Supplementary Commentary


Abstract of the original article: Research in the neurosciences continues to provide evidence that sleep plays a role in the processes of learning and memory. There is less of a consensus, however, regarding the precise stages of memory development during which sleep is considered a requirement, simply favorable, or not important. This article begins with an overview of recent studies regarding sleep and learning, predominantly in the procedural memory domain, and is measured against our current understanding of the mechanisms that govern memory formation. Based on these considerations, I offer a new neurocognitive framework of procedural learning, consisting first of acquisition, followed by two specific stages of consolidation, one involving a process of stabilization, the other involving enhancement, whereby delayed learning occurs. Psychophysiological evidence indicates that initial acquisition does not rely fundamentally on sleep. This also appears to be true for the stabilization phase of consolidation, with durable representations, resistant to interference, clearly developing in a successful manner during time awake (or just time, per se). In contrast, the consolidation stage, resulting in additional/enhanced learning in the absence of further rehearsal, does appear to rely on the process of sleep, with evidence for specific sleep-stage dependencies across the procedural domain. Evaluations at a molecular, cellular, and systems level currently offer several sleep specific candidates that could play a role in sleep-dependent learning. These include the upregulation of select plasticity-associated genes, increased protein synthesis, changes in neurotransmitter concentration, and specific electrical events in neuronal networks that modulate synaptic potentiation.

Refinements and confinements in a two-stage model of memory consolidation

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Abstract: Matthew Walker’s model overcomes the unrefined classical concept of consolidation as a unitary process. Presently still confined in its scope to selective data mainly referring to procedural motor learning, the model nonetheless provides a valuable starting point for further refinements, which would be required for a more comprehensive account of different types and aspects of human memory consolidation.

Memory consolidation, the ability to keep and “engrave” newly acquired information for later use, is one of the fundamental brain functions underlying the impressive adaptiveness of human behavior. But how exactly is this important function accomplished? Walker provides a timely model as an attempt to answer this unresolved question. By proposing two distinct stages of memory consolidation – time-dependent stabilization and sleep-dependent enhancement – the model refines the classical perspective of memory consolidation as a unitary, monolithic process and nicely integrates findings from different lines of research. However, the presented model is based on a limited set of data and appears to require further refinements for a more comprehensive account of different types and aspects of memory consolidation. Specifically, we suggest extending the model in the following three areas:

1. The model is supposed to be valid for procedural memory, but within this domain it strongly focuses on available data from only one task type, namely procedural motor learning. Although Walker also refers to some findings from studies on visual texture discrimination (a prototype of perceptual procedural learning), there are important data that would not fit into the model. For example, in several studies visual discrimination performance did not show signs of stabilization during wakefulness. In fact, several retests without intervening sleep did not lead to stabilization, but to a performance decrement. Any learning of this discrimination task has been related to sleep, involving a coordinated interplay between slow-wave sleep (SWS) and subsequent REM sleep (Gais et al. 2000; Mednick et al. 2003; Stickgold et al. 2000a; 2000b). There are likewise findings within the domain of procedural motor learning that are not accounted for by the model. For instance, performance in a finger-to-thumb opposition task was found to be significantly enhanced across 8 hours of daytime wakefulness in one study (Fischer et al. 2002). Although sleep during the same period resulted in additional enhancement, this outcome does not support the general concept of a pure maintaining function of wake time after training in this task. More studies using interference probes at different time delays after training, also considering circadian aspects, would be needed to specify the exact progress of consolidation-based memory stabilization and/or enhancement during periods of wakefulness.

2. Although overcoming the monolithic view of memory consolidation, Walker’s model is still based on the traditional concept of memory consolidation as a mere quantitative strengthening (“enhancement”) of newly acquired memory traces. However, in certain cases the memory trace may also undergo a process of restructuring during the consolidation process, resulting in a qualitative rather than only quantitative change in behavior. Several studies have provided hints at such structural change in memory representations as a result of the consolidation process. Korman et al. (2003) reported in a procedural motor task a kind of qualitative change, indicated by a shift from effector-independent to
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effect-dependent performance, after multisession training that was composed of five single training sessions spaced apart by 1 to 3 days. The restructuring in this case may have emerged from an interplay between processes of labilization at training and reconsolidation during subsequent sleep (Nader 2003; Walker et al. 2003). We demonstrated recently that sleep can facilitate restructuring processes in a sequential reaction time task, where sleep enhanced the probability of gaining explicit insight into a hidden task structure (Wagner et al. 2004). There is also first evidence from brain imaging studies that sleep-dependent consolidation is linked to a specific reorganization in the underlying neuronal representation of motor skills in parallel with increasing behavioral automation (Fischer et al., in press; Walker et al. 2005).

3. Walker deliberately confines his model to procedural memory and excludes the domain of declarative (explicit) memory. It would be interesting to test to what extent predictions derived from the model could also apply to declarative memory functions, as a great part of the literature on human memory consolidation deals with declarative memory, which has also been shown to benefit from sleep in many studies (e.g., Ekstrand 1977; Jenkins & Dallenbach 1924; Pihlbl & Born 1997; Wagner et al. 2001). The transient storage of information in hippocampal networks could serve a stabilization of newly encoded declarative memories, similar to that assumed for procedural memories. Moreover, the assumed processes of hippocampal reactivation during sleep allowing an integration of the information into long-term memories may share some essential features of the processes of “memory enhancement” proposed by Walker. A more comprehensive model would attempt to include declarative aspects of memory as well, particularly on the background that much of the research on neural bases of sleep-associated memory formation, also cited by Walker, refers to mechanisms within the hippocampus, which is specifically implicated in declarative memory. Also, some of these neural mechanisms seem to apply to both declarative and procedural types of memory. Thus, a replay of previously encoded materials could be essential for sleep-associated consolidation of procedural and declarative memories (Hasselmo 1999; Maquet et al. 2000; McNaughton et al. 2003). Also, glutamate receptor–dependent long-term potentiation can be modulated by the same transmitters in the hippocampus and neocortex whereby both types of memories would be similarly influenced (Brocher et al. 1992; Izquierdo & Medina 1997). Interestingly, new findings also indicate that, in certain tasks involving components of procedural motor learning, explicit and implicit mechanisms can interact with sleep-related processing to differentially change task performance (Robertson et al. 2004; Wagner et al. 2004), supporting also from this perspective a more integrative approach to procedural and declarative types of memory.

Together, these points show that the assumption of only two relevant subprocesses underlying memory consolidation would apparently be insufficient to account for the whole complexity of human memory consolidation even if restricted to the procedural memory system. Different memory tasks and even different memory aspects within the same task involve different brain mechanisms, which in turn can be affected in very different ways by sleep- or time-dependent processes of memory consolidation. With the model’s open category of “additional processes,” Walker offers a good starting point for such extensions. Thus, this promising model will serve as the germ for the development of more refined and less confined theoretical frameworks, which would eventually include the entire range of different phenomena within human memory consolidation. Having broken the theoretical monolith of memory consolidation in a first step is the principal merit of Walker’s model.

References