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GUEST EDITORIAL

Sleep to make more of your memories: Decoding hidden rules from encoded information

Does memory processing during sleep enhance the abstraction of regularities?

Research of the last decades has established the central role sleep plays for the consolidation and formation of long-term memory [1]. But the story does not end with mere stabilization of representations. In memory research, consolidation is thought of as a process that transforms a labile memory representation into a more stabile representation, whereby the memory representation is reorganized and also undergoes qualitative changes [2,3]. During consolidation of an experienced episode, details of this episode may be forgotten and only the core information may enter long-term storage sites, where this information is integrated with pre-existing knowledge. It is a long-held view that this consolidation process eventually leads to the formation of abstracted and general memories, that only represent the "gist" of the experiences, which amongst others includes the regularities and rules, and the common semantic information inherent to the many episodes encountered during everyday life [4]. It is the outcome of such active consolidation and transformation of memory that is considered to eventually enable higher-cognitive capabilities underlying the formation of cognitive schemas, problem-solving, the gain of insight and creativity [5]. Testing for the respective qualitative changes in memory goes beyond simply testing recall of an exact copy of the information initially encoded – like in tests of learned vocabulary – but, it typically requires more complex task paradigms where the recall test targets precisely the information that is thought to be abstracted during the consolidation process, for example, the "hidden regularities" in the task materials. Given that sleep consolidates memory, the central question is: does sleep, in this process, also enhance the abstraction of rules and regularities from encoded information? In their review article "Sleep and the Extraction of Hidden Regularities: A Systematic Review and the Importance of Temporal Rules", Itamar Lerner and Mark Gluck provide a profound psychological analysis of the diverse findings on this issue in humans [6].

Why is this question so important? Because it targets a basic problem of memory. Our brain has principally limited capacities to store information. By extracting rules and generalized knowledge, the amount of information that resides in long-term memory can be effectively reduced. Considering the vast uptake of information on a daily basis, to abstract gist information that is selectively stored for the long-term during sleep, represents a highly adaptive process that is integral to healthy brain functioning, as it optimizes the use of limited neuronal resources. Simultaneously, such generalized knowledge is more easily accessible and can be more flexibly used in different contexts. At the neuronal level, the abstraction of gist information during sleep is a process most closely linked to the "dual function" of sleep, i.e., to globally downscale synapses involved in the representation of irrelevant information, but to spare from this process of downscaling, and to even upscale synapse ensembles contributing to relevant "gist" memories. Indeed, this dual function of sleep is the central theme of two widely accepted theories about the cognitive function of sleep, the "synaptic homeostasis hypothesis" (SHY) and the "active systems consolidation" concept [3,7,8].

The first and foremost answer Lerner and Gluck give to the central question of their review is: yes, sleep does enhance the abstraction of hidden rules and regularities from previously encoded information. In times of a replication crisis that has gripped psychology, this is a most important result. The majority of the reviewed studies observed some kind of improvement in the detection of regularities when sleep had followed encoding of the task materials compared with a wake control condition where the participants remained awake during the respective post-encoding interval. The review provides no study example showing the opposite, that post-encoding wake enhances this capability, which would be expected on statistical grounds in the case of an overall null effect.

Nevertheless, there is a substantial number of studies that failed to find a sleep-dependent enhancement in the extraction of regularities. It is the merit of Lerner and Gluck's review to identify specific psychological conditions that favor regularity extraction processes during subsequent sleep: the *temporality* of the regularity and the *explicitness* in recognizing the regularity. That is, sleep appears to support that participants gain an explicit, i.e., conscious, knowledge of a regularity hidden in the stimulus materials when the regularity is of a temporal rather than stationary nature.

What is a temporal regularity? Temporal regularities refer to a predictable sequential order in the stimulus material (i.e., "*event A at time t predicts a later event B*" [6]), and have been mostly investigated using different versions of the serial reaction time task (SRTT). In the classical SRTT, naïve participants respond as fast and as accurately as possible by pressing one of several buttons, with each button corresponding to a different spatial position of the presented stimulus [9]. Unbeknownst to the participant, the order in which the stimuli are presented is not random but follows a repeating sequential pattern. The gradual abstraction of this regular sequential pattern is associated with faster responses and less errors over time – such effects being considered "implicit" – but

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can also lead to the explicit recognition of the sequence rule, in which case the participant is able to verbally report this sequence. Sleep is well-known to enhance abstraction of this sequence knowledge, and participants after sleep can also easier apply this sequence knowledge in other contexts (e.g., [10]). By contrast, stationary regularities refer to commonalities in the stimulus materials that are present independently of any temporal order in which it may be presented. An often-used example are object categorization tasks that require the participant to classify unknown objects into different categories according to certain features which, in this case, represent the hidden rules. To explain why sleep selectively enhances the explicit detection of temporal rules, as opposed to stationary rules, Lerner and Gluck propose the "Temporal Scaffolding Hypothesis" which refers to the fact that neuronal replay of temporal sequences during sleep occurs at a much faster rate than the sequence occurred in real time at encoding. This increases the likelihood that cell ensembles representing the elements of the sequence jointly fire within a time window allowing for Hebbian plasticity whereby the association between the respective sequence elements is synaptically strengthened.

Temporal versus stationary regularity

With the "Temporal Scaffolding Hypothesis" Lerner and Gluck indeed offer a very compelling explanation of how sleep, at the neuronal level, might promote the abstraction of temporal regularities, stimulating not only future research but also some conceptual considerations, the first concerning the distinction between temporal and stationary regularities. Lerner and Gluck's hypothesis well concurs with active systems consolidation concepts putting the hippocampal neuronal replay of newly encoded memories at the core of the sleep-dependent consolidation process [3,4,11]. However, in focusing on temporal sequence replay, these concepts are altogether challenged by recent studies suggesting that strict temporal sequentiality of replay in hippocampal networks may not be a prerequisite for the enhancing effect of sleep on memory (e.g., [12–14]). On the other side, tasks with "stationary" rules can also include relevant temporal aspects. For example, in object categorization tasks the participant typically learns to classify the objects based on similarities among the objects, with the objects sequentially presented over more or less extended time intervals. One might expect that the abstraction of stationary invariants in such tasks (with sequential presentation of more or less similar objects) likewise profits from a time-compressed neuronal replay that brings more closely together in time the features that are common to the objects of a specific category.

Indeed, sleep can have a profound enhancing effect on category learning. For example, infants appeared to learn object categories (such that they were able to correctly categorize novel objects never seen before) only when they had napped after a first learning session but not, when they remained awake after this learning session, and this ability was strongly associated with NonREM sleep spindle activity during the nap [15]. Using a modified Deese-Roediger-McDermott (DRM) task that was based on visual shapes to minimize influences of prior knowledge, we found a distinct benefiting effect of post-encoding sleep on the abstraction of the gist shapes that occurred only at a recall test one year later, which underlines the slow nature of these abstraction processes [16]. In fact, the review by Lerner and Gluck confirms that 15 of 22 studies employing tasks with a stationary rule found some enhancing effect of sleep which is closely comparable to the rate of 31 out of 45 studies revealing a sleep effect on detection of a temporal rule. However, these rates of sleep effects are similar only when both explicit and implicit measures of rule detection are considered. (In only 1 of 9 studies sleep facilitated the explicit detection of a stationary regularity.)

Explicit versus implicit detection of regularities

Thus, the concept of explicitness vs implicitness appears to be key to understanding how effects of sleep on the abstraction of regularities express themselves. There are two basically different views on this concept: one assumes that explicit and implicit measures of retrieval represent different paths of access to one and the same memory, the other links explicit and implicit recall to separate memory traces. For example, based on the assumption that implicit and explicit recall taps into the same memory, research in infants who are not able to give an explicit verbal report, commonly relies on implicit measures of memory, with no differences expected if there were explicit memory measures available. However, one of the very few studies comparing the effects of sleep on memory between explicit (verbal report) and implicit recall measures (eye fixations) revealed only moderate correlations between these measures, explaining about 32% of the variance [17]. Likewise, there was no correlation between the effects of sleep on implicit and explicit measures of sequence knowledge in an SRTT [10]. This suggests that explicit and implicit recall refers to – at least partially – differing traces of the memory that might be formed in separate memory systems with different underlying brain structures [18]. These systems interact, and it has been proposed that sleep enhances the co-operation between these systems [11,19]. Against the backdrop of Lerner and Gluck's review, the fascinating question arises, how these systems interact during sleep-consolidation to support the abstraction of regularities.

Strengthening simple associations versus higher-cognitive processing

Finally, in their review Lerner and Gluck ask whether sleep by enhancing the detection of hidden regularities, promotes a high-level cognitive learning process. Alternatively, sleep might facilitate simple associative processes by strengthening synaptic connectivity in local ensembles, which would be used to achieve complex learning during succeeding wakefulness, e.g., while performing the retest. This is a fundamental question inasmuch the assumption of sleep merely strengthening simple associations challenges active systems consolidation accounts which assume that consolidation during sleep induces a reorganization and transformation of the memory representation, and that only such transformation eventually enables the abstraction of regularities [8]. Computational work has shown that strengthening of simple associations suffices to explain the sleep effect, at least, on the implicit detection of regularities [6,20]. On the other side, using for example fMRI, experimental studies have demonstrated that sleep does reorganize newly encoded representations, leading to a stronger cortical representation of the memory in particular involving the prefrontal cortex [21–23].

Altogether, Lerner and Gluck present an exciting review about a function of sleep – to abstract hidden regularities from newly encoded memories – that is clearly more important than that of simply "consolidating" memories in the word's strict sense. Temporality of rules and explicitness of their detection are key features in this process to be further researched. Yet, the main challenge of future research remains to determine how memory processing during sleep makes possible the complexity of human higher-cognitive processing during wakefulness.

Conflicts of interest

The authors do not have any conflicts of interest to disclose.

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