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Seeing the Forest through the Trees

Commentary on Sterpenich et al. Memory reactivation during rapid eye movement sleep promotes its generalization and integration in cortical stores. SLEEP 2014;37:1061-1075.

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It is often said that a person is the sum of her memories. Memory allows us to relive our past, and in so doing provides us with a sense of our previous and present selves. But new evidence suggests that our memories are as important for the future as they are for the past.[1] This requires thinking of a memory less as a high fidelity and static representation of prior experience, and more as a powerfully flexible construct that is nonetheless prone to errors and inaccuracies. A study by Sterpenich and colleagues[2] in the current issue of *SLEEP* brings this important insight into the field of sleep and memory research, and suggests a role for REM sleep in memory flexibility.

We often talk about sleep "consolidating" memories, or fixing them in the brain. Several studies have demonstrated that the neural activity observed during wakeful learning can be reactivated during subsequent periods of sleep. This in turn aids memories, with reactivation during deep, slow wave sleep (SWS) being especially beneficial if one wants to recall information in veridical format—or in exactly the same way one originally encountered it.[3] A clever group of studies,[4] including the Sterpenich study,[2] provide causal evidence for sleep's role in memory processing by demonstrating that a sensory cue, if originally paired with a memory at the time of learning, can improve memory retention when that cue is re-delivered during sleep. For example, in a recent study by Diekelmann et al., participants were trained on a task similar to the memory game "Concentration" either in the presence or absence of an odor that would later serve as a memory cue. They then either stayed awake or went to sleep, during which time they were re-exposed to the odor. Odors applied during SWS stabilized memories in hippocampal-cortical networks, which in turn benefited subsequent task performance.[5]

Such studies support the traditional view of memory consolidation as a stabilizing or "stamping in" of newly learned information. In contrast to traditional consolidation theory, however, are studies showing that seemingly permanent memories can be returned to a labile state following reactivation, at which point they can be modified.[6] Indeed, in the study mentioned above,[5] if the odor cue was re-presented during wakefulness (instead of SWS) memories were *labilized*, allowing them to be modified and updated with similar information. Although rendering a memory modifiable can lead to memory distortion, it also allows for adaptive generalizations to take place when we encounter related information.

But what happens when memories are reactivated during REM sleep? Would REM sleep, a brain state similar in some respects to the awake brain,[7-9] also allow for generalization in memory? The report by Sterpenich and colleagues[2] begins to answer this question by examining the behavioral and neurofunctional consequences of memory reactivation during REM sleep. Participants in several experimental groups first encoded blocks of valenced faces that were each paired with a separate tone (one tone for negative faces, a different tone for neutral faces). They then slept overnight in the laboratory. In the first group, both tones were presented during REM sleep. In the second group, both tones were presented during stage 2 NREM sleep. In the third group, no tones were presented during sleep. Finally, a fourth group did not hear the tones during encoding but were presented with the tones during REM sleep. As predicted, subjects were best at remembering the faces when the tones were presented during REM sleep (i.e., group 1), presumably because reexposure to the tone served as a reminder and triggered reactivation of the memory traces. This notion is bolstered by the fact that Sterpenich found that neural activity was increased in cortical areas during retrieval, including an occipital area involved in face perception, and the middle temporal gyrus, which is involved in the perception of synchronous visual and auditory stimuli.[2]

Clearly, reactivation during REM sleep benefited memory performance, likely due to increased activity and connectivity in the cortical areas mentioned above. But the story is both more complex and more interesting, because in addition to correctly remembering studied faces, participants in the REM reactivation group also falsely remembered similar but unstudied faces. Rather than remembering the specifics of every face, subjects seem to have generalized across stimuli, emphasizing gist over veridical detail. Although a role for sleep in generalization has been seen before,[10] and REM has been implicated in this process,[8,9] the study by Sterpenich[2] is the first to demonstrate that reactivation of memories during REM sleep leads to the integration of new memories within cortical semantic networks. Thus, while cues presented during SWS promote veridical memory consolidation by boosting hippocampo-cortical communication,[11] the current study suggests that cues presented during REM sleep favor gist processing and semantic integration by potentiating cortico-cortical circuits. The very act of integrating information into cortical stores likely supports modification of the memory trace, favoring general, "schematic" characteristics over detailed, veridical ones.[8,9]

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An interesting next step in this line of work would be to reactivate only emotional or neutral memories during REM sleep in an attempt to confirm REM's role in emotional memory processing. By reactivating both types of memories during sleep, this study was not ideally suited to answer this question. However, understanding the role of memory reactivation during REM sleep is important, given clinical conditions characterized by changes to both REM sleep and memory. Depression, for example, is associated with a negative memory bias, where people focus excessively on negative information at the expense of neutral and positive information.[12] Perhaps reactivating positive and neutral memories during REM sleep would provoke a normalization of memory processing where positive and neutral memories would become more salient and generalizable than negative ones, thereby ameliorating depressive symptoms.

Memory research makes clear that our long-term memories are not faithful reproductions, but rather reconstructions or even distortions of experience.[13] While this might seem maladaptive, such plasticity in memory allows us to flexibly recombine stored information in order to develop insight into hidden rules,[14] draw inferences,[15] integrate information,[16] and adaptively generalize across exemplars in order to extract the gist of experience.[7-10] If it weren't for these higher-level abilities, we would be mired in superfluous details, apt to miss important connections, and be less adept at detecting subtle patterns based on similarities in input. In other words, we wouldn't be able to see "the forest through the trees." The study by Sterpenich[2] suggests that REM sleep, rather than solidifying veridical memory details in the brain in a manner similar to SWS, instead promotes the ability to get the gist.

CITATION

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