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The role of sleep in memory

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We sleep less than ever before. Occupational stress, familial commitments and an increasing number of distractions make it difficult for us to get the traditional eight hours of sleep. Many success stories about people sleeping only a few hours a day pressure us to think that we need to sleep less in order to be successful. Consequently, sleep deprivation has become such a common phenomenon that some people do not even realize their exhaustion. However, demanding schedules for doctors persist and trainees are forced to learn to sleep less. Apparently, the sleep quality and satisfaction among medical students and residents is relatively low, and many of them try to compensate for their lack of sleep by taking caffeine pills or coffee. Is sleep really something we should strive to cut back on? What are the consequences of frequent sleep deprivation on our ability to learn? In the following paper, we will look at the present knowledge of the role of sleep in memory consolidation.

What is sleep? Although often perceived as a passive and inactive period, there are many physiological and neurological changes occurring during sleep. Sleep can be divided into rapid eye movement (REM) sleep and non-rapid eye movement (NREM) sleep. The latter can be further divided into light sleep (stages 1 and 2) and slow wave sleep (SWS, stages 3 and 4). Sleep gets progressively deeper from stages 1 to 4. Each sleep cycle proceeds from lighter sleep to SWS and then to REM, and this SWS to REM cycle is repeated several times throughout the night. The first half of the sleep is predominantly SWS, whereas the last half of the sleep is predominantly REM.

One of the most exciting and ongoing debates in the field of sleep research is whether or not sleep contributes to memory and if it does, how so? Memories are initially "encoded" when the brain engages in novel experience and action. These memories, however, require consolidation, which consists of stabilization and enhancement. A large number of studies offer a substantive body of evidence supporting the role of sleep in what is known as sleep-dependent memory processing. Evidence of sleep-dependent memory has been found in many species, including humans and non-human primates, cats, rats, and mice using a variety of behavioural paradigms. These studies offer mixed conclusions about the role of sleep in simple, emotion-free declarative memories. For example, a recent study has shown that facial recognition memory was unaffected by subjects deprived of sleep for 35 hours. However, other studies indicate that both SWS and REM sleep contribute to consolidation of complex, emotionally salient declarative memories. For instance, even though the aforementioned sleep-deprived subjects remembered familiar faces, they had much more difficulty remembering in which of the two sets of photos the faces had appeared. In other words, their memory for the context of the faces was significantly decreased. It is interesting to note that while large doses of caffeine reduced the feelings of sleepiness and improved the ability of the sleep-deprived subjects to remember in which set the faces had appeared, the level of recall was still significantly below the level of the non-sleep-deprived subjects.

There is little doubt that sleep plays a critical role in post-training consolidation of procedural or skill memory. Recent studies have shown that memory stabilization largely occurs during wakefulness, whereas memory enhancement occurs primarily, if not exclusively, during sleep; through this enhancement either previously lost memories are restored or additional learning is produced, both without the need for any further practice. Thus, through sleep, the enhancement phase of memory consolidation causes the active retention of memory instead of its decay.

The enhancement phase occurs during slow wave sleep

SWS is most prominent during early sleep. It is characterized by the appearance of slow oscillations, spindles and sharp wave-ripple field potential oscillations on an electroencephalogram (EEG). These various types of wave activities originate in different centres of the brain and are thought to play a role in memory consolidation. In the hippocampal-neocortical model of memory consolidation, it is proposed that the active memory accumulated during wakefulness is stored as fragments predominantly in the hippocampus as well as in neocortical regions. Studies have shown that by utilizing transcranial direct current stimulation, one can artificially induce increased SWS and enhanced hippocampal-dependent declarative memory consolidation. It is hypothesized that during periods of SWS, slow oscillations originating from the neocortex repeatedly stimulate the newly stored information in the hippocampus and cause their reactivation. This reactivation is associated with the presence of sharp wave-ripple activity as well as spindle activity. The sharp wave-ripple activity originates from the hippocampus, while the spindle activity originates from the reticular nucleus of the thalamus, which travels to the entire neocortex via the thalamocortical circuitry. The process of reactivation essentially allows recently stored memories in the hippocampus to help educate more
permanent stores within the neocortex. This is mediated by spindle activity, which causes changes in calcium permeability of pyramidal neurons (important neocortical neurons in the relay of input into the neocortex). Varying calcium levels have been shown to play a role in the expression of genes that affect long-term plastic changes associated with memory formation and maintenance.

In addition to memory consolidation, SWS has also been shown to aid in the encoding and formation of new memory in the subsequent wakefulness period. It has been well characterized that neuronal synapses possess great plasticity and can alternate between long-term potentiation (LTP) and depression. Calcium influx and delivery of specific receptors to the excitatory synapses facilitate these changes. The delivery of excitatory receptors to the synapses increases the synaptic strength and LTP, and this process is found to be more prominent during wakefulness in rats. This indicates that strong synaptic circuits cannot be maintained indefinitely due to limitations on energy, space, and saturation. Hence, the down-regulation of these receptors observed in SWS may be crucial for the homeostasis of neuronal plasticity. However, this does not mean that sleep is devoid of LTP activities, and it is hypothesized that this process occurs during REM sleep. Animal studies have shown that exposure to a novel environment during wakefulness is associated with increased expression of immediate early genes during sleep. They in turn activate several receptors, which induce LTP. The process of "transferring" memory from its temporary hippocampal storage sites to its more permanent neocortical sites has also been suggested to play a role in priming hippocampal structures for the formation of new memories. fMRI imaging studies support this hypothesis by showing significant reduction in hippocampal activity following sleep deprivation during memory encoding activity compared to controls. Furthermore, recent studies evaluating the effect of SWS on the acquisition of temporal memory (memory of when events occur) showed a significant deficiency in temporal memory recall in the sleep deprived group compared to controls. This experiment controlled for confounding variables such as stress from the lack of sleep by allowing a 36 hour sleep 'rejuvenation' period for both groups. Furthermore, it has been shown that even a nap of significant duration, containing SWS, shows significant correlation with enhanced declarative memory. Moreover, physiological and behavior studies have shown the importance of SWS on the consolidation of new and old memories and thus can be thought to play an integral role in the effective acquisition and storage of new information.

The role of rapid eye movement sleep

REM sleep represents the late stage of the sleep cycle. It is characterized by reduced muscle tone and fast, low-voltage EEG waves. Early behavioural studies led to the development of the hypothesis that REM sleep is involved in memory consolidation. Following a period of intense learning, it has been shown that there is an increase in REM density and the number of rapid eye movements. Altering the levels of REM during sleep may affect memory acquisition. Donepezil, an acetylcholinesterase inhibitor used for treatment in Alzheimer’s, induces an increase in REM sleep. This increase is linked to an enhancement of memory performance. In contrast, a decrease in REM sleep inhibits learning, as seen in REM deprivation studies in both animals and humans. Physiologically, the discharge patterns in the hippocampus during training on a circular track task (a common experimental setup to test for spatial recognition memory) are also mimicked during REM sleep, which suggests that the learned task is replayed while asleep. The increase in the amount of REM sleep post-learning, change in memory performance by altering the amount of REM sleep, and evidence of learning during REM sleep provide support for the aforementioned hypothesis. Recently the role of REM in memory consolidation has been called into question. The REM depression studies
have been criticized for the use of the "platform-technique," where an animal is placed on a small platform surrounded by water. As the animal enters the REM stage of the sleep cycle, its muscles relax causing it to fall in and thereby disrupting that stage of sleep. This technique produces a high level of stress in the animal, resulting in confounding factors such as hyperactivity, anxiety and irritability. Furthermore, depressed patients treated with monoamine oxidase inhibitors, which block REM sleep, do not show memory impairments. The inconsistent results with respect to the REM sleep-memory consolidation hypothesis have led to a debate in the field, with some suggesting that REM sleep is only important for procedural memory.

Conclusion

Despite the controversial role of REM sleep in memory consolidation, there is no doubt that sleep has a profound influence on how we learn. Medical students are constantly torn between the need to stay up and learn those extra few pages, and getting the sleep required. However, many studies have shown a decrease in memory acquisition and consolidation with a lack of sleep. Although staying up late may help students get the few extra points needed to pass a course, it will hinder the ability to retain what has been learned. Future doctors must optimize learning habits today to take better care of patients tomorrow.

References