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Research report

Sleep not just protects memories against forgetting, it also makes them more accessible

Nicolas Dumay [a,b,*]

[a] Department of Psychology, University of Exeter, United Kingdom
[b] BCBL. Basque Center on Cognition, Brain and Language, Spain

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ABSTRACT

Two published datasets (Dumay & Gaskell, 2007, *Psychological Science*; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010, *Journal of Neuroscience*) showing a positive influence of sleep on declarative memory were re-analyzed, focusing on the "fate" of each item at the 0-h test and 12-h retest. In particular, I looked at which items were retrieved at test and "maintained" (i.e., not forgotten) at retest, and which items were not retrieved at test, but eventually "gained" at retest. This gave me separate estimates of protection against loss and memory enhancement, which the classic approach relying on net recall/recognition levels has remained blind to. In both free recall and recognition, the likelihood of maintaining an item between test and retest, like that of gaining one at retest, was higher when the retention interval was filled with nocturnal sleep, as opposed to day-time (active) wakefulness. And, in both cases, the effect of sleep was stronger on gained than maintained items. Thus, if sleep indeed protects against retroactive, unspecific interference, it also clearly promotes access to those memories initially too weak to be retrieved. These findings call for an integrated approach including both passive (cell-level) and active (systems-level) consolidation, possibly unfolding in an opportunistic fashion.

> "The analysis of recall patterns has clearly shown that the "average" item is a highly abstract and elusive entity having no readily identifiable counterparts in the empirical realm." (Tulving, 1967, p. 183).

1. Introduction

In a study titled "Obliviscence during sleep and waking" Jenkins and Dallenbach (1924) had two of their colleagues learn lists of nonsense syllables either in the morning or late evening. By testing recall after intervals ranging between one and eight hours, these researchers found that the presence of sleep in the retention interval had a protective influence: forgetting curves were less steep for intervals filled with sleep than for those filled with active wake.

Nine decades down the forgetting curves, the beneficial impact of sleep on memory is well established (see Wixted & Cai, 2014, for a review). We know that the sooner the learner sleeps after encoding, the better the memory retention (Ekstrand, 1972; Gais, Lucas, & Born, 2006; Payne et al., 2012). We also know that which sleep component is key to the

* Department of Psychology, University of Exeter, Perry Road, Exeter, EX4 4QG, United Kingdom.
E-mail address: nicolas.dumay@gmail.com.
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consolidation process depends on the type of knowledge to be consolidated. For instance, the conscious recollection of factual information or of our past experience (i.e., "declarative" memory) almost exclusively benefits from slow-wave (slow oscillations) sleep (Plihal & Born, 1997, 1999; Yaroush, Sullivan, & Ekstrand, 1971). By contrast, the positive effect of sleep on newly learnt perceptual or motor skills (i.e., procedural memory) shows a more complex picture, in which REM (rapid-eye movement) and non-REM sleep brain correlates have been implicated, sometimes in synergy (e.g., Gais, Plihal, Wagner, & Born, 2000; Gaskell et al., 2014; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Rasch, Gais, & Born, 2009; Stickgold, James, & Hobson, 2000).

One of the current debates, however, is whether sleep makes declarative (hippocampus-dependent) memories more vivid, and thus more accessible, than they were just after encoding, or if instead sleep merely protects them from the deleterious effect of retroactive interference. According to the "active consolidation" account (Diekelmann & Born, 2010), sleep is key to memory consolidation because slow-wave sleep promotes "neural replay" (Wilson & McNaughton, 1994). In slow-wave sleep, new memories encoded in the hippocampus are repeatedly re-activated, which drives concurrent reactivation of cortical regions implicated in their initial capture (Ji & Wilson, 2007). By this feedback from the hippocampus to the cortex, or "systems consolidation", newly acquired memories are effectively re-experienced, with the result that cortical representations are strengthened. They are also better integrated in pre-existing cortical networks, because replay also reactivates similar, long-consolidated material. Hence, according to this account, which emphasizes the role of the hippocampus as the sparring partner of the neocortex, sleep has the potential to make memories more accessible.

In contrast, theories grounded in the notion of retroactive interference (Wixted, 2004; see also Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011) insist that, during slow-wave sleep, synaptic plasticity in the hippocampus is null. Consequently, hippocampal resources that would otherwise be allocated to new encoding can now be used to consolidate, at the cell level, memories formed prior to (slow-wave) sleep. Amongst these memories, those formed earlier during the wake should be more eroded. Thus, memory consolidation is fundamentally the antidote to retroactive, unspecific interference and thus reduces its product: forgetting. Any factor that reduces the encoding activities of the hippocampus *ipso facto* promotes consolidation. As this account assumes that hippocampal consolidation triggers systems consolidation, anything that is forgotten by the hippocampus cannot be recovered via neural replay (Wixted & Cai, 2014, p. 30). Thus, according to the anti-forgetting view, sleep—like any other interval of reduced encoding—can at best stabilize newly formed declarative memories; it cannot make them more accessible.

So far, the "active consolidation" account has received strong empirical support from demonstrations that declarative memories are better preserved if, while in slow-wave sleep, participants are cued by an odor or sound also present during encoding (Rasch, Buchel, Gais, & Born, 2007), or by translation equivalents, in the case of word lists (Schreiner & Rasch, 2014). Frustratingly, however, the data supposedly speaking to the issue of sleep-dependent trace enhancement remain ambiguous, providing little support for the idea.

I suggest that this state of affairs is due to the fact that researchers have been relying exclusively on net performance. However, as Tulving (1964, 1967), amongst others, pointed out, this approach is inherently blind to fluctuations at the item level. Consequently, even though the typically observed pattern is that the sleep group simply shows less forgetting than the wake group, it may well be that a sleep-dependent trace enhancing mechanism is actually counteracting the effect of a task-specific component that worsens performance at retest. Conversely, and by the same logic, finding that the sleep group shows more improvement at retest (compared to the initial test) than the wake group does not necessarily provide evidence for sleep-dependent trace enhancement. A sleep-dependent anti-forgetting mechanism could just supplement a task-specific component which, irrespective of group, helps to maintain/improve performance. Therefore, without information on the trajectory of each item between test and retest, it is misguided to use declarative tasks and make inferences about consolidation mechanisms supposedly acting on individual representations.

Consequently, in the present research I tracked the "fate" of individual items from an initial test to a post-sleep (or post-wake) retest to better assess the impact of sleep on memory. Specifically, I distinguished between items that were retrieved at test and "maintained" (i.e., not forgotten) at retest, and items that were not retrieved at test, but were eventually recovered (i.e., "gained") at retest—a phenomenon typically referred to as "reminiscence". This gave me separate estimates of protection against loss and of memory enhancement. These provide a means to determine whether sleep only boosts protection against loss, which would support the anti-forgetting account (Wixted, 2004), or whether it also boosts memory accessibility, which would support the active consolidation account (Diekelmann & Born, 2010).

Item-fate analysis is routinely performed in cognitive psychology (Ballard, 1913; Brown, 1923; Erdelyi, 1984; Tulving, 1964, 1967, just to cite the pioneers). However, it is only recently that Fenn and Hambrick (2013) used this approach to look at the effect of sleep, unfortunately rather unconvincingly, as I will demonstrate. Fenn and Hambrick had 354 participants learn pairs of semantically related items (e.g., table-chair) either in the evening or in the morning. After testing recall of the second member of each pair (e.g., table-?) immediately and after twelve hours, and finding improvement for both groups, they classified responses following the above "maintained versus gained" distinction. As sleep had its strongest impact on maintained items (+1.35 item compared to wake; *vs* +.44 for gained), the authors concluded that "[…] loss prevention may primarily account for the effect of sleep on declarative memory consolidation" (p. 501).

As can be seen on their Fig. 1, however, performance was dangerously close to ceiling, especially at the 12-h retest (on average, 35 items recalled out of 40). To reassure the reader, Fenn and Hambrick crosschecked their results, excluding all participants with a retest score four items (i.e., the average improvement across the two groups), or less, away from the ceiling (see their Footnote 4 and Supplemental Materials). This