

A complementary learning systems model of how sleep moderates retrieval practice effects

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Abstract:

While many theories assume that sleep is critical in stabilizing and strengthening memories, our recent behavioral study (Liu & Ranganath, 2021) suggests that sleep does not simply stabilize memories. Instead, it plays a more complex role, integrating information across two temporally distinct learning episodes. In the current study, we simulated the results of Liu and Ranganath (2021) using our biologically plausible computational model, TEACH, developed based on the complementary learning systems (CLS) framework. Our model suggests that when memories are activated during sleep, the reduced influence of temporal context establishes connections across temporally-separated events through mutually training between the hippocampus and neocortex. In addition to providing a compelling mechanistic explanation for the selective effect of sleep, this model offers new examples of the diverse ways in which the cortex and hippocampus can interact during learning.

Introduction

In the field of learning and memory, many theories assume that sleep plays a critical role in stabilizing or strengthening memories for events, such that they are resistant to interference. More detailed theories, such as the “Active Systems Consolidation” theory, propose that neural representations of recent events are spontaneously activated (i.e., “sleep replay”) during slow-wave sleep (SWS), thereby strengthening these representations and improving retention (Diekelmann & Born, 2010; Geva-Sagiv & Nir, 2019; Klinzing, Niethard, & Born, 2019; Tamminen, Ralph, & Lewis, 2013; Tamminga, Stan, & Wagner, 2010). However, we also know that repeatedly reactivating memories during wake can enhance the retention of recently learned information, independent of sleep. These findings raise the question of whether sleep confers unique benefits or is simply the same as what happens when we repeatedly access memory while awake (Antony, Ferreira, Norman, & Wimber, 2017)

In this paper, we explore the possibility that sleep does play a special role, enabling the brain to discover connections between events that occurred at different times. Using a biologically-based computational model of cortico-hippocampal interactions, based on the Complementary Learning Systems (CLS) framework (O'Reilly, Bhattacharyya, Howard, & Ketz, 2014), we modeled behavioral results showing that events that are initially learned across longer temporal delays can become integrated during sleep. Our model suggests that when memories are activated during sleep, the reduced influence of temporal context establishes connections across temporally-separated events through mutually training between the hippocampus

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and neocortex. Below, we describe how the model helps to bridge the gap between the effects of sleep on memory and the effects of reactivating memories during wake.

The selective effects of sleep on memory

Although the Active Systems Consolidation theory predicts that memory reactivation during SWS should promote memory consolidation, available evidence does not consistently support the idea. Behavioral effects of sleep-mediated consolidation have been inconsistent across studies and paradigm-dependent (Cordi & Rasch, 2021). For example, some studies showed that sleep could protect associative memories against interference (Ellenbogen, Hulbert, Jiang, & Stickgold, 2009; Ellenbogen, Payne, & Stickgold, 2006), two recent studies failed to replicate this finding (Bailes, Caldwell, Wamsley, & Tucker, 2020; Pöhlchen & Schönauer, 2020).

Rather than strengthening all memories or slowing forgetting, sleep is more likely to have selective effects. For example, some studies have found that sleep improved memory for shared properties of newly learned semantic categories (Schapiro et al., 2017) and facilitated the incorporation of new information into existing semantic knowledge (Tamminen et al., 2013). Other studies suggest that sleep selectively facilitates weakly learned information (e.g., Schapiro, McDevitt, Rogers, Mednick, & Norman, 2018). These findings suggest that SWS does not simply stabilize memories, and instead, it might play a more complex role, reorganizing representations of past experience (Lewis & Durrant, 2011; Singh, Norman, & Schapiro, 2022).

Empirical results that challenge the Active Systems Consolidation theory

It is well established that repeatedly reactivating memories during waking, also known as “retrieval practice,” improves the retention of information that is retrieved. As noted above, active systems consolidation theory proposes that memories are stabilized through sleep replay during SWS. Although the precise mechanisms by which this occurs are not described in detail, in its simplest form, active systems consolidation theory would predict that the effects of sleep on memory should mimic the effects of retrieval practice during waking (Antony et al., 2017). In other words, sleep and retrieval practice might differ in their efficacy but otherwise promote retention in a similar fashion.

Here, we simulate recent evidence that raises an important challenge for theories proposing that memory consolidation is mediated by simple effects of memory reactivation during SWS (Liu & Ranganath, 2021). It is well known that retrieval of a target item during waking states can affect the retention of items that are not retrieved, facilitating retention of items that are well integrated with the target and causing forgetting of items that compete with the target. We recently examined how these “spillover” effects of retrieval practice might interact with sleep-mediated consolidation in three different experiments that varied several factors (Liu & Ranganath, 2021). Specifically, subjects learned scene-word associations, and each scene was associated with two different words (*pairmates*) that were either semantically related or unrelated (Figure 1).

We (Liu & Ranganath, 2021) did not find a global effect of sleep on retention, nor did we find that sleep generally increased or reduced the effects of retrieval practice on unstudied items. For instance, retrieval of one scene-word association always enhanced retention of pairmates studied in the same list context (“temporally-close”). Conversely, retrieval of a target consistently reduced retention of pairmates that were in different lists (“temporally-far”) and unrelated to the retrieved target. Critically, only one of our findings was directly affected by sleep: retrieval practice impaired retention of temporally-far, semantically-related pairs if subjects were unable to sleep during the retention interval, but it facilitated retention of these items if subjects were able to sleep. In other words, sleep reversed the negative effects of retrieval practice, enabling participants to “rescue” memories that might otherwise be lost due to interference.

The results of Liu and Ranganath (2021) are, to some extent, consistent with the “Complementary Learning Systems” (CLS) framework (McClelland, McNaughton, & O’Reilly, 1995; O’Reilly et al., 2014). Ac-

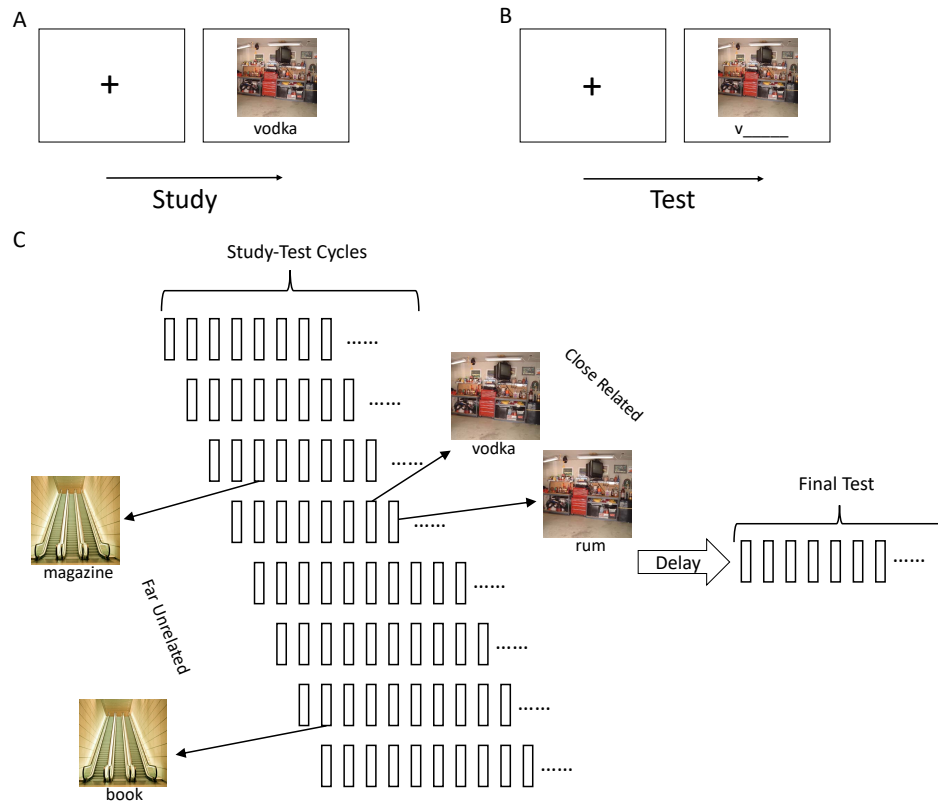


Figure 1: Paradigm and behavioral results of Liu and Ranganath (2021). A. Illustration of Study procedure. B. Illustration of Test procedure during retrieval practice and the final test. C. Illustration of the overall experimental paradigm. The delay was manipulated between-subject as wake vs. sleep.

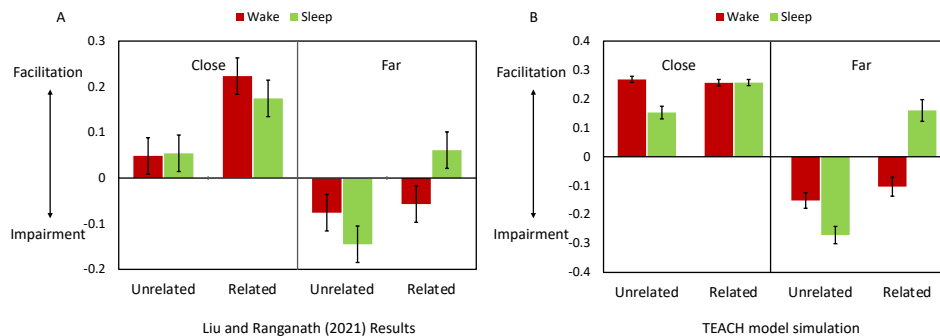


Figure 2: A. Behavioral results of Liu and Ranganath (2021). B. Simulation results of the TEACH model. Graph shows mean final test recall differences between Non-target and Control trials separately as a function of temporal proximity (Close vs Far) and semantic relatedness. Error bars denote 95% confidence intervals.

According to CLS, the hippocampus enables fast learning of specific pieces of information (i.e., episodic-like memory), whereas the neocortex supports slow learning that supports generalization (i.e., semantic memory). In this framework, reactivation of hippocampal representations during sleep enables the hippocampus to “teach” the neocortex such that new information can be incorporated without disrupting pre-existing neocortical representations (McClelland et al., 1995; O’Reilly et al., 2014). This framework fits with Liu and Ranganath’s finding (2021) that sleep uniquely enabled subjects to integrate information across temporally

distinct but related learning episodes. However, in the original framework, like the active systems consolidation hypothesis, consolidation was simply envisioned as an effect of reactivating hippocampal memories. As such, it cannot account for the different effects of retrieval practice during wake and putative reactivation of memories during sleep.

The current model

Here, we sought to gain traction on how sleep-mediated consolidation could produce such a specific effect on memory that was qualitatively different from the effects of awake memory retrieval. We propose a novel extension of the biologically-based CLS model of hippocampal function (O'Reilly et al., 2014), referred to as the TEACH (TEsting Activated Cortico-Hippocampal interaction)

We start with the assumption that underlies active systems consolidation theory: the hippocampus interacts with the neocortex during SWS. Consistent with other theories, the model assumes that, during waking, hippocampal memories are retrieved through a combination of item and temporal context cues and that the hippocampus trains the neocortex during memory retrieval (e.g., Antony et al., 2017; Ferreira, Charest, & Wimber, 2019; Ritvo, Turk-Browne, & Norman, 2019)(see Liu, O'Reilly, & Ranganath, 2021, for a review) During waking retrieval practice, temporal context acts as a barrier, such that reactivation of one memory in the hippocampus will not lead to retrieval of related memories learned in different contexts.

In addition to assuming the hippocampus trains the neocortex, our model incorporates both directions of cortico-hippocampal interactions. Specifically, following recent empirical findings (Rothschild, Eban, & Frank, 2017), the model assumes that, during sleep, the reactivation of associations starts in the neocortex. Because the temporal context is disabled during sleep, semantic connections in the neocortex provide a way in which the cortex effectively trains the hippocampus to learn about these connections. We also assume that recently activated associations, such as those experienced during retrieval practice, are prioritized for replay during sleep. This assumption is based on the empirical finding (Liu & Ranganath, 2021) that retrieval practice of one of the two associations impairs memory for the other association without sleep. However, such impairment switched to facilitation after sleep. This pattern suggests that retrieval practice moderates the effect of sleep on the untested association. We will discuss how this assumption is congruent with the literature in the General Discussion.

In the remainder of the paper, we first present the methods, including a high-level summary of the principles and mechanisms in our computational model, followed by our simulation results of the Liu and Ranganath (2021) data. Then we discuss connections to other related computational and theoretical work and implications for future work, including further testable predictions of our framework.

Methods

Overview of the model

The model simulates both the hippocampal and neocortical systems (Figure 3), and the two learning systems are bidirectionally connected, and we assume that the hippocampal and neocortical systems jointly contribute to memory retrieval, consistent with the CLS framework (O'Reilly et al., 2014). Specifically, retrieval of a specific item can be seen as falling on a continuum, with varying degrees of dependence on the two learning systems depending on the task, item, and other variables.

One essential principle of the CLS framework is that the hippocampus is capable of rapid learning, whereas neocortical areas exhibit slow learning rates, and that cortico-hippocampal interactions can speed up the process of cortical learning, such that new information can be incorporated without disrupting pre-existing representations (McClelland et al., 1995; O'Reilly et al., 2014). These interactions could occur when memories are recalled during the waking state, or when recently learned information is reactivated by

the hippocampus during sleep. This idea is consistent with recent theories (e.g., Antony et al., 2017; Ferreira et al., 2019; Liu et al., 2021; Ritvo et al., 2019) suggesting that online reactivation (such as retrieval) of recently acquired memories in the hippocampus can drive learning in the neocortex. Other recent studies have shown that communication between the hippocampus and neocortex during sleep can be initiated in the neocortex, and there is a cortical-hippocampal-cortical loop of information flow during sleep (Rothschild et al., 2017).

The model was implemented using the Leabra framework (O'Reilly, Hazy, & Herd, 2017; O'Reilly & Rudy, 2000), which supports both cortical and hippocampal systems within one overall model. The hippocampal system has recently been updated with a more complete implementation of error-driven learning mechanisms in areas CA1 and CA3 (Zheng, Liu, Nishiyama, Ranganath, & O'Reilly, 2022), building on earlier work (Ketz, Morkonda, & O'Reilly, 2013).

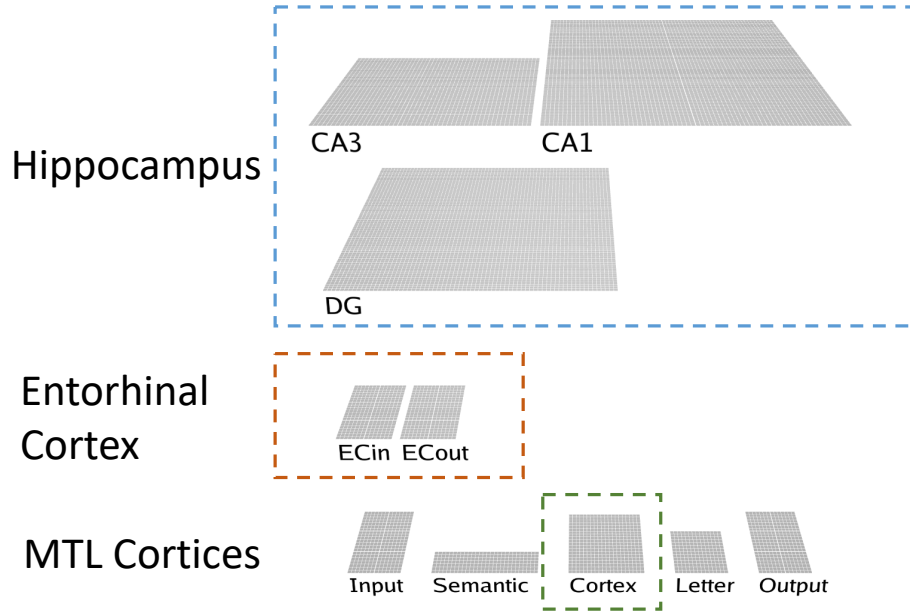


Figure 3: Overview of the TEACH model architecture

Learning in neural networks occurs by modifying synaptic weights between sending and receiving neurons. The Leabra framework is based on the combined contributions of two distinct, widely-used learning rules: Hebbian and error-driven. Hebbian learning posits that synaptic weights are strengthened when they are co-activated (“cells that fire together, wire together”) (Hebb, 1949), and it serves as a kind of heuristic bias toward encoding statistical correlations in the Leabra model. Error-driven learning provides the most important form of learning, by adjusting weights to minimize errors in a network’s performance, as in the widely-used error backpropagation algorithm (Rumelhart, Hinton, & Williams, 1986). Leabra uses a biologically-plausible form of error-driven learning that leverages bidirectional connectivity to communicate error signals in the same way that any other neural activity is communicated, with synaptic learning sensitive to two different phases of activity over time that represent an expectation followed by an outcome or target state (O’Reilly, 1996; O’Reilly & Rudy, 2000).

To directly examine the necessity of the hypotheses, we simulated three alternative models of sleep, namely, the Sleep-PriWeak model, in which non-tested and pairs were prioritized for replay, the Sleep-All model, in which all pairs were equivalently replayed, and the Sleep-AddRP model, in which sleep was equivalent to additional retrieval practice.

The neocortical system

The neocortex supports basic sensory-motor processing and higher-level semantic and association knowledge, captured by the Input, Output, Letter, Semantic, and Cortex layers in our model. We simplify the model by driving the Input and Output layers with fixed patterns of the task events, containing information about scene-word pairs and temporal context (as random vectors). These vectors are represented as six pools of 49 neurons (as a 7x7 matrix). One pool represents the scene cue, two pools represent the two words that are associated with the scene, one pool represents the first letters of the words, which also serve as cues at test, and the remaining two pools represent the temporal context. Each input pattern was constructed by randomly assigning 20% neurons as active and the rest of the neurons as inactive.

The relevant long-term semantic knowledge for spelling and semantic associations of the items used in the study are separately encoded in the Letter and Semantic layers. The Letter layer receives information from the letter pool of the input layer and encodes the orthographic spelling of the words, sending its output to the word pools of the Output and the hippocampal system. The Semantic layer receives information from each of the word pools of the Input layer and encodes semantic representations of the words, sending its output to both word pools of the Output and the hippocampal system. Activation of a word will partially activate semantically related words through the Semantic layer. The Semantic layers are pre-trained before learning the scene-word associations. The contribution of Semantic to the hippocampal system is inhibited by the temporal context input, capturing a hypothesized controlled task-based top-down biasing function of the form typically attributed to the prefrontal cortex (Miller & Cohen, 2001).

We assume that the novel scene-word associations that are established within the context of the task are learned most strongly in the neocortex by the MTL cortical areas surrounding the hippocampal formation, including the perirhinal cortex, which has been implicated in higher-order associative learning of this form (Inhoff & Ranganath, 2017; Ranganath & Ritchey, 2012; Ritchey, Libby, & Ranganath, 2015). In the model, this occurs in the connections from the scene and word pools of the Input layer to the Cortex layer, which then drives corresponding pools of the Output layer that represents the relevant output signal. Biologically, this output signal is likely conveyed by deep layer neurons and their projections, which exist in every neocortical area. The Output layer also receives information from the output of the hippocampus, via its entorhinal cortex output layer. According to the CLS framework, the cortical layers use a slower learning rate and learn more overlapping representations than the hippocampus. Therefore, during initial learning, the difference between the fast-learning hippocampal and slower-learning cortical representations generates error signals that drive learning in these neocortical pathways.

The hippocampal system

The hippocampal system in our model receives cortical inputs into its entorhinal cortex input layer (ECin, representing the superficial layers of EC), which then projects to both the DG and area CA1 in the hippocampus. For simplicity, the ECin just mirrors the same pool structure as the Input layer. The DG layer is larger than ECin and features high levels of inhibition, resulting in only very sparse representations that functionally separate the patterns of highly similar inputs from ECin, which then drive the CA3, which also receives direct ECin projections. Our recent model of error-driven learning in the hippocampus shows how the DG input to CA3 can drive error-driven learning relative to the direct ECin pathway inputs. Consistent with the classic Hebb-Marr model of the hippocampus, the recurrent connections among CA3 neurons support pattern completion, where an activated representation can retrieve its previously learned associations. The CA3 then drives the CA1, which functions as a sparse auto-encoder for all information in the EC input / output pathway, activating any retrieved memory elements onto the Ecout (deep entorhinal layers). The CA1 can learn over the course of a theta cycle via error-driven learning as described in Ketz et al. (2013).

Note that there are two separable hippocampal loops: a *monosynaptic* pathway (containing only a single

synapse within the hippocampus (from ECin \rightarrow CA1 \rightarrow Ecout), and a *trisynaptic* pathway (from ECin \rightarrow DG \rightarrow CA3 \rightarrow CA1 \rightarrow Ecout).

The network size parameters of this model are summarized in Table 1.

Table 1: Parameters for network sizes

Network Layer	Size
Input Pool Size	7x7
Input Number of Pools	2x3
ECin Pool Size	7x7
ECin Number of Pools	2x3
ECout Pool Size	7x7
ECout Number of Pools	2x3
DG Size	70x70
CA3 Size	50x50
CA1 Pool Size	30x35
CA1 Number of Pools	2x3
Letter Size	14x14
Semantic Size	14x14
Cortex Size	20x20

Note. The numbers for pool sizes indicate the number of neurons in each specific pool.

Model training

The main training involved 12 unique scene patterns, with each scene paired with two word patterns or *pairmates*, resulting in 24 scene-word associations and 12 groups of pairmates sharing the same scene. The factorial experimental design incorporated four factors: retrieval practice, temporal distance, semantic relatedness, and sleep. The retrieval practice manipulation resulted in three types of trials: For some of the scene-word associations, one pairmate, the retrieval *target*, was retrieval-practiced after the initial study. We refer to the non-practiced pairmate as a *non-target*. Finally, for *control* associations, neither of the pairmates were practiced.

The temporal distance manipulation focused on the distance between the practiced scene-item association and the unpracticed pairmate. Unpracticed pairmates were either *adjacent* (i.e., the two associations were presented with the same temporal context) and *far* (i.e., the two associations were studied with different temporal contexts). In the far condition, the non-target was always studied in an earlier list than the target to ensure that participants learned both associations before retrieval practice. The semantic relatedness factor was manipulated by whether the Semantic layer was pre-trained, that is, whether activation of one pairmate could also activate the other pairmate. Finally, as described in more detail below, the sleep factor was manipulated by whether the sleep training procedure was given. Training in all the conditions used the same set of 32 associations, and after training and testing of each condition, the model was re-initialized with the same random seeds. We trained the model with 20 independent runs with a new random seed used for each run.

Pre-training

During pre-training of the semantic relationships, each word was presented to the input layer. In the *related* condition, both the same word and the related word used in model training were presented to the ECin layer as the target pattern, to drive error-driven learning of the semantic relationships. In the *unrelated*

condition, the same word and an unused random word pattern were presented to the ECin layer. To ensure strong semantic relationships, pre-training of each word was repeated for 30 times ("epochs").

Initial study

During the initial study phase, the scene-word associations were presented to the input layer in succession. In the *close* condition, the two pairmates associated with one scene were trained next to each other, and all the associations were trained with the same temporal context pattern. In the *far* condition, one pairmate associated with each scene was trained with the first temporal context pattern, and the second pairmates were trained with a different temporal context pattern. During each initial study trial, the correct input pattern from the ECin layer directly drives a corresponding pattern over the EOut layer at the end of the theta cycle, to drive error-driven learning in the hippocampus (Ketz et al., 2013; Zheng et al., 2022).

Retrieval practice

In conditions involving retrieval practice, the initial study phase was followed by the retrieval practice phase, in which half of the associations were tested. During a retrieval practice trial, only the scene was presented to the input layer along with the first letter and the temporal context. The model was supposed to complete the missing target pattern in the EOut layer through the hippocampal learning system and in the CORout layer through the neocortical learning system. Unlike the initial study phase, the correct pattern was not provided to the model, consistent with the behavioral experiment (Liu & Ranganath, 2021) in which no feedback was provided. The EOut pattern served as the target for the CORout layer, and the difference between the two layers created the error signal that trained the neocortical system.

Sleep

In conditions involving sleep, the sleep procedure was simulated after the retrieval practice phase. During sleep, the scene-word associations were presented to the input layer without temporal context. As introduced earlier, the relative weight of Semantic input to ECin was stronger when the temporal context input was shut off. Thus, input words could also activate semantically related words in ECin. Similar to the initial study phase, the ECin pattern drives EOut at the end of the theta cycle, driving error-driven learning. Following the assumption that retrieval practiced associations are prioritized to replay during sleep, after training of all associations, retrieval practiced associations were trained for additional epochs. Different training rules were applied for the alternative models. Specifically, for the Sleep-PriWeak model, associations that were not retrieval practiced received additional training epochs; for the Sleep-All model, all associations were trained for the same number of epochs; for the Sleep-AddRP model, the sleep session was identical to the retrieval practice session.

Model testing

During the final test, weight updating (i.e., learning) was disabled. Only the scene and first letter were presented for each final test trial. The model performance was evaluated by the d' of the output layer, defined as $d' = Z(\text{Hit rate}) - Z(\text{False alarm rate})$, where the hit rate was the proportion of active units in the original target that was also active in the retrieved pattern of the output layer, and the false alarm rate was the proportion of inactive units that were active in the output layer.

Results

Following the behavioral study (Liu & Ranganath, 2021), our primary analyses focused on d' differences between the non-target and control trials on the final test. The behavioral results of accuracy difference between non-target and control trials showed a three-way interaction between Temporal Distance, Semantic

Relatedness, and Sleep. Specifically, retrieval practice facilitated retention of temporally adjacent non-targets and impaired recall of temporally far and unrelated non-targets regardless of sleep, retrieval practice impaired recall of temporally far and related non-targets but retrieval practice facilitated retention of these items after post-learning sleep.

Teach Model Results

Simulations with the TEACH model replicated the entire pattern of results summarized above. Figure 4 shows the results of the model simulation. A 2 (Temporal Distance: adjacent, far) X 2 (Semantic Relatedness) X 2 (Sleep vs. Wake) ANOVA revealed 3-way interactions ($F(1,38)=20.21$, $p<.001$, $\eta_p^2=.35$). To break down this complex pattern of results, planned comparisons were conducted to examine whether retrieval practice facilitated or impaired recall of the non-target trials compared with the control trials in each condition.

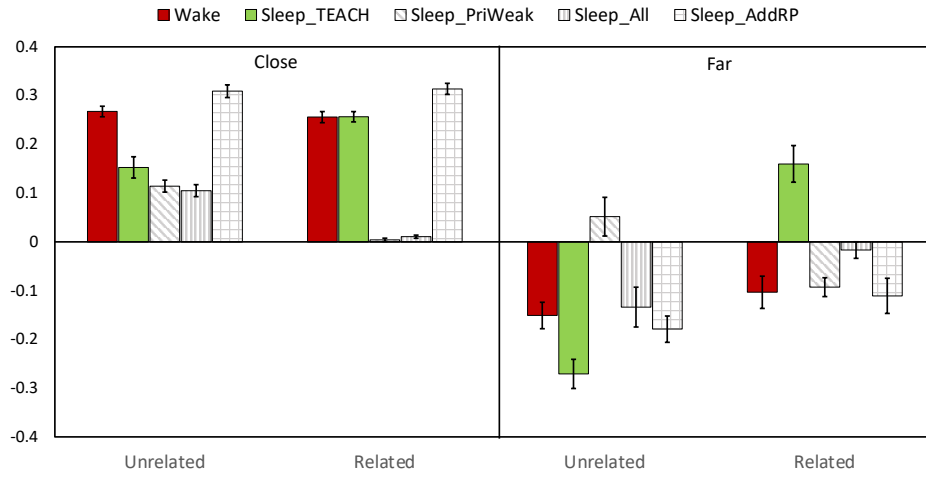


Figure 4: Results of the TEACH and alternative models

Consistent with the behavioral results, regardless of sleep and semantic relatedness, retrieval practice facilitated retention for temporally adjacent non-targets. Specifically, the recall performance for non-targets was significantly better than that for control trials in each of the temporally adjacent conditions (related/sleep: $t(19)=24.21$, $p<.001$, $d=5.41$; unrelated/sleep: $t(19)=6.99$, $p<.001$, $d=1.56$; Related/wake: $t(19)=22.43$, $p<.001$, $d=5.02$; unrelated/wake: $t(19)=24.71$, $p<.001$, $d=5.53$).

Regardless of sleep, retrieval practice impaired recall of temporally far and unrelated non-targets. Specifically, the recall performance for non-targets was significantly better than that for control trials in far and unrelated conditions (sleep: $t(19)=9.05$, $p<.001$, $d=2.02$; wake: $t(19)=5.57$, $p<.001$, $d=1.25$).

Without sleep, retrieval practice impaired recall of temporally far and related non-targets, but retrieval practice facilitated retention of these items after post-learning sleep. Recall performance for non-target was better than that for control trials in the far and related condition with sleep ($t(19)=4.25$, $p<.001$, $d=.95$), but worse than the for control trials without sleep ($t(19)=3.13$, $p=.006$, $d=.70$).

Alternative Model Results

Our next simulations considered the viability of alternative assumptions that might explain the results of Liu and Ranganath (2021). First, we considered the possibility that sleep replay might be qualitatively similar to retrieval practice. To simulate the results under this assumption, we ran a version of the model (Sleep-

AddRP) in which sleep was identical to additional retrieval practice epochs. While the Sleep-AddRP model also showed facilitation effects in temporally adjacent conditions (related: $t(19)=26.90$, $p<.001$, $d=6.01$; unrelated: $t(19)=23.11$, $p<.001$, $d=5.17$) and impairment in the far and unrelated condition ($t(19)=6.46$, $p<.001$, $d=1.45$), different from the behavioral results (Liu et al., 2021), it showed impairment, instead of facilitation in the far and related condition ($t(19)=2.99$, $p=.007$, $d=.67$).

Next, we considered alternative assumptions about the prioritization of specific associations to be replayed during sleep. For example, one possibility is that, rather than prioritizing strongly learned associations, weakly learned associations might be disproportionately reactivated during sleep. Therefore, we ran a version of the model (Sleep-PriWeak) in which associations that were not retrieval practiced (including both non-targets and control trials) received additional training epochs during sleep. Consistent with the TEACH model, the Sleep-PriWeak model showed facilitation in the close and unrelated condition ($t(19)=3.13$, $p=.006$, $d=.70$). However, this model also did not capture the key finding that retrieval practice facilitated far and related non-targets after sleep. Instead, it showed impairment ($t(19)=4.69$, $p<.001$, $d=1.05$). There were no significant effects found in the close and related ($t(19)=1.23$, $p=.23$, $d=.28$) and the far and unrelated ($t(19)=1.29$, $p=.22$, $d=.28$) conditions.

Finally, we considered the possibility that replay is completely random, such that any association might be equally likely to be replayed. In this simulation (Sleep-All), all associations received the same number of training epochs during sleep. Similar with other alternative models, the Sleep-All model did not show facilitation effect in the far and related condition ($t(19)=.97$, $p=.35$, $d=.22$). The results of the other three conditions were consistent with the TEACH model. Specifically, retrieval practice facilitated the recall of non-targets in the in temporally adjacent conditions (related: $t(19)=3.17$, $p=.005$, $d=.71$; unrelated: $t(19)=8.32$, $p<.001$, $d=1.86$) and impaired recall in the far and unrelated condition ($t(19)=3.19$, $p=.005$, $d=.71$).

General Discussion

Substantial evidence suggests that retrieving recently learned information can significantly improve retention of the reactivated information. Although substantial evidence suggests that memories of recent experiences might be reactivated during sleep, the effects of sleep on retention are not equivalent to the effects of retrieval practice (Liu & Ranganath, 2021). Here, we show that a biologically inspired model of cortico-hippocampal interactions can account for the effects of sleep and retrieval practice on integrating semantically related information. This model captures the key results of Liu and Ranganath (2021), which showed that retrieval practice could facilitate the retention of untested semantically related information if subjects had the opportunity to sleep between retrieval practice and the final test, even if the retrieval practice target and non-target were learned across two temporally distinct episodes. It is noteworthy that these results cannot be explained by the idea that sleep is equivalent to retrieval practice, as shown in the Sleep-AddRP model. Instead, our modeling suggests that the reduced influence of temporal context on memory activation during sleep can account for the complex effects of sleep on memory, enabling information learned across different points in time to be integrated in a way that could not happen during retrieval practice.

The role of temporal context during wake

Our modeling of the Liu and Ranganath (2021) task showed that the effects of retrieval practice on untested information during wake were determined by temporal context. In the model, during encoding, the hippocampus bound inputs about picture-word associations with entorhinal cortex (EC) activity patterns that gradually change over time (Howard & Kahana, 2002; Tsao et al., 2018). During retrieval practice, the hippocampus, triggered by the picture cue and list context, could recover the target pattern from the original activity (i.e., "pattern completion," (O'Reilly et al., 2014)). Note that, in the close condition, both

the cue and the list context overlapped between retrieval practice targets and non-targets that subjects were not instructed to retrieve. Our simulations revealed that, because of the overlap in cue and list context information, the hippocampus recovered information about both the target and the non-target from the same list. The hippocampal output of the target and non-target provided a training signal for the neocortex during retrieval practice (Liu et al., 2021). Specifically, learning in our model primarily relied on error-driving learning. When the relevant non-target was retrieved with the target in the hippocampus, the diversity between the more accurate hippocampal representation and the less accurate neocortical created an error signal which trained the neocortical representation and facilitated later recall of both targets and non-targets.

In contrast to the near condition, in the far condition, non-targets were associated with different list contexts. As a result, during retrieval practice, only the target along with irrelevant noise could be recovered. In other words, the list context acted as a barrier that kept memories separated from each other. Thus, the diversity between retrieved irrelevant noise in the hippocampus and the neocortical representation also created an error signal that led to interference in the neocortex.

One of the key insights derived from our simulations is that retrieval-induced facilitation and forgetting can both emerge through changes in the neocortical representation—retrieval practice facilitates neocortical learning of nonpracticed associates from the same context and disrupts representations of nonpracticed associations from different contexts.

Our simulations also provide new insights into the relationship between retrieval-induced forgetting and retrieval-induced facilitation. Specifically, the dynamics of the model in the far condition align with theories that emphasize interference as a factor in retrieval-induced forgetting (e.g., Dodd, Castel, & Roberts, 2006; Jonker, Seli, & MacLeod, 2013; MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003; Perfect et al., 2004; Raaijmakers & Jakab, 2013; Verde, 2012), and theories proposing that integration is a key factor in promoting retrieval induced facilitation (Anderson & McCulloch, 1999; Chan, 2009). In both cases, temporal context determines whether retrieval practice will create interference or facilitate integration.

The role of temporal context during sleep

Our simulations with TEACH also revealed how sleep can mediate the effects of retrieval practice on untested information. As mentioned earlier, during wake, temporal context plays a key role in determining whether retrieval practice will increase competition or facilitate retrieval of non-practiced items. Temporal context acted as a barrier during the wake condition, such that successful retrieval of the target pattern could spread to the non-target sharing the same context, but retrieval did not extend across lists. In contrast, we simulated reactivation during sleep by disabling the temporal context input. This was critical in accounting for the entire pattern of results, such that the impairment caused by retrieval practice switched to facilitation after sleep. When temporal context input was deactivated during sleep, the result was a loss of this temporal context barrier keeping memories separated from each other, which in turn enabled the cortical semantic layer to drive learning in the EC layer. Thus, far-related items benefitted from reactivation during sleep because reactivating a picture-word association could activate the semantically-related word, which was also paired with the picture but encoded with different context input. In contrast, far-unrelated items did not benefit from sleep because input from the semantic layer was not sufficient to reactivate unrelated non-targets.

Our simulations suggest that the deactivation of temporal context input during sleep was critical for accounting for the full pattern of results. We think this assumption is a reasonable assumption for the following reasons: First, temporal context is usually assumed to reflect the outcome of a number of processes that support conscious, goal-directed activity, and context is widely believed to be used to cue recall of studied information (Polyn & Kahana, 2008). Presumably, due to the loss of consciousness, it is unlikely that these processes would contribute to reactivation during sleep. For instance, in our case, participants encoded each pair in the context of a list of learned associations, and during retrieval practice, information

about the list context could be intentionally used to cue retrieval. In contrast, reactivation during sleep is not driven by a current goal or task, and as such, it seems unlikely that context would be used to cue hippocampal reactivation during sleep.

A second factor to consider is that brain activity states fundamentally differ between wake and sleep. For instance, the PFC is engaged during active task performance like memory encoding and retrieval practice, but evidence from multiple studies suggests that the PFC is deactivated during sleep (Hobson & Pace-Schott, 2002). For example, Braun et al. (1997) showed cerebral blood flow in the PFC was reduced during both slow-wave sleep and rapid eye movement sleep. The PFC has been widely implicated as an important source of temporal context that feeds into the hippocampus (Jenkins & Ranganath, 2010, 2016; Polyn & Kahana, 2008; Reeders, Hamm, Allen, & Mattfeld, 2021). Thus, it is reasonable to think that, because PFC is deactivated during sleep, retrieval might be driven more heavily by semantic associations, rather than temporal context.

Bidirectional interactions between the hippocampus and neocortex

Another key principle to emerge from the current model is that the effects of sleep on memory emerge from bidirectional interactions between the hippocampus and neocortex. Our model assumes that, during sleep, reactivation in the neocortex trains the hippocampus with both the directly reactivated target pattern from the input layer and the semantically related non-target pattern generated from the neocortical semantic layer. In other words, reactivation during sleep, enabled the neocortex to train the hippocampus to strengthen links between related pairmates, even if they were not learned in the same context. Pattern completion in the hippocampus, in turn, trained the cortical representation further. Put another way, our model suggests that the neocortex and hippocampus train each other during sleep.

Notably, this assumption diverges from the one-way relationship between hippocampus and neocortex envisioned in the original CLS framework (McClelland et al., 1995). Specifically, McClelland et al. (1995) proposed that the hippocampus “teaches” the neocortex during sleep, and they simulated this effect by comparing the effects of fast learning and slow interleaved learning in connectionist models. Whereas fast learning produced catastrophic interference (see also McCloskey & Cohen, 1989), and slow, interleaved learning allowed the new information to be readily learned without disrupting existing representations, such that the model could pick up the shared structure across most of the learned items.

Our model, in contrast, is based on recent evidence that memory consolidation involves bidirectional interactions between the hippocampus and neocortex. The dialogue between the hippocampus and neocortex may be initiated in the neocortex (Rothschild et al., 2017). In other words, reactivation in the neocortex may precede and trigger reactivation in the hippocampus. For example, prior studies found that reactivation in the visual cortex and auditory cortex preceded reactivation in the hippocampus and demonstrated that cortical reactivation patterns could predict subsequent hippocampal reactivation (Ji & Wilson, 2007).

Retrieval practiced associations are prioritized for reactivation during sleep

Another important factor revealed in our simulations was prioritized reactivation of retrieval practiced associations during sleep. Indeed, the switch from impairment to facilitation after sleep was not shown in the Sleep-Weak and Sleep-All models. We found that, if non-practiced (i.e., weakly learned) associations were prioritized for reactivation or all previously learned associations were equivalently reactivated, the benefit of sleep in retrieval practiced associations was less or equal to control association. Thus the impairment caused by retrieval practice could not be overcome during sleep.

We think that it is reasonable to assume that practiced associations are prioritized for reactivation during sleep, as it would be adaptive to preferentially retain experiences that are salient or important enough to be retrieved fairly often. However, this assumption might seem to be at odds with studies examining interactions

between sleep and retrieval practice effects. For example, Bäuml, Holtermann, and Abel (2014) showed that, without feedback during retrieval practice, sleep produced larger benefits for restudied than retrieval practiced information (see also Antony & Paller, 2018). Thus, the testing effect was reduced after sleep. However, if corrective feedback was provided after retrieval practice, the benefit of sleep was comparable in restudied, and retrieval practiced items, eliminating the modulating role of sleep (Abel et al., 2019). This pattern suggests that the effect of sleep may be explained by the distribution-based bifurcation model of the testing effect (Halamish & Bjork, 2011; Kornell, Bjork, & Garcia, 2011). Specifically, without feedback, retrieval practice strongly strengthens correctly retrieved items while leaving forgotten items unaffected, whereas restudy strengthens all restudied items to the same moderate degree. The strength of forgotten items may be too far from the retrieval threshold and cannot reach the threshold even with sleep. Therefore, on average, the sleep benefit is reduced in the retrieval practice condition. On the contrary, with feedback, the strength of forgotten items is raised above or close to the threshold, enabling these items to benefit from sleep. Therefore, the modulation role of sleep is eliminated.

Future Directions

It is noteworthy that other mechanisms may also potentially account for the integration of related information during sleep. For example, (Singh et al., 2022) simulated the alternation between SWS, during which the hippocampus trained the neocortex with newly acquired memory, and REM sleep, during which the neocortex primarily replayed the consolidated remote memory without influence from the hippocampus. Therefore, it is possible that the replay of semantic connections during REM sleep directly overwrites the impairment of non-targets caused by retrieval practice and leads to facilitation. However, the switch from impairment to facilitation is less likely to be hippocampal-independent and exclusively driven by REM sleep. If so, the model would need to prioritize REM sleep extensively to overcome the interference created by the hippocampus. Future modeling work may incorporate the alternation between SWS and REM sleep. Future neuroimaging work may test whether the integration of related information during sleep involves both the hippocampus and neocortex.

Conclusion

In summary, the current model provides a compelling mechanistic explanation for why we might integrate memories overnight. Moreover, this model offers some interesting new examples of the diverse ways in which the cortex and hippocampus can interact during learning. During retrieval practice, the hippocampus effectively trains the cortex through its ability to pattern complete the associated word and drive activation of that word in the cortex, causing a small but behaviorally significant impact on the cortical connections between the word and the picture (Liu et al., 2021). However, during sleep, the roles are reversed. The semantic connections among the words allow the cortex to train the hippocampus to learn about this connection effectively. This case also suggests that the hippocampus may not always engage in pattern separation to keep memories separate. However, it may also learn systematic connections among different memories, providing a precursor to further slow semantic learning in the cortex, as envisioned in the standard CLS model. Thus, these systems may work together synergistically while still having very different biases in the way they learn overall. Finally, this work provides a novel way of understanding the conditions under which retrieval-induced forgetting vs. retrieval-induced facilitation should be observed (Liu et al., 2021; Liu & Ranganath, 2021), according to the overall dynamics of representational patterns being pushed further apart vs. integrated together.

References

- Abel, M., Haller, V., Köck, H., Pötschke, S., Heib, D., Schabus, M., & Bäuml, K.-H. T. (2019). Sleep reduces the testing effect—But not after corrective feedback and prolonged retention interval. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 45, 272–287. (Place: US Publisher: American Psychological Association) doi: 10.1037/xlm0000576
- Anderson, M. C., & McCulloch, K. C. (1999). Integration as a general boundary condition on retrieval-induced forgetting. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 25, 608–629. (Place: US Publisher: American Psychological Association) doi: 10.1037/0278-7393.25.3.608
- Antony, J. W., Ferreira, C. S., Norman, K. A., & Wimber, M. (2017). Retrieval as a Fast Route to Memory Consolidation. *Trends in Cognitive Sciences*, 21(8), 573–576. Retrieved 2022-10-05, from <https://www.sciencedirect.com/science/article/pii/S1364661317300992> doi: 10.1016/j.tics.2017.05.001
- Antony, J. W., & Paller, K. A. (2018). Retrieval and sleep both counteract the forgetting of spatial information. *Learning & Memory*, 25(6), 258–263. Retrieved 2022-11-18, from <http://learnmem.cshlp.org/content/25/6/258> (Company: Cold Spring Harbor Laboratory Press Distributor: Cold Spring Harbor Laboratory Press Institution: Cold Spring Harbor Laboratory Press Label: Cold Spring Harbor Laboratory Press Publisher: Cold Spring Harbor Lab) doi: 10.1101/lm.046268.117
- Bailes, C., Caldwell, M., Wamsley, E. J., & Tucker, M. A. (2020). Does sleep protect memories against interference? A failure to replicate. *PLoS ONE*, 15(2), e0220419. Retrieved 2022-11-18, from <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7018054/> doi: 10.1371/journal.pone.0220419
- Braun, A. R., Balkin, T. J., Wesenten, N. J., Carson, R. E., Varga, M., Baldwin, P., ... Herscovitch, P. (1997). Regional cerebral blood flow throughout the sleep-wake cycle. An H2(15)O PET study. *Brain: A Journal of Neurology*, 120 (Pt 7), 1173–1197. doi: 10.1093/brain/120.7.1173
- Bäuml, K.-H. T., Holterman, C., & Abel, M. (2014). Sleep can reduce the testing effect: it enhances recall of restudied items but can leave recall of retrieved items unaffected. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 40(6), 1568–1581. doi: 10.1037/xlm0000025
- Chan, J. C. (2009). When does retrieval induce forgetting and when does it induce facilitation? Implications for retrieval inhibition, testing effect, and text processing. *Journal of Memory and Language*, 61(2), 153–170. Retrieved from <http://dx.doi.org/10.1016/j.jml.2009.04.004> (Publisher: Elsevier Inc.) doi: 10.1016/j.jml.2009.04.004
- Cordi, M. J., & Rasch, B. (2021). How robust are sleep-mediated memory benefits? *Current Opinion in Neurobiology*, 67, 1–7. doi: 10.1016/j.conb.2020.06.002
- Diekelmann, S., & Born, J. (2010). The memory function of sleep. *Nature Reviews Neuroscience*, 11(2), 114–126. Retrieved 2022-11-18, from <https://www.nature.com/articles/nrn2762> (Number: 2 Publisher: Nature Publishing Group) doi: 10.1038/nrn2762
- Dodd, M. D., Castel, A. D., & Roberts, K. E. (2006). A strategy disruption component to retrieval-induced forgetting. *Memory & Cognition*, 34(1), 102–111. (Place: US Publisher: Psychonomic Society) doi: 10.3758/BF03193390
- Ellenbogen, J. M., Hulbert, J. C., Jiang, Y., & Stickgold, R. (2009). The sleeping brain's influence on verbal memory: boosting resistance to interference. *PloS One*, 4(1), e4117. doi: 10.1371/journal.pone.0004117
- Ellenbogen, J. M., Payne, J. D., & Stickgold, R. (2006). The role of sleep in declarative memory consolidation: passive, permissive, active or none? *Current Opinion in Neurobiology*, 16(6), 716–722. doi:

10.1016/j.conb.2006.10.006

- Ferreira, C. S., Charest, I., & Wimber, M. (2019). Retrieval aids the creation of a generalised memory trace and strengthens episode-unique information. *NeuroImage*, 201, 115996. doi: 10.1016/j.neuroimage.2019.07.009
- Geva-Sagiv, M., & Nir, Y. (2019). Local Sleep Oscillations: Implications for Memory Consolidation. *Frontiers in Neuroscience*, 13. Retrieved 2022-11-18, from <https://www.frontiersin.org/articles/10.3389/fnins.2019.00813>
- Halamish, V., & Bjork, R. A. (2011). When does testing enhance retention? A distribution-based interpretation of retrieval as a memory modifier. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 37, 801–812. (Place: US Publisher: American Psychological Association) doi: 10.1037/a0023219
- Hebb, D. O. (1949). *The organization of behavior; a neuropsychological theory*. Oxford, England: Wiley. (Pages: xix, 335)
- Hobson, J. A., & Pace-Schott, E. F. (2002). The cognitive neuroscience of sleep: neuronal systems, consciousness and learning. *Nature Reviews. Neuroscience*, 3(9), 679–693. doi: 10.1038/nrn915
- Howard, M. W., & Kahana, M. J. (2002). A distributed representation of temporal context. *Journal of Mathematical Psychology*, 46(3), 269–299. (Place: Netherlands Publisher: Elsevier Science) doi: 10.1006/jmps.2001.1388
- Inhoff, M. C., & Ranganath, C. (2017). Dynamic Cortico-hippocampal Networks Underlying Memory and Cognition: The PMAT Framework. In D. E. Hannula & M. C. Duff (Eds.), *The Hippocampus from Cells to Systems: Structure, Connectivity, and Functional Contributions to Memory and Flexible Cognition* (pp. 559–589). Cham: Springer International Publishing. Retrieved 2021-04-30, from https://doi.org/10.1007/978-3-319-50406-3_18 doi: 10.1007/978-3-319-50406-3_18
- Jenkins, L. J., & Ranganath, C. (2010). Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. *The Journal of Neuroscience*, 30, 15558–15565. (Place: US Publisher: Society for Neuroscience) doi: 10.1523/JNEUROSCI.1337-10.2010
- Jenkins, L. J., & Ranganath, C. (2016). Distinct neural mechanisms for remembering when an event occurred. *Hippocampus*, 26(5), 554–559. doi: 10.1002/hipo.22571
- Ji, D., & Wilson, M. A. (2007). Coordinated memory replay in the visual cortex and hippocampus during sleep. *Nature Neuroscience*, 10(1), 100–107. doi: 10.1038/nn1825
- Jonker, T. R., Seli, P., & MacLeod, C. M. (2013). Putting retrieval-induced forgetting in context: An inhibition-free, context-based account. *Psychological Review*, 120(4), 852–872. (Place: US Publisher: American Psychological Association) doi: 10.1037/a0034246
- Ketz, N., Morkonda, S. G., & O'Reilly, R. C. (2013). Theta Coordinated Error-Driven Learning in the Hippocampus. *PLOS Computational Biology*, 9(6), e1003067. Retrieved 2021-05-01, from <https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1003067> (Publisher: Public Library of Science) doi: 10.1371/journal.pcbi.1003067
- Klinzing, J. G., Niethard, N., & Born, J. (2019). Mechanisms of systems memory consolidation during sleep. *Nature Neuroscience*, 22(10), 1598–1610. Retrieved 2022-11-18, from <https://www.nature.com/articles/s41593-019-0467-3> (Number: 10 Publisher: Nature Publishing Group) doi: 10.1038/s41593-019-0467-3
- Kornell, N., Bjork, R. A., & Garcia, M. A. (2011). Why tests appear to prevent forgetting: A distribution-based bifurcation model. *Journal of Memory and Language*, 65(2), 85–97. Retrieved 2022-11-18, from <https://www.sciencedirect.com/science/article/pii/S0749596X11000416> doi: 10.1016/j.jml.2011.04.002
- Lewis, P. A., & Durrant, S. J. (2011). Overlapping memory replay during sleep builds cognitive schemata.

- Trends in Cognitive Sciences*, 15(8), 343–351. doi: 10.1016/j.tics.2011.06.004
- Liu, X. L., O'Reilly, R. C., & Ranganath, C. (2021). Chapter Four - Effects of retrieval practice on tested and untested information: Cortico-hippocampal interactions and error-driven learning. In K. D. Federmeier & L. Sahakyan (Eds.), *Psychology of Learning and Motivation* (Vol. 75, pp. 125–155). Academic Press. Retrieved 2022-10-05, from <https://www.sciencedirect.com/science/article/pii/S0079742121000232> doi: 10.1016/bs.plm.2021.07.003
- Liu, X. L., & Ranganath, C. (2021). Resurrected memories: Sleep-dependent memory consolidation saves memories from competition induced by retrieval practice. *Psychonomic Bulletin & Review*, 28, 2035–2044. (Place: Germany Publisher: Springer) doi: 10.3758/s13423-021-01953-6
- MacLeod, C. M., Dodd, M. D., Sheard, E. D., Wilson, D. E., & Bibi, U. (2003). In opposition to inhibition. In *The psychology of learning and motivation: Advances in research and theory*, Vol. 43 (pp. 163–214). New York, NY, US: Elsevier Science.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102, 419–457. (Place: US Publisher: American Psychological Association) doi: 10.1037/0033-295X.102.3.419
- McCloskey, M., & Cohen, N. J. (1989). Catastrophic Interference in Connectionist Networks: The Sequential Learning Problem. In G. H. Bower (Ed.), *Psychology of Learning and Motivation* (Vol. 24, pp. 109–165). Academic Press. Retrieved 2022-11-18, from <https://www.sciencedirect.com/science/article/pii/S0079742108605368> doi: 10.1016/S0079-7421(08)60536-8
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167–202. doi: 10.1146/annurev.neuro.24.1.167
- O'Reilly, R. C. (1996). Biologically Plausible Error-Driven Learning Using Local Activation Differences: The Generalized Recirculation Algorithm. *Neural Computation*, 8(5), 895–938. (Conference Name: Neural Computation) doi: 10.1162/neco.1996.8.5.895
- O'Reilly, R. C., Hazy, T. E., & Herd, S. A. (2017). The Leabra cognitive architecture: How to play 20 principles with nature and win! In *The Oxford handbook of cognitive science* (pp. 91–115). New York, NY, US: Oxford University Press.
- O'Reilly, R. C., & Rudy, J. W. (2000). Computational principles of learning in the neocortex and hippocampus. *Hippocampus*, 10, 389–397. (Place: US Publisher: John Wiley & Sons) doi: 10.1002/1098-1063(2000)10:4<389::AID-HIPO5>3.0.CO;2-P
- O'Reilly, R. C., Bhattacharyya, R., Howard, M. D., & Ketz, N. (2014). Complementary Learning Systems. *Cognitive Science*, 38(6), 1229–1248. Retrieved 2022-10-05, from <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1551-6709.2011.01214.x> (_eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1551-6709.2011.01214.x>) doi: 10.1111/j.1551-6709.2011.01214.x
- Perfect, T. J., Stark, L.-J., Tree, J. J., Moulin, C. J. A., Ahmed, L., & Hutter, R. (2004). Transfer appropriate forgetting: The cue-dependent nature of retrieval-induced forgetting. *Journal of Memory and Language*, 51(3), 399–417. Retrieved 2021-04-30, from <https://www.sciencedirect.com/science/article/pii/S0749596X04000646> doi: 10.1016/j.jml.2004.06.003
- Polyn, S. M., & Kahana, M. J. (2008). Memory search and the neural representation of context. *Trends in Cognitive Sciences*, 12(1), 24–30. doi: 10.1016/j.tics.2007.10.010
- Pöhlchen, D., & Schönauer, M. (2020). Sleep-dependent memory consolidation in the light of rapid neocortical plasticity. *Current Opinion in Behavioral Sciences*, 33, 118–125. (Place: Netherlands Publisher: Elsevier Science) doi: 10.1016/j.cobeha.2020.02.001
- Raaijmakers, J. G. W., & Jakab, E. (2013). Rethinking inhibition theory: On the problematic status of the inhibition theory for forgetting. *Journal of Memory and Language*, 68(2), 98–122. (Place: Netherlands

- Publisher: Elsevier Science) doi: 10.1016/j.jml.2012.10.002
- Ranganath, C., & Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nature Reviews Neuroscience*, 13(10), 713–726. Retrieved 2022-10-05, from <https://www.nature.com/articles/nrn3338> (Number: 10 Publisher: Nature Publishing Group) doi: 10.1038/nrn3338
- Reeders, P. C., Hamm, A. G., Allen, T. A., & Mattfeld, A. T. (2021). Medial prefrontal cortex and hippocampal activity differentially contribute to ordinal and temporal context retrieval during sequence memory. *Learning & Memory (Cold Spring Harbor, N.Y.)*, 28(4), 134–147. doi: 10.1101/lm.052365.120
- Ritchey, M., Libby, L. A., & Ranganath, C. (2015). Cortico-hippocampal systems involved in memory and cognition: the PMAT framework. *Progress in Brain Research*, 219, 45–64. doi: 10.1016/bs.pbr.2015.04.001
- Ritvo, V. J. H., Turk-Browne, N. B., & Norman, K. A. (2019). Nonmonotonic Plasticity: How Memory Retrieval Drives Learning. *Trends in Cognitive Sciences*, 23(9), 726–742. doi: 10.1016/j.tics.2019.06.007
- Rothschild, G., Eban, E., & Frank, L. M. (2017). A cortical-hippocampal-cortical loop of information processing during memory consolidation. *Nature Neuroscience*, 20(2), 251–259. doi: 10.1038/nn.4457
- Rumelhart, D. E., Hinton, G. E., & Williams, R. J. (1986). Learning representations by back-propagating errors. *Nature*, 323(6088), 533–536. Retrieved 2022-10-05, from <https://www.nature.com/articles/323533a0> (Number: 6088 Publisher: Nature Publishing Group) doi: 10.1038/323533a0
- Schapiro, A. C., McDevitt, E. A., Chen, L., Norman, K. A., Mednick, S. C., & Rogers, T. T. (2017). Sleep Benefits Memory for Semantic Category Structure While Preserving Exemplar-Specific Information. *Scientific Reports*, 7(1), 14869. Retrieved 2022-11-18, from <https://www.nature.com/articles/s41598-017-12884-5> (Number: 1 Publisher: Nature Publishing Group) doi: 10.1038/s41598-017-12884-5
- Schapiro, A. C., McDevitt, E. A., Rogers, T. T., Mednick, S. C., & Norman, K. A. (2018). Human hippocampal replay during rest prioritizes weakly learned information and predicts memory performance. *Nature Communications*, 9(1), 3920. Retrieved 2022-11-18, from <https://www.nature.com/articles/s41467-018-06213-1> (Number: 1 Publisher: Nature Publishing Group) doi: 10.1038/s41467-018-06213-1
- Singh, D., Norman, K. A., & Schapiro, A. C. (2022). A model of autonomous interactions between hippocampus and neocortex driving sleep-dependent memory consolidation. *Proceedings of the National Academy of Sciences*, 119(44), e2123432119. Retrieved 2022-11-18, from <https://www.pnas.org/doi/10.1073/pnas.2123432119> (Publisher: Proceedings of the National Academy of Sciences) doi: 10.1073/pnas.2123432119
- Tamminen, J., Ralph, M. A. L., & Lewis, P. A. (2013). The role of sleep spindles and slow-wave activity in integrating new information in semantic memory. *The Journal of Neuroscience*, 33, 15376–15381. (Place: US Publisher: Society for Neuroscience) doi: 10.1523/JNEUROSCI.5093-12.2013
- Tamminga, C. A., Stan, A. D., & Wagner, A. D. (2010). The hippocampal formation in schizophrenia. *The American Journal of Psychiatry*, 167(10), 1178–1193. doi: 10.1176/appi.ajp.2010.09081187
- Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J. J., Moser, M.-B., & Moser, E. I. (2018). Integrating time from experience in the lateral entorhinal cortex. *Nature*, 561(7721), 57–62. Retrieved 2021-05-01, from <https://www.nature.com/articles/s41586-018-0459-6> (Number: 7721 Publisher: Nature Publishing Group) doi: 10.1038/s41586-018-0459-6
- Verde, M. F. (2012). Retrieval-induced forgetting and inhibition: A critical review. In *The psychology of learning and motivation*, Vol. 56 (pp. 47–80). San Diego, CA, US: Elsevier Academic Press. doi: 10.1016/B978-0-12-394393-4.00002-9
- Zheng, Y., Liu, X. L., Nishiyama, S., Ranganath, C., & O'Reilly, R. C. (2022). Correcting the heb-

bian mistake: Toward a fully error-driven hippocampus. *PLOS Computational Biology*, 18(10), e1010589. Retrieved 2022-11-18, from <https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1010589> (Publisher: Public Library of Science)
doi: 10.1371/journal.pcbi.1010589