The role and mechanisms of sleep on memory consolidation

Jiahe Huang
Martin Luther School-Kaifeng New Century, Shanghai,200120,China

Abstract. In addition to its physiological functions, sleep also has a consolidating effect on memory, and current research has found sleep could promote the consolidation of declarative, procedural, and emotional memory. Possible mechanisms of sleep-enhanced memory include the the systemic consolidation theory, dual-process theory, the synaptic homeostasis theory, and the sequence hypothesis. In the future, more research need to examine the neural mechanisms of sleep-enhanced memory consolidation, and the use of simultaneous EEG-MRI will be a meaningful attempt to help us better understand the specific neural processes of sleep-enhanced memory consolidation.

Keywords: Sleep, Memory; Memory Consolidation; Potential Mechanism.

1. Introduction

Sleep is an important physiological activity that plays a very important role in the human life course. Now, with the development of cognitive neuroscience, sleep has gradually become a research hotspot. Specifically, many studies have focused on the role of sleep on memory consolidation. In this paper, first, we will descrie the effects of sleep on the consolidation of different types of memories, then elucidate the possible mechanisms of sleep on memory consolidation, and finally provide our own view of the direction of sleep on memory consolidation. We believe that this paper can introduce the important role and mechanisms of sleep on memory to non-specialists; at the same time, it will stimulate important thinking about the sleep's role.

2. Consolidation effects of sleep on memory

Memory is not a whole, it can be divided into different types according to different distinguishing criteria, for example, Based on the duration of memory, it can be classified as sensory memory, short-term memory and long-term memory (Shiffrin & Atkinson, 1969). Based on the properties of memory, long term memory can be further classified into declarative, procedural and emotional memory (Tulving, 1972). Currently, in the field of sleep memory consolidation, the main focus is on long-term memory, so this paper will illustrate the effect of sleep on memory work from the three classifications of declarative memory, procedural memory and emotional memory.

2.1 Consolidation effects of sleep on declarative memory

As early as 1924, jenkins and helgadottir found that sleepers had significantly higher rates of correct retesting of memorised material on waking up on day 2 compared to non-sleepers (jenkins and helgadottir, 1924). Subsequent studies further demonstrated that normal sleep, shorter naps, and even after a short nap (6 min) significantly improved memory, which suggesting sleep has a significant consolidating effect on declarative memory (Marshall et al., 2006). Gais et al. (2006) also found in memory material with closer semantic connections (word pairs of cued and target word pairings) that, compared to conditions in which sleep was not experienced, slept people would have better performance in the memory retest phase.

However, it has also been suggested that the gains in memory effects from sleep observed in previous studies were not stable and could not be observed across multiple tests with consistent and stable results. A study by Ellenhogen et al. (2006) soon countered these arguments. Ellenhogen and colleagues first had subjects in the sleep and wakefulness groups learn a set of paired word tasks (A-B), and after a 12 h interval, learn another set of paired words (A-C) separately. The test was then conducted and it was found that the sleep group showed a stronger ability to inhibit interfering memories (A-C) in the (A-B) recall task, i.e., there was no interference with the memory of the A-C pairs due to the memory intrusion of the A-C pairs, whereas the memory of the A-B pairs of the wakeful group of subjects was interfered with by the memory intrusion of the A-C pairs. This suggests that even if memory performance does not improve after sleep, it does not mean that sleep does not play a role in memory consolidation, because the consolidating effect of sleep on memory can also be reflected in the inhibitory effect of sleep on the relevant interfering memories.

2.2 Consolidation effects of sleep on procedural memory

Procedural memory is also a hot topic of research in sleep-promoted memory consolidation, as declarative memory may be too simple for academics and only examines the subject's literacy, whereas procedural memory tends to examine the subject's memory for a certain skill, which may be more practical.

The current study found that in a finger sequence tapping task, procedural memory was significantly improved in terms of speed and accuracy after subjects experienced sleep compared to the awake group, and the more complex the motor skill the more significant the improvement was after sleep (Kuriyama et al., 2009). Nishida et al. found that even a short sleep (60-90 minutes) improved procedural memory task performance (Nishida & Walker, 2007). Stickgold and colleagues proposed the hypothesis of the consolidation and reconsolidation process of memory. After information is encoded perceptually to form a memory, it goes through the following stages autonomously with the participation of the unconscious mind: reactivation, stabilisation, degradation, and reconsolidation (Stickgold & Walker, 2007). The process of memory consolidation goes through two main stages: the time-dependent memory stabilisation stage and the sleep-dependent memory enhancement stage. Researchers believe that during the first 6 h after memory formation, memory is still in an unstable stage, and if similar procedural motor skills are used to interfere with the memory, memory can only improve after the sleep phase. During the reconsolidation phase, the reactivation of memories can leave them in an unstable state, if similar memory disturbances occur, it can lead to a significant decline in consolidated memory, but little is known about the time window for reconsolidation and the specific function of reconsolidation.

However, some scholars believe that the experimental design in this field is not sophisticated enough, therefore, Cai and Rickard (2009) used a more sophisticated experimental design to avoid influence of unrelated factors, and the results did not find that sleep can improve procedural memory. Therefore, the specific details of the consolidation of sleep on procedural memory need to be observed and summarised.

Walker et al. (2002) found that the consolidation effect of sleep on procedural memory is proportional to the non-rapid eye movement (NREM) stage 2 (N2) sleep phase, and thus proposed that N2 sleep is related to consolidation of procedural memory. Morin et al. (2008) concluded that the spindle wave of N2 is related to procedural memory consolidation, while rapid eye movement (REM) sleep is more related to the formation of complex motor skills. It has also been suggested that in addition to the N2 sleep period, the REM sleep period also has an effect on procedural memory consolidation. Barakat et al. (2011) found that the spindle wave in REM sleep plays an important role in procedural memory consolidation. Based on this, the effect of sleep on procedural memory consolidation still needs to be examined in further studies.

2.3 Consolidation effects of sleep on emotional memory

Finally, it is the consolidation effect of sleep on emotional memory, which has been the focus of attention in recent years, and some scholars have even begun to explore whether it is possible to consolidate the positive emotional memory while eliminating the negative emotional memory through sleep, so as to achieve the effect of improving the subject's state of mind and emotion. Of course, this is not within the scope of this paper, but it will likely become a future focus of the field. Overall, most of the current research has found that sleep has a very significant effect on emotional memory.

Wagner et al. (2006) found that subjects who experienced 3 h of sleep after completing an emotional memory task were able to extract emotional memories more accurately and meticulously compared to the control group in a memory testing test 4 years later. Payne et al. (2008) found that sleep was selective for emotional memory consolidation, i.e., experiencing sleep resulted in stronger memory processing of the negative emotional memory component of the mixed pictures, suggesting that sleep has different consolidation mechanisms for neutral and negative emotional memories. This mechanism of selective consolidation of negative memories has a positive effect on human beings' ability to identify and remember dangerous stimuli in time and adapt to the survival environment.

It is now believed that emotional events can regulate the neural activity of memory-related brain regions such as the amygdala and the hippocampus, etc. Yoo et al. (2007) found that 35 h of sleep deprivation significantly increased the signal strength of the amygdala, whereas the functional connectivity between the amygdala and the medial prefrontal cortex was significantly decreased, which suggests that sleep regulates the neural activity of the amygdala and thus regulates the neural activity of emotional memories. The study found that functional connectivity in the medial prefrontal cortex, precuneus, amygdala, and occipital cortex was strengthened in people with three consecutive nights of normal sleep compared to the first night of sleep deprivation but the last two nights of normal sleep, and also found that functional connectivity in the amygdala and medial prefrontal cortex was strengthened compared to the previous one in memory retesting after 6 months. It is inferred that sleep-dependent memory consolidation is crucial on the first night after memory learning, and that sleep triggers the interaction of neural activities in different brain regions and activates long-term memory storage pathways (Gais et al., 2007).

The systematic review by Walker and van der Helm (2009) put forward the hypothesis of the forgetting and consolidation process of sleep on emotional memories: the REM stage plays an important role in the consolidation process of emotional memories. Emotional memories form initial memory traces through the amygdala and hippocampus in the wakefulness stage under the synergy of monoaminergic neurotransmitters, and the memories are consolidated in the neocortex in the sleep stage through the action of cortical slow shock waves and hippocampal theta waves as well as acetylcholine; when it is necessary to extract the emotional memories, the activation of the relevant memory emotional state will be gradually reduced due to the time gradually lengthening, but the specific content of the memories is not affected by the time course. It is suggested that deprivation of REM stage sleep affects the formation of human emotional memory, which is very important for the elimination of negative emotions. Recently, some scholars have begun preliminary attempts, and it is believed that this will become a hot topic of research in the future.

3. Mechanisms of Sleep for Memory Consolidation

Having described the effects of sleep on the consolidation of many types of memory, we will briefly summarise the mechanisms by which sleep promotes memory consolidation. Several major mechanistic explanations exist, including: the dual-process theory, the synaptic homeostasis theory, the systemic consolidation theory, and the sequence hypothesis.

3.1 Dual process theory

Initially, research focused on the role of sleep stages on memory consolidation, and it was simply assumed that hippocampal activation in slow-wave sleep stages consolidated declarative memories, while REM stages consolidated non-declarative memories (Plihal & Born, 1997). With the increasing depth of research, more and more scholars believe that declarative memory and spatial memory rely more on the slow-wave sleep stage; procedural memory relies more on the N2 stage or REM stage; and emotional memory relies more on the REM stage. Brain plasticity during sleep is not a single process. Rather, there are unique sleep-related memory consolidation mechanisms for different sleep stages and different brain regions and different types of learning throughout the night (Stuckgold, 2005).

3.2 Synaptic homeostasis theory

The synaptic homeostasis hypothesis suggests that the neural basis of learning memory is the plasticity of the central nervous system, and that during wakefulness the organism receives external stimuli that cause extensive enhancement of synaptic connections. During sleep, synaptic connections are proportionately weakened to baseline levels by electrophysiological slow oscillatory activity, particularly slow-wave activity (Tononi, 2006). Exploration of the neural architecture of Drosophila has revealed an increase in the morphology and number of synapses during the waking phase and a corresponding decrease during sleep. Furthermore, the extent to which synapses increase during wakefulness is proportional to the learning experience and confirms that the Fmrl gene has an important role in the weakening of synaptic connections (Bushey et al., 2011).

3.3 Systemic consolidation theory

Information perceived by humans is temporarily stored in the hippocampus and gradually transferred to the neocortex for long-term storage (Diekelmann & Born, 2010). Sleep regulates the synchronisation between neurons in the thalamus. LTP is the cellular basis of learning memory. During the slow-wave sleep phase, cholinergic neurotransmitters and glucocorticoids are in a lower state of release. This hormonal state and electrophysiological activity synergistically ensure spontaneous reactivation of hippocampal memory traces and promote their consolidation into the neocortex, while the increased release of cholinergic neurotransmitters and glucocorticoids during the REM stage has a significant effect on both affective memory consolidation and procedural memory enhancement.

3.4 Sequential hypothesis

Normal sleep stages, depth and sequence are important for memory consolidation, which is only facilitated by the NREM stage immediately followed by the REM stage. In the slow wave sleep stage. In the slow-wave sleep stage, individuals' waking memory information and past experiences are separated and unrelated to each other; while in the REM stage, waking memories form a broader connection through reorganisation, assimilation and abstraction, and cognitive activities in this stage are closely related to the formation of dreams and prediction of the future (Walker & Stickgold, 2010).

4. Conclusion and future direction

Overall, it appears that sleep currently promotes memory consolidation, including many different types of memories. A question that needs to be elucidated, however, is what are the specific brain neural mechanisms by which sleep promotes memory consolidation. While this paper presents a number of possible theoretical hypotheses, to date there is still a lack of direct neural mechanisms for each theory. Therefore, future studies could use a variety of neuroscience imaging techniques, such as fmri and eeg as mentioned earlier, and in addition, fusion of fmri and EEG would be a better approach. This is because fmri has high spatial resolution but loses temporal resolution, while EEG has high temporal resolution but loses spatial resolution. Therefore, the use of synchronised EEG-fmri technique will be an important approach, which can ensure that we can carry out the exploration of the neural mechanisms of sleep for memory consolidation with high spatial and temporal resolution at the same time.

References

[1] Amélie, M., Julien, D., Valérie, D., Marc, B., Hadj, T. A., Maria, K., Habib, B., Avi, K., Ungerleider, L. G., & Julie, C. (2008). Motor sequence learning increases sleep spindles and fast frequencies in post-training sleep. Sleep(8), 1149-1156.

[2] Barakat, M., Doyon, J., Debas, K., Vandewalle, G., Morin, A., Poirier, G., Martin, N., Lafortune, M., Karni, A., & Ungerleider, L. G. (2011). Fast and slow spindle involvement in the consolidation of a new motor sequence. Behavioural brain research, 217(1), 117-121.

[3] Bushey, D., Tononi, G., & Cirelli, C. (2011). Sleep and Synaptic Homeostasis: Structural Evidence in Drosophila. Science, 332(6037), 1576.

[4] Cai, D. J., & Rickard, T. C. (2009). Reconsidering the role of sleep for motor memory. Behavioral Neuroscience, 123(6), 1153-1157.

[5] Dallenbach, J. K. M. (1924). Obliviscence during Sleep and Waking. American Journal of Psychology, 35(4), 605-612.

[6] Diekelmann, S., & Born, J. (2010). The memory function of sleep. Nat Rev Neurosci, 11(2), 114-126.

[7] Ellenbogen, J. M., Hulbert, J. C., Stickgold, R., Dinges, D. F., & Thompson-Schill, S. L. (2006). Interfering with Theories of Sleep and Memory: Sleep, Declarative Memory, and Associative Interference. Current Biology, 16(13), 1290-1294.

[8] Gais, S., Albouy, G., Boly, M., Dang-Vu, T. T., Darsaud, A., Desseilles, M., Rauchs, G., Schabus, M., Sterpenich, V., Vandewalle, G., Maquet, P., & Peigneux, P. (2007). Sleep transforms the cerebral trace of declarative memories. Proc Natl Acad Sci U S A, 104(47), 18778-18783.

[9] Gais, S., Lucas, B., & Born, J. (2006). Sleep after learning aids memory recall. Learn Mem(3).

[10] Marshall, L., Helgadottir, H., Molle, M., & Born, J. (2006). Boosting slow oscillations during sleep potentiates memory. Nature, 444(7119), p. 610-613.

[11] Nishida, M., Pearsall, J., Buckner, R. L., & Walker, M. P. (2008). REM Sleep, Prefrontal Theta, and the Consolidation of Human Emotional Memory. Cerebral Cortex, 19(5), 1158-1166.

[12] Nishida, M., & Walker, M. P. (2007). Daytime naps, motor memory consolidation and regionally specific sleep spindles. PLoS One, 2(4), e341.

[13] Payne, J. D., Stickgold, R., Swanberg, K., & Kensinger, E. A. (2008). Sleep preferentially enhances memory for emotional components of scenes. Psychol Sci, 19(8), 781-788.

[14] Plihal, Werner, Born, & Jan. (1997). Effects of Early and Late Nocturnal Sleep on Declarative and Procedural Memory. Journal of Cognitive Neuroscience.

[15] Shiffrin, R. M., & Atkinson, R. C. (1969). Storage and retrieval processes in long-term memory. Psychological Review, 76(76), 179-193.

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

[17] Stickgold, R., & Walker, M. P. (2007). Sleep-dependent memory consolidation and reconsolidation. Sleep Medicine, 8(4), 331-343.

[18] Tononi, G., & Cirelli, C. (2006). Tononi G, Cirelli C. Sleep function and synaptic homeostasis. Sleep Med Rev 10: 49-62. Sleep Medicine Reviews, 10(1), 49-62.

[19] Tulving, E. (1972). Episodic and Semantic Memory. Organization of Memory.

[20] Wagner, U., Hallschmid, M., Rasch, B., & Born, J. (2006). Brief sleep after learning keeps emotional memories alive for years. Biol Psychiatry, 60(7), 788-790.

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

[22] Walker, M. P., & Els, V. D. H. (2009). Overnight therapy? The role of sleep in emotional brain processing. Psychological Bulletin, 135(5), 731-748.

[23] Walker, M. P., & Stickgold, R. (2010). Overnight alchemy: sleep-dependent memory evolution. Nature Reviews Neuroscience.

[24] Yoo, S. S., Gujar, N., Hu, P., Jolesz, F. A., & Walker, M. P. (2007). The human emotional brain without sleep--a prefrontal amygdala disconnect. Curr Biol, 17(20), R877-878.

[25]