Updating internal cognitive models during sleep

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It is well-known that a night of good sleep reinforces various cognitive functions, including memory processing (see Lim & Dinges, 2010 for a review). Specifically, the consolidation of newly acquired memories is thought to benefit from sleep (Rasch and Born, 2013), based on studies showing improved performance (e.g., memory enhancement or reduced forgetting, depending on the task) after sleep than after a similar time spent awake (Chambers, 2017).

Although the effect of sleep on the consolidation (i.e., the process of transforming newly acquired information into long-term memories) of explicit, hippocampal-dependent, declarative memory seems to be widely supported (see Rasch & Born, 2013 for a review), the impact of sleep on more complex functions seems to be less clear. For example, studies testing the effect of sleep on tasks requiring a constant updating of information in working memory, such as rapid serial visual presentation tasks and sequence learning, have provided conflicting results (Cellini et al., 2015; Durrant, Taylor, Cairney, & Lewis, 2011; Fischer, Drosopoulos, Tsen, & Born, 2006; Nemeth et al., 2010). Nevertheless, accumulating evidence suggests that sleep is an essential period for extracting the overarching rules underlying a set of new information (i.e., the gist) and to integrate them into existing knowledge, leading to an update of existing schemas (Lewis, Knoblich, & Poe, 2018; Stickgold & Walker, 2013).

Grounded on this literature, a recent study published in *The Journal of Neuroscience*, (Lutz and colleagues 2018) investigated the effects of overnight sleep on the formation, consolidation and abstraction of an internal cognitive model (i.e., a schema representing upcoming stimuli), using a predictive coding approach. Predictive coding theories hypothesize that information processing is organized hierarchically (Raus & Pourtois, 2013). That is, we would use our learned models to predict upcoming congruent stimuli (top-down processing), whereas we would use the stimuli themselves (when incongruent with our models) to modify our predictions and update our models (bottom-up processing) (Rao & Ballard, 1999). In other words, model-congruent stimuli would be processed in a top-down modality, whereas model-incongruent stimuli would be processes in a bottom-up one.

In the study of Lutz et al. (2018), subjects were tested before and after a retention period consisting of either a night of undisturbed sleep or a period of wake consisting of controlled, non-strenuous and non-learning routine activities (between group design: sleep vs. wake). In order to generate internal models, participants were trained on a 12-item implicit deterministic sequence of visual stimuli. Stimuli were grayscale Gabor gratings sequentially appearing at six peripheral locations on a computer screen, tilted either at an angle of 45° or 135° from a central fixation point. Participants had to indicate the position of each stimulus pressing the appropriate button on a keyboard. Thirty minutes after the training phase, participants completed the pre-retention test. In the test phase sequences, stimuli deviating from the original learned sequence were introduced. Specifically, in the test phase, sequences contained standard (congruent with the original sequence), deviant (incongruent from the original sequence) and "follower standard" stimuli, i.e., a standard stimulus which comes right after a deviant one which is supposed to elicit a behavior more likely similar to deviant than standard stimuli. The same sequences were then retested after the retention period, consisting of either sleep or wake. Importantly, to test the effects if sleep on the abstraction of internal models and their use across different temporal contexts, the authors manipulated the response-to-stimulus intervals (i.e., the delay between when a subject made a response and when the next stimulus was presented) between pre- and post-retention assessment (e.g. long response-to-stimulus intervals in pre-phase and short response-to-stimulus intervals in post-phase).

The authors reasoned that if sleep supports the consolidation of an internal implicit sequence model, then subjects tested after a period of sleep should show increased error rates for deviant stimuli, compared with subjects tested after wakefulness, because their predictive model is more consolidated and their sequence learning is stronger. In other words, if the sequence is well consolidated in an internal model, participants should make an error whenever the present sequence deviates from the standard. Moreover, because a consolidated predictive model should allow one to restore behavior as soon as the environment again reveals as predicted and produce appropriate motor responses, a more consolidated internal sequence model should be also reflected in reduced error rates for follower standard stimuli Lutz et al. (2018).

Consistent with these hypotheses, in the post-retention assessment, the sleep group showed higher error rates for deviant stimuli than the awake group. Moreover, the sleep group showed a greater increase in the prediction strength index (i.e., error rates for deviant stimuli minus error rates for follower-standard stimuli) from pre-to-post retention compared with the awake group. Error rates for follower-standard stimuli were comparable to standard stimuli in the post-sleep group, whereas in the awake group, error rates for follower-standard items were than for standard stimuli. Finally, when response-to-stimulus intervals varied from pre- to -post retention assessment, the prediction strength was increased after sleep but not after wake, reflecting the positive effect of sleep on the abstraction of internal model that can be used in different temporal contexts.

This study showed that the sleeping brain is able to update internal models based on information acquired during wakefulness in order to better predict the external situations during the next waking period. However, how the sleeping brain updates internal models remains unclear. According to Honey et al. (2017), internal models are shaped by a continuous switching between externally and internally biased processing modes. In the externally biased mode, input from the environment shapes the ongoing neural activity in a button-up fashion, whereas in the internally biased mode neural activity reflects a top-down process that guides the perception and prediction of the external world. In this framework, the wake-sleep alternation is considered one of the switching situations between internal and external modes. Moreover, even within sleep, Honey et al. (2017) propose another switching mechanism: during non-rapid eye movement sleep (NREM), the sleeping brain processes external-like input via hippocampal replay (Ólafsdóttir, Bush, & Barry, 2018), whereas during rapid eye movement sleep (REM), which is characterized by an increased long-range cortico-cortical effective connectivity (Massimini et al., 2010) and by a high cholinergic tone (Hasselmo & McGaughy, 2004), the brain switches to an internally biased mode, promoting memory integration and model updating. Thus, this within-sleep switching mechanism may promote the consolidation of newly acquired external information during NREM and their integration into pre-existing models during REM sleep. These models are then used during wakefulness to interact with the external world and can be updated during the following sleeping period.

The hypothesis that internal-model updating mainly (but not exclusively) occurs during REM sleep has been also suggested by theoretical work (Llewellyn, 2016). In this work, Llewellyn also proposed a distinction between predictive and prospecting coding. Predictive coding refers to the anticipation of upcoming input during wake based on a specific ongoing event, whereas prospective coding creates offline probabilistic patterns (i.e., schema of plausible sequences of events created during sleep or resting periods) based on past events. According to Llewellyn (2016), during REM the sleeping brain scans memories in order to find meaningful regularities between events and uses these regularities to create associations between the events. These associations generate prospective codes that can be used during wakefulness as a predictive as well as a perceptual/attentional codes to prepare and adapt our behaviors to constantly changing external events.

These theoretical models concerning how sleep influences the updating of internal models fit well with the findings by Lutz et al. (2018). However, Lutz et al. (2018) monitored sleep between testing session via actigraphy, which cannot provide information about sleep architecture (e.g., time spent in NREM and REM) or on the neural dynamics during sleep. Future studies, building on the work of Lutz et al. (2018) should test the specific roles of REM sleep and neural activity during sleep in influencing prospective/predictive coding.

In summary, the study by Lutz et al. (2018) provides evidence for a role of sleep in reinforcing the consolidation and abstraction of an internal sequence model. Which specific sleep stages facilitate these processes is yet to be clarified. Traditionally, REM sleep has been recognized as a key physiological state supporting the consolidation of implicit memories (Whitehurst, Cellini, McDevitt, Duggan, & Mednick, 2016). However, it is likely that both NREM and REM sleep interact to consolidate the regularities present in the environment and to use this information to update internal cognitive models. This idea prompts several questions: What is the impact of sleep disruption on the updating of internal models? In particular, what are the consequences for clinical populations characterized by abnormal REM sleep, such as narcolepsy or depression (Pillai, Kalmbach, & Ciesla, 2011)? Moreover, given that the quantity of NREM and REM sleep varies across the human lifespan (Ohayon, Carskadon, Guilleminault, & Vitiello, 2004), what are the consequences of age-dependent sleep changes on the updating of internal models? Further studies, combining behavioral, neurophysiological, and computational approaches, should address these questions to shed light on how our brains create and modify internal cognitive models.

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