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Examining sleep's role in memory generalization and specificity through the lens of targeted memory reactivation

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Two vital memory functions — remembering specific experiences and generalizing across many experiences — are in tension with each other. In the complementary-learning-systems model, the hippocampus allows for fast learning of unique episodic memories while the cortex slowly extracts regularities from overlapping representations. Whereas episodic memories undergo consolidation over protracted time periods, many questions remain about how memory generalization evolves over time. Sleep's role in consolidating individual memories has been convincingly demonstrated using targeted memory reactivation, a method whereby memories can be selectively strengthened through the unobtrusive presentation of learning-related stimuli during sleep. In this review, we argue that targeted memory reactivation can help advance understanding of memory transformation and the contrast between specificity and generalization.

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Introduction

Declarative memory encompasses the ability to remember specific experiences and to generalize across multiple experiences (i.e. event and fact learning). For example, if you went to an aquarium you would spot an unusually shaped ocean sunfish and commit its specific, unique features to memory. Yet, perhaps you have seen many kinds of sea creatures while scuba diving, so the sunfish could strike you as similar, but not quite identical, to a filefish. A complementary-learning-systems orientation [1,2] would posit that the hippocampus quickly encodes individual memories (a specific sighting of a unique sea creature) whereas the cortex slowly extracts regularities from overlapping representations (generalizing based on cumulative experiences with many sea creatures). Does sleep similarly impact these two memory functions, or are specificity and memory generalization afforded special and distinct processing during sleep?

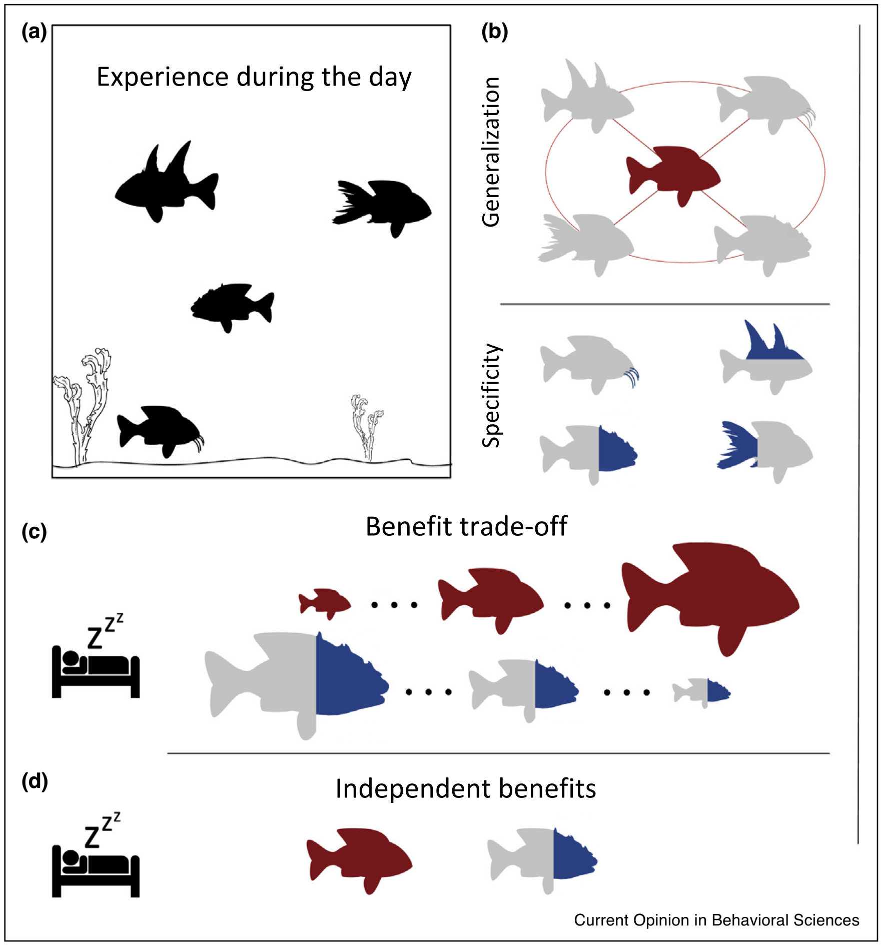
Memory consolidation refers to the process of stabilizing and integrating memories within the brain. Consolidation may largely depend on the reactivation of previously acquired memories [3]. Although memory reactivation can occur during wake or sleep, the unique circumstances of sleep may be advantageous in allowing reactivation to occur with minimal competition from other information processing. Additionally, some researchers argue that sleep provides an opportunity for communication between the hippocampus and the neocortex to allow for decontextualization in conjunction with a transfer of information to extrahippocampal regions [4]. Generalization could be considered a consequence of transformation whereby memories become less hippocampal-dependent and rely more on distributed traces across the neocortex. Others argue that the reactivation of overlapping memories during sleep strengthens the shared features and leads to generalization [5].

Considering the current models of sleep's role in memory, it is unclear if detailed memory representations are in direct conflict with generalized gist representations or whether the two coexist (Figure 1). Strengthening of overlapping memory traces may result in a loss of unique detailed features. Alternatively, generalization and memory for specifics could coexist such that shared features across representations are strengthened to create a new network without losing unique features of episodic memories.

Sleep's impact on declarative memory for specifics

Sleep's protective role against forgetting has been recognized as far back as the 1920s [6], but this idea did not catch on quickly in memory research. Recent emphasis on the period of sleep known as slow-wave sleep (SWS) coincided with a surge of interest in this topic [7]. A landmark observation was that rodent hippocampal place cells display firing patterns during sleep that recapitulate

Figure 1



Memory consolidation for specific details and generalization over sleep. This diagram provides a schematic illustration of how memory consolidation may occur over sleep. **(a)** In this example, a person sees a set of different fish. **(b)** Memory of the experience evolves over time in two ways. In generalization (top), shared features among the fish contribute to a gist representation or abstracted prototype (represented in red). Memory for unique features of each fish (represented in blue) may also be consolidated to support specific remembering (bottom). Generalization and specificity may both be influenced by memory consolidation during sleep. **(c)** One hypothesis is that memory consolidation could help generalization over sleep (schematized as increasing size of red prototype), at the cost of memory for specifics (schematized as decreasing size of blue specifics), or *vice-versa*. **(d)** Alternatively, sleep consolidation could preserve memory for specifics and generalized memories independently of each other.

those in previous wake exploration [8,9]. In particular, replay in the rodent hippocampus was shown to be temporally coordinated with memory reactivation in the visual cortex during SWS [10].

Research into human memory also supports the idea that sleep, and SWS in particular, is important for memory for specifics. This form of memory can be considered in relation to the neural process of pattern separation, whereby memory representations can be distinctive when they overlap minimally with each other [11]. Distinct representations allow for the successful retrieval of specific details and discriminating between similar representations in the face of potential interference. To study pattern separation, many researchers employ the mnemonic-similarity task, in which participants are first exposed to a series of objects and categorize them as either indoor or outdoor objects, followed by a recognition test with novel objects, old objects, and highly similar objects [12,13,14•,15]. Accurate recognition of old objects with low false-alarm rates, particularly for the highly similar objects, is indicative of high memory specificity, due presumably to effective pattern separation. Using such a task, researchers compared a 12-hour delay including either sleep or wake [13]. They found that sleep preserved memory specificity more than when participants remained awake.

These findings were corroborated by results from another study with a 9-hour retention interval during the day or overnight with electroencephalographic (EEG) monitoring [14•]. Hanert *et al.* found that high specificity in recognition was positively correlated with two sleep physiology signals, slow oscillations (0.5–1 Hz) and sleep spindles. Sleep spindles are rapid bursts of neural activity at 11–16 Hz, which can be observed during SWS [16,17] and are correlated with improved performance on declarative memory tasks [18–20]. These electrophysiological findings were taken as evidence for sleeps' ability to improve hippocampal representations and enhance performance on highly specific memory tasks.

Memory generalization during sleep

There are many ways to study the process of generalization [21]. For example, investigators have used procedures in which participants gradually learned to extract relationships among various abstract stimuli, to solve a puzzle based on repeated mathematical procedures, to produce a word that fits multiple constraints, or various other language tasks.

In a 2007 experiment, Ellenbogen *et al.* presented participants with pairs of abstract images that fit into a complex hierarchical structure, followed by a memory test with new pairs [22]. Relational knowledge was assessed by determining whether participants inferred $A > C$ (where '$>$' means 'should be selected over') after learning of $A > B$ and $B > C$, with no prior exposure to the A/C pair. This generalized knowledge for the underlying structure of stimuli (also known as transitive inference) was stronger after a period of sleep compared to a period of being awake. However, measures of sleep or sleep-stage were not available, so it was unclear which aspects of sleep may have improved generalization.

A more recent study tested how sleep could improve insight for a hidden rule [23]. The researchers used the number-reduction task, which can be solved either by a sequence of simple math operations or by using a faster, hidden rule. The study replicated an earlier finding [24] that those who slept were more likely to discover the rule. Also, beta power (17–25 Hz) predicted which participants would discover the rule, but only during SWS.

Although this study implicates SWS in memory generalization, in other relevant studies SWS has not consistently been the most important sleep stage. Rapid eye movement (REM) sleep, which tends to be more prevalent in the second half of the night, has been associated with integrating unassociated information for creative problem solving [25]. Using the remote-associates task, where participants see three cue words and must identify a fourth word linked with all three (i.e. crab, pie, and pine are all linked by apple), researchers compared wake participants with sleep groups that either did or did not enter REM sleep during an afternoon nap [26]. Only the REM sleep group improved on the task by integrating unassociated information to find solutions. Although the authors concluded that REM sleep is important for integration, there may have been confounding factors that led some subjects to have more REM. Also, other studies have not always found REM sleep correlated with problem solving [27]. In fact, a recent experiment using magic tricks and classic insight problems found no effect of sleep on problem solving at all [28].

Contrasting specificity and generalization during sleep

The experiments described thus far examined either memory for specifics or generalization. It could be advantageous to analyze both types of memory in tandem. This tactic was utilized in a study where learning of Chinese characters was followed by a 90-min afternoon nap or wake period [29]. Recalling the meaning of studied characters was relatively worse after a delay with sleep compared to wake, but generalization was improved, operationalized in this study as the ability to recognize common symbols shared across characters (i.e. the symbol for woman is included in the characters for maid, princess, and nurse).

In another study also supporting the idea that sleep is preferentially beneficial for generalization [30••], participants viewed artificial images composed of shared features (defining categories) and unique features (identifiers for individuals). Sleep was associated with relatively better memory only for the former.

Researchers have also tested 15-month-olds' generalization abilities through exposure to triplets of spoken words in an artificial language with hidden dependencies between the first and final words [31]. Infants either napped or stayed awake for a 4-hour delay before a subsequent test. Whereas memory for the previously heard strings was evident in the wake group, an ability to abstract the grammatical relation and apply it to new strings of nonsense words was significant only in the sleep group. Together, these studies indicate that even a short period of sleep may preferentially influence generalized memory over memory for specifics.

In another study comparing sleep and wake groups across a 12-hour delay, participants completed a dot-pattern-classification task, where they categorized constellation-like images [32]. Researchers found that overnight sleep improved categorization of new stimuli but had no effect on recognition of old stimuli.

In a longer-delay study that tested generalization in a visual-categorization paradigm, researchers tested participants after a 10-hour period containing sleep or wake, and then again 1 year later [33•]. Participants who slept after learning were relatively better at recognition specificity at the 10-hour delay, but there was no difference between the groups on generalization. However, after a year delay, only the sleep group showed gist knowledge in their categorization performance, even though specific items were not remembered in either group.

A reasonable inference based on this evidence is that generalized memory and memory for specific details can be in competition with each other, with sleep enhancing memory generalization but not specific memories. However, this hypothesis is challenged by numerous studies showing that sleep improves memory for specifics [e.g. 13,34]. There are at least three possible explanations for this apparent conflict. First, the experimental designs above may have emphasized general features to the detriment of specifics during learning. Second, perhaps these paradigms lacked sufficient sensitivity to specificity effects. Finally, maybe both memory types benefit from sleep, depending on different sleep stages or sleep physiology.

All the above studies compared memory following wake versus sleep, sometimes emphasizing different sleep stages. However, these sleep and wake conditions vary in many ways, including alertness, degree of interference, and circadian factors. Accordingly, results from sleep-versus-wake designs are subject to interpretive limitations such that sleep's role in promoting memory generalization and specificity has remained equivocal. However, alternative experimental strategies that avoid these shortcomings could be employed.

Future prospects using targeted memory reactivation

Memory reactivation during sleep can be biased using targeted memory reactivation (TMR), an experimental tool that allows researchers to direct reactivation for specific items during sleep. The procedure typically starts with a learning session including one or more special stimuli that are linked with aspects of learning. The same stimuli can then be presented during sleep — carefully to avoid producing arousal — in an attempt to reactivate memories [35,36]. A recent meta-analysis of the TMR literature to date demonstrated that such cues were effective during SWS and stage-2 sleep [37].

Many early studies using TMR focused on spatial memory where individual items are associated with cues and a specific location on a grid [38,39]. These designs are particularly powerful for detecting small, specific changes between cued and noncued items, as measured by error between an item's studied location and the location recalled by the participant at test. TMR has been applied to investigate memory consolidation for a broad array of memory types [e.g. 40–42]. Though most studies using TMR have focused on its impact on the specific aspects of remembering, TMR offers advantages for investigating sleep's role in both memory generalization and specificity. Relying on within-subject comparisons between cued and noncued information, for example, avoids confounds with differential alertness, time of day, demand characteristics, and potential interference from waking experience. Although some evidence suggests that TMR-induced consolidation may differ in some respects from spontaneous reactivation [e.g. 43], it remains a useful tool for understanding memory transformation over sleep.

One recent TMR experiment explored sleep's contribution to generalization by using lexical competition between words and nonwords [44•]. The researchers hypothesized that cueing during sleep would lead to better lexical integration of artificial words. Results showed no direct effect of TMR. However, for cued words, REM sleep was correlated with better integration of new information within existing knowledge. That is, participants took longer to make judgments for stimuli confusable with cued relative to the noncued words when they spent more time in REM sleep, indicating that TMR facilitated the extent to which words were embedded in the lexicon. While touching on generalization, this study does not reveal what aspect of generalization leads to competition nor does it test for specificity.

Rather than focusing on competition between specific words, researchers in another study used TMR to test grammatical rule abstraction [45]. Participants learned grammatical rules through a language task and then participated in a second, unrelated task. During an afternoon nap, participants were cued for either the grammar task or the unrelated task, and those who were exposed to the language phrases during sleep showed a relative gain in grammar learning. Whereas these findings reinforce the notion that memory reactivation can impact generalization, the performance criteria at learning were such that it was not straightforward to assess memory for specific phrases at test.

Insofar as sleep's role in the consolidation process for specific episodic memories and gist is not well understood, manipulating reactivation via TMR provides a suitable tool for seeking answers to these questions. Future TMR experiments should be designed with a variety of learning materials and procedures to test both integrated knowledge as well as specifics of the items studied. Ideally, these two features can be examined in parallel such that researchers can identify if they rely on different processes or represent a trade-off whereby specificity declines as generalized knowledge is gained (or *vice-versa*).

For example, analogical problem solving could be used to put generalization and memory specificity in opposition [46]. Participants could attempt to solve a series of word problems with distinct features, half of which would be cued during sleep. Upon waking, participants would attempt to solve an analogous problem with different details, testing both for problem solving (generalization of the underlying structure) and details of the specific problems.

Additionally, better understanding of how TMR cues bias consolidation during sleep and whether reactivation is specific to the item or applies to a general context will improve experimental design for all studies going forward [47]. Harnessing TMR to causally affect memory consolidation may prove crucial in teasing apart hypotheses regarding sleep's role in generalization and the possible trade-off between generalized and specific memories. We might discover that different sleep-physiology signals relate to how brain networks are engaged to preferentially yield either generalization or maintenance of details. Further studies might find that sleep promotes generalization at the expense of memory for specifics. Alternately, as schematized in Figure 1, sleep may both promote the integration of specific memories into broader schemas while also protecting the specific of those memories. Experimental approaches that take into account the dual role of consolidation in facilitating memory for specifics as well as generalization are crucial to improving our understanding of sleep's role in memory.

Conflict of interest statement

Nothing declared.

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- •• of outstanding interest

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