Filling one gap by creating another: Memory stabilization is not all-or-nothing, either

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Abstract: Walker proposes that procedural memory formation involves two specific stages of consolidation: wake-dependent stabilization, followed by sleep-dependent enhancement. If sleep-based enhancement of procedural memory formation is now well supported by evidence obtained at different levels of cognitive and neurophysiological organization, wake-dependent mechanisms for stabilization have not been demonstrated as convincingly, and still require more systematic characterization.

In a laudable effort to move beyond simplistic "all-or-nothing" views on the role of sleep in memory consolidation, Walker proposes that memory traces acquired during a learning episode further undergo at least two distinct sorts of modifications after practice has ended (that is, "off-line"): consolidation-based stabilization (CBS) and consolidation-based enhancement (CBE). The first set of processes would be dependent on wakefulness, while the second would be dependent on sleep. While we certainly agree with the author that previous characterizations of the role of sleep during memory formation has tended to focus on simplistic distinctions, it also appears to us that Walker's own proposal, in which a sharp distinction is made between wake-dependent CBS and sleep-dependent CBE, falls into the same trap.

Admittedly, it is now well established that sleep plays an important role in CBE-like processes. In Walker's proposal, the enhancement component of memory consolidation is akin to what the sleep community used to characterize as a sleep-dependent memory consolidation process. In attributing a specific role to sleep for memory enhancement, however, Walker also asks us to consider that wakefulness plays a specific role in stabilization – a process during which recently acquired information stabilizes at the level attained at the end of a practice session and through which it becomes more resistant to interference. We found, however, that the evidence presented by the author in support of this otherwise interesting hypothesis is far less consistent than the evidence that supports the notion that sleep plays a significant role in memory enhancement.

Indeed, looking at the experimental data, the vigilance state-dependency of memory stabilization seems to vary according to whether the task involves perceptual or motor components. To see this, consider first the visuo-perceptual Texture Discrimination Task (TDT). Performance on this task, as measured at the end of a wake interval subsequent to the end of the training session, generally shows no improvement (Stickgold et al. 2000a), and, more important, appears to decrease with further practice unless a 30-minute nap is allowed, in which case further decay is stopped (Mednick et al. 2002). Interestingly, performance reverts to the initial levels after a longer (60-minute) nap (Mednick et al. 2002). Actual improvement is observed only after a night of sleep (Gais et al. 2000; Stickgold et al. 2000a; 2000b) or after a longer, 90-minute, nap (Mednicket al. 2003), both characterized by the orderly succession of SWS and REM periods. Because performance actually decreases across repetitions separated by wake intervals, one would tend to think that the perceptual memory trace was in fact not at all stabilized during wakefulness. On the contrary, the fact that performance only stabilizes after a nap suggests that memory stabilization takes place during the initial period of sleep, which is dominated by SWS. This interpretation may find further support in the demonstration that overnight performance improvement in texture discrimination is best explained by the amount of SWS in the first part of the night plus the amount of REM sleep in the last part of the night (Stickgold et al. 2000b). We therefore conclude that memory stabilization in a visuo-perceptual procedural task such as the TDT does not appear to depend primarily on a specific wake-dependent mechanism, but, rather, on the occurrence of specific sleep-dependent mechanisms.

Next, consider another type of task involving motor rather than perceptual procedural learning, such as the Finger Tapping Task (FTT). The time course of memory consolidation for this task follows a different course that better fits with Walker's proposal. In the FTT, a slight increase in performance is observed either with repeated practice or with elapsed wake time, albeit overnight improvement remains significantly larger (Fischer et al. 2002; Walker et al. 2002; 2003b). Most important, presentation of interfering material after 30 minutes significantly disrupts performance, which seems not to be the case anymore after a few hours (Walker et al. 2003b). Change in the robustness of a motor memory within a few hours after acquisition has been previously examined by Shadmehr and Brashers-Krug (1997), who elegantly proposed that the recruitment of activity in neuronal circuits following motor practice establishes a reverberating pattern that gradually decays in the short term, and that may serve as the teacher signal for a slower but more robust form of memory storage. Should we therefore conclude that stabilization of memory only occurs during wakefulness? Not necessarily so. Performance stabilization for procedural (or declarative) memory can also be observed after restricted periods of time mostly dominated by REM sleep (or SWS, respectively) (Plihal & Born 1997; 1999a).

A final issue that we wonder about is the functional relationship between stabilization and enhancement components. Walker et al. (2003a) have previously argued that there is a stochastic relationship between the fast components of memory formation, as revealed by the rate of improvement within training sessions and the level attained during initial practice, and the slow, off-line components, which are assumed to be specifically sleep-dependent. However, using the procedural serial reaction time task (SRTT), we have recently reported (Peigneux et al. 2003) that the reactivation of learning-related cortical areas during REM sleep is proportional to the level of performance achieved at the end of the training session. It therefore appears that the cellular processes that subtend the fast, initial "stabilization" stages modulate the subsequent consolidation-based enhancement that takes place during sleep. Understanding this interaction is clearly an important challenge for future research. Hence, while Walker has offered a comprehensive speculative discussion on the biological mechanisms of learning and of synaptic plasticity during sleep, his proposal falls a bit short when it comes to understanding the neurobiological mechanisms that support stabilization and, most important, the relationships between the latter and the mechanisms of enhancement.

New perspectives on sleep disturbances and memory in human pathological and psychopharmacological states

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Abstract: Matthew Walker's article has prompted us to consider neuropsychiatric disorders and pharmacological effects associated with sleep alterations, and aspects of memory affected. Not all disorders involving insomnia show memory impairment, and hypersomnias can be associated with memory deficits. The use of cholinergic medication in dementia indicates that consideration of the link between sleep and memory is more than academic.

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