliability to this finding that sleep spindle waves facilitate memory consolidation^[43-44] and are considered to be a mechanistic vehicle for memory consolidation^[45-47]. In a study by Schmidt^[48], it was shown

that encoding strength predicted the sleep spindle wave condition that occurs in post-learning naps. In addition, Baran in a study on schizophrenia^[49], found that impairment of sleep-dependent memory consolidation mechanisms correlated with reduced sleep spindle wave activity, and suggested that sleep spindle wave activity may be an entry point for studying therapeutic mechanisms.

Antony argued that even if an individual has not yet slept, a stage similar to the consolidation process in sleep is experienced within the brain during online retrieval of learning material^[50]. From this, it can be speculated that the portion of information that is remembered with greater strength may be fairly well consolidated prior to the onset of sleep, which in turn makes stronger memories weaken the need for further consolidation during sleep^[33]. Some researchers have used directed memory reactivation techniques for experimental memory reinforcement during naps, and found that only memories with weaker encoding strengths showed better consolidation after sleep, suggesting that directed memory reactivation techniques tend to produce better post-sleep memory performance for memories with weaker encoding strengths^[51-52].

In some studies, researchers have used the level of semantic relatedness as an indirect manipulative index to classify the level of memory strength, and learning material with low semantic relatedness usually produces memories with weaker memory strength^[33]. In the Lo study, two experimental conditions^[22], sleep and wakefulness, were set up as controls and subjects were assigned processed word pairs to memorize, while differences in consolidation effects between short daytime and long nighttime sleep were explored. The results showed that the beneficial effects on word pairs with low related semantics were greater than those with high related semantics, both in the post-study short daytime sleep and the post-study long nighttime sleep. Translated, the benefits of sleep were more pronounced for low semantic relevance learning materials compared to high semantic relevance learning materials, which in turn suggests that a more pronounced sleep-dependent memory consolidation effect was demonstrated for weaker memories. There are also other studies reflecting similar results^[53].

One explanation for the inability of stronger memories to be prioritized for consolidation could be due to stronger cortical memory representations resulting from extensive repetitive processing of the learning material^[54], from which it can be deduced that repetitive processing of specific information results in the relevant memory traces being imprinted sufficiently strongly, and that stronger memories are already sufficiently consolidated before bedtime such that sleep does not, or could not, have a further have a consolidating reinforcing effect on them, and so instead consolidates the weaker memories, making the weaker memories appear to benefit more from sleep^[25,33].

4. Conclusions

Although there are conflicting studies on the prioritization of sleep-dependent memory consolidation and there is no conclusive evidence to systematically explain this phenomenon, these studies have revealed the beneficial effects of sleep on memory to varying degrees. These studies provide valuable insights into people's daily learning, which can help people develop more personalized and efficient learning methods and approaches in the future, and may even help people find ways to improve the efficiency of knowledge absorption and the conversion rate of fragmented memory. However, sleep-dependent memory consolidation is a complex field, whether strong memory is more dependent on sleep consolidation or weak memory is more dependent on sleep consolidation, we still need to explore and validate its operation mechanism and application mode in the future, so as to provide more theoretical support for the field of memory performance and sleep.

References

- [1] Chouhan, N. S., & Sehgal, A. (2022). Consolidation of Sleep-Dependent Appetitive Memory Is Mediated by a Sweet-Sensing Circuit. *Journal of Neuroscience*, 42(18), 3856-3867.
- [2] Diekelmann, S., & Born, J. (2010). The memory function of sleep. *Nature Reviews Neuroscience*.
- [3] Rasch, B., & Born, J. (2013). About Sleep's Role in Memory. *Physiological Reviews*, 93(2), 681-766.
- [4] Iber, C., Ancoli-Israel, S., Chesson, A. L., & Quan, S. F. (2007). *The AASM Manual for the Scoring of Sleep and Associated Events: Rules, Terminology and Technical Specifications*. American Academy of Sleep Medicine Westchester, (1).
- [5] Hobson, J., McCarley, R., & Wyzinski, P. (1975). Sleep cycle oscillation: reciprocal discharge by two brainstem neuronal groups. *Science*, 189(4196), 55-58.
- [6] Tronson, N. C., & Taylor, J. R. (2007). Molecular mechanisms of memory reconsolidation. *Nature Reviews Neuroscience*, 8(4), 262-275.
- [7] McGaugh, James, & L. (2000). Memory—A Century of Consolidation. *Science*, 287(5451), 248-248.
- [8] Duncan, C. P. (1949). The retroactive effect of electroshock on learning. *Journal of Comparative and Physiological Psychology*, 42(1), 32-44.
- [9] Mcgaugh, J. L. (1966). Time-dependent processes in memory storage. *Science*, 8(742), 153-1351.
- [10] Krakauer, J. W., & Shadmehr, R. (2006). Consolidation of motor memory. *Trends in neurosciences*, 29(1), 58-64.
- [11] Walker, M., Stickgold, R., Alsop, D., Gaab, N., & Schlaug, G. (2005). Sleep-dependent motor memory plasticity in the human brain. *Neuroscience*, 133(4), 911-917.
- [12] Genzel, L., & Wixted, J. T. (2017). Cellular and Systems Consolidation of Declarative Memory. *Studies in Neuroscience, Psychology and Behavioral Economics*, 3-16.
- [13] Hughes, R. J., Sack, R. L., & Lewy, A. J. (1997). The role of melatonin and circadian phase in age-related sleep-maintenance insomnia: Assessment in a clinical trial of melatonin replacement. *Sleep*, 21(1), 52.
- [14] Murty, V. P., Tompary, A., Adcock, R. A., & Davachi, L. (2017). Selectivity in Postencoding Connectivity with High-Level Visual Cortex Is Associated with Reward-Motivated Memory. *Journal of Neuroscience*, 37(3), 537-545.
- [15] Staresina, B. P., Alink, A., Kriegeskorte, N., & Henson, R. N. (2013). Awake reactivation predicts memory in humans. *Proceedings of the National Academy of Sciences*, 110(52), 21159–21164.
- [16] Schlichting, M. L., & Preston, A. R. (2016). Hippocampal-medial prefrontal circuit supports memory updating during learning and post-encoding rest. *Neurobiology of Learning and Memory*, 134, 91-106.
- [17] Maquet, P., Schwartz, S., Passingham, R., & Frith, C. (2003). Sleep-related consolidation of a visuomotor skill: Brain mechanisms as assessed by functional magnetic resonance imaging. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 23(4), 1432-1440.
- [18] Walker, M. P. (2004). Issues surrounding sleep-dependent memory consolidation and plasticity. *Cellular and Molecular Life Sciences*, 61(24), 3009-3015.
- [19] Stefan Fischer, M. H., Eisner, A. L., & Born, J. (2002). Sleep forms memory for finger skills. *Proceedings of the National Academy of Sciences of the United States of America*, 99(18), 11987-11987.
- [20] Maquet, P., Laureys, S., Peigneux, P., Fuchs, S., Petiau, C., Phillips, C., Aerts, J., Del Fiore, G., Degueldre, C., Meulemans, T., Luxen, A., Franck, G., Van Der Linden, M., Smith, C., & Cleeremans, A. (2000). Experience-dependent changes in cerebral activation during human REM sleep. *Nature Neuroscience*, 3(8), Article 8.
- [21] Peigneux, P., Laureys, S., Fuchs, S., Destrebecqz, A., Collette, F., Delbeuck, X., Phillips, C., Aerts, J., Del Fiore, G., & Degueldre, C. (2003). Learned material content and acquisition level modulate cerebral reactivation during posttraining rapid-eye-movements sleep. *NeuroImage*, 20(1), 125-134.
- [22] Lo, J. C., Dijk, D.-J., & Groeger, J. A. (2014). Comparing the Effects of Nocturnal Sleep and Daytime Napping on Declarative Memory Consolidation. *PLoS ONE*, 9(9), e108100.
- [23] Sio, U. N., Monaghan, P., & Ormerod, T. (2013). Sleep on it, but only if it is difficult: Effects of sleep on problem solving. *Memory & Cognition*, 41(2), 59e166.
- [24] Kuriyama, K., Stickgold, R., & Walker, M. P. (2013). Sleep-dependent learning and motor-skill complexity. *Learning & Memory*, 11, 705-713.
- [25] Denis, D., Mylonas, D., Poskanzer, C., Bursal, V., & Stickgold, R. (2020). Sleep spindles facilitate selective memory consolidation. *Cold Spring Harbor Laboratory*.
- [26] Schapiro, A. C., McDevitt, E. A., Chen, L., Norman, K. A., Mednick, S. C., & Rogers, T. T. (2017). Sleep Benefits Memory for Semantic Category Structure While Preserving Exemplar-Specific Information. *Scientific Reports*, 7(1), 14869.
- [27] Wang, B. (2020). Effect of post-encoding emotion on long-term memory: Modulation of emotion category and memory strength. *The Journal of General Psychology*, 4, 1-27.
- [28] McDevitt, E. A., Duggan, K. A., & Mednick, S. C. (2015). REM sleep rescues learning from interference. *Neurobiology of Learning and Memory*, 122, 51-62.
- [29] Wilhelm, I., Diekelmann, S., Molzow, I., Ayoub, A., & Born, J. (2011). Sleep selectively enhances memory expected to be of future relevance. *Journal of Neuroscience the Official Journal of the Society for Neuroscience*, 31(5), 1563-1569.

- [30] Payne, J. D., Stickgold, R., Swanberg, K., & Kensinger, E. A. (2008). *Sleep Preferentially Enhances Memory for Emotional Components of Scenes*. SAGE Publications, 8.
- [31] Sterpenich, V., Schie, M. K. M. V., Catsiyannis, M., Ramyeed, A., & Schwartz, S. (2021). *Reward biases spontaneous neural reactivation during sleep*. *Nature Communications*, 12(1).
- [32] Craik; Robert S. Lockhart (1972). *Levels of processing: A framework for memory research*. *Journal of Verbal Learning and Verbal Behavior*, 11(6), 0-684.
- [33] Petzka, M., Charest, I., Balanos, G. M., & Staresina, B. P. (2021). *Does sleep-dependent consolidation favour weak memories?* *Cortex*, 134, 65-75.
- [34] Schapiro, A. C., McDevitt, E. A., Rogers, T. T., Mednick, S. C., & Norman, K. A. (2018). *Human hippocampal replay during rest prioritizes weakly learned information and predicts memory performance*. *Nature Communications*, 9(1), Article 1.
- [35] Bursley, J. K., Nestor, A., Tarr, M. J., & Creswell, J. D. (2016). *Awake, Offline Processing during Associative Learning*. *PLOS ONE*, 11(4), e0127522.
- [36] Denis, D., Schapiro, A.C., Poskanzer, C., Bursal, V., Charon, L., Morgan, A., and Stickgold, R (2020). *The roles of item exposure and visualization success in the consolidation of memories across wake and sleep*. *Learning and Memory*. 27. 451-456.
- [37] Murray, B. D., & Kensinger, E. A. (2012). *The effects of emotion and encoding strategy on associative memory*. *Memory & Cognition*, 40(7), 1056-1069.
- [38] Diekelmann, S., Wilhelm, I., & Born, J. (2009). *The whats and whens of sleep-dependent memory consolidation*. *Sleep Medicine Reviews*, 13(5), 309-321.
- [39] Hoddes, E., Dement, W. C., & Zarcone, V. (1972). *The development and use of the Stanford sleepiness scale (SSS)*. *Journal of Sleep Research*, 1(1):35-39
- [40] Rauchs, G., Feyers, D., Landeau, B., Bastin, C., Luxen, A., Maquet, P., & Collette, F. (2011). *Sleep Contributes to the Strengthening of Some Memories Over Others, Depending on Hippocampal Activity at Learning*. *The Journal of Neuroscience*, 31(7), 2563-2568.
- [41] Schapiro, A. C., Reid, A. G., Morgan, A., Manoach, D. S., Verfaellie, M., & Stickgold, R. (2019). *The hippocampus is necessary for the consolidation of a task that does not require the hippocampus for initial learning*. *Hippocampus*, 29(11), 1091-1100.
- [42] Baena, D., Cantero, J. L., Lluís Fuentemilla, & Atienza, M. (2020). *Weakly encoded memories due to acute sleep restriction can be rescued after one night of recovery sleep*. *Nature Publishing Group*, 1.
- [43] Cox, R., Hofman, W. F., & Talamini, L. M. (2012). *Involvement of spindles in memory consolidation is slow wave sleep-specific*. *Learning & Memory*, 19(7), 264-267.
- [44] Schabus, M., Gruber, G., Parapatits, S., Sauter, C., Klösch, G., Anderer, P., Klimesch, W., Saletu, B., & Zeitlhofer, J. (2004). *Sleep Spindles and Their Significance for Declarative Memory Consolidation*. *Sleep*, 27(8), 1479-1485.
- [45] Schmidt, C., Peigneux, P., Muto, V., Schenkel, M., Knoblauch, V., Münch, M., De Quervain, D. J.-F., Wirz-Justice, A., & Cajochen, C. (2006). *Encoding Difficulty Promotes Postlearning Changes in Sleep Spindle Activity during Napping*. *The Journal of Neuroscience*, 26(35), 8976-8982.
- [46] Fernandez, L. M. J., & Luthi, A. (2019). *Sleep Spindles: Mechanisms and Functions*. *Physiological Reviews*, 100(2).
- [47] Peyrache, A., & Seibt, J. (2020). *A mechanism for learning with sleep spindles*. *Philosophical Transactions of the Royal Society B Biological Sciences*, 375(1799), 20190230.
- [48] Schmidt, C. (2006). *Encoding Difficulty Promotes Postlearning Changes in Sleep Spindle Activity during Napping*. *Journal of Neuroscience*, 26(35), 8976-8982.
- [49] Baran, B., Correll, D., Vuper, T. C., Morgan, A., Durrant, S. J., Manoach, D. S., & Stickgold, R. (2018). *Spared and impaired sleep-dependent memory consolidation in schizophrenia*. *Schizophrenia Research*, 199, 83-89.
- [50] Antony, J. W., Ferreira, C. S., Norman, K. A., & Wimber, M. (2017). *Retrieval as a fast route for consolidation*. *Trends in Cognitive Sciences*, 21(8), 573-576.
- [51] Cairney, S. A., Lindsay, S., Sobczak, J. M., Paller, K. A., & Gaskell, M. G. (2016). *The benefits of targeted memory reactivation for consolidation in sleep are contingent on memory accuracy and direct cue-memory associations*. *Sleep*, 39(5), 1139-1150.
- [52] Creery, J. D., Oudiette, D., Antony, J. W., & Paller, K. A. (2015). *Targeted memory reactivation during sleep depends on prior learning*. *Sleep*, 38(5), 755-763.
- [53] Payne, J. D., Tucker, M. A., Ellenbogen, J. M., Wamsley, E. J., Walker, M. P., Schacter, D. L., & Stickgold, R. (2012). *Memory for Semantically Related and Unrelated Declarative Information: The Benefit of Sleep, the Cost of Wake*. *PLoS ONE*, 7(3), e33079.
- [54] Brodt, S., Gais, S., Beck, J., Erb, M., Scheffler, K., & Schöner, M. (2018). *Fast track to the neocortex: A memory engram in the posterior parietal cortex*. *Science*, 362(6418), 1045-1048.