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Title: Reap while you sleep: consolidation of memories differs by how they were sown

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Abstract:

Newly formed memories are spontaneously reactivated during sleep, leading to their strengthening. This reactivation process can be manipulated by reinstating learning-related stimuli during sleep, a technique termed targeted memory reactivation. Numerous studies have found that delivering cues during sleep improves memory for *simple* associations, in which one cue reactivates one tested memory. However, real-life memories often live in rich, complex networks of associations. In this review, we will examine recent forays into investigating how targeted sleep reactivation affects memories within *complex* paradigms, in which one cue can reactivate multiple tested memories. A common theme across studies is that reactivation consequences do not merely depend on *whether* memories reside in complex arrangements, but on *how* memories interact with one another during acquisition. We therefore emphasize how intricate study design details that alter the nature of learning and/or participant intentions impact the outcomes of sleep reactivation. In some cases, complex networks of memories interact harmoniously to bring about mutual memory benefits; in other cases, memories may interact antagonistically and produce selective impairments in retrieval. Ultimately, although this burgeoning area of research has yet to be systematically explored, results suggest that the fate of reactivated stimuli within complex arrangements depends on how they were learned.

Keywords: memory reactivation, memory consolidation, sleep, episodic memory, memory interference

A wealth of research has bloomed in recent decades around the idea that sleep affects memory functioning. Although not a new idea (Benson & Feinberg, 1977; Heine, 1914; Jenkins & Dallenbach, 1924; Yaroush et al., 1971), this newfound growth was spurred by neurophysiological findings that cellular activity underlying new learning is reactivated (Buzsáki, 1989; Pavlides & Winson, 1989; Wilson & McNaughton, 1994) – and even replayed in a similar spatiotemporal pattern (Ji & Wilson, 2007; Lee & Wilson, 2002; Nádasdy et al., 1999) – during post-learning sleep. Other studies have shown that reactivation and related physiological phenomena in rodents are modified by important learning variables such as reward (Carey et al., 2019; Dupret et al., 2010; Peyrache et al., 2011). Moreover, markers of reactivation are causally related to later behavioral performance (Aleman-Zapata et al., 2022; Ego-Stengel & Wilson, 2010; Fernández-Ruiz et al., 2019; Girardeau et al., 2009; Gridchyn et al., 2020), demonstrating that reactivation during sleep is a dynamic and critical process for stabilizing newly formed memories.

Intriguingly, reactivation during sleep can be manipulated by presenting stimuli that had been linked with learning before sleep. Research using this technique – termed targeted memory reactivation (TMR) – started during the second half of the 20th century (e.g., Guerrien et al., 1989) but exploded in the late 2000s, following the publication of two seminal studies (see Hu et al., 2020 for meta-analysis). Rasch et al. (2007) had participants learn on-screen spatial locations of pairs of objects amid the presence of a rose odor. They were then presented with the odor during subsequent slow wave sleep (SWS), subsequent rapid eye movement sleep, or not at all. Participants who were exposed to the odor during SWS improved their performance on a morning memory test, whereas those in the other groups did not. Therefore, Rasch et al. (2007) showed that reactivating a learning context during sleep – and specifically SWS – benefited memory. Later, Rudoy et al. (2009) showed that reactivation can be even more specific. They had participants learn spatial locations of objects along with a specific, congruent sound (e.g., “meow” for cat). Participants then took an afternoon nap, during which the experimenters cued half of the sounds when participants entered non rapid eye movement sleep, which includes SWS. In a post-nap memory test, memory was better for cued than uncued objects, showing that cues can reactivate individual memories. These experiments nicely demonstrated that reactivation aids memory in humans and can be manipulated using straightforward associations among stimuli.

As a technique, TMR has been instrumental in uncovering how different forms of learning benefit from sleep (Hu et al., 2020). However, a major goal of research is to capture how humans remember in the real world. Real-world memories do not live in a vacuum, but rather in dense, interconnected networks of associations that are linked together based on shared time and space, among other features. As an example, imagine that you visit a chic coffee shop. Upon entering, you encounter a long line, sparking concerns about being late for an upcoming meeting. While waiting in line, you realize that you forgot your wallet, but luckily a stranger comes to your rescue and covers the cost. A complex episodic memory like that differs substantially from those commonly used in lab-based memory experiments. The sound of coffee grinding, linked with this complex scenario, could elicit any number of associations during wakefulness: nervousness about being late, the artistic sensibilities of the coffee shop’s vibe, the delicious smell of coffee, the self-punishment of forgetting your wallet, the appreciation felt for the stranger you encountered, and/or a host of other possibilities. Memory processing related to this event during sleep may be equally complex and layered. Which memories would the sleeping brain process when exposed to the same grinding sound?

Here we cover recent ventures into understanding reactivation under such complex arrangements during sleep (Fig 1). We define complex arrangements as those wherein memory cues are tightly related to multiple tested items. According to this definition, the study by Rasch et al. (2007), which involved a one-to-many relationship between the odor and its learning context consisting of multiple tested memories, is of higher complexity than that of Rudoy et al. (2009), which involved one-to-one relationships between sound cues and tested memories. We designate paradigms like the latter experiment as "simple", despite there being some variation within them (Box 1). While TMR experiments in real-world settings are scant (though see Gao et al., 2020; Knötzele et al., 2023; Neumann et al., 2020; Vidal et al., 2022), recent experiments have made inroads into how reactivation drives memory benefits and impairments in complex situations. We will review these findings and argue that an underlying theme is that the specifics of the learning experience determine the consolidation trajectories of associated memories, which we refer to as the consolidation trajectory hypothesis**.** Specifically, we will argue that if the interconnected elements incorporated in a complex memory are learned harmoniously, they will be jointly promoted during sleep, whereas if they were antagonistically pitted against one another during learning, these dynamics will be replicated during sleep. We will conclude by considering alternative accounts and by suggesting new avenues of research that serve to both investigate the links between wake and sleep memory dynamics and to further advance the ecological validity of sleep and memory studies.

Box 1: Variations on simple reactivation experiments. Even seemingly simple associations used in targeted memory reactivation (TMR) experiments vary in several noteworthy dimensions (Fig 1, "Simple"). First, many simple experiments involve only a single association, wherein the cueing stimulus (i.e., the stimulus presented during sleep) is also the cue for the memory at retrieval, such as between two vocabulary words, e.g., "Winst"-"Gewinn" (Schreiner & Rasch, 2015). Other experiments involve two associations – one between the cue and some reference object and one between that object and another associate, e.g., meow-cat and cat-location in Rudoy et al. (2009). Rarely, some TMR studies do not involve associations at all, incorporating an auditory presentation of the to-be-recalled memory itself rather than a cue (Ai et al., 2018; Tilley, 1979). We group all these instances under the term "simple" because there remains a route from a single cue to a single tested memory. Second, cues often have an *a priori* link to their reactivated memory (e.g., "meow" reactivating a cat's spatial location; Creery et al., 2015; Rudoy et al., 2009), but that is not always the case. Sometimes these associations are learned *de novo*, whereby cues first become linked with other stimuli before further learning (e.g., "meow"-Brad Pitt is learned before the spatial location of the image of Brad Pitt; Antony, Cheng, et al., 2018; Cairney et al., 2018). A final aspect in which all TMR studies exploring declarative memories vary is the specifics of the task. The most commonly used tasks are spatial (i.e., memory for on-screen positions; e.g., Rudoy et al., 2009) and verbal paired-associates tasks (i.e., memory for the association between two words; e.g., Schreiner & Rasch, 2015). Despite these delineations, TMR has benefited memory in studies using all of these simple paradigms.

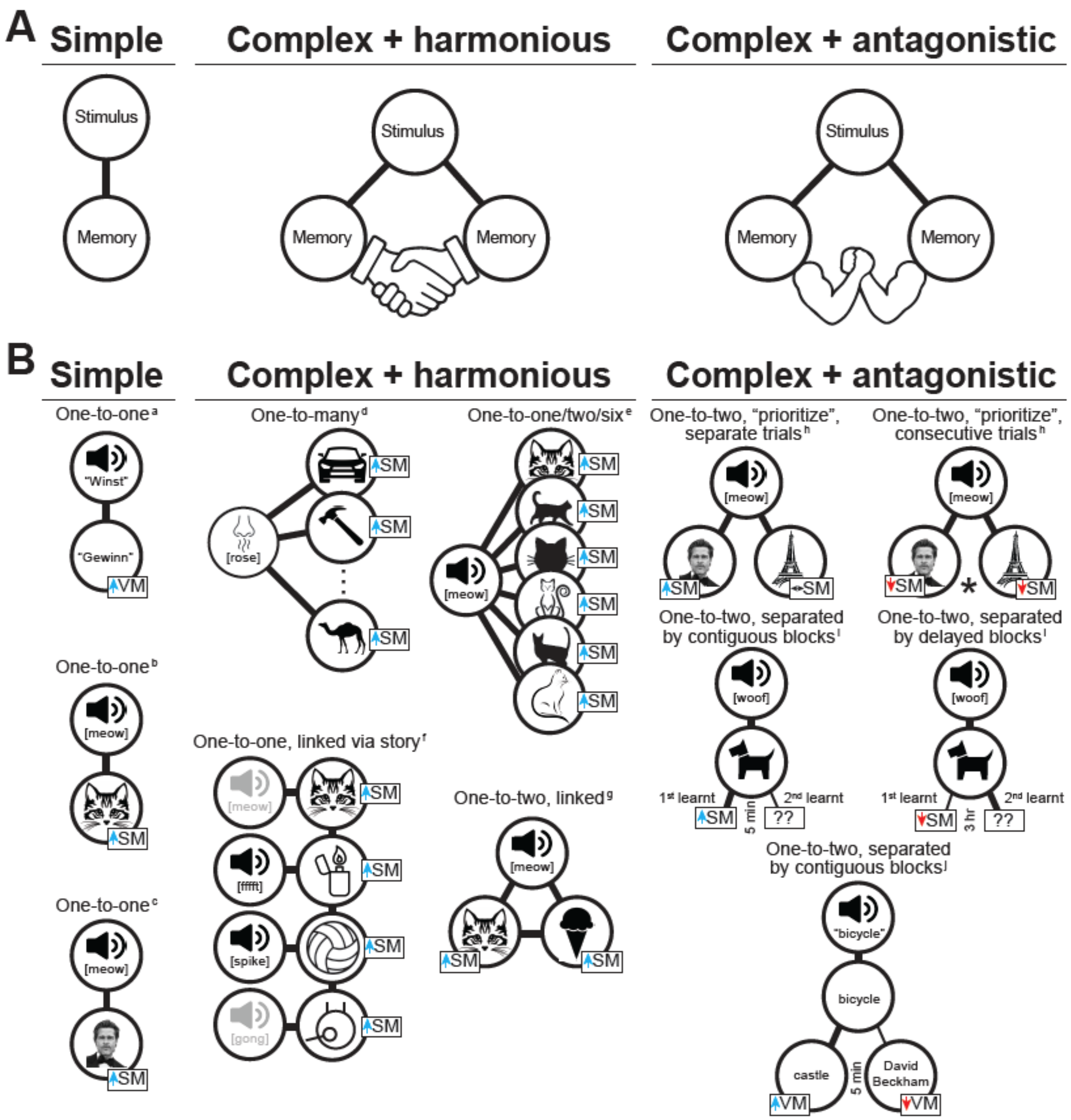

Figure 1: Taxonomy of targeted memory reactivation studies based on experimental design. (a) Targeted memory reactivation (TMR) experiments involve the unobtrusive presentation of memory-related stimuli during sleep. Most experiments (simple designs; left) include a single reactivation cue ("Stimulus") linked with a single associated memory ("Memory"). In this review, we discuss experiments in which multiple memories are linked with the same cue (complex memories). We argue that the memory trajectories in complex designs diverge based on the type of interaction between the associates, and we distinguish between two types of experimental paradigms: harmonious paradigms, in which TMR-linked memories do not directly compete during wakefulness, and antagonistic paradigms, in which TMR-linked memories compete with each other during wakefulness. (b) Examples of simple- and complex-design studies testing the impact of TMR on reactivation consequences. Details on the design of each study can be found in the main text. Whereas simple designs largely lead

to TMR benefits[a-c], the consequences of TMR in complex designs differ based on whether multiple memories interact harmoniously or antagonistically. Harmonious paradigms[d-g] have resulted in memory benefits to items linked together during learning[f], and these benefits were sometimes correlated among items[g]. In antagonistic paradigms[h-j], TMR cues have impaired some subset of memories[i,j] or made one memory less likely to benefit[h]. SM: spatial memory; VM: verbal memory; ??: untested; *: impaired if both items were well-learned; gray color: uncued during sleep. References – [a]: Schreiner & Rasch (2015); [b]: Rudoy et al. (2009); [c]: Antony, Piloto, et al. (2018); [d]: Rasch et al. (2007); [e]: Schechtman et al. (2021); [f]: Schechtman et al. (2022b) [g]: Vargas et al. (2019) [h]: Antony, Cheng, et al. (2018); [i]: Oyarzun et al. (2017) [j]: Joensen et al. (2022). Where applicable, line strength differences reflect relative pre-sleep association strengths.

Beyond the reactivation of simple memories during sleep

The theoretical rationale explaining why TMR aids simple associations appears straightforward: TMR cues likely promote the reactivation of the associated memory trace (Bendor & Wilson, 2012; Rothschild et al., 2017) and strengthen the memory via Hebbian, repetition-induced plasticity (Buzsáki, 1989; Hebb, 1949). The behavioral contribution of TMR in complex paradigms has been generally established as well, as detailed below, but the complexities arising from the interactions between multiple memories in studies using these designs have raised novel questions which were previously unexplored. For example, in Rasch et al. (2007) and other studies using similar designs (e.g., Bar et al., 2020; Diekelmann et al., 2011; Seibold et al., 2018; Shanahan et al., 2018), the odor cue benefited mean performance for many individual memories (Fig 1, “Complex + harmonious”), but this could have arisen in multiple ways. For instance, did the overall average TMR benefit mask complexity in how individual items were impacted by the cues (e.g., a larger subset were strengthened, some were unaffected, some were weakened)? Did it reactivate multiple memories simultaneously, or is a limited subset reactivated at any given point in time? Did the cue first reactivate neural representations of the learning context, which later evoked individual, context-linked memories at random?

In reviewing this nascent literature, there does not appear to be a one-size-fits-all answer to these questions, but rather these dynamics change depending on how the information was learned. In the following sections, we discuss the ramifications of harmonious and antagonistic dynamics between elements under complex memory arrangements and how the nature of their learning determined their fate.

Reactivating multiple memories together

Complex designs have targeted up to dozens of memories with a single odor cue (e.g., 30 memories in Neumann et al., 2020). However, these studies did not compare the consequences of reactivating multiple vs. single memories. Such comparisons are crucial to understanding how consolidation benefits are split among multiple reactivated memories.

Can multiple memories be strengthened at once or is a single memory sampled and strengthened at any given time? Are reactivation benefits necessarily divided between the various tested elements of a given cue? In other words, is there a “reactivation bottleneck” that provides diluted benefits on a per-cue basis? A recent meta-analysis of TMR studies found that the effect sizes for olfactory cueing was not significantly different than that for auditory cueing

(Hu et al., 2020, Table 2C). Since most olfactory TMR studies involve multiple memories and most auditory studies involve single memories (but see Ngo & Staresina, 2022), this could be seen as evidence that the benefits of cueing are similar regardless of the number of reactivated memories. Alternatively, they may reflect some inherent difference between modalities.

Schechtman et al. (2021) investigated this question by having participants learn the on-screen spatial location of one, two, or six distinct exemplars from the same category, all linked with the same sound (e.g., six images of cats linked with a single 'meow' sound). These exemplars were learned in separate training blocks, resulting in multiple memories that were grouped together in categorical sets of different sizes, ranging from one to six exemplars. Then, during sleep, half of the sets from each of the three set-size conditions were cued. Contrary to the idea of a reactivation bottleneck, they found that TMR benefits for memories (i.e., change in memory relative to controls) did not differ by cueing-group size. Individual memories within sets of six and two items benefitted to the same degree as single reactivated memories.

Linking memories via context

These results suggested that multiple memories can be reactivated in parallel without compromising the benefits they incur. Moreover, they put the spotlight on the possible role of the cognitive networks linking memories together (e.g., the connections between the different cat-related memories). Although the results of multi-item studies (e.g., Rasch et al., 2007; Schechtman, Antony, et al., 2021; Shanahan et al., 2018) can be explained by assuming that the one stimulus reactivates each individual memory independently, a more parsimonious explanation is that the stimulus reactivates the "glue" linking these memories together (e.g., the learning setting or task in Rasch et al., 2007; the common object in Schechtman, Antony, et al., 2021; object categories in Shanahan et al., 2018; for evidence that contextual cues benefit procedural memories, see Laventure et al., 2018, 2016; Picard-Deland & Nielsen, 2022; Picard-Deland et al., 2021). In other words, these TMR studies suggest that the cues first activate a neural representation of context associated with the cueing group, and this reactivation propagates down to individual memories (Fig 5b of Schechtman, Antony, et al., 2021).

Context is a notoriously vague concept. In using the term, 'context', we endorse the three criteria suggested by Stark et al. (2018): Context must be stable over time, behaviorally relevant, and – most importantly for our purposes – it must have a 1-to-n connection with embedded memories, where n > 1. In other words, context is any form of common core that serves to bind multiple memories together, whereby these memories are linked with this core more than they are with one another directly. Contexts vary in multiple dimensions, including time, space, and semantic relatedness.

To investigate the role of context in consolidation during sleep, Schechtman et al. (2022) tested whether targeting specific memories reinstates their context, thereby benefiting other contextually bound memories. Contexts were operationalized by having participants generate stories incorporating a set of objects, creating contextually bound sets. Then, for some of these sets, half of the objects were reactivated during sleep. A subsequent test demonstrated that this procedure impacted memory for the objects that were directly cued. Crucially, however, TMR also impacted memory for uncued objects that were contextually bound to the cued one, suggesting that the context incorporating the memories was involved in processing during sleep.

This study was among the first to provide direct evidence for context reinstatement during sleep-related memory reactivation (see also Schechtman et al., 2023).

The idea that TMR benefits extend to contextually linked memory raises some methodological questions regarding the paradigm more broadly. Most TMR studies are done in a within-subject manner, comparing cued and uncued memories within the same task and experimental setting. However, these two factors are contextual in nature, suggesting that uncued memories may themselves benefit to a certain degree from cueing. Some evidence indeed suggests that TMR may impact uncued memories. For example, a mixed design study examining the effects of TMR on motor performance found a between-subject benefit for the TMR group, but no within-subject benefit for the cued locations relative to the non-cued ones (Johnson et al., 2020). Similarly, TMR benefited uncued spatial memory for items linked with low expected monetary compensation (Oudiette et al., 2013). Notwithstanding, most TMR studies to date have lacked the proper control to consider the effects of uncued memories directly (i.e., including both cued and uncued memories in one group of participants and a separate non-TMR control group with which the uncued memories can be compared). It seems likely that TMR impacts memory to a degree that is correlated with the contextual associations between the cues and memories. In other words, the tighter the contextual link between a cue and a memory, the more it will benefit. Therefore, uncued memories are likely impacted by cueing, but to a far lesser degree than the cued ones, as reflected in the reliable within-subject TMR effects that have been shown across tasks and protocols (Hu et al., 2020).

Comparing correlated benefits within cueing groups

Studies finding benefits for multiple memories linked within the same group or context raise the question of the interdynamics within these cued groups. Do TMR effects correlate among members of a cued group? To test this, Vargas et al. (2019) had participants first memorize pairs of objects, one of which (e.g., cat) was congruently related to a concurrent sound (e.g., "meow") while the other was random (e.g., ice cream cone). The cueing group therefore consisted of a sound along with two objects. Next, participants simultaneously learned the locations of both grouped objects against a background spatial grid. During a nap, half of the sounds served as TMR cues. The authors found that memory for both grouped objects – the ones related and the ones unrelated to the sounds – benefitted from cueing. Additionally, the authors found that the positive pairwise correlations between memory scores for grouped objects were maintained better across the nap in the cued relative to the uncued groups, demonstrating that TMR benefits were positively linked within each cued group. Therefore, Vargas et al. (2019) showed that memory for two grouped objects – under the conditions in which they were learned simultaneously – could benefit from cueing in a correlated manner.

The benefits in Vargas et al. (2019) and Schechtman et al. (2021) align well with the well-established benefits of integration in other (wake) paradigms, such as boundary conditions surrounding retrieval-induced forgetting, fan effects, and other forms of memory interference. Retrieval-induced forgetting occurs when retrieval of one association (e.g., fruit-pear) produces forgetting of a related, non-presented association (e.g., fruit-apple) (Anderson et al., 1994). This effect is eliminated by encouraging subjects to integrate the words beforehands (Anderson & McCulloch, 1999; see Bäuml & Hartinger, 2002; Carroll et al., 2007 for a similar effect). Similarly, the negative consequences of fan effects – whereby associating multiple targets with the same cue word impairs memory for the targets – can be reduced or eliminated by encouraging integration among the target words (Moeser, 1979; Reder & Anderson, 1980). Moreover, in classic A-B, A-C paradigms, whereby a cue is first linked with one target (A-B; e.g., chair-horse) before being linked to another target (A-C; e.g., chair-plant), interference is often found to negatively impact recollection for both A-B and A-C associations. That is, there is both retroactive interference for the A-B association relative to non-interfering associations (i.e., A-B followed by D-E; Barnes & Underwood, 1959; Briggs, 1954), and proactive interference for the A-C association relative to non-interfering associations (Young, 1955). However, reminding subjects of previously learned (A-B) associations during new A-C learning – thereby encouraging integration of the two – often eliminates these interference effects or even produces facilitation relative to non-interfering conditions (Antony et al., 2022; Garlitch & Wahlheim, 2020; Hintzman, 2011; Jacoby et al., 2015). Additionally, explicitly creating integrated, closed-loop configurations, such as by having subjects learn each link in a triad consisting of A-B, B-C, and A-C, seems to benefit memory more than related, open-loop configurations, such as having subjects learn A-B, B-C, and C-D (Horner et al., 2015; Horner & Burgess, 2014; Ngo et al., 2019). Altogether, these findings from wake support the idea that the nature of the paradigm and learning instructions strongly impact the level of integration among memories.

Weakening memories during sleep

Notably, correlated benefits do not arise in every paradigm and under every set of learning instructions. Moreover, not every study finds TMR-related benefits – some have found TMR-related *impairments*. Antony, Cheng, et al. (2018) conducted an experiment in which each cue (e.g., “meow”) was linked with two items (e.g., Brad Pitt and the Eiffel Tower) (Fig 1, “Complex + antagonistic”). During a spatial learning phase, subjects were offered a high reward for remembering one of the grouped items at the final test and a low reward for the other. Critically, subjects learned these items in one of two conditions. In the separate learning condition, two items from separate groups were learned back-to-back, followed by a 5-s rehearsal period during which subjects were asked to prioritize their rehearsals for one item over another. Thus, the two grouped items with the same cue were not learned together in this condition. Conversely, in the consecutive learning condition, the two items learned back-to-back before the 5-s rehearsal periods belonged to the same cueing group. When the grouped items were separated during spatial learning, the authors found cueing benefits, but in a different way than Vargas et al. (2019): when one grouped item benefited from cueing, the other item was *less* likely to benefit. These results suggested that when the items were learned separately, cues seemed to pick a winner among the grouped items. Conversely, when the grouped items were learned consecutively, cueing benefits were eliminated entirely. Moreover, when both items were well learned, cueing (relative to no cueing) *impaired* the memories. In this case, cueing may have evoked competition that was created during spatial learning when the two grouped items were in direct conflict.

Differences in learning paradigms are not the only factor determining the fate of reactivated memories; another factor is experimental timing. Oyarzun et al. (2017) investigated the effects of TMR in a spatial variant of an A-B, A-C learning task. First, two on-screen spatial locations for the same object were learned along with a congruent sound (A-B; e.g., Dog-

Location A and Dog-Location B, along with a "woof"). Then, after either a five-minute or three-hour delay, subjects learned a new association, whereby one of the two locations remained the same but the other was novel (A-C). After this phase, half of the sound cues were presented during sleep before subjects were awakened and tested on all A-B associations. The authors found that in the five-minute delay condition, cueing benefited A-B memory, in line with typical TMR memory benefits. However, in the three-hour delay condition, cueing *impaired* A-B memory. Which factors could have led to these diametrically opposing results? The relative strength of A-B and A-C likely differed at the two delays: after the five-minute delay, A-B and A-C would be relatively equivalent in strength, whereas after the three-hour delay, A-B would be weaker than A-C. Indeed, the authors conducted control experiments showing that A-B memories were weaker after the delay. This interpretation aligns with prior findings suggesting that competing memory traces vary in their level of dominance, which determines which among multiple memory traces that are linked with a given cue can be altered (Bridge & Voss, 2015; Eisenberg et al., 2003). One intriguing question is whether A-B memory traces remained intact, but their retrieval was impaired via output interference (Runquist, 1975), which could arise if the A-C associations were strengthened. Alternatively, it may be that A-B associations were weakened, in line with findings that weak-to-moderate reactivation can in some cases produce memory weakening relative to no reactivation at all (Lewis-Peacock & Norman, 2014).

Two lingering questions from Oyarzun et al. (2017) were what fate befell the later-learned A-C memories and how the A-B and A-C memories interacted. Joensen et al. (2022) addressed these questions by having subjects separately learn associations between objects and both the names of famous people and descriptions of physical locations (e.g., Bicycle-David Beckham and Bicycle-Castle) in consecutive phases. Then, they cued some of the object words during sleep and tested memory for the same associations. Similar to the five-minute condition in Oyarzun et al. (2017), they found that TMR benefited A-B associations (i.e., the association learned first out of the two). Intriguingly, however, the same TMR cues impaired A-C associations. Moreover, their correlational analyses suggested that TMR (relative to no TMR) led to *anti-correlations* between A-B and A-C memories. In other words, their results showed that the more memory for one item in an association improved, the more its counterpart was weakened. The authors also found that A-C associations were initially weaker than A-B, and therefore their results may have arisen due to a stronger likelihood of reactivating A-B over A-C, followed by either output interference between the memories at retrieval or a weakened A-C memory trace (Joensen et al., 2022).

You reap what you sow: putting it all together

Results in complex memory designs seem to point in a dizzying array of directions: TMR benefits or impairs memories and produces correlated, uncorrelated, or anticorrelated benefits among them. Which factors determine the consequences of reactivation? In this section, we argue that the configuration of memories during acquisition marks their consolidation path. Trivially, the specifics of memory encoding determine their trajectories, regardless of sleep or consolidation. Our hypothesis – which we term the consolidation trajectory hypothesis – suggests that the benefits of sleep are encoding-dependent (see Gibson et al., 2022; Heib et al., 2015 for endorsements of this idea in non-TMR paradigms). Using an ANOVA as an analogy, current models of memory could be said to focus on the main effects of both encoding and sleep on subsequent retrieval. In our hypothesis, we suggest that encoding and sleep interact with each other in complex ways, as described below.

The predominant factors promoting overall benefits among memories seem to be either study designs with no inherent competition among items (Klinzing et al., 2018; Ngo & Staresina, 2022; Rasch et al., 2007; Rihm et al., 2014; Seibold et al., 2018) or designs that implicitly or explicitly encourage subjects to integrate and group memories together. In Schechtman et al. (2022), this was encouraged explicitly by linking items via the creation of a narrative context. In Vargas et al. (2019), this likely occurred because both associated memories were learned simultaneously during both the initial phase and the spatial memory phase. We refer collectively to these experimental designs as harmonious because, due to the lack of direct competition or encouraged integration, there is no necessary reason why a cue should elicit some subset of memories more strongly than others. Conversely, TMR impairments can occur if associations directly compete for access to a cue and one of them is less dominant than others at the time of cueing (Joensen et al., 2022; Oyarzun et al., 2017) or if both memories are well-learned and directly compete during learning (competitive pair learning in Antony, Cheng, et al., 2018). We refer to these experimental designs as antagonistic because the presentation of a cue elicits direct competition among linked memories.

We will now examine how some subtle differences in study designs alter consolidation trajectories. In Schechtman et al. (2021), participants learned locations for two of the same type of item linked by the same sound (e.g., one cat's location followed by another cat's location, both accompanied by the same 'meow' sound). In contrast to Oyarzun et al. (2017) and Joensen et al. (2022), both linked objects seemed to benefit from TMR. One explanation for this difference is that the sound in Schechtman et al. (2021) was associated with a single category (cats) but the memory traces remained distinct (i.e., there were different cats in different locations rather than the same cat in two locations). Conversely, in both the five-minute delay condition in Oyarzun et al. (2017) and in Joensen et al. (2022), one central aspect of the memory was common to both memories (i.e., A was common to both A-B and A-C memories). In other words, the first element reactivated by the cue in these two studies (the visual dog in Oyarzun et al., 2017, and the visual word, bicycle, in Joensen et al., 2022) was *common* to both interfering memories. As a thought experiment, if an experiment (similar to Schechtman et al., 2021) had participants learn two different spatial locations for the same cat on different blocks (rather than different cats) and asked them to recall the first or second location, we speculate that the TMR cue would produce direct competition between the two location memories. This would constitute an antagonistic design by our definition, and we would expect TMR to produce impairments similar to Oyarzun et al., 2017 and Joensen et al., 2022. Therefore, these intricate study design considerations seem critical in determining how TMR affects memories.

If indeed consolidation trajectories are sown during encoding, as we suggest, the underlying theme seems to be that task instructions, along with participant motivations and their thought processes while completing a task, strongly influence what happens when memories are later reactivated (see Table 1 for a non-exhaustive list of design considerations that may determine whether a complex design will be harmonious or antagonistic). This idea has never been directly addressed in any TMR study, and direct empirical support for it is insufficient. To directly test this idea, researchers could have participants learn the same information in the same learning order but with different instructions. For example, researchers could have participants learn A-B, A-C pairs while encouraging them to encode the A-C association separately from the A-B one or, alternatively, instruct them to think back and integrate both associations (Richter et al., 2016). Under this account, the former condition should result in diverging effects (Joensen et al., 2022; Oyarzun et al., 2017), whereas the latter condition should result in unanimous TMR benefits, perhaps in a correlated fashion between A-B and A-C memories.

Altogether, the results obtained in studies using complex designs suggest that TMR provides a privileged opportunity for peering into the state of the original memory trace. Unlike examinations of memory during wakefulness, sleep involves a minimal state of awareness, and therefore offers a unique opportunity to drive consolidation trajectories by exacerbating initial differences (i.e., increase contrasts) based on learning. That is, if pre-sleep learning facilitates antagonistic relations among memories that do not allow them to co-activate without interference, TMR may expose these relationships by enhancing the contrasts (with unanimous benefits occuring for memory sets with harmonious relations).

Table 1: Non-exhaustive list of experimental design considerations that may determine whether a complex design is harmonious or antagonistic. Future studies should empirically test whether any one element or a combination of elements could sufficiently determine the nature of the association between memories and drive consolidation trajectories. References – [a]: Oyarzun et al. (2017); [b]: Antony, Cheng, et al. (2018); [c]: Schechtman et al. (2022).

	Antagonistic	Harmonious
Instructions	During acquisition, present the associated memories as competing over the same figurative cognitive space (e.g., in a paired-associated language learning task, frame the new associate as a completely different meaning of the probe; “SVANG means both bottle and compass in language A”).	During acquisition, present the associated memories as independent and/or coexistent (e.g., in a paired-associated language learning task, frame the new associate as a word in an entirely separate language; “SVANG means bottle in language A and compass in language B”).
Timing	Timing may interact with competition[a]. If instructions are to prioritize some nearby items over others, present the cue-linked memories nearby in time[b].	If instructions are to prioritize some nearby items over others, separate the cue-linked memories in time.[b]
Context	Embed memories in conflicting or interfering contexts (e.g., highly similar yet distinct learning contexts)[a].	Embed memories in the same context (or highly distinct contexts) such that they will coexist without interference[c].
Competition	Incentivize one memory over the other through compensation (e.g., framing, monetary, intrinsic motivation, curiosity)[b].	Avoid pitting memories one against another (leaving them independently predisposed)[b] or make them mutually beneficial (e.g., only rewarded if both are recalled correctly), encouraging integration.

Alternatives to the consolidation trajectory hypothesis

The underlying theme across complex study designs is that the interconnections between memories upon their formation determines the consolidation dynamics. However, despite our focus on this interpretation throughout this review, alternative explanations are also plausible. The following paragraphs propose other processes that may contribute to the observed results, which are not necessarily mutually exclusive with the idea that interactions among memory traces during encoding set the course for subsequent changes upon reactivation.

Does consolidation itself evoke competition?

One alternative interpretation is that these dynamics between memories may not be set while awake and unleashed while asleep. Rather, they may be fleshed out during sleep based on the memory traces formed during wakefulness, which may not interact with one another initially. Consolidation during sleep involves the transformation of memory traces, with specific implications for memories with overlapping traces and shared features (Lewis & Durrant, 2011; McClelland et al., 1995; Schapiro et al., 2017). Although this process is hypothesized to identify commonalities to promote generalization, the underlying cost may be the loss of memory for specific details, which may explain the detrimental effects of reactivation for some memories (Witkowski et al., 2020).

To demonstrate this idea, we return to the overlapping associations used by Joensen et al. (2022), which resulted in anti-dependent changes in memory between pairs (e.g., Bicycle-Castle improved and Bicycle-Beckham was weakened). As mentioned above, an attractive explanation for these results is that overlapping and competing memory traces were formed upon initial encoding. An alternative model posits that these traces were formed independently and were only pitted against each other as part of the transformation they underwent as a result of being cued during sleep. This explanation is supported by the lack of significant anti-dependence between pairs before sleep (Joensen et al., 2022). The studies presented in this review do not provide data that can tease these hypotheses apart, and the question of whether interference is formed by reactivation or simply exacerbated by it remains open. Future studies using non-report metrics, such as direct neural measures of memory representations and the overlaps amongst them – before, during, and after sleep – may be instrumental in resolving this issue (e.g., Cowan et al., 2020; Tompary & Davachi, 2017).

Does intent matter?

Previous paragraphs have focused on the interactions between the memory traces within complex designs, arguing that the seeds for the consolidation trajectory are sown during encoding and then come into play during sleep. However, experiences are not recorded verbatim; rather, the interpretation, motivation, and intention of the participants are modulating factors in memory encoding. Often, participants are aware that the A-C pair they are required to remember intersects with a previous A-B pair, and may have their own interpretation of the task demands: they may try to integrate A-B with A-C; they may try to mentally replace their previous memory with the new one; or they may view the two as separate altogether. These intentions may themselves impact consolidation. Waking memories may be flagged with a meta-memory component (for example, that they were in competition with another memory), and that layer on top of the memory may itself be reactivated. Put differently, the intentionality involved in encoding may be ingrained in the memory and reactivated itself. From a neurocognitive (rather than purely psychological) perspective, the term intention can be translated into the activation of a certain brain network engaged in a certain action. For the sake of this argument, we view these perspectives as complementary.

There is some evidence demonstrating that memory-related intentionality is reactivated during sleep in a manner that impacts the associated memories. One line of work that supports this notion involves forgetting during sleep. Simon et al. (2018) had participants engage in a directed forgetting task, which is thought to engage inhibitory brain mechanisms (e.g., Wylie et al., 2008). In this version of the task, participants were instructed to forget previously perceived words when they were followed by a two-second tone. Then, during sleep, sounds from an unrelated memory task were presented, followed by the tone three seconds later. A memory test demonstrated that this procedure impaired retrieval performance for the cued memories. Therefore, the intent to inhibit the memory (and the neurocognitive inhibitory process itself) were linked with the tone during encoding and then reactivated in conjunction with the cued memories, thereby shifting the outcome toward memory weakening as opposed to strengthening.

Simon et al. (2018) used different cues to independently reactivate both the intention to forget and an unrelated to-be-forgotten memory. However, intentionality can also be embedded within the initial memory and actively shape its subsequent reactivation. This was demonstrated in another TMR study using motivated forgetting to selectively weaken memories (Schechtman et al., 2020). In this study, the same sound was used to cue both the instructions to forget and the specific memories that were to-be-forgotten. In a two-step training protocol, sounds were first linked with specific memories and then linked with the instructions–and, supposedly, intent–to forget those memories. One of these sounds was then cued during sleep. As a result, memories linked with that sound specifically were weakened. Based on the classic premise of TMR, which does not incorporate intent, memories in this group should have been enhanced similarly to those in other studies involving multiple memories linked with a single cue (e.g., Rasch et al., 2007). The finding that memory was weakened in this study suggests that the instructions to forget (and the intentionality that these instructions supposedly produced) played a decisive role in the consolidation process.

There is some evidence that intentionality carries over from wakefulness to sleep even when TMR is not involved. Multiple studies have shown that sleep selectively enhances memories that are prioritized either due to perceived future relevance (i.e., information on future test; van Dongen et al., 2012; Wilhelm et al., 2011) or due to larger expected rewards (Fischer & Born, 2009; Oudiette et al., 2013; Sterpenich et al., 2021). However, studies trying to replicate these effects have not been uniformly successful, and the robustness and generalizability of these effects remains questionable (see Davidson et al., 2021 for review). Regardless of sleep's specific role, however, there is a plethora of evidence suggesting that consolidation in a broader sense does preferentially promote memories of future relevance in an adaptive manner (Cowan et al., 2021). The question of whether intentionality carries over to sleep remains largely unanswered, but its effects on sleep-specific consolidation may be dependent on boundary conditions that have yet to be fully fleshed out. Closing this gap would require designs that contrast the consequences of reactivation between several identically structured tasks that differ only in the designated intent (i.e., as defined by the provided instructions). For example, in a modification of Simon et al. (2018), subjects could learn both 'remember' and 'forget' cues before they learn paired associates linked to TMR cues, and these intent cues could be similarly presented after the TMR cues during sleep. Alternatively, subjects could learn paired associates linked with TMR cues simultaneously with a 'remember' / 'forget' designation, after which TMR cues (alone) could reactivate the designated intention and predict different memory outcomes relative to uncued items.

More broadly, the notion of sleep-related reactivation of intent aligns with studies showing that concepts other than memories can be reactivated during sleep. For example, presenting relaxing words during sleep was shown to improve objective and subjective sleep quality, supposedly through reactivation of the concept of relaxation (Beck et al., 2021). Another study showed that TMR cues could be used to reinforce self-esteem training (L. Chen et al., 2021). Similarly, a recent study demonstrated that reactivation linked with an imagery rehearsal task reduced the occurrence of nightmares in patients suffering from nightmare disorder (although it remains unclear whether this effect stems from reactivation of the imagery operation or reactivation of imagery-related memories; Schwartz et al., 2022). Other studies have instructed participants to process words presented during sleep in certain ways and demonstrated that this guidance impacted processing during sleep. For example, Kouider et al. (2014) had participants engage in a categorization task which involved pressing either the left or right button after hearing a word during wakefulness. They then showed that EEG evidence for the same action can be observed following word presentation during sleep, suggesting that the action itself was reactivated in a category-selective way.

Taken together, these findings support the idea that high-order cognitive entities such as intents, concepts, and actions can be reactivated during sleep. To date, reactivation studies have focused on the reactivation of memory *representations*, whereas the results presented here put forward the notion that memory *operations* may also be reactivated during sleep (Cowell et al., 2019). However, as with many new fields, the lack of clear terminological and methodological frameworks impedes progress, making the task of operationalizing these cognitive entities extremely challenging. Establishing such a framework is beyond the scope of this review, but we hope that our descriptive overview will advance future endeavors towards addressing these questions.

The impact of memory strength

Learning multiple interlinked memories in complex designs naturally creates differences in multiple dimensions among those memories. Of importance, some memories may enter sleep stronger than others. Although memory strength is hard to define, in sleep and memory experiment contexts it is typically measured as pre-sleep retrieval performance (e.g., Creery et al., 2015; Schechtman, Lampe, et al., 2021) or operationalized through behavioral manipulation (e.g., Denis et al., 2020; Joensen et al., 2022). Complex designs often drive some memories to be stronger than others, whether intentionally or not. Are the observed differences in memory trajectories a result of these differences in strengths rather than their interactions during encoding? Indeed, previous TMR studies using simple designs have found that memory strength impacts TMR benefits, with higher benefits to memories of intermediate or low strengths (Cairney et al., 2016; Creery et al., 2015; Schechtman, Lampe, et al., 2021).

However, we believe that it is unlikely that memory strength alone drives the results in complex designs. First, operationalizing memory strength through manipulation is not always straightforward. For example, an argument can be made that an item learned first would be stronger than an item learned second because of the lack of interference upon encoding (e.g., Joensen et al., 2022). However, an opposite argument can also be made – that an item learned earlier in time is negatively impacted by memory decay whereas a more recently acquired memory is stronger (e.g., Oyarzun et al., 2017). Second, at least one attempt to directly manipulate memory strength in a complex design has shown no clear effects. As mentioned above, Antony, Cheng, et al. (2018) used reward to manipulate memory strength. When memories were encoded separately and reactivated using a common cue, only one item benefited whereas the other did not. Importantly, however, memory strength (or reward) did not determine which memory benefited and which did not. Therefore, although memory strength undoubtedly impacts consolidation, we argue that it does not, in itself, explain the complex encoding-dependent dynamics revealed by TMR studies.

Box 2: Are spontaneous and targeted memory reactivation (TMR) similar or different?

Much of this review has focused on how learning paradigms interact with TMR to determine memory fate. We argue that understanding this interaction under controlled reactivation settings informs our general understanding of endogenous processing during sleep. However, one critical question in determining how well the TMR results apply to typical sleeping conditions involves the extent to which spontaneous reactivation during sleep and TMR differ. In support of their similarity, TMR success relies on the same physiological signals that support spontaneous memory reactivation. Spontaneous reactivation seems to occur optimally when it coincides with two prominent EEG events: slow oscillations and spindles. Slow oscillations are ~0.8 Hz oscillations that coordinate interactions between the hippocampus and neocortex and reactivation during slow-wave sleep (Diekelmann & Born, 2010; Helfrich et al., 2019). Sleep spindles are brief bursts of neural activity (0.5 – 2 s; 11-15 Hz) occurring between the thalamus and cortex that similarly coordinate hippocampal-neocortical interactions and overlap with hippocampal reactivation events (Antony et al., 2019; McCormick & Bal, 1997; Siapas & Wilson, 1998). Intriguingly, TMR efficacy can differ based on when cues are delivered with respect to the slow oscillation phase (Batterink et al., 2016; Ngo & Staresina, 2022; Xia et al., 2023; though see Goldi et al., 2019; J. Y. Wang et al., 2022). Additionally, TMR cues delivered shortly after spindles, which are unlikely to produce other beneficial post-cue spindles due to the presence of a 3-6 second spindle refractory period, are less effective than those delivered outside of the refractory period (Antony, Piloto, et al., 2018; Wang et al., 2019). These findings suggest that TMR *hijacks* spontaneous reactivation processes and supports the idea that outcomes for complex memory arrangements under TMR resemble spontaneous outcomes.

However, even in these studies, TMR cues could result in a reactivation event that differs – however subtly, on a cellular or ensemble level – from spontaneous reactivation. Proving definitively that there are no differences between targeted and spontaneous reactivation neurally will be difficult. Measuring spontaneous reactivation in humans, despite promising and impressive in-roads (Deuker et al., 2013; Schonauer et al., 2017; Schreiner et al., 2021), is coarse (often limited to the level of categories like places or objects, though see Deuker et al., 2013) and commonly yields low decoding accuracies. Moreover, unlike targeted reactivations, which have post-cue periods in which reactivation events are expected (Abdellahi et al., 2021; Belal et al., 2018; Cairney et al., 2018; Ngo & Staresina, 2022; Schechtman et al., 2022b; Wang et al., 2019), spontaneous reactivation occurs unpredictably, which makes identifying clear moments as reactivation events challenging. One potential avenue to resolve this issue would be to use data at the level of the neural ensemble in non-human rodents (Bendor & Wilson, 2012; Rothschild et al., 2017) or intracranial experiments in humans (Creery et al., 2022). These invasive techniques enable the detection of reactivation patterns on the neuronal level for both spontaneous and targeted events with high fidelity. If reactivation evidence during the period shortly after a TMR cue resembles evidence during spontaneous epochs, this would lend strong support to their being similar.

These problems will likely require many well-considered and well-controlled experiments to solidify progress in this area. Ultimately, given how spontaneous reactivation and TMR depend on the same hallmarks of sleep physiology, it may be best to regard the two reactivation types as similar if measured differences are very subtle or undetectable.

Future directions and concluding remarks

Our understanding about the mechanisms through which TMR impacts cognition has expanded substantially since its resurgence after the publication of Rasch et al. (2007) 15 years ago, and it has recently been shown to support learning in applied settings (Gao et al., 2020; Knötzele et al., 2023; Neumann et al., 2020; Vidal et al., 2022). However, real-world memories are often complex, and it is therefore important to understand the role of sleep reactivation in supporting their retrieval. We believe that the studies covered in this review have produced major insights informing our understanding of these complexities, and we hope our review has helped to identify common threads as well as knowledge gaps within the current literature.

More broadly, we envision two other directions for research on reactivation within complex learning arrangements. First, researchers could investigate the impact of sleep reactivation for even more complex networks of knowledge, such as arrangements with unique sets of commonalities among memories (e.g., Schapiro et al., 2017) or varying levels of interconnections as determined by nodes and links within a graph structure (e.g., Feld et al., 2022; Garvert et al., 2017). Second, applied research could similarly investigate how sleep reactivation supports more complex types of learning, such as reinforcing knowledge about the structure of the atom, framing an argument on a social issue like affirmative action, or generating insights about a novel engineering problem or analyses of a pre-read Emily Dickinson poem. These domains are naturally more difficult to control experimentally, but they have the added benefit of generalizing to everyday life (Yarkoni, 2022). In parallel, lab-based studies examining the effects of sleep on memory should employ more naturalistic designs involving complex stimuli such as videos (e.g., Antony et al., 2021; J. Chen et al., 2016) or virtual-reality-like experiences (e.g., K. C. Simon et al., 2022). Altogether, research on how sleep reactivation supports complex memories is at an exciting juncture, and we hope this review has helped to frame its commonalities and guide its future developments.

References

Abdellahi, M. E. A., Koopman, A. C. M., Treder, M. S., & Lewis, P. A. (2021). *Targeting targeted memory reactivation: Characteristics of cued reactivation in sleep* (p. 2021.12.09.471945). bioRxiv. https://doi.org/10.1101/2021.12.09.471945

Ai, S. Z., Yin, Y. L., Chen, Y., Wang, C., Sun, Y., Tang, X. D., Lu, L., Zhu, L. S., & Shi, J. (2018). Promoting subjective preferences in simple economic choices during nap. *Elife*, *7*, 21. https://doi.org/10.7554/eLife.40583

Aleman-Zapata, A., Morris, R. G. M., & Genzel, L. (2022). Sleep deprivation and hippocampal ripple disruption after one-session learning eliminate memory expression the next day. *Proceedings of the National Academy of Sciences*, *119*(44), e2123424119. https://doi.org/10.1073/pnas.2123424119

Anderson, M. C., Bjork, R. A., & Bjork, E. L. (1994). Remembering can cause forgetting: Retrieval dynamics in long-term memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *20*(5), 1063–1087. https://doi.org/10.1037//0278-7393.20.5.1063

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. https://doi.org/10.1037/0278-7393.25.3.608

Antony, J. W., Cheng, L. Y., Brooks, P. P., Paller, K. A., & Norman, K. A. (2018). Competitive learning modulates memory consolidation during sleep. *Neurobiology of Learning and Memory*, *155*, 216–230. https://doi.org/10.1016/j.nlm.2018.08.007

Antony, J. W., Hartshorne, T. H., Pomeroy, K., Gureckis, T. M., Hasson, U., McDougle, S. D., & Norman, K. A. (2021). Behavioral, Physiological, and Neural Signatures of Surprise during Naturalistic Sports Viewing. *Neuron*, *109*(2), 377-390.e7. https://doi.org/10.1016/j.neuron.2020.10.029

Antony, J. W., Piloto, L., Wang, M., Pacheco, P., Norman, K. A., & Paller, K. A. (2018). Sleep Spindle Refractoriness Segregates Periods of Memory Reactivation. *Current Biology*, *28*(11), 1736-1743 e4. https://doi.org/10.1016/j.cub.2018.04.020

Antony, J. W., Romero, A., Vierra, A. H., Luenser, R. S., Hawkins, R. D., & Bennion, K. A. (2022). Semantic relatedness retroactively boosts memory and promotes memory interdependence across episodes. *ELife*, *11*, e72519. https://doi.org/10.7554/eLife.72519

Antony, J. W., Schonauer, M., Staresina, B. P., & Cairney, S. A. (2019). Sleep Spindles and Memory Reprocessing. *Trends Neurosci*, *42*(1), 1–3. https://doi.org/10.1016/j.tins.2018.09.012

Bar, E., Marmelshtein, A., Arzi, A., Perl, O., Livne, E., Hizmi, E., Paz, R., Sobel, N., Dudai, Y., & Nir, Y. (2020). Local Targeted Memory Reactivation in Human Sleep. *Curr Biol*. https://doi.org/10.1016/j.cub.2020.01.091

Barnes, J. M., & Underwood, B. J. (1959). “Fate” of first-list associations in transfer theory. *Journal of Experimental Psychology*, *58*, 97–105. https://doi.org/10.1037/h0047507

Batterink, L. J., Creery, J. D., & Paller, K. A. (2016). Phase of Spontaneous Slow Oscillations during Sleep Influences Memory-Related Processing of Auditory Cues. *J Neurosci*, *36*(4), 1401–1409. https://doi.org/10.1523/jneurosci.3175-15.2016

Bäuml, K.-H., & Hartinger, A. (2002). On the role of item similarity in retrieval-induced forgetting. *Memory (Hove, England)*, *10*(3), 215–224. https://doi.org/10.1080/09658210143000362

Beck, J., Loretz, E., & Rasch, B. (2021). Exposure to relaxing words during sleep promotes slow-wave sleep and subjective sleep quality. *Sleep*, *44*(11), zsab148. https://doi.org/10.1093/sleep/zsab148

Belal, S., Cousins, J., El-Deredy, W., Parkes, L., Schneider, J., Tsujimura, H., Zoumpoulaki, A., Perapoch, M., Santamaria, L., & Lewis, P. (2018). Identification of memory reactivation during sleep by EEG classification. *NeuroImage*, *176*, 203–214.

https://doi.org/10.1016/j.neuroimage.2018.04.029

Bendor, D., & Wilson, M. A. (2012). Biasing the content of hippocampal replay during sleep. *Nat Neurosci*, *15*(10), 1439–1444. https://doi.org/10.1038/nn.3203

Benson, K., & Feinberg, I. (1977). The beneficial effect of sleep in an extended Jenkins and Dallenbach paradigm. *Psychophysiology*, *14*, 375–384. https://doi.org/10.1111/j.1469-8986.1977.tb02967.x

Bridge, D. J., & Voss, J. L. (2015). Binding among select episodic elements is altered via active short-term retrieval. *Learning & Memory*, *22*(8), 360–363. https://doi.org/10.1101/lm.038703.115

Briggs, G. E. (1954). Acquisition, extinction, and recovery functions in retroactive inhibition. *Journal of Experimental Psychology*, *47*, 285–293. https://doi.org/10.1037/h0060251

Buzsáki, G. (1989). Two-stage model of memory trace formation: A role for “noisy” brain states. *Neuroscience*, *31*(3), 551–570. https://doi.org/10.1016/0306-4522(89)90423-5

Cairney, S. A., Guttesen, A. A. V., El Marj, N., & Staresina, B. P. (2018). Memory Consolidation Is Linked to Spindle-Mediated Information Processing during Sleep. *Current Biology*, *28*(6), 948-954.e4. https://doi.org/10.1016/j.cub.2018.01.087

Cairney, S. A., Lindsay, S., Sobczak, J. M., Paller, K. A., & Gaskell, M. G. (2016). The Benefits of Targeted Memory Reactivation for Consolidation in Sleep are Contingent on Memory Accuracy and Direct Cue-Memory Associations. *Sleep*, *39*(5), 1139–1150. https://doi.org/10.5665/sleep.5772

Carey, A. A., Tanaka, Y., & van der Meer, M. A. A. (2019). Reward revaluation biases hippocampal replay content away from the preferred outcome. *Nature Neuroscience*. https://doi.org/10.1038/s41593-019-0464-6

Carroll, M., Campbell-Ratcliffe, J., Murnane, H., & Perfect, T. (2007). Retrieval-induced forgetting in educational contexts: Monitoring, expertise, text integration, and test format. *European Journal of Cognitive Psychology*, *19*(4–5), 580–606.

https://doi.org/10.1080/09541440701326071

Chen, J., Honey, C. J., Simony, E., Arcaro, M. J., Norman, K. A., & Hasson, U. (2016). Accessing Real-Life Episodic Information from Minutes versus Hours Earlier Modulates Hippocampal and High-Order Cortical Dynamics. *Cerebral Cortex*, *26*(8), 3428–3441. https://doi.org/10.1093/cercor/bhv155

Chen, L., Wang, Y., Zhang, Y., & Wang, Y. (2021). A new application of TMR: A study on implicit self-esteem. *Current Psychology*. https://doi.org/10.1007/s12144-021-01883-5

Cowan, E., Liu, A., Henin, S., Kothare, S., Devinsky, O., & Davachi, L. (2020). Sleep spindles promote the restructuring of memory representations in ventromedial prefrontal cortex through enhanced hippocampal-cortical functional connectivity. *The Journal of Neuroscience*, 1946–19. https://doi.org/10.1523/jneurosci.1946-19.2020

Cowan, E. T., Schapiro, A. C., Dunsmoor, J. E., & Murty, V. P. (2021). Memory consolidation as an adaptive process. *Psychonomic Bulletin & Review*, *28*(6), 1796–1810. https://doi.org/10.3758/s13423-021-01978-x

Cowell, R. A., Barense, M. D., & Sadil, P. S. (2019). A Roadmap for Understanding Memory: Decomposing Cognitive Processes into Operations and Representations. *ENeuro*, *6*(4). https://doi.org/10.1523/ENEURO.0122-19.2019

Creery, J. D., Brang, D. J., Arndt, J. D., Bassard, A., Towle, V. L., Tao, J. X., Wu, S., Rose, S., Warnke, P. C., Issa, N. P., & Paller, K. A. (2022). Electrophysiological markers of memory consolidation in the human brain when memories are reactivated during sleep. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(44), e2123430119. https://doi.org/10.1073/pnas.2123430119

Creery, J. D., Oudiette, D., Antony, J. W., & Paller, K. A. (2015). Targeted Memory Reactivation during Sleep Depends on Prior Learning. *Sleep*, *38*(5), 755–763. https://doi.org/10.5665/sleep.4670

Davidson, P., Jönsson, P., Carlsson, I., & Pace-Schott, E. (2021). Does Sleep Selectively

Strengthen Certain Memories Over Others Based on Emotion and Perceived Future Relevance? *Nature and Science of Sleep*, *13*, 1257–1306. https://doi.org/10.2147/NSS.S286701

Denis, D., Schapiro, A. C., Poskanzer, C., Bursal, V., Charon, L., Morgan, A., & Stickgold, R. (2020). The roles of item exposure and visualization success in the consolidation of memories across wake and sleep. *Learn Mem*, *27*(11), 451–456. https://doi.org/10.1101/lm.051383.120

Deuker, L., Olligs, J., Fell, J., Kranz, T. A., Mormann, F., Montag, C., Reuter, M., Elger, C. E., & Axmacher, N. (2013). Memory consolidation by replay of stimulus-specific neural activity. *J Neurosci*, *33*(49), 19373–19383. https://doi.org/10.1523/jneurosci.0414-13.2013

Diekelmann, S., & Born, J. (2010). The memory function of sleep. *Nat Rev Neurosci*, *11*(2), 114–126. https://doi.org/10.1038/nrn2762

Diekelmann, S., Buchel, C., Born, J., & Rasch, B. (2011). Labile or stable: Opposing consequences for memory when reactivated during waking and sleep. *Nature Neuroscience*, *14*(3), 381–386. https://doi.org/10.1038/nn.2744

Dupret, D., O'Neill, J., Pleydell-Bouverie, B., & Csicsvari, J. (2010). The reorganization and reactivation of hippocampal maps predict spatial memory performance. *Nature Neuroscience*, *13*(8), 995–1002. https://doi.org/10.1038/nn.2599

Ego-Stengel, V., & Wilson, M. A. (2010). Disruption of ripple-associated hippocampal activity during rest impairs spatial learning in the rat. *Hippocampus*, *20*(1), 1–10. https://doi.org/10.1002/hipo.20707

Eisenberg, M., Kobilo, T., Berman, D. E., & Dudai, Y. (2003). Stability of retrieved memory: Inverse correlation with trace dominance. *Science*, *301*(5636), 1102–1104. https://doi.org/10.1126/science.1086881

Feld, G. B., Bernard, M., Rawson, A. B., & Spiers, H. J. (2022). Sleep targets highly connected global and local nodes to aid consolidation of learned graph networks. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-17747-2

Fernández-Ruiz, A., Oliva, A., Fermino de Oliveira, E., Rocha-Almeida, F., Tingley, D., & Buzsáki, G. (2019). Long-duration hippocampal sharp wave ripples improve memory. *Science (New York, N.Y.)*, *364*(6445), 1082–1086. https://doi.org/10.1126/science.aax0758

Fischer, S., & Born, J. (2009). Anticipated reward enhances offline learning during sleep. *J Exp Psychol Learn Mem Cogn*, *35*(6), 1586–1593. https://doi.org/10.1037/a0017256

Gao, C., Fillmore, P., & Scullin, M. K. (2020). Classical Music, Educational Learning, and Slow Wave Sleep: A Targeted Memory Reactivation Experiment. *Neurobiology of Learning and Memory*, 107206. https://doi.org/10.1016/j.nlm.2020.107206

Garlitch, S. M., & Wahlheim, C. N. (2020). The role of reminding in retroactive effects of memory for older and younger adults. *Psychology and Aging*, *35*, 697–709. https://doi.org/10.1037/pag0000427

Garvert, M. M., Dolan, R. J., & Behrens, T. E. (2017). A map of abstract relational knowledge in the human hippocampal–entorhinal cortex. *ELife*, *6*, e17086. https://doi.org/10.7554/eLife.17086

Gibson, T., Cross, Z. R., & Chatburn, A. (2022). Theta Activity During Encoding Interacts With NREM Sleep Oscillations to Predict Memory Generalization. *Frontiers in Human Neuroscience*, *16*. https://www.frontiersin.org/articles/10.3389/fnhum.2022.821191

Girardeau, G., Benchenane, K., Wiener, S. I., Buzsaki, G., & Zugaro, M. B. (2009). Selective suppression of hippocampal ripples impairs spatial memory. *Nature Neuroscience*, *12*(10), 1222–1223. https://doi.org/10.1038/nn.2384

Goldi, M., van Poppel, E. A. M., Rasch, B., & Schreiner, T. (2019). Increased neuronal signatures of targeted memory reactivation during slow-wave up states. *Scientific Reports*, *9*(1), 2715. https://doi.org/10.1038/s41598-019-39178-2

Gridchyn, I., Schoenenberger, P., O’Neill, J., & Csicsvari, J. (2020). Assembly-Specific

Disruption of Hippocampal Replay Leads to Selective Memory Deficit. *Neuron*, *106*(2), 291-300.e6. https://doi.org/10.1016/j.neuron.2020.01.021

Guerrien, A., Dujardin, K., Mandal, O., Sockeel, P., & Leconte, P. (1989). Enhancement of memory by auditory stimulation during postlearning REM sleep in humans. *Physiology & Behavior*, *45*(5), 947–950. https://doi.org/10.1016/0031-9384(89)90219-9

Hebb, D. O. (1949). *The organization of behavior; a neuropsychological theory* (pp. xix, 335). Wiley.

Heib, D. P. J., Hoedlmoser, K., Anderer, P., Gruber, G., Zeitlhofer, J., & Schabus, M. (2015). Oscillatory theta activity during memory formation and its impact on overnight consolidation: A missing link? *Journal of Cognitive Neuroscience*, *27*(8), 1648–1658. https://doi.org/10.1162/jocn_a_00804

Heine, R. (1914). *Über Wiedererkennen und rückwirkende Hemmung*. Johann Ambrosius Barth.

Helfrich, R. F., Lendner, J. D., Mander, B. A., Guillen, H., Paff, M., Mnatsakanyan, L., Vadera, S., Walker, M. P., Lin, J. J., & Knight, R. T. (2019). Bidirectional prefrontal-hippocampal dynamics organize information transfer during sleep in humans. *Nature Communications*, *10*(1), 3572. https://doi.org/10.1038/s41467-019-11444-x

Hintzman, D. L. (2011). Research Strategy in the Study of Memory: Fads, Fallacies, and the Search for the “Coordinates of Truth.” *Perspectives on Psychological Science*, *6*(3), 253–271. https://doi.org/10.1177/1745691611406924

Horner, A. J., Bisby, J. A., Bush, D., Lin, W.-J., & Burgess, N. (2015). Evidence for holistic episodic recollection via hippocampal pattern completion. *Nature Communications*, *6*(1), Article 1. https://doi.org/10.1038/ncomms8462

Horner, A. J., & Burgess, N. (2014). Pattern completion in multielement event engrams. *Current Biology: CB*, *24*(9), 988–992. https://doi.org/10.1016/j.cub.2014.03.012

Hu, X., Cheng, L. Y., Chiu, M. H., & Paller, K. A. (2020). Promoting memory consolidation during sleep: A meta-analysis of targeted memory reactivation. *Psychol Bull*, *146*(3), 218–244. https://doi.org/10.1037/bul0000223

Jacoby, L. L., Wahlheim, C. N., & Kelley, C. M. (2015). Memory consequences of looking back to notice change: Retroactive and proactive facilitation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *41*, 1282–1297. https://doi.org/10.1037/xlm0000123

Jenkins, J. G., & Dallenbach, K. M. (1924). Obliviscence during sleep and waking. *The American Journal of Psychology*, *35*(4), 605–612.

Ji, D., & Wilson, M. A. (2007). Coordinated memory replay in the visual cortex and hippocampus during sleep. *Nature Neuroscience*, *10*(1), 100–107. https://doi.org/10.1038/nn1825

Joensen, B. H., Harrington, M. O., Berens, S. C., Cairney, S. A., Gaskell, M. G., & Horner, A. J. (2022). Targeted memory reactivation during sleep can induce forgetting of overlapping memories. *Learning & Memory (Cold Spring Harbor, N.Y.)*, *29*(11), 401–411. https://doi.org/10.1101/lm.053594.122

Johnson, B. P., Scharf, S. M., Verceles, A. C., & Westlake, K. P. (2020). Sensorimotor performance is improved by targeted memory reactivation during a daytime nap in healthy older adults. *Neurosci Lett*, 134973. https://doi.org/10.1016/j.neulet.2020.134973

Klinzing, J. G., Kugler, S., Soekadar, S. R., Rasch, B., Born, J., & Diekelmann, S. (2018). Odor cueing during slow-wave sleep benefits memory independently of low cholinergic tone. *Psychopharmacology*, *235*(1), 291–299. https://doi.org/10.1007/s00213-017-4768-5

Knötzele, J., Riemann, D., Frase, L., Feige, B., van Elst, L. T., & Kornmeier, J. (2023). Presenting rose odor during learning, sleep and retrieval helps to improve memory consolidation: A real-life study. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-28676-z

Kouider, S., Andrillon, T., Barbosa, L. S., Goupil, L., & Bekinschtein, T. A. (2014). Inducing task-relevant responses to speech in the sleeping brain. *Current Biology: CB*, *24*(18), 2208–2214. https://doi.org/10.1016/j.cub.2014.08.016

Laventure, S., Fogel, S., Lungu, O., Albouy, G., Sevigny-Dupont, P., Vien, C., Sayour, C., Carrier, J., Benali, H., & Doyon, J. (2016). NREM2 and Sleep Spindles Are Instrumental to the Consolidation of Motor Sequence Memories. *PLoS Biol*, *14*(3), e1002429. https://doi.org/10.1371/journal.pbio.1002429

Laventure, S., Pinsard, B., Lungu, O., Carrier, J., Fogel, S., Benali, H., Lina, J. M., Boutin, A., & Doyon, J. (2018). Beyond spindles: Interactions between sleep spindles and boundary frequencies during cued reactivation of motor memory representations. *Sleep*. https://doi.org/10.1093/sleep/zsy142

Lee, A. K., & Wilson, M. A. (2002). Memory of Sequential Experience in the Hippocampus during Slow Wave Sleep. *Neuron*, *36*(6), 1183–1194. https://doi.org/10.1016/S0896-6273(02)01096-6

Lewis, P. A., & Durrant, S. J. (2011). Overlapping memory replay during sleep builds cognitive schemata. *Trends Cogn Sci*, *15*(8), 343–351. https://doi.org/10.1016/j.tics.2011.06.004

Lewis-Peacock, J. A., & Norman, K. A. (2014). Competition between items in working memory leads to forgetting. *Nature Communications*, *5*(1), Article 1. https://doi.org/10.1038/ncomms6768

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*(3), 419–457. https://doi.org/10.1037/0033-295x.102.3.419

McCormick, D. A., & Bal, T. (1997). Sleep and arousal: Thalamocortical mechanisms. *Annual Review of Neuroscience*, *20*, 185–215. https://doi.org/10.1146/annurev.neuro.20.1.185

Moeser, S. D. (1979). Retrieval interference in the independent storage of related episodic traces. *Canadian Journal of Psychology / Revue Canadienne de Psychologie*, *33*, 185–192. https://doi.org/10.1037/h0081715

Nádasdy, Z., Hirase, H., Czurkó, A., Csicsvari, J., & Buzsáki, G. (1999). Replay and Time

Compression of Recurring Spike Sequences in the Hippocampus. *The Journal of Neuroscience*, *19*(21), 9497–9507. https://doi.org/10.1523/jneurosci.19-21-09497.1999

Neumann, F., Oberhauser, V., & Kornmeier, J. (2020). How odor cues help to optimize learning during sleep in a real life-setting. *Scientific Reports*, *10*(1), 1227. https://doi.org/10.1038/s41598-020-57613-7

Ngo, C. T., Horner, A. J., Newcombe, N. S., & Olson, I. R. (2019). Development of Holistic Episodic Recollection. *Psychological Science*, *30*(12), 1696–1706. https://doi.org/10.1177/0956797619879441

Ngo, H.-V. V., & Staresina, B. P. (2022). Shaping overnight consolidation via slow-oscillation closed-loop targeted memory reactivation. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(44), e2123428119. https://doi.org/10.1073/pnas.2123428119

Oudiette, D., Antony, J. W., Creery, J. D., & Paller, K. A. (2013). The role of memory reactivation during wakefulness and sleep in determining which memories endure. *J Neurosci*, *33*(15), 6672–6678. https://doi.org/10.1523/jneurosci.5497-12.2013

Oyarzun, J. P., Moris, J., Luque, D., de Diego-Balaguer, R., & Fuentemilla, L. (2017). Targeted Memory Reactivation during Sleep Adaptively Promotes the Strengthening or Weakening of Overlapping Memories. *J Neurosci*, *37*(32), 7748–7758. https://doi.org/10.1523/jneurosci.3537-16.2017

Pavlides, C., & Winson, J. (1989). Influences of hippocampal place cell firing in the awake state on the activity of these cells during subsequent sleep episodes. *J Neurosci*, *9*(8), 2907–2918.

Peyrache, A., Battaglia, F. P., & Destexhe, A. (2011). Inhibition recruitment in prefrontal cortex during sleep spindles and gating of hippocampal inputs. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(41), 17207–17212. https://doi.org/10.1073/pnas.1103612108

Picard-Deland, C., Aumont, T., Samson-Richer, A., Paquette, T., & Nielsen, T. (2021). Whole-body procedural learning benefits from targeted memory reactivation in REM sleep and task-related dreaming. *Neurobiology of Learning and Memory*, *183*, 107460. https://doi.org/10.1016/j.nlm.2021.107460

Picard-Deland, C., & Nielsen, T. (2022). Targeted memory reactivation has a sleep stage-specific delayed effect on dream content. *Journal of Sleep Research*, *31*(1), e13391. https://doi.org/10.1111/jsr.13391

Rasch, B., Buchel, C., Gais, S., & Born, J. (2007). Odor cues during slow-wave sleep prompt declarative memory consolidation. *Science*, *315*(5817), 1426–1429. https://doi.org/10.1126/science.1138581

Reder, L. M., & Anderson, J. R. (1980). A partial resolution of the paradox of interference: The role of integrating knowledge. *Cognitive Psychology*, *12*, 447–472. https://doi.org/10.1016/0010-0285(80)90016-X

Richter, F. R., Chanales, A. J. H., & Kuhl, B. A. (2016). Predicting the integration of overlapping memories by decoding mnemonic processing states during learning. *NeuroImage*, *124*, 323–335. https://doi.org/10.1016/j.neuroimage.2015.08.051

Rihm, J. S., Diekelmann, S., Born, J., & Rasch, B. (2014). Reactivating memories during sleep by odors: Odor specificity and associated changes in sleep oscillations. *Journal of Cognitive Neuroscience*, *26*(8), 1806–1818. https://doi.org/10.1162/jocn_a_00579

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. https://doi.org/10.1038/nn.4457

Rudoy, J. D., Voss, J. L., Westerberg, C. E., & Paller, K. A. (2009). Strengthening individual memories by reactivating them during sleep. *Science*, *326*(5956), 1079. https://doi.org/10.1126/science.1179013

Runquist, W. N. (1975). Interference among memory traces. *Memory & Cognition*, *3*, 143–159.

https://doi.org/10.3758/BF03212891

Schapiro, A. C., Turk-Browne, N. B., Botvinick, M. M., & Norman, K. A. (2017). Complementary learning systems within the hippocampus: A neural network modelling approach to reconciling episodic memory with statistical learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1711), 20160049. https://doi.org/10.1098/rstb.2016.0049

Schechtman, E., Antony, J. W., Lampe, A., Wilson, B. J., Norman, K. A., & Paller, K. A. (2021). Multiple memories can be simultaneously reactivated during sleep as effectively as a single memory. *Communications Biology*, *4*(1), 25. https://doi.org/10.1038/s42003-020-01512-0

Schechtman, E., Heilberg, J., & Paller, K. A. (2022). Made together, replayed together: Context reinstatement during sleep guides memory consolidation. *BioRxiv*, 2022.03.28.486140. https://doi.org/10.1101/2022.03.28.486140

Schechtman, E., Heilberg, J., & Paller, K. A. (2023). Context matters: Changes in memory over a period of sleep are driven by encoding context. *Learning & Memory (Cold Spring Harbor, N.Y.)*, *30*(2), 36–42. https://doi.org/10.1101/lm.053634.122

Schechtman, E., Lampe, A., Wilson, B. J., Kwon, E., Anderson, M. C., & Paller, K. A. (2021). Sleep reactivation did not boost suppression-induced forgetting. *Sci Rep*, *11*(1), 1383–1383. https://doi.org/10.1038/s41598-020-80671-w

Schechtman, E., Witkowski, S., Lampe, A., Wilson, B. J., & Paller, K. A. (2020). Targeted memory reactivation during sleep boosts intentional forgetting of spatial locations. *Scientific Reports*, *10*(1), 2327. https://doi.org/10.1038/s41598-020-59019-x

Schonauer, M., Alizadeh, S., Jamalabadi, H., Abraham, A., Pawlizki, A., & Gais, S. (2017). Decoding material-specific memory reprocessing during sleep in humans. *Nature Communications*, *8*, 15404. https://doi.org/10.1038/ncomms15404

Schreiner, T., Petzka, M., Staudigl, T., & Staresina, B. P. (2021). Endogenous memory reactivation during sleep in humans is clocked by slow oscillation-spindle complexes. *Nature Communications*, *12*(1), 3112. https://doi.org/10.1038/s41467-021-23520-2

Schreiner, T., & Rasch, B. (2015). Boosting Vocabulary Learning by Verbal Cueing During Sleep. *Cerebral Cortex*, *25*(11), 4169–4179. https://doi.org/10.1093/cercor/bhu139

Schwartz, S., Clerget, A., & Perogamvros, L. (2022). Enhancing imagery rehearsal therapy for nightmares with targeted memory reactivation. *Current Biology*, S0960982222014774. https://doi.org/10.1016/j.cub.2022.09.032

Seibold, M., Rasch, B., Born, J., & Diekelmann, S. (2018). Reactivation of interference during sleep does not impair ongoing memory consolidation. *Memory*, *26*(3), 377–384. https://doi.org/10.1080/09658211.2017.1329442

Shanahan, L. K., Gjorgieva, E., Paller, K. A., Kahnt, T., & Gottfried, J. A. (2018). Odor-evoked category reactivation in human ventromedial prefrontal cortex during sleep promotes memory consolidation. *Elife*, *7*, 21. https://doi.org/10.7554/eLife.39681

Siapas, A. G., & Wilson, M. A. (1998). Coordinated interactions between hippocampal ripples and cortical spindles during slow-wave sleep. *Neuron*, *21*(5), 1123–1128.

Simon, K. C., Clemenson, G. D., Zhang, J., Sattari, N., Shuster, A. E., Clayton, B., Alzueta, E., Dulai, T., de Zambotti, M., Stark, C., Baker, F. C., & Mednick, S. C. (2022). Sleep facilitates spatial memory but not navigation using the Minecraft Memory and Navigation task. *Proceedings of the National Academy of Sciences*, *119*(43), e2202394119. https://doi.org/10.1073/pnas.2202394119

Simon, K., Gomez, R. L., & Nadel, L. (2018). Losing memories during sleep after targeted memory reactivation. *Neurobiology of Learning and Memory*, *151*, 10–17. https://doi.org/10.1016/j.nlm.2018.03.003

Stark, S. M., Reagh, Z. M., Yassa, M. A., & Stark, C. E. L. (2018). What’s in a context? Cautions, limitations, and potential paths forward. *Neurosci Lett*, *680*, 77–87. https://doi.org/10.1016/j.neulet.2017.05.022

Sterpenich, V., van Schie, M. K. M., Catsiyannis, M., Ramyead, A., Perrig, S., Yang, H.-D., Van De Ville, D., & Schwartz, S. (2021). Reward biases spontaneous neural reactivation during sleep. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-021-24357-5

Tilley, A. J. (1979). Sleep learning during Stage 2 and REM sleep. *Biological Psychology*, *9*, 155–161. https://doi.org/10.1016/0301-0511(79)90035-8

Tompary, A., & Davachi, L. (2017). Consolidation Promotes the Emergence of Representational Overlap in the Hippocampus and Medial Prefrontal Cortex. *Neuron*, *96*(1), 228-241.e5. https://doi.org/10.1016/j.neuron.2017.09.005

van Dongen, E. V., Thielen, J. W., Takashima, A., Barth, M., & Fernandez, G. (2012). Sleep supports selective retention of associative memories based on relevance for future utilization. *PLoS ONE*, *7*(8), e43426. https://doi.org/10.1371/journal.pone.0043426

Vargas, I. M., Schechtman, E., & Paller, K. A. (2019). Targeted memory reactivation during sleep to strengthen memory for arbitrary pairings. *Neuropsychologia*, *124*, 144–150.

Vidal, V., Barbuzza, A. R., Tassone, L. M., Brusco, L. I., Ballarini, F. M., & Forcato, C. (2022). Odor cueing during sleep improves consolidation of a history lesson in a school setting. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-14588-x

Wang, B., Antony, J. W., Lurie, S., Brooks, P. P., Paller, K. A., & Norman, K. A. (2019). Targeted memory reactivation during sleep elicits neural signals related to learning content. *J Neurosci*. https://doi.org/10.1523/jneurosci.2798-18.2019

Wang, J. Y., Heck, K. L., Born, J., Ngo, H. V., & Diekelmann, S. (2022). No difference between slow oscillation up- and down-state cueing for memory consolidation during sleep. *Journal of Sleep Research*, e13562. https://doi.org/10.1111/jsr.13562

Wilhelm, I., Diekelmann, S., Molzow, I., Ayoub, A., Molle, M., & Born, J. (2011). Sleep selectively enhances memory expected to be of future relevance. *J Neurosci*, *31*(5), 1563–1569. https://doi.org/10.1523/jneurosci.3575-10.2011

Wilson, M. A., & McNaughton, B. L. (1994). Reactivation of hippocampal ensemble memories during sleep. *Science*, *265*(5172), 676–679.

Witkowski, S., Schechtman, E., & Paller, K. A. (2020). Examining sleep's role in memory generalization and specificity through the lens of targeted memory reactivation. *Current Opinion in Behavioral Sciences*, *33*, 86–91. https://doi.org/10.1016/j.cobeha.2020.01.007

Wylie, G. R., Foxe, J. J., & Taylor, T. L. (2008). Forgetting as an active process: An FMRI investigation of item-method-directed forgetting. *Cerebral Cortex*, *18*(3), 670–682. https://doi.org/10.1093/cercor/bhm101

Xia, T., Antony, J. W., Paller, K. A., & Hu, X. (2023). Targeted memory reactivation during sleep influences social bias as a function of slow-oscillation phase and delta power. *Psychophysiology*, *n/a*(n/a), e14224. https://doi.org/10.1111/psyp.14224

Yarkoni, T. (2022). The generalizability crisis. *Behavioral and Brain Sciences*, *45*, e1. https://doi.org/10.1017/S0140525X20001685

Yaroush, R., Sullivan, M. J., & Ekstrand, B. R. (1971). Effect of sleep on memory. II. Differential effect of the first and second half of the night. *Journal of Experimental Psychology*, *88*(3), 361–366.

Young, R. K. (1955). Retroactive and proactive effects under varying conditions of response similarity. *Journal of Experimental Psychology*, *50*, 113–119. https://doi.org/10.1037/h0047382