Neuropsychologia 138 (2020) 107328

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: http://www.elsevier.com/locate/neuropsychologia

Dynamic internal states shape memory retrieval

Hannah Tarder-Stoll[a,1,*], Manasi Jayakumar[a,*,1], Halle R. Dimsdale-Zucker[a], Eren Günseli[a], Mariam Aly[a,b]

[a] Department of Psychology, Columbia University, USA
[b] Affiliate Member, Zuckerman Mind Brain Behavior Institute, Columbia University, USA

ARTICLE INFO

Keywords:
Episodic memory
Goal states
Neuromodulation
Goal-directed attention
Medial temporal lobe
Prefrontal cortex

ABSTRACT

Why do we sometimes easily retrieve memories, but other times appear to forget them? We often look to our external environment for retrieval cues, but another way to optimize memory retrieval is to be in a mental state, or mode, that prioritizes access to our internal representation of the world. Such a 'retrieval mode' was proposed by Endel Tulving (1983), who considered it a neurocognitive state in which one keeps the goal of memory retrieval in mind. Building on Tulving's proposal, we review converging evidence from multiple lines of research that emphasize the importance of internal states in the instantiation of retrieval modes that optimize successful remembering. We identify three key factors that contribute to a retrieval mode by modulating either the likelihood or the content of retrieval: (1) an intention to remember or forget (either in the present or the future), (2) attentional selection of goal-relevant memories and suppression of distractors, and (3) fluctuating levels of acetylcholine in the hippocampus. We discuss empirical evidence that these internal states individually influence memory retrieval and propose how they may interact synergistically. Characterizing these dynamic internal factors is an important key for unlocking our understanding of the organization and accessibility of our memories.

1. Introduction

A crucial component of memory is the ability to retrieve stored information, such as the name of a familiar person or where we know them from. Why we sometimes easily retrieve this information, but other times appear to forget it, has vexed memory researchers for decades. One piece of the puzzle is that retrieval does not happen in isolation but is supported by contextual information present during encoding. This is reflected in Tulving's influential encoding specificity hypothesis, which postulates that memory retrieval is optimized when there is a match between the external context at encoding and that at retrieval (Tulving and Thomson, 1971). Another way to optimize memory retrieval, however, is to be in a mental state, or mode, that prioritizes access to our internal representation of the world. Accordingly, Tulving proposed the idea of a *retrieval mode* as a neurocognitive state that one engages when they intend to retrieve a memory (Tulving, 1983) — a mode that may impact whether we retrieve information and what we retrieve. Such a mode involves attention that is focused on information relevant for retrieving that memory, and may be instantiated even before a retrieval cue is apprehended (Lepage et al., 2000). We propose that its core components include intention (to retrieve a memory), attention (focused on goal-relevant features), and an internal neuromodulatory state that is optimized for remembering even prior to the act of retrieval itself.

This focus on internal states reflects a shift in the field's efforts to understand the factors that help or hinder memory retrieval: In the 1980s, 1990s, and early 2000s, much effort was devoted to understanding how external factors contribute to memory success or failure. For example, spacing and frequency of studying to-be-learned material (Bahrick et al., 1993; Roediger and Karpicke, 2006); the presence of semantically-related information during learning (Roediger and McDermott, 1995); information encountered prior to retrieval, even when it is below the threshold of awareness (Tulving and Schacter, 1990); the presence of affective information (Kensinger et al., 2007); and the use of external mnemonic support (Vortac et al., 1995; Block and Morwitz, 1999; Rajaram and Pereira-Pasarin, 2007) can all impact memory performance.

Tulving made the critical observation that these external factors must act through the mental state of the individual: "[…] *an effective*

---

* Corresponding authors. 406 Schermerhorn Hall, 1190 Amsterdam Ave, MC 5501, New York, NY, 10027, USA.
E-mail addresses: hrt2116@columbia.edu (H. Tarder-Stoll), mj2873@columbia.edu (M. Jayakumar).

[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.neuropsychologia.2019.107328
Received 1 July 2019; Received in revised form 13 December 2019; Accepted 22 December 2019

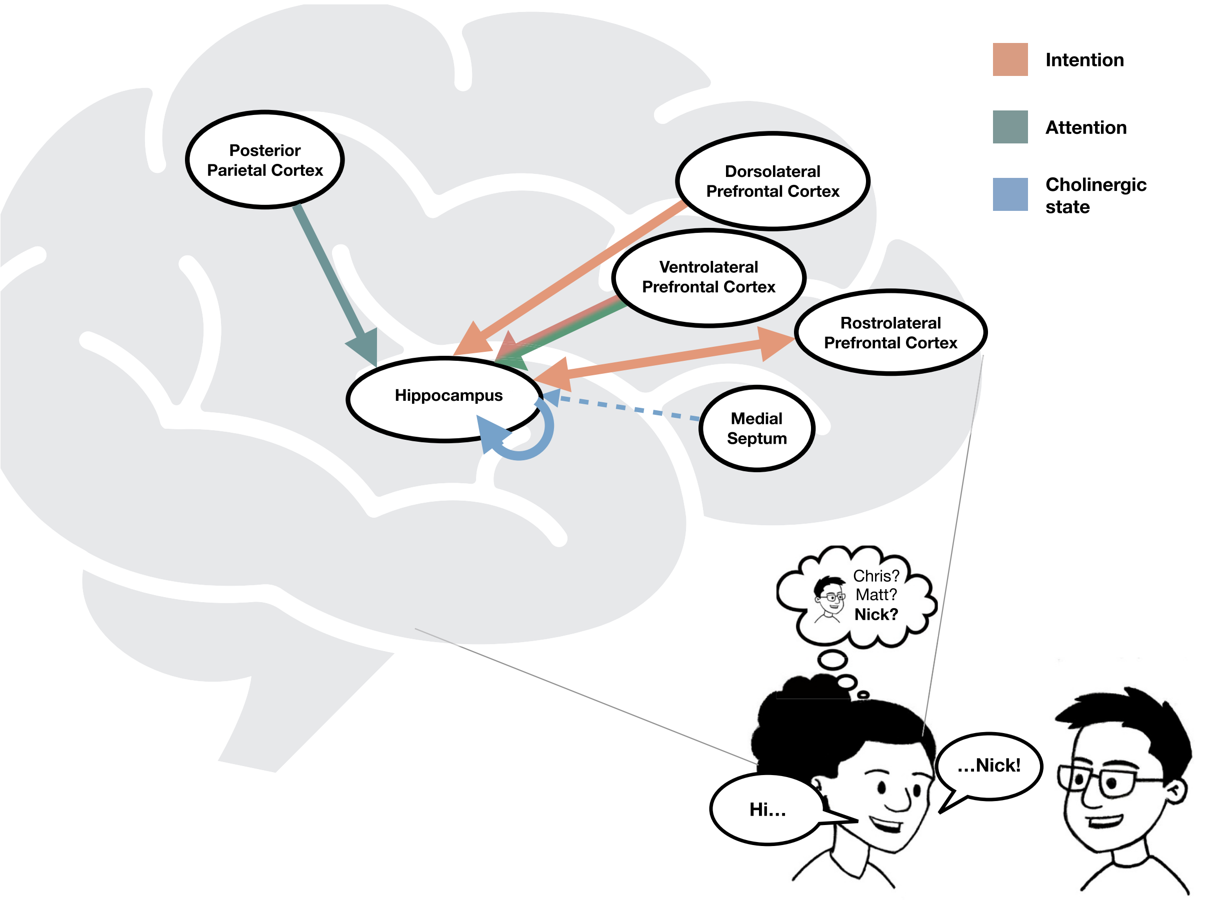

Fig. 1. | How intentions, attention, and neuromodulatory states contribute to retrieval mode. Here, we illustrate a subset of the cognitive and neural mechanisms by which intentions, attention, and neuromodulatory states interact to instantiate and maintain retrieval mode. Other neural interactions likely exist but are not as well characterized and hence not included in this figure. Imagine that you run into an acquaintance at a departmental party and are attempting to retrieve their name. The intention to retrieve their name helps suppress competing memories (e.g., names of your former romantic partners) and competing perceptual distractors (e.g., the table of snacks) while focusing attentional resources on goal-relevant information (e.g., names that are familiar from work). These processes are enacted through top-down control mechanisms in the dorsolateral prefrontal cortex and ventrolateral prefrontal cortex. Specifically, dorsolateral and ventrolateral prefrontal cortex act to set intentions, and ventrolateral prefrontal cortex guides selective attention. These regions support these functions, at least in part, by modulating the hippocampus to prioritize goal-directed memory retrieval and to suppress memories that are intended to be forgotten. Simultaneously, the posterior parietal cortex focuses attention towards hippocampal memories, and aids in the construction and representation of recovered information. Whether or not you ultimately retrieve the name of your colleague may also depend on localized neuromodulatory states: Reduced acetylcholine release from the medial septum into the hippocampus (indicated by the dashed blue line) improves memory retrieval by enhancing pattern completion in recurrent hippocampal connections. These internal states therefore synergistically contribute to remembering in the present moment. Finally, they allow us to set intentions to remember in the future (e.g., to remember to pass on a message from one colleague to another). Such prospective intentions are supported by interactions between the rostrolateral prefrontal cortex and hippocampus. Together, this network of regions acts to initiate and maintain retrieval mode: by setting intentions to retrieve (both in the present and in the future), by modulating attention, and by optimizing neuromodulatory states for retrieval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

retrieval cue is a product of the rememberer's mental activity both at the time of the formation of the engram and the time of attempted retrieval" (Tulving, 1983, p. 175). Therefore, even though many factors that modulate memory are present in the individual's external environment, the manner in which they act is via generating an internal mental state that can facilitate successful remembering. An additional critical assumption suggested by the retrieval mode hypothesis is that other factors beyond what the individual is presented with can change their internal mental state and have consequences for what is remembered.

Although Tulving recognized the importance of retrieval mode, the factors that bias this mode have only become clear in recent years. In particular, the emerging work on how intentions, attention, and neuromodulatory states affect memory retrieval has helped inform our understanding of retrieval mode. We argue that these three factors work together synergistically to maintain internal states that are optimized for remembering (Fig. 1). For example, take the case where we encounter someone at a party. We have met them previously, and, as they approach, we start searching our memory for their name. Thus, our *intention* is to retrieve their name. This intention, or goal, guides our *attention* to focus on relevant details that may jog our memory. Yet, even with the goal to retrieve a name, and our attention focused on this goal, we can either succeed or fail. One factor that may influence the likelihood of retrieval success is *neuromodulatory systems* in the brain, particularly acetylcholine. Modulation of acetylcholine levels can shift the hippocampus from an externally-oriented state (a bias toward attending to and encoding new information) to an internally-oriented state (a bias toward memory retrieval) (Hasselmo and Schnell, 1994; Hasselmo et al., 1995; Hasselmo et al., 1996; Hasselmo and Fehlau, 2001; Meeter et al., 2004; Duncan et al. 2012b; Patil and Duncan, 2018).

Although intentions, attention, and acetylcholine levels may all have their separate effects, they also interact (Honey et al., 2017). For example, acetylcholine levels can fluctuate with our goals and attentional focus (Turchi and Sarter, 1997; St Peters et al., 2011; Newman et al., 2012). Intentions or goals can affect what we choose to pay

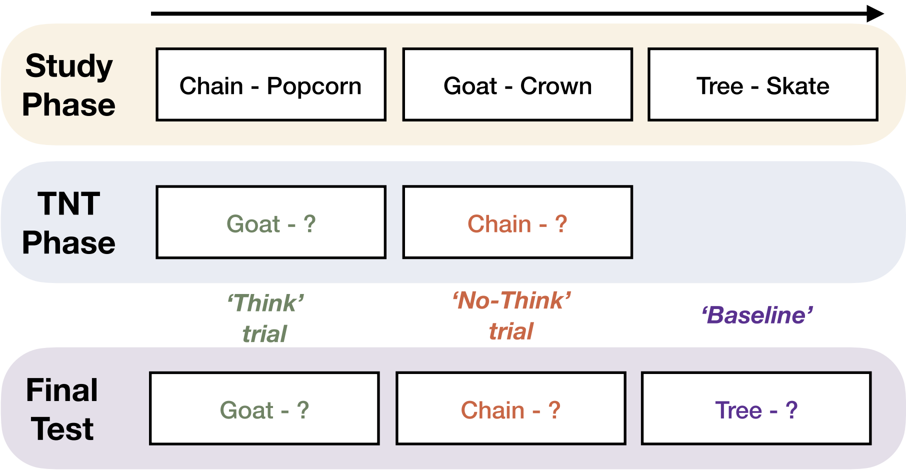

Fig. 2. | Think/No-Think paradigm. Participants first learn pairs of items (e.g., word-word pairs), one at a time (study phase). Then, in the Think/No-Think (TNT) phase, participants are presented with some of the items from the study phase, one at a time. Only one member of a given pair (the cue) is shown, and participants are asked to either retrieve ('think') or suppress ('no-think') the other member of the pair (the target). Finally, memory for the study phase pairs is tested with cued recall. Tested pairs include ones that received a 'think' instruction in the TNT phase, ones that received a 'no-think' instruction, and 'baseline' pairs that were not presented in the TNT phase.

attention to in the environment (Schmitz et al., 2017). Thus, although we will consider these factors partly in isolation, their interactions are flexible and bidirectional.

We will start by reviewing how intentions can guide memory: how they affect what we remember and forget, in the present and the future. We then highlight how attention can affect retrieval: how dividing attention or selectively focusing it can modulate memory for goal-relevant and -irrelevant features. We will then link these top-down cognitive factors to the neural background in which they occur by considering how neuromodulatory states can optimize the brain for encoding vs. retrieval. We will conclude by discussing how intentions, attention, and neuromodulatory states interact and suggest directions for future research.

2. How do intentions guide what we remember?

Retrieval mode is a neurocognitive state in which one holds the intention, or goal, of memory retrieval in mind (Lepage et al., 2000). The intention to retrieve a memory both sets up, and is a part of, retrieval mode. In this section, we discuss the effects of intention on memory retrieval by highlighting converging lines of research. We first examine motivated forgetting studies and discuss the intention to remember or forget a memory in the present. Then, we examine how we can form intentions to remember an event in the future, drawing on evidence from studies of prospective memory. We argue that an intention to remember vs. forget shifts a person's internal state towards or away from a retrieval mode, respectively. We also discuss some gaps in our theoretical knowledge of goal states and their influence on retrieval, and outline future directions.

2.1. *Intention to remember or forget in the present*

Think back to the scenario in the Introduction, and imagine trying to retrieve a name of someone who is moving towards you at a party. The intention to retrieve the name of this person is set up by seeing them approach. As you try to retrieve their name, you may remember that this person is a colleague of your former romantic partner. Not wanting to reminisce about your former partner in that moment, you set up another intention: to suppress memories that involve your former partner. Your intentions to remember (the approaching individual's name) or not remember (information about your former partner) influence your retrieval success (Fig. 1).

Studies on motivated forgetting aim to characterize this process.[2] These studies often use the Think/No-Think (TNT) paradigm to examine intentions to remember or forget (Anderson and Green, 2001; Anderson et al., 2004; Kuhl and Wagner, 2009; Anderson and Hanslmayr, 2014). Here, participants first study cue-target pairs (e.g., word pairs or picture pairs; Fig. 2) in preparation for a cued recall test. In the TNT phase, participants are presented with cue items in isolation. For some cue items, participants are asked to retrieve the target ('think' trials); for other cue items, participants are asked to suppress retrieval of the target ('no-think' trials). Other studied cue-target pairs are not presented in the TNT phase at all ('baseline' trials). Finally, after the TNT phase, memory for the 'think', 'no-think', and 'baseline' items is tested.

These studies show that memory for the 'think' items is better than memory for the 'no-think' items, consistent with a benefit for rehearsal. Interestingly, memory for the 'no-think' items is worse than memory for 'baseline' items. This phenomenon, *suppression-induced forgetting*, suggests that intentionally suppressing retrieval degrades a memory more than the act of not retrieving that memory at all (Kuhl and Wagner, 2009; Anderson and Hanslmayr, 2014). Furthermore, the more 'no-think' repetitions an item receives, the worse memory is for that item (Anderson and Green, 2001). Different theories have been proposed to explain these findings, including inhibition (Anderson and Green, 2001; Anderson and Huddleston, 2012), thought-substitution (Hertel and Calcaterra, 2005; LeMoult et al., 2010; Prete et al., 2015) and recovery interference (Tomlinson et al., 2009) accounts. A detailed review of these accounts is beyond the scope of this paper (see Raaijmakers, 2018 for a review), but we will expand on some of them briefly below.

Neuroimaging studies show that intentional retrieval suppression during 'no-think' trials (vs. 'think' trials) is associated with enhanced activity in ventrolateral and dorsolateral prefrontal cortex and reduced hippocampal activity (Anderson et al., 2004; Depue et al., 2007; Butler and James, 2010; Benoit and Anderson, 2012; Levy and Anderson, 2012). Additionally, fronto-hippocampal interactions are commonly

---

[2] Some studies of motivated forgetting use *directed forgetting* tasks, in which individuals are told to either remember or forget items relatively soon after they are encoded (in advance of a subsequent memory test). However, these manipulations may primarily tap encoding or post-encoding processes (Anderson and Hanslmayr, 2014). Given our focus is on intentions at *retrieval*, we do not include these studies here.

observed during suppression (Paz-Alonso et al., 2013; Gagnepain et al., 2014). Think/No-Think tasks therefore suggest that top-down prefrontal control over hippocampal memory retrieval is important for implementing intentions to forget. (Fig. 1; For a detailed review of these neuroimaging studies, see Anderson and Hanslmayr, 2014).

Recently, a modified Think/No-Think paradigm was used to explore whether the effects of memory suppression linger in time (Hulbert et al., 2016). As in the classic Think/No-Think paradigm, participants first learned a series of word pairs. In the modified retrieval suppression phase (i.e., the TNT phase), the word retrieval cues (which were paired with 'think' or 'no-think' instructions) were interspersed with images of objects ('bystanders'). Participants were asked to make judgements on the bystander objects, but were never told to remember them. At the end of the experiment, a surprise memory test was conducted: Participants were asked to either recall the bystander objects or perform an old/new recognition task on them. As in other Think/No-Think studies, memory was also tested for the word pairs ('think', 'no-think', and 'baseline').

As expected, retrieval suppression was associated with reduced hippocampal activity, and produced worse memory for the to-be-suppressed items compared to the to-be-remembered items. Furthermore, activity in lateral prefrontal cortex was higher for retrieval suppression vs. remembering (i.e., 'no-think' vs. 'think' trials). The extent to which prefrontal cortex activity was enhanced on 'no-think' (vs. 'think') trials was correlated with suppression of the hippocampus on 'no-think' (vs. 'think') trials. This suggests that prefrontal control mechanisms might be acting to suppress hippocampal memory retrieval in a goal-directed fashion (Hulbert et al., 2016).

Intriguingly, participants' memory for the 'bystander' objects was worse when they were surrounded by 'no-think' compared to 'think' trials. This indicates that suppressing memory retrieval is followed by a period of worse encoding, inducing an 'amnesic shadow'. This amnesic shadow was observed only with retrieval suppression and not with a thought substitution task or the inclusion of a distractor task. This suggests that the act of suppression itself is critical for the accompanying impairment of encoding — other means of forgetting do not similarly disrupt the formation of new memories (Hulbert et al., 2016). We will return to these encoding/retrieval interactions in the Discussion (Section 5.2).

Top-down inhibition of the hippocampus by the prefrontal cortex might therefore be one mechanism by which intentions to forget are realized (Kuhl et al., 2007; Kuhl and Wagner, 2009; Anderson and Hanslmayr, 2014). Recent studies have suggested that the inhibitory neurotransmitter GABA might also play an important role in the goal-directed modulation of memory (Schmitz et al., 2017). Higher levels of hippocampal GABA predict more forgetting of to-be-suppressed memories, and are associated with stronger fronto-hippocampal connectivity during memory suppression. Thus, functional interactions between the hippocampus and other cortical regions, as well as neuromodulatory mechanisms intrinsic to the hippocampus, are both important for the intentional control of forgetting. We return to neuromodulatory influences on memory in Section 4, where we discuss acetylcholine, and in Section 5.2, where we discuss dopamine.

A variation of the Think/No-Think task — the thought substitution task — is also used to study motivated forgetting. Here, instead of asking participants to suppress retrieval during 'no-think' trials, participants are asked to substitute the 'no-think' target with another thought. Behavioral evidence of forgetting is similar in tasks that use 'no-think' and thought substitution instructions (Hertel and Calcaterra, 2005; Benoit and Anderson, 2012; Prete et al., 2015; Hulbert et al., 2016). However, the neuroimaging findings diverge. While retrieval suppression is associated with greater activity in the dorsolateral prefrontal cortex, thought substitution is associated with increased activity in the ventrolateral prefrontal cortex (Benoit and Anderson, 2012; Anderson and Hanslmayr, 2014). Additionally, activity in the dorsolateral prefrontal cortex is negatively correlated with hippocampal activity for direct suppression ('no-think') but positively correlated with hippocampal activity for thought substitution (Kuhl et al., 2007; Benoit and Anderson, 2012). These results suggest that motivated forgetting can be achieved through thought substitution or through direct suppression, but the underlying neural mechanisms differ. This difference in neural mechanisms could be a result of the difference in cognitive demands: The Think/No-Think task involves suppression of a memory, and the thought substitution task requires another thought to be constructed. However, given the debate regarding the exact cognitive mechanisms underlying forgetting effects in the Think/No-Think task (Raaijmakers, 2018), further research is required to understand variation in neural correlates across tasks.

In conclusion, studies using Think/No-Think and thought substitution tasks suggest that top-down prefrontal control mechanisms and fronto-hippocampal interactions are important in fulfilling the intention to forget. We propose that the intention to forget sets up an internal state that interferes with retrieval, with lasting consequences for access to those memories. Conversely, the intention to remember sets up an internal state that prioritizes the active maintenance and retrieval of memories. If so, neural markers of a retrieval state (Quamme et al., 2010; Richter et al., 2016) should be reduced following instructions to suppress a memory and enhanced followed an intention to remember — thus providing a direct link between intentions and retrieval mode.

2.2. *Intention to remember in the future*

So far, we've considered how the intention to remember or forget in the present can influence our memory. But how does the intention to remember in the future affect our memory? Building on our example of a friend approaching you at a party (Fig. 1), say you remember that their name is Nick. You have a quick conversation, and, at the end, Nick asks you to say hi to a mutual friend, Caroline. At this point, you may set an intention to say hi to Caroline from Nick. The next time you see Caroline, you retrieve this intention and you pass on the greeting from Nick. In this example, the intention to retrieve was not for the current or present moment, but rather an intention to remember for the future. Here, we will explore this phenomenon by reviewing studies on *prospective memory*.

2.2.1. *Behavioral studies*

Prospective memory refers to our ability to remember to carry out an action or retrieve a memory in the future. In studies of prospective memory, participants receive an instruction to perform some action in the future (the prospective memory task; such as saying hello to Caroline from Nick in our earlier example), and must hold that intention in mind during performance of an ongoing task. The relationship between the ongoing task and the prospective memory task can be manipulated so that they either tax similar (*focal processing* conditions) or distinct (*non-focal processing* conditions) cognitive processes (McDaniel and Einstein, 2000; Einstein and McDaniel, 2005). For example, a prospective memory task might be to respond with a unique key press when a word is presented in a turquoise color (Anderson and McDaniel, 2019). A non-focal condition might involve an ongoing lexical decision task; it is non-focal because the ongoing task requires accessing semantic information while the prospective memory task requires accessing perceptual features. Conversely, a focal condition might have an ongoing task in which participants judge if the presented words are in a warm or cool color. This is focal because both the ongoing task and the prospective memory task require accessing perceptual information about color (Anderson and McDaniel, 2019).

Whether the ongoing task and the prospective memory task tax similar or distinct cognitive processes turns out to have important implications for behavior. Performance on the prospective memory task is worse for non-focal compared to focal processing conditions (McDaniel and Einstein, 2000; Einstein and McDaniel, 2005; Scullin et al., 2010; Uttl, 2011; Mullet et al., 2013; Anderson and McDaniel, 2019). Moreover, responses on the ongoing task are slower when the prospective memory task is non-focal, relative to a baseline condition with no prospective memory task (Smith, 2003; Einstein and McDaniel, 2005, 2010; Scullin et al., 2010; Anderson and McDaniel, 2019). This slowing is not consistently observed when comparing a focal prospective memory task to a baseline with no prospective memory task (Einstein and McDaniel, 2005; Harrison et al., 2014; Anderson and McDaniel, 2019).

McDaniel and Einstein (2000) introduced the *multiprocess framework* to explain this pattern of results. According to this framework, there are two pathways by which prospective memory can succeed: monitoring and spontaneous retrieval (McDaniel and Einstein, 2000; Einstein and McDaniel, 2005). Both involve an initial setting of a prospective memory intention, but the way in which the intention is later retrieved differs. Monitoring involves a top-down attentional control process that maintains the prospective memory intention and constantly searches for the prospective memory target in the environment. Spontaneous retrieval involves a bottom-up process in which the appearance of the prospective memory target automatically triggers the retrieval of the intention (McDaniel and Einstein, 2000; Einstein and McDaniel, 2005; McDaniel et al., 2015; Anderson and McDaniel, 2019). The framework suggests that either pathway can be employed depending on task demands and the environment. Focal processing in particular may bias the system towards spontaneous retrieval (Einstein and McDaniel, 2005; McDaniel et al., 2015).

The finding that focal processing conditions are associated with better prospective memory performance is reminiscent of transfer-appropriate processing (Morris et al., 1977; Meier and Graf, 2000). Specifically, although transfer-appropriate processing traditionally refers to improved memory when processing demands between encoding and retrieval overlap, it can also be applied to understand why prospective memory is better when the processing demands of the ongoing and prospective memory tasks overlap (Meier and Graf, 2000).

Two other theoretical frameworks have been developed to explain the mechanisms underlying prospective memory fulfillment. One framework argues that successful prospective memory can be brought about solely through the process of monitoring. In this framework, the amount of resources allocated to the prospective memory intention depends on ongoing task demands: Monitoring can be continuously sustained when ongoing task demands are low, or may occur as a more subtle attentional allocation when ongoing task demands are high (Smith, 2003). Another framework is a *delay theory* account (Loft and Remington, 2013; Heathcote et al., 2015), which suggests that behavioral slowing on the ongoing task while holding a prospective memory intention in mind allows for increased accrual of prospective-memory-related information. This delay theory account is supported by drift-diffusion and linear ballistic accumulator models (see Heathcote et al., 2015 and references therein). Recent evidence, however, seems to suggest that the multiprocess theory better explains human behavioral data (Anderson and McDaniel, 2019), and this remains arguably the more dominant theory in the field.

How might the maintenance of a retrieval mode affect the success of prospective memory? Spontaneous retrieval of a prospective memory intention may not require retrieval mode at all, because it occurs relatively automatically. However, the more effortful monitoring process might benefit from a mode in which the intention is actively kept in mind to facilitate retrieval of the prospective action. Hence, we propose that, when prospective memory intentions have to be maintained actively, they act to initiate and maintain a retrieval mode that helps the identification of goal-relevant cues in the environment.

2.2.2. *Neuroimaging studies*

The rostral prefrontal cortex (also referred to as frontopolar cortex or anterior prefrontal cortex) has typically been implicated in maintaining intentions or goals, e.g., maintaining task sets (Sakai and Passingham, 2003; Sakai, 2008; Bengtsson et al., 2009), task switching (Burgess et al., 2000; Gilbert et al., 2005; Rowe et al., 2007), maintaining prospective actions or intentions over a delay (Lau et al., 2004; Haynes et al., 2007), and maintaining subgoals en route to a main goal (Koechlin et al., 1999; Braver and Bongiolatti, 2002). This suggests a role for this region in prospective memory, because such memory requires the maintenance of an intention to remember.

Indeed, many studies have found a role for both the rostrolateral and rostromedial prefrontal cortex in prospective memory (Okuda et al., 1998, 2007; Lepage et al., 2000; Burgess et al., 2003; Simons et al., 2005; Simons et al., 2006; Gilbert et al., 2009; Reynolds et al., 2009; Benoit and Anderson, 2012; Momennejad and Haynes, 2012) and some have sought to dissociate their functions (Burgess et al., 2003; Simons et al., 2005; Gilbert et al., 2009; Benoit and Anderson, 2012; Momennejad and Haynes, 2012). The involvement of rostromedial prefrontal cortex in prospective memory seems to vary as a function of task demands (Burgess, Gonen-Yaacovi and Volle, 2011). Conversely, rostrolateral prefrontal cortex is consistently implicated in prospective memory (Okuda et al., 1998, 2007; Lepage et al., 2000; Burgess et al., 2003; Simons et al., 2006; Gilbert et al., 2009; Reynolds et al., 2009). For example, patients with unilateral rostrolateral prefrontal cortex lesions have difficulty with task switching (such as between an ongoing task and a prospective memory task) or multitasking, and have impaired maintenance of prospective memory (Rowe et al., 2007; Volle et al., 2011) (For a detailed review of studies implicating rostral prefrontal cortex in prospective memory, see Burgess, Gonen-Yaacovi and Volle, 2011).

Thus, the rostrolateral prefrontal cortex is involved in, and is necessary for, successful prospective memory. But *how* does it contribute to prospective memory? This is an important question because successful prospective memory involves many stages — encoding, maintenance, and retrieval of the intention — only some of which may depend on the function of any given brain region. If prospective memory fails, behavioral studies may not be able to determine at which stage this failure occurred. But neuroimaging studies can clarify how the different stages of prospective memory unfold by examining which brain regions are linked to each stage of this process. Recent studies have attempted to determine this with multivariate pattern analysis and connectivity approaches.

One such study (Gilbert, 2011) examined intention formation, maintenance, and retrieval of prospective memory. Univariate analyses revealed that activity in bilateral hippocampus was linked to encoding (but not maintenance or retrieval) of the prospective memory intention. Maintenance of this intention was then linked to activity in bilateral lateral prefrontal cortex, particularly rostrolateral prefrontal cortex. Interestingly, a subsequent multivoxel pattern analysis was unable to decode the content of the prospective memory intention in rostrolateral prefrontal cortex (i.e., whether the intention was for a word or image, Gilbert, 2011). However, functional connectivity analysis indicated increased coupling between rostrolateral prefrontal cortex and frontal and temporal regions (including lateral occipito-temporal cortex, lateral temporal cortex, and superior frontal gyrus) during prospective memory maintenance. This suggests that rostrolateral prefrontal cortex plays a role in maintaining prospective memory intentions, perhaps by coordinating with task- and content-sensitive regions (Gilbert, 2011).

Momennejad and Haynes (2013) found converging evidence for the role of rostrolateral prefrontal cortex in maintaining prospective memory intentions. Participants maintained a prospective memory intention during a delay that was either filled with an ongoing task or was task-free. Conjunction analyses showed that rostrolateral prefrontal cortex was active during the maintenance of prospective memory intentions for both types of delay. Furthermore, multivariate analyses revealed that the content of the prospective memory intention could be decoded in this region. These findings contradict those of Gilbert (2011), who was not able to decode prospective memory intentions in the rostrolateral prefrontal cortex. One reason for these contradictory findings could be the different tasks used: The Momennejad and Haynes (2013) study required maintenance of abstract task sets and changing stimulus-response mappings, while the Gilbert (2011) study required maintenance of individual, concrete stimuli and a single type of response. However, the results from Gilbert (2011) are null effects and hence caution should be applied when interpreting them.

Given the cognitive stages required to actualize prospective memory intentions (i.e., encoding, maintenance, and retrieval), another brain region that might be involved is the hippocampus. Some work suggests that the hippocampus plays a role in encoding (but not maintaining or retrieving) prospective memory intentions (e.g. Gilbert, 2011). However, other studies find that the demand to maintain intentions in mind can modulate hippocampal engagement. For instance, increased hippocampal activity is observed when an internally generated goal matches perceptual input in a working memory task (Duncan et al., 2009). Furthermore, the hippocampus codes for prospective goals and intentions (Johnson et al., 2007; Brown et al., 2016). Putting these findings together, evidence suggests that the hippocampus may be important for encoding memory-based intentions, as well as maintaining them for future action.

In sum, prospective memory studies highlight important roles for the rostrolateral prefrontal cortex and hippocampus in setting and maintaining intentions to remember in the future. The hippocampus encodes prospective memory intentions (Gilbert, 2011), while both the hippocampus (Duncan et al., 2009) and rostrolateral prefrontal cortex (Rowe et al., 2007; Gilbert, 2011; Momennejad and Haynes, 2013) seem to play roles in maintaining those intentions. Whether the rostrolateral prefrontal cortex also represents the content of prospective memory intentions needs further investigation. One possibility is that the rostrolateral prefrontal cortex may interact with the hippocampus to set, maintain, and retrieve prospective intentions; such interactions would be in line with the importance of hippocampal-prefrontal communication for memory-guided behavior (Simons and Spiers, 2003; Shapiro et al., 2014; Eichenbaum, 2017). Future neuroimaging and patient research will shed light on the separate, and interacting, roles of these regions in prospective memory.

2.3. Interim conclusions

Here, we reviewed evidence that intentions powerfully affect memory. Retrieval suppression studies suggest that top-down control mechanisms coordinated by the prefrontal cortex implement an intention to limit remembering. This prefrontal cognitive control acts by down-regulating memory retrieval in the hippocampus to facilitate forgetting. These studies are complemented by those of prospective memory, which highlight a role for the hippocampus in encoding intentions to remember in the future. Such intentions are then maintained by the rostrolateral prefrontal cortex, via its interactions with task- and content-sensitive brain regions (Fig. 1). Future studies will be needed to determine whether and how the mechanisms underlying intentions to remember in the future (i.e., prospective memory) differ from those for intentions to retrieve a past memory. Nevertheless, these two lines of research converge in showing that intentions play a crucial role in maintaining a retrieval mode.

Thus, we propose that the intention to remember might set up an internal state that is conducive to maintaining and retrieving memories, whereas the intention to forget might disrupt such a state. This disruption could occur either through: 1) a shift away from a retrieval mode and toward an encoding mode (see Section 5.2), or 2) a shift toward processing information (thoughts, memories) that are unrelated to the to-be-suppressed content. While there is mixed evidence to support the former (see Hulbert et al., 2016, and Section 2.1), the latter may be supported through a shift in the allocation of attentional resources (Anderson et al., 1994; Levy and Anderson, 2002; also see Section 3.2). A promising area for future research is to determine how intentions to remember or forget alter neural representations of retrieval mode, and how such an alteration may be instantiated via interactions between dorsolateral prefrontal cortex, rostrolateral prefrontal cortex, and the hippocampus.

3. How does attention shape retrieval?

Intentions are an important first step to retrieving a memory, but they are not sufficient. In addition to setting the intention to retrieve, we also need to select target memories among a vast array of competing ones (e.g., retrieve Nick's name among the names of all other people we know; see Fig. 1). Such selection is distinct from the intention to retrieve. For example, prior studies have operationalized *retrieval mode* as the intention to retrieve and *retrieval orientation* as the selection of particular stimulus features, and discovered that retrieval mode vs. orientation have distinct EEG signatures (Herron and Wilding, 2004; Rugg and Wilding, 2000). Here, we consider retrieval mode as a broader concept that encapsulates both intentions to retrieve and attention to particular stimulus features, but this work nevertheless supports our claim that these two components are dissociable. How, then, does attentional selection contribute to retrieval?

Evidence from multiple lines of research demonstrates that selection during retrieval requires goal-directed cognitive control and attention (Cabeza et al., 2008, 2011; Kuhl and Wagner, 2009). Although there is debate about whether attentional selection from episodic memory involves similar or different neural networks as attentional selection during perception (Cabeza et al., 2008, 2011; Hutchinson et al., 2009), there is consensus that attention is an important factor for episodic memory retrieval (Aly and Turk-Browne, 2017). Below, we review this evidence, which comes from studies of divided attention, selective attention, and the retrieval of memory in the face of distracting information.

Together, these studies suggest that attention — both internally and externally directed — may act to prioritize goal-relevant features to aid remembering. Thus, attentional states may contribute to a retrieval mode by highlighting the features most relevant for the recovery of a desired memory and suppressing those features that are not relevant — including distractors in the external world and goal-irrelevant memories.

3.1. Divided attention: Attention to retrieval vs. to other tasks

The behavioral effects of attention on memory retrieval are often studied by having participants retrieve memories while also performing a secondary task. If attention is critical for memory retrieval, retrieval should suffer when attention is divided. Indeed, memory accuracy is lower when participants perform a secondary task during retrieval, vs. when attention is fully focused (Jacoby et al., 1989). However, the costs of divided attention at retrieval are smaller than the costs at encoding (Baddeley et al., 1984; Craik et al., 1996). For example, any type of secondary task is detrimental for memory encoding; however, dual-task costs at retrieval can be selective to, or larger for, secondary tasks that tax the same modality as the retrieved content (Fernandes and Moscovitch, 2000). These results suggest that attention, although less critical for retrieval than for encoding, can shape the contents of memory.

Why does attention play a larger role in encoding vs. retrieval? One possibility is that memory retrieval, particularly recollection, is a two-step process (Moscovitch, 2008; for a similar model, see Tulving, 1985): The first step is fast, unconscious, and automatic; the second step is slow, conscious, and effortful. As such, only the second step may require focused attention. If the relatively more implicit components of recollection require little attention, then perhaps implicit forms of memory retrieval, in general, are not attentionally demanding. This turns out to be the case: Although attention plays a role in the retrieval of both implicit and explicit memories, it is more important for explicit memory retrieval (Jacoby et al., 1989; Clarke and Butler, 2008). Thus, attention might be preferentially required for retrieved memories to reach conscious awareness, but attention may not be necessary for the act of memory retrieval itself.

If accessing memories does not require attention per se, then what specific part of retrieval is attentionally demanding? One candidate process is the act of selecting a task-relevant memory among multiple retrieved associations: Attention may focus memory retrieval on a specific, target memory and inhibit related, competing memories. According to this explanation, when attention is divided, spontaneous or involuntary memory retrieval may dominate a decision even when that retrieval is not goal-relevant or desirable.

For example, in one study (Anderson et al., 2011), participants separately studied words and drawings. On each trial of a subsequent recognition test, participants were presented with a word superimposed on a drawing. They were asked to make old/new judgments for one of the two stimulus categories (e.g., make recognition judgments on words, and ignore drawings). For any given word-drawing stimulus, both stimuli could be new (not previously studied), both could be old (previously studied), or one could be old and the other new. Spontaneous recognition was defined as making an incorrect 'old' judgment for a new target item when the distractor item was old. This task was conducted under either full or divided attention (where attention was divided with a secondary digit-monitoring task). There were more spontaneous recognition errors when attention was divided vs. fully focused. Moreover, when attention was fully focused, older adults made more errors than younger adults. These results suggest that preventing task-irrelevant recognition from affecting behavior requires cognitive control or goal-directed attention — which is disrupted in older adults (Hasher and Zacks, 1988; Ardila and Rosselli, 1989; Dempster, 1992). Together, these results suggest that divided attention is particularly detrimental for goal-directed memory retrieval — a process that might require selective attention to the target memory in the face of distracting memories.

3.2. The role of attention in selecting which memory to retrieve

Adaptive mnemonic functioning requires selectively retrieving task-relevant memories among competing ones. What neural mechanisms allow such goal-directed retrieval? One brain region that is involved in controlling goal-directed attention is the prefrontal cortex (Corbetta and Shulman, 2002; Asplund et al., 2010; Kim et al., 2016), which establishes cognitive control by storing goal representations — goal representations that can be used to guide selective attention or perform a multitude of other tasks (Miller and Cohen, 2001). Thus, it is likely that the prefrontal cortex is also involved in directing internal, goal-directed attention during memory retrieval.

Studies of patients with prefrontal cortex damage confirm this prediction. These patients can often accurately recognize previously acquired knowledge but struggle to recall it on their own (recall is thought to tax cognitive control more than recognition). For example, patients with bilateral prefrontal cortex damage show deficits in recalling remote public events (e.g., *Who killed John Lennon?*). However, they can perform similarly to healthy individuals when asked to choose the answer among multiple options (e.g., *Was it John Hinkley, Sarah Jane Moore, Mark Chapman, or David Roth?*; Mangels et al., 1996; for reviews see Wheeler et al., 1995; Baldo and Shimamura, 2002). Similar recall vs. recognition dissociations in prefrontal cortex lesion patients have been reported for odor memory (Baldo and Shimamura, 2002) and autobiographical memory (Kopelman et al., 1999). These results suggest that the prefrontal cortex is necessary for attentional selection among stored memories in a goal-directed fashion: Prefrontal cortex lesions may impair the active search for memory but not memory access per se (also see Aly et al., 2011).

If the prefrontal cortex is indeed involved in attentional selection of to-be-retrieved memories, then its involvement should increase as competition for retrieval increases. This was tested in an fMRI study in which participants practiced person-location associations (e.g., *a hippie is in the park*). Importantly, the number of locations associated with each person was either one, two, or three, and likewise, each location was associated with either one, two, or three people (Sohn et al., 2003). In the recognition test, participants were presented with person-location pairs that were either intact (e.g., hippie-park) or re-paired (e.g., hippie-classroom, where 'hippie' and 'classroom' were never studied together during encoding). Participants' task was to indicate if the pair was previously studied or new. Pairs of items that have more associations should elicit greater competition during memory retrieval, and therefore should place a greater demand for attentional selection among competing memories.

Behaviorally, recognition performance was less accurate and slower for item pairs that had a larger number of associations. This finding replicates the seminal *fan effect* (Anderson, 1974). Importantly, during the recognition test, univariate activity in bilateral dorsolateral and ventrolateral prefrontal cortex was higher for person-location pairs that had a high (vs. low) number of associations. These results are consistent with a role for the prefrontal cortex in controlling attentional selection of to-be-retrieved memories in the face of competition.

But how does selective attention resolve competition between memories during retrieval? There are two explanations that are not mutually exclusive: attentional facilitation of target memories and attentional suppression of competing memories. Supporting evidence for the coexistence of target facilitation and competitor suppression comes from the *retrieval-induced forgetting* literature. Retrieval-induced forgetting refers to the finding that retrieval improves memory for the retrieved content but weakens memories that compete with the retrieved content, relative to 'neutral', noncompeting memories that are not retrieved (Anderson et al., 1994; Levy and Anderson, 2002; Jonker et al., 2013; Raaijmakers, 2018). The coexistence of benefits for target memories and costs for competing memories suggests that selective attention at retrieval operates not only by facilitating the target memory but also by suppressing competing memories (see Section 2.1).

Further support for the active suppression of competing memories at retrieval comes from an fMRI study by Wimber and colleagues (Wimber et al., 2015). In this study, participants first learned a series of cue words, each of which was paired with two images. Then, in the fMRI scanner, participants were presented with the cue words one at a time, and selectively recalled the first image associated with each word. They then indicated if that image was a face, object, or scene. For example, during the learning phase, the word 'sand' might be paired with an image of Marilyn Monroe and later with an image of a hat. At the selective retrieval phase, when presented with 'sand', 'face' would be the correct response because the target memory is Marilyn Monroe (the first image studied with 'sand'). 'Object' would be an intrusion error because the competing memory (the second image studied with 'sand') is a hat. During this selective retrieval phase, participants viewed each target word four times, each time retrieving the associated first image. The percentage of intrusion errors decreased as the same target was repeatedly retrieved. This suggests that competing memories might have been weakened over time, leading to reduced competition and a decreased need for attentional selection.

At the end of the fMRI scan, participants received a memory test that required them to recognize studied images among similar foils. Recognition accuracy was lower for competing images (e.g., the hat) compared to baseline images that were not shown during the selective retrieval phase (e.g., a pair of goggles) (Wimber et al., 2015). These behavioral results replicate the retrieval-induced forgetting phenomenon and provide support for the suppression of competing memories at retrieval: Attending to, and retrieving, one item among competitors boosts memory for the attended item and hurts memory for the competitors. Furthermore, competing memories were suppressed at a neural level: Markers of competing memories in the brain (e.g., a pattern of activity in ventral visual cortex linked to perceiving a hat) decreased as target memories (e.g., Marilyn Monroe) were retrieved more often. Intriguingly, neural markers of these competing memories were suppressed below the level of noncompeting memories of the same category (e.g., a pair of goggles). This suppression was linked to later forgetting of those competing memories, and was higher when ventrolateral prefrontal cortex activity was higher. This offers further evidence that the prefrontal cortex is important for resolving competition among memories at retrieval, perhaps through a mechanism of selective attention.

There is nevertheless a caveat: A follow-up study using a similar experimental procedure failed to replicate the behavioral findings of Wimber et al. (2015) (Potter et al., 2018). Specifically, in two new datasets, Potter et al. (2018) found no reliable forgetting difference between competing memories and baseline memories. Although retrieval-induced forgetting has been replicated repeatedly in the literature, a failure to demonstrate this effect in the paradigm used by Wimber et al. (2015) makes their findings of neural suppression difficult to interpret: If there is no behavioral marker of memory suppression, what is the neural suppression capturing? Thus, it remains an open question whether attentional selection of target memories is accompanied by weakening of neural representations for competing memories.

The retrieval-induced forgetting phenomenon shows that competition for retrieval decreases with repeated retrieval of a target memory: Competing memories are weakened every time a target memory is retrieved (Bjork, 1988; Anderson et al., 1994; Levy and Anderson, 2002). If the ventrolateral prefrontal cortex is involved in the attentional prioritization of target memories, then its involvement should decrease across repeated retrieval of the same target memory. Indeed, repeated retrieval is associated with decreased activity in the ventrolateral prefrontal cortex and inferior frontal gyrus (Kuhl et al., 2007; Wimber et al., 2015). This finding supports a role for these regions in the attentional prioritization of target memories, presumably via both attentional selection of target memories and suppression of competing memories. This role might be mediated by the availability of the neurotransmitter dopamine (Wimber et al., 2011), a topic that we will return to in Section 5.2. Repetition-related activity declines in the prefrontal cortex have also been observed for task switching and the resolution of proactive interference in working memory (for a review, see Badre and Wagner, 2007). Thus, the conflict-resolution functions of the prefrontal cortex extend beyond long-term memory retrieval.

In Section 3.1, we described the effects of dual-task costs on retrieval, costs that likely arise because of disrupted *executive control* over attention (Logan and Gordon, 2001). Here, we summarized the role of the prefrontal cortex in selective attention. Although described separately, executive control and selective attention interact with one another during retrieval. For example, retrieval-induced forgetting is present when retrieval is performed alone, but not when retrieval takes place concurrently with a secondary task (Román et al., 2009). This finding suggests that selective attention to target memories and suppression of competing memories requires executive control — control that is reduced when one has to perform a second task at the same time. Further support for the interaction between executive control and selective attention comes from Ortega et al. (2012). In this study, low demands from a secondary task were sufficient to impair retrieval-induced forgetting for older adults, while higher demands were needed for such impairment to be observed for younger adults. Given executive control declines in aging (Braver and Barch, 2002), this finding further supports an important role for such control in selecting among memories. Together, these studies suggest that the deterioration of executive control, by aging and/or a secondary task, results in an impairment in the ability to suppress competing memories during retrieval.

3.3. *Internally vs. externally oriented attention*

Attentional prioritization of target memories during retrieval is crucial given the competition among memories. Similar competition exists in the external world: Perceptual input is too rich for our limited processing capacity. As a result, unless attended, information right in front of our eyes is sometimes not consciously perceived (e.g., inattentional blindness; Mack and Rock, 1998). Does selective attention operate similarly for memory retrieval and perception? Research suggests that there are both similarities and differences. For example, suppression of competing information at retrieval might be an instance of a more general ability to inhibit distraction. Individuals with high working memory capacity not only demonstrate higher retrieval-induced forgetting effects — suggesting that they are better at inhibiting unwanted distractions in memory (Aslan and Bäuml, 2011) — but are also better at inhibiting distractors during perception (Vogel et al., 2005). However, there is debate about whether (external) attention during perception and (internal) attention during memory retrieval rely on overlapping (Cabeza et al., 2008, 2011) or dissociable (Hutchinson et al., 2009; Sestieri et al., 2010) neural mechanisms, particularly in the posterior parietal cortex.

Nevertheless, there is a great deal of evidence that internal attention mechanisms in posterior parietal cortex are important for gating access to our memories — perhaps via instantiation of a retrieval mode. Evidence for this comes from a study investigating the different ways in which we can make memory judgments: recollection vs. familiarity. Recollection involves the recovery of specific episodic details about a previous experience; familiarity refers to a feeling of knowing that something has been experienced before, despite an inability to bring to mind qualitative details about the prior event (Yonelinas et al., 2010). Because recollection requires the recovery of specific episodic details, it is more effortful than familiarity and may require focused internal attention toward details that are stored in memory. Therefore, the increased demands of recollection indicate that it, particularly, may benefit from a retrieval mode. This prediction was confirmed in an fMRI study (Quamme et al., 2010): prior to the onset of a retrieval cue, patterns of activity in posterior parietal cortex reflected whether participants were in a retrieval mode that prioritized recollection (vs. familiarity), and this internal 'recollection' attentional state predicted access to episodic details.

These and other studies have therefore provided compelling evidence that the posterior parietal cortex plays an important role in attention to memory (Fig. 1; Wagner et al., 2005; Ciaramelli et al., 2010). This has motivated frameworks in which the role of the posterior parietal cortex in memory is limited to attentional selection at retrieval, as opposed to representing retrieved memory content (Cabeza et al., 2008; Ciaramelli et al., 2008). Indirect support for this attentional account comes from patient studies: Patients with damage to the posterior parietal cortex do not tend to exhibit large episodic memory deficits, suggesting that retrieved memories might be represented elsewhere (Cabeza et al., 2008). Moreover, posterior parietal cortex activity reflects the subjective experience of remembering, or confidence in memory, as opposed to objective recall performance (Chua et al., 2006; Moritz et al., 2006; Kim and Cabeza, 2007; Simons et al., 2010). Based on these results, the parietal cortex has been suggested to be involved in attentional selection during retrieval, rather than the representation of retrieved memories (for review, see Cabeza et al., 2012).

This purely attentional account of posterior parietal cortex involvement in memory is popular but has faced challenges. Using multivariate pattern analyses, multiple studies have decoded retrieved content from activity in the posterior parietal cortex (Wagner et al., 2005; Kuhl et al., 2013; Kuhl and Chun, 2014; Bird et al., 2015; St-Laurent et al., 2015; Bonnici et al., 2016; Lee and Kuhl, 2016; Lee et al., 2019). Furthermore, goal-directed attentional selection results in enhanced representations of target memories in the posterior parietal cortex (Favila et al., 2018). These results suggest that this region is not only involved in attentional selection of to-be-retrieved target memories but also represents the content of those memories.

Although posterior parietal cortex represents the content of retrieved memories, it likely does not store those memories itself. This is because, as noted earlier, lesions in parietal cortex do not typically produce large impairments in episodic memory (Cabeza et al., 2008; Berryhill, 2012). If the posterior parietal cortex does not store memories itself, how does it come to represent them? One possibility is that representations of memories in posterior parietal cortex depend on retrieval mechanisms in the hippocampus. Bidirectional connections between the hippocampus and posterior parietal cortex (Cabeza et al., 2008) may enable parietal attention mechanisms to modulate the hippocampus and the hippocampus to trigger memory reactivation in parietal cortex. Indeed, posterior parietal cortex is thought to exert top-down control over the hippocampus (Cabeza et al., 2008) to focus internal attention in the service of memory retrieval. Hippocampal pattern completion (Treves and Rolls, 1992) — the retrieval of complete memories from a partial cue — may then trigger the reactivation of memories in posterior parietal cortex, driving the subjective experience of remembering. This is consistent with studies that show i) that the quality of retrieved memories is correlated with functional connectivity between the hippocampus and posterior parietal cortex (Cooper and Ritchey, 2019), and ii) that such connectivity is associated with recollection of autobiographical memory details (McCormick et al., 2013). These studies raise the possibility that hippocampal memory retrieval may contribute to the reactivation of memory content in parietal cortex (Lee and Kuhl, 2016; Lee et al., 2019) but this remains to be directly tested in future studies.

3.4. *Attentional states and hippocampal retrieval*

So far, we have reviewed evidence that the prefrontal cortex and posterior parietal cortex play important roles in attentional selection of memories (Fig. 1). Another brain region that is likely at the intersection of attention and memory is the hippocampus, given its importance in memory and its involvement in attention behaviors (Aly and Turk-Browne, 2016a, 2016b, 2017). How do attentional states at retrieval influence hippocampal memory signals? One possibility is that attention has a relatively minor effect on hippocampal memory retrieval: If the first stage of hippocampal recollection is relatively automatic and obligatory, attention may not be necessary (Moscovitch, 2008). Conversely, because attention strongly modulates hippocampal encoding (Davachi and Wagner, 2002; Uncapher and Rugg, 2009; Carr et al., 2013; Aly and Turk-Browne, 2016a), then it may also modulate hippocampal retrieval.

Indeed, some studies find modulation of hippocampal activity as a function of selective attention at retrieval. For example, hippocampal activity levels were modulated in a recognition task depending on whether participants were attending to perceptual or semantic information (Hashimoto et al., 2012). In another study, correct vs. incorrect responses were associated with increased activity levels in posterior hippocampus when the task was to assess the relative recency of items and in anterior hippocampus when the task was to assess the novelty of items (Dudukovic and Wagner, 2007). Finally, activity in the hippocampus was modulated depending on whether, during recognition, the task was to detect changes in the layout of rooms or changes in their furniture (Duncan et al., 2012a). These studies provide evidence for modulation of hippocampal memory retrieval by selective attention (for a review, see Aly and Turk-Browne, 2017).

The attentional states that modulate hippocampal memory retrieval seem to involve selecting different features of a retrieved memory (e.g., perceptual vs. semantic aspects of a retrieved image, novelty vs. recency of retrieved words, or layout vs. furniture in a retrieved room). In contrast, studies in which attention is divided between memory retrieval and a secondary task do not find modulation of hippocampal activity (e.g. Iidaka et al., 2000) or find reductions in hippocampal activity only when the secondary task taxes the same processing modality as memory retrieval (Fernandes et al., 2005). Thus, it is possible that the hippocampus is primarily modulated by attentional demands when retrieval requires selection among the features of a memory but not when attention is simply reduced as a whole.

Such selection also operates in the direction of not selecting a particular memory: Intentions to forget or suppress particular memories result in downregulation of hippocampal activity (Benoit and Anderson, 2012; Benoit et al., 2015; Anderson et al., 2016). These findings suggest that attention might modulate hippocampal activity in two ways: to facilitate the selective retrieval of target memories and to suppress retrieval of unwanted memories (see Section 2.1).

3.5. *The role of attention in the face of perceptual distraction during retrieval*

Because attention is limited, memory retrieval might suffer in the face of distracting, task-irrelevant information even when this information can be ignored. One fMRI study tested this idea by comparing cued-recall performance when participants' eyes were closed vs. when they were open and irrelevant visual stimuli were presented. Recollection of episodic memory details was diminished when distracting information was presented — even though distractors were completely task-irrelevant (Wais et al., 2010; also see, Vredeveldt et al., 2011). Furthermore, hippocampal activity was lower in the presence of distractors, suggesting that task-irrelevant information can compete for attention and impair access to hippocampal memories. The cost of visual interference on recall performance was also linked to changes in prefrontal cortex function: There was reduced functional connectivity between the inferior frontal gyrus and visual association cortex during visual distraction. In another study, perturbation of the inferior frontal gyrus with repetitive transcranial magnetic stimulation increased the extent to which task-irrelevant visual distractors impaired retrieval (Wais et al., 2012a). Together, these results suggest that the lateral prefrontal cortex, and its functional coupling with the hippocampus and association cortex, is crucial for preventing attentional distraction by irrelevant perceptual input during memory retrieval. Because lateral prefrontal cortex has also been linked to the instantiation of retrieval mode (Lepage et al., 2000), these studies together suggest that this region might be critical for maintaining a retrieval mode in the face of distraction (Wais et al., 2010; Wais et al., 2012b).

Further support for this argument comes from studies that compare the effect of visual distraction in older vs. younger adults (Wais et al., 2012b). Participants engaged in an incidental encoding task and later recalled the studied objects. Recall took place either while participants' eyes were closed, while they looked at a gray screen, or while they looked at distracting information. The cost of visual distraction on episodic memory retrieval was defined as the recall accuracy difference between the distractor-present and eyes-closed conditions. This distraction cost was higher for older compared to younger adults. This is consistent with findings that older adults show decreased ability to suppress irrelevant information during cognitive tasks (Hasher et al. 1999; Gazzaley et al., 2005; Gazzaley et al., 2008; Luo and Craik, 2008). Thus, it is possible that higher distraction costs for older adults during memory retrieval are a result of deficits in the ability to use attention to focus on goal-relevant memories and suppress distracting information. These results, along with the studies mentioned above (Wais et al., 2010; Wais et al., 2012b), raise the possibility that effective recruitment of the prefrontal cortex — which declines with healthy aging (Whelihan and Lesher, 1985; West, 1996; Braver and Barch, 2002) — is important for reducing distraction during memory retrieval by focusing attention on goal-relevant information and suppressing goal-irrelevant information.

3.6. *Interim conclusions*

Attention plays a crucial role in the selection of target memories and the suppression of competing memories. This attentional prioritization of memory retrieval relies on the prefrontal cortex. Posterior parietal cortex also plays a role in the attentional modulation of memory: it directs attention to, and represents, retrieved memory contents. Finally, hippocampal memory retrieval is modulated by selective attention to particular features of a memory, and is reduced when attention is diverted away from a particular memory in order to suppress it.

These studies together suggest an important role for attention in shaping the contents of memory. Because at any given moment many memories may come to mind, attentional selection is important for focusing limited resources on desired memories and suppressing competing ones. Such an attentional weighting of memories may contribute critically to the instantiation and maintenance of retrieval

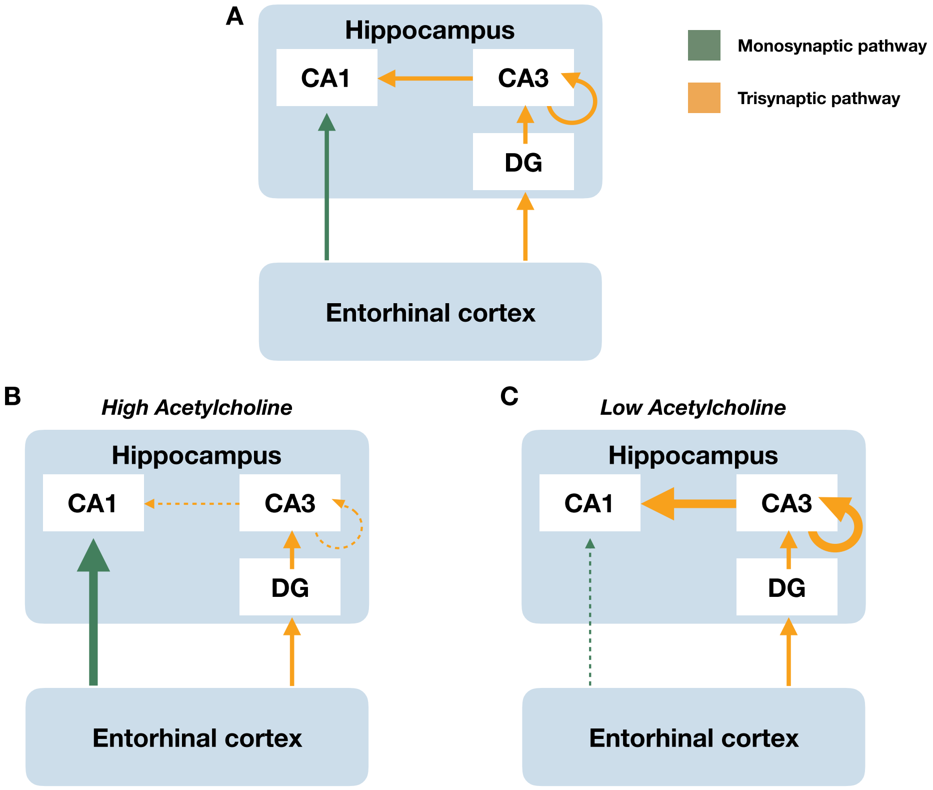

Fig. 3. | The influence of acetylcholine on retrieval mode. **(A)** Schematic of hippocampal architecture. The monosynaptic pathway (green) connects entorhinal cortex (ERc) to CA1. This pathway is thought to optimize encoding of current experience. The trisynaptic pathway (orange) connects ERc to dentate gyrus (DG), DG to CA3, and CA3 to CA1. CA3-CA1 and recurrent CA3 connections are thought to optimize retrieval through CA3's role in pattern completion. Because CA1 receives both ERc and CA3 input, CA1 can compare retrieved memories to current experiences. **(B)** High cholinergic states in the hippocampus suppress CA3-CA1 and recurrent CA3 connections (dashed orange lines) while simultaneously prioritizing ERc-CA1 connections (thick green line). Because the monosynaptic pathway optimizes encoding, high acetylcholine biases the hippocampus away from retrieval and toward an encoding state. **(C)** Low cholinergic states in the hippocampus enhance CA3-CA1 and recurrent CA3 connections (thick orange lines) and suppress ERc-CA1 connections (dashed green line). Given the role of CA3 in pattern completion, low acetylcholine biases the hippocampus toward a retrieval mode. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

mode: Attention selects the most relevant features for the currently desired memory, thus serving to both initiate and maintain memory retrieval in the service of our goals. Specifically, features of the target memory that are attended can act as retrieval cues that aid the search and recovery of related information in memory. In this way, selective attention can initiate memory search for goal-relevant features and maintain such targeted search in the face of potential distraction by recalled information that is task-irrelevant.

4. How do neuromodulatory states affect retrieval mode?

Attention and intention to retrieve memories can be considered top-down goal states that are engaged by an individual. In addition to these voluntary factors, the neural background in which memory retrieval occurs is likely critical: The success of memory retrieval may depend on neuromodulatory states that are in place even before a memory cue is encountered. Returning to our scenario, this suggests that fluctuations in neurochemical states can influence whether Nick's name is remembered, even before he approaches you at the party (Fig. 1). Indeed, converging evidence from rodent work and computational modeling implicate the neurotransmitter acetylcholine in the induction of oscillating encoding and retrieval states. Although computational theories of cholinergic encoding and retrieval states are not new (Hasselmo and Schnell, 1994; Hasselmo, 1995; Hasselmo and Barkai, 1995; Hasselmo et al., 1995, 1996; Meeter et al., 2004), their proposed mechanisms for memory formation and retrieval are only beginning to be tested in humans (Duncan et al.,2012b; Duncan and Shohamy, 2016; Patil and Duncan, 2018). These cholinergic states are a potential physiological basis for retrieval modes because they influence hippocampal function in a way that can optimize access to the external vs. internal environment. Such effects of cholinergic states on retrieval mode can be conceptualized in one of two ways. First, cholinergic states may be the physiological mechanism by which cognitive states (e.g., attention) guide retrieval (see Section 5.1). Second, cholinergic states may at least sometimes act independently of intention and attention, and serve to influence retrieval in a more automatic fashion. In this section, we will first summarize how cholinergic states can bias the hippocampus toward memory retrieval and away from encoding. Then, we will bridge neurocomputational frameworks of acetylcholine function with Tulving's retrieval mode hypothesis (Tulving, 1983).

4.1. Hippocampal architecture

In order to appreciate how acetylcholine can toggle the hippocampus between encoding and retrieval modes, it is necessary to first consider how information is processed within the hippocampus (Fig. 3). Specifically, the unique architecture and connectivity of hippocampal subfields provides insight into how this region performs operations that are critical for forming and retrieving memories. For the purpose of this review, we will focus mainly on hippocampal subfields CA1, CA3, and dentate gyrus (DG), as well as the entorhinal cortex (ERc), which is the main source of cortical input to the hippocampus (Lavenex and Amaral, 2000).

Two pathways in the hippocampus are thought to be critical for memory encoding and retrieval. The *monosynaptic pathway* directly connects ERc to CA1 (Fig. 3a; Lavenex and Amaral, 2000; van Strien et al., 2009). ERc also synapses with DG, which then sends information to CA3. CA3 then synapses with CA1 via the Schaffer collaterals, and also has strong recurrent synaptic connections. The three-synapse circuit between ERc-DG, DG-CA3, and CA3-CA1 is known as the *trisynaptic pathway* (Fig. 3a; Lavenex and Amaral, 2000; van Strien et al., 2009).

This architecture enables the hippocampus to perform various operations that are thought to be critical for memory. Two of these operations are *pattern separation* — the encoding of new information in a manner that is distinct from similar memories (Yassa and Stark, 2011) — and *pattern completion* — the retrieval of a full memory given a partial cue (Treves and Rolls, 1992). The DG, via its sparse coding properties, is implicated in pattern separation (O'Reilly and McClelland, 1994; Leutgeb et al., 2007; Bakker et al., 2008; Yassa and Stark, 2011; Berron et al., 2016; for reviews see Kesner and Rolls, 2015; Duncan and Schlichting, 2018). CA3, which receives input from DG, is likewise involved in pattern separation (O'Reilly and McClelland, 1994; Leutgeb et al., 2007; Bakker et al., 2008; Norman, 2010). However, the strong recurrent connections of CA3 are also linked to pattern completion (Treves and Rolls, 1992; O'Reilly and McClelland, 1994; Neunuebel and Knierim, 2014; Kesner and Rolls, 2015; Duncan and Schlichting, 2018). CA1 receives input from both ERc and CA3 (Lavenex and Amaral, 2000), putting it in an ideal location to compare retrieved memories (from CA3) to currently experienced events (from ERc; Duncan, et al., 2012a; Chen et al., 2015).

Thus, hippocampal structure and function are well-suited for both memory encoding and memory retrieval. How, then, is the switch between encoding and retrieval flipped?

4.2. *Hippocampal function prioritizes retrieval or encoding*

The encoding of new, distinct experiences (pattern separation) and the retrieval of relevant, related memories (pattern completion) place opposing demands on the hippocampus. To resolve this apparent tension, recent work has proposed that the hippocampus prioritizes encoding vs. retrieval by operating in distinct states that can be mapped onto the functional architecture of hippocampal subfields (Hasselmo et al., 2002; Carr and Frank, 2012; Hasselmo and Stern, 2014; Colgin, 2016).

Encoding states may be subserved by the monosynaptic pathway. Bottom-up information from sensory areas is strongly represented in ERc (Felleman and Van Essen, 1991; Lavenex and Amaral, 2000). Thus, enhanced ERc-CA1 connectivity may result in a prioritization of new sensory input, leading to an *encoding state*. Conversely, *retrieval states* may rely on connections between hippocampal subfields CA3 and CA1: These connections allow pattern-completed memories in CA3 to be sent to CA1 and then transmitted outside of the hippocampus (Treves and Rolls, 1992; Neunuebel and Knierim, 2014; Kesner and Rolls, 2015).

In support of this view, work in rodents has shown that CA3-CA1 gamma coherence increases during retrieval-like behaviors, such as navigating toward a choice point in a T-maze, where a memory-guided decision must be made (Montgomery and Buzsáki, 2007). High-resolution fMRI studies in humans lend further support for the differential involvement of CA3-CA1 and ERc-CA1 connectivity in retrieval and encoding, respectively (Duncan et al., 2014; Bein et al., 2019). Duncan et al. (2014) found that the strength of connectivity between CA2/CA3/DG and CA1 predicted performance in an associative retrieval task, in line with a retrieval state (CA2, CA3, and DG activity is difficult to separate in fMRI studies). In contrast, CA2/CA3/DG-CA1 connectivity decreased while ERc-CA1 connectivity increased in response to mnemonic prediction errors (Bein et al., 2019). This finding is consistent with an encoding state, because prediction errors drive new learning (Greve et al., 2017) and memory updating (Long et al., 2016; Sinclair and Barense, 2018).

Furthermore, other studies find more direct evidence for a trade-off between encoding and retrieval in the brain and in behavior. In one such study, participants made perceptual decisions about a stream of trial-unique images. When participants implicitly learned that these trial-unique images contained category-level regularities (e.g., a forest predicts a beach), better multivariate classification of an upcoming category (e.g., a beach) in the hippocampus was negatively correlated with incidental episodic encoding of the current item (e.g., a trial unique forest; Sherman and Turk-Browne, 2018). This suggests that a retrieval state in the hippocampus impaired simultaneous encoding, consistent with what would be expected if these states trade off in the brain. Importantly, such a result may reflect an automatic trade-off between encoding and retrieval, because participants were performing an unrelated perceptual task.

Other studies find that attending to or encoding one aspect of a task leads to poorer memory retrieval for a concurrent task (Fernandes and Moscovitch, 2000; Wais et al., 2010; Aly and Turk-Browne, 2017). Although these studies are consistent with an executive-control account of dual task costs (see Section 3.1), they may also point to a behavioral trade-off between encoding and retrieval, given the evidence of such a trade-off in the hippocampus.

Taken together, these studies suggest a dissociation between encoding and retrieval states in behavior and in the hippocampus, and point to CA3-CA1 connectivity as potentially important for memory retrieval. Therefore, the state of our brain — and, specifically, the state of the hippocampus — can place us in a mode that prioritizes memory retrieval.

4.3. *Acetylcholine shifts the balance between encoding and retrieval*

How does the hippocampus dynamically shift between encoding and retrieval states? Rodent work and computational modeling suggest that cholinergic modulation may be a key driver in toggling between states (Hasselmo and Schnell, 1994; Hasselmo, 1995; Hasselmo and Barkai, 1995; Hasselmo et al., 1995, 1996; Meeter et al., 2004) Specifically, high levels of acetylcholine bias the hippocampus toward an encoding state, while low levels of acetylcholine bias the hippocampus toward a retrieval mode (Figs. 1 and 3).

High acetylcholine is associated with encoding in the hippocampus because acetylcholine release enhances ERc-CA1 connections (Fig. 3b; Newman et al., 2012). This allows sensory information from ERc (Lavenex and Amaral, 2000) to be transmitted to the hippocampus and to affect ongoing behavior and memory encoding. Furthermore, cholinergic agonists enhance long-term potentiation in ERc (Cheong et al., 2001) and CA1 (Huerta and Lisman, 1993, 1995), allowing environmental input to more strongly affect representations in the hippocampus. Simultaneously, high acetylcholine suppresses CA3-CA1 synaptic connections as well as CA3 recurrent connections (Hasselmo and Schnell, 1994; Hasselmo et al., 1995; Vogt and Regehr, 2001; Kremin and Hasselmo, 2007). Because CA3 is important for pattern completion (Treves and Rolls, 1992; Neunuebel and Knierim, 2014; Kesner and Rolls, 2015) — a key element of recovering memories — this inhibition should impair memory retrieval. Taken together, these findings show that high acetylcholine prioritizes ERc input to CA1, suppresses CA3 input to CA1, and enhances synaptic plasticity in ERc and CA1. These functional changes are associated with enhanced input about the environment and suppression of memory retrieval mechanisms, biasing the hippocampus toward an encoding state (for review, see Hasselmo, 2006).

Conversely, low acetylcholine in the hippocampus is associated with retrieval (Fig. 3c). This is because low acetylcholine is associated with weaker ERc-CA1 connectivity, stronger activity of CA3 recurrent connections, and stronger CA3-CA1 connectivity (Hasselmo and Schnell, 1994; Newman et al., 2012). Such connectivity changes prioritize memory retrieval (via CA3) at the cost of encoding (via ERc-CA1).

Thus, computational models and work in non-human animals have yielded converging evidence for a role of acetylcholine in modulating encoding vs. retrieval modes in the hippocampus. However, both bodies of work have had limited influence on studies of human memory, in part due to the challenges of conducting pharmacological manipulations in humans. Recent studies in our lab (Ruiz and Aly, 2019) have approached this challenge in a tractable way by comparing the behavior of nicotine cigarette smokers when they have just smoked versus abstained from smoking for 12 hours (nicotine is a cholinergic agonist; Brody et al., 2006). By using such designs in conjunction with hippocampally dependent tasks, we can start to understand how cholinergic modulation can affect encoding vs. retrieval states. These and other pharmacological manipulations will be useful in explicitly testing the predictions of computational models in humans.

4.4. Behavioral evidence in line with cholinergic retrieval states

Although it has been difficult to *directly* test the predictions of these computational models in humans, several recent studies have tested these predictions *indirectly*. If the exchange between encoding and retrieval modes is modulated by acetylcholine, then each state should linger on the order of seconds, consistent with the known timecourse of cholinergic modulation of the hippocampus (Hasselmo and Fehlau, 2001; Meeter et al., 2004). This time-varying aspect of cholinergic modulation has motivated studies that use the temporal dynamics of behavior as an indirect window into cholinergic modulation of retrieval states (Duncan et al. 2012b; Duncan and Shohamy, 2016; Patil and Duncan, 2018). These studies typically manipulate novelty and familiarity as a proxy for variable cholinergic levels, as more acetylcholine is released in the hippocampus when rodents explore a novel vs. familiar environment (Giovannini et al., 2001). Therefore, exposure to novel stimuli should increase acetylcholine release and bias the hippocampus toward an encoding state. Conversely, exposure to familiar stimuli should decrease acetylcholine release in the hippocampus, leading to a retrieval state and, thus, enhanced retrieval success.

Relying on this logic, several studies have used novelty and familiarity to putatively manipulate acetylcholine levels (Duncan et al., 2012b; Duncan and Shohamy, 2016; Patil and Duncan, 2018). In one such study, participants were presented with a continuous stream of objects. These objects could be 'new' (never seen before), 'similar' (an alteration of a previously seen object), or 'old' (repetition of a previously seen object). Participants judged whether each item was new, old, or similar. The purpose of including 'similar' objects was to tax pattern separation: Responding correctly to these objects requires differentiating them from other very similar objects in memory (Duncan et al., 2012b).

Critically, some 'similar' objects were preceded by 'new' objects, whereas other 'similar' objects were preceded by 'old' objects. 'New' objects were predicted to lead to a high cholinergic state, which should prioritize memory encoding, and improve the ability to perform pattern separation (Yassa and Stark, 2011). Conversely, the familiarity of 'old' objects was predicted to lead to a low cholinergic state, which should prioritize memory retrieval and impair the ability to perform pattern separation (Duncan et al., 2012b).

If these encoding vs. retrieval modes linger for several seconds (consistent with the temporal dynamics of acetylcholine) (Hasselmo and Fehlau, 2001; Meeter et al., 2004), then participants should be in a retrieval state when they encounter 'similar' objects presented just after 'old' objects. Being in a retrieval state should facilitate pattern completion (or, conversely, hurt pattern separation), leading participants to falsely endorse 'similar' objects as 'old'. Indeed, accuracy was lower for 'similar' objects preceded by an 'old' object vs. 'similar' objects preceded by a 'new' object. Thus, being in a retrieval state can hurt one's ability to encode two similar items as being distinct (Duncan et al., 2012b). In contrast, recent exposure to familiar objects enhances integrative encoding, a process that relies on the retrieval of previously stored associations (Duncan et al.,2012b). Together, these findings suggest that novelty vs. familiarity can toggle the system between encoding/pattern separation and retrieval/pattern completion, respectively. This is consistent with predictions of how acetylcholine should act in the hippocampus (Hasselmo and Schnell, 1994; Hasselmo, 1995).

Using a similar behavioral manipulation, another study found that recent exposure to familiar (vs. novel) objects enhanced associative retrieval, but did not influence item memory (Patil and Duncan, 2018). Associative retrieval — being able to identify which pair of items was studied together — requires pattern completion: Given one member of the pair, an individual must retrieve, or 'complete', the memory to determine the other member of the pair. Item recognition, in contrast, does not require pattern completion or associative processing and may therefore be accomplished by regions outside of the hippocampus, such as the perirhinal cortex (Davachi et al., 2003). The selective benefit for preceding familiarity on associative memory is therefore consistent with the instantiation of a retrieval mode in the hippocampus. Importantly, consistent with the timescale of cholinergic modulation of the hippocampus (Hasselmo and Fehlau, 2001; Meeter et al., 2004), the effect of recent familiarity on associative memory decreased over several seconds (Patil and Duncan, 2018).

Retrieval states can have a pervasive effect on our behavior, beyond judgments of memory. We sometimes make decisions by consulting a specific prior memory. For example, we may choose to return to a lunch spot because we remember having a delicious sandwich there one time (Bornstein et al., 2017). Thus, familiarity-induced retrieval states might increase our reliance on episodic memory retrieval when making decisions. Indeed, participants were more likely to retrieve, and use, episodic memories after they had just seen a familiar vs. novel scene (Duncan and Shohamy, 2016).

Together, these studies indicate that the presence of familiar information can induce a retrieval state, which prioritizes access to stored mnemonic representations, often at the cost of encoding but to the benefit of integration (as in Duncan et al., 2012b) and decision making (Duncan and Shohamy, 2016). These behavioral effects may be mediated by a cholinergic mechanism (Duncan et al., 2012b; Duncan and Shohamy, 2016; Patil and Duncan, 2018).

Separately, a large body of work has shown that familiar spatial contexts enhance memory retrieval. These studies were not motivated by cholinergic dynamics; rather, they were tests of the encoding specificity hypothesis (Tulving and Thomson, 1971). The key finding is that exposure to a familiar spatial context can facilitate memory retrieval (Robin & Moscovitch, 2014, 2017; Robin et al., 2016; Robin et al., 2019). A critical difference between the effect of familiar spatial contexts (as in the encoding specificity studies) and the effect of familiarity-induced retrieval states (Duncan et al., 2012b) is the relevance of the familiar item/context to the retrieved memory. While familiar spatial contexts enhance retrieval of memories related to that context (Robin et al., 2019), retrieval states induced by familiarity can enhance retrieval of unrelated associations (Duncan et al., 2012b; Duncan and Shohamy, 2016; Patil and Duncan, 2018). Importantly, by separating the induction of a retrieval state from the act of retrieval itself, this illustrates that retrieval may depend partly on our pre-existing internal state (Quamme et al., 2010). Similar to Tulving's retrieval mode hypothesis (Tulving, 1983; Lepage et al., 2000), cholinergic retrieval states highlight the importance of internal, rather than external, context and draw a distinction between the likelihood of retrieval and the contents of retrieval.

4.5. Interim conclusions

The aforementioned behavioral studies are in line with neurocomputational models of cholinergic retrieval states — but these studies do not test these theories directly because acetylcholine is not explicitly manipulated (Duncan et al., 2012b; Duncan and Shohamy, 2016; Patil and Duncan, 2018). Future studies with pharmacological manipulations will be critical for directly testing cholinergic encoding vs. retrieval states in the hippocampus (for one such approach, see Ruiz and Aly, 2019).

We have discussed the link between high acetylcholine levels and encoding, but this link comes with a strong caveat. Work in non-human animals shows that ablation of cholinergic septohippocampal projections does not impair performance across multiple behavioral tasks, including ones of learning and memory (Parent and Baxter, 2004; Baxter et al., 2013; McHugh et al., 2015). This raises the possibility that, although acetylcholine may balance encoding and retrieval states, it does not play a necessary role that cannot be compensated for by other mechanisms. What might those other mechanisms be?

One potential candidate is theta oscillations. These oscillations occur rapidly, on the order of milliseconds, but nevertheless influence memory retrieval (Sederberg et al., 2003; Staudigl et al., 2010; Addante et al., 2011; Staudigl and Hanslmayr, 2013). The peak vs. trough of theta may be optimal for encoding and retrieval, in line with a state-based account of hippocampal function (Colgin, 2016; Kerrén et al., 2018). Acetylcholine and theta interact: In rodents, cholinergic antagonists disrupt the modulation of theta by encoding-like behaviors (Newman et al., 2012; Newman et al., 2013). For example, one study found that as rodents explored novel vs. familiar environments, CA1 firing shifted toward the peak vs. trough of the theta phase, respectively. Furthermore, a cholinergic antagonist attenuated the shift toward the theta peak in novel environments (Douchamps et al., 2013). Such interactions between theta and acetylcholine remain underexplored in humans.

Taken together, research on acetylcholine, the hippocampus, and memory — from computational modeling, non-human animals, and humans — converges in suggesting that the hippocampus can be biased to prioritize retrieval when in a low cholinergic state. Critically, the induction of this retrieval state is separable from the contents of retrieval, illustrating the importance of our pre-existing internal state for successful remembering (Quamme et al., 2010).

5. Discussion

In this review, we explored Tulving's hypothesis of a retrieval mode as an internal neurocognitive state that facilitates remembering (Tulving, 1983). We examined how intention, attention, and neuromodulators create internal states that facilitate successful retrieval. Intentions can guide what information we remember or forget in the present, and shape how and what we remember in the future. Attention plays an important role in the selection of relevant memories and the suppression of competing memories, tasks, or perceptual distractors. Finally, neuromodulatory systems, particularly the cholinergic system, can help toggle the brain between states that are optimized for encoding vs. retrieval.

Although we have focused on intention, attention, and neuromodulatory states as important features of retrieval mode, we do not claim that they are the only important factors. For example, expectations may alter our internal states and contribute to retrieval mode: Expectations interact with, and complement, attention (Summerfield and Egner, 2009). Furthermore, although we separately examined intention, attention, and neuromodulatory states, these factors likely interact in complex ways in real life. Below, we briefly examine such interactions.

5.1. Interactions between intention, attention, and cholinergic states

5.1.1. Attention and intention

Early formulations of retrieval mode proposed that both intentions and attention are critical contributors (Lepage et al., 2000), and they likely influence each other in a bidirectional fashion (for EEG evidence showing a dissociation between intentions and attention during retrieval, see Herron and Wilding, 2004). For instance, when we set the intention to retrieve a memory, we may bring attentional resources online to keep the goal active and help focus memory search on goal-relevant features. Indeed, the phrase *goal-directed attention* highlights the importance of goals (or intentions) on attentional selection (Corbetta and Shulman, 2002). Studies of memory intentions (e.g., motivated forgetting and prospective memory; Kuhl and Wagner, 2009; Burgess Gonen-Yaacovi and Volle, 2011; Anderson and Hanslmayr, 2014; Anderson and McDaniel, 2019), and studies of attentional modulation of memory (e.g., selective attention and retrieval-induced forgetting; Baldo and Shimamura, 2002; Wimber et al., 2015), provide some evidence to substantiate the interaction between intention and attention.

First, studies of how intentions affect memory often highlight the role of attention. For instance, studies of retrieval suppression suggest the involvement of a top-down inhibitory control process in successful forgetting (Benoit and Anderson, 2012; Levy and Anderson, 2012; Paz-Alonso et al., 2013; Gagnepain et al., 2014). This control process might involve goal-directed attention directed toward memory suppression (Levy and Anderson, 2002; Hulbert et al., 2016). Similarly, theories of prospective memory intentions often call on attentional processes. For example, the multiprocess theory of prospective memory proposes a monitoring pathway with an attentional control process that maintains the prospective memory intention in mind and searches for the target (McDaniel and Einstein, 2000; Einstein and McDaniel, 2005; McDaniel et al., 2015; Anderson and McDaniel, 2019).

Along with similarities in cognitive operations, neural signatures of attention and intention overlap. The prefrontal cortex is implicated in intention setting, as in motivated forgetting (Anderson and Hanslmayr, 2014) and in prospective memory (Gilbert, 2011; Momennejad and Haynes, 2013). The prefrontal cortex is also linked to goal-directed attentional selection between competing memories (Corbetta and Shulman, 2002; Asplund et al., 2010; Kim et al., 2016), retrieval-induced forgetting (Wimber et al., 2015), and goal-relevant retrieval in the face of distraction (Wais et al., 2010). Indeed, some studies of prospective memory demonstrate that attention and intention both draw on prefrontal cortex function (Simons et al., 2006; Benoit et al., 2012). One parsimonious account is that individuals first engage in a process of intention setting, which then drives attentional selection — with both of these processes dependent on prefrontal cortex function.

Intentions therefore likely affect attention, but what about the reverse? As we attend to ongoing tasks or to the outside world, a change in our attentional focus might bring to mind a previously stored intention to retrieve a memory or engage in some action. Indeed, this is a component of the multiprocess theory of prospective memory: The appearance of a prospective memory target can spontaneously reactivate a prospective memory intention (McDaniel and Einstein, 2000; Einstein and McDaniel, 2005; McDaniel et al., 2015; Anderson and McDaniel, 2019). In such cases, bottom-up attentional capture by the prospective memory target could be the mechanism through which the retrieval of prospective memory intentions occurs. Returning to our earlier scenario, Caroline might capture our attention as she walks by in the hallway, leading us to remember our intention to pass along a message from Nick (Fig. 1). Alternatively, attention might bypass intention and trigger memory retrieval directly, a possibility that should be explored in future work.

In sum, intention and attention are closely intertwined: Intentions to retrieve particular memories change attentional states in a way that optimizes remembering. Attention can then affect subsequent goal states in a feedback loop. Studies that attempt to separate the process of setting an intention from the enactment of a corresponding attentional set will be important (Günseli and Aly, 2019). Such approaches can help identify the overlapping and unique cognitive and neural underpinnings of intention and attention.

5.1.2. Attention and acetylcholine

One of the neuromodulatory systems that is closely tied to attention is acetylcholine (Newman et al., 2012). Thus, although we discussed the role of acetylcholine as that of shifting the hippocampal balance between encoding and retrieval, its function can also be conceptualized as modulating attentional states.

Specifically, encoding modes (high acetylcholine) can be considered states that optimize attention to the external world, while retrieval modes (low acetylcholine) can be considered states that optimize attention to the internal world. Indeed, theoretical models postulate that the brain fluctuates between internally and externally biased states (for a review, see Honey et al., 2017). In the hippocampus, this constitutes a fluctuation between retrieval vs. encoding (Hasselmo and Schnell, 1994; Hasselmo, 1995; Hasselmo and Barkai, 1995; Hasselmo et al., 1995, 1996; Meeter et al., 2004). In this framework, then, acetylcholine and attention are tightly linked: Acetylcholine can toggle the hippocampus between internally vs. externally directed attention.

There is some evidence that attention directed toward internal memory retrieval can modulate the hippocampus (Dudukovic et al., 2009; Duncan et al., 2012a; Hashimoto et al., 2012). Likewise, emerging work has found evidence for modulation of the hippocampus by externally oriented attention (Aly and Turk-Browne, 2016a, 2016b; 2017; Cordova et al., 2019): Different (external) attentional states directed at identical stimuli produce distinct patterns of activity in the hippocampus. One hypothesis is that externally oriented attention modulates hippocampal representations via acetylcholine (Newman et al., 2012; Honey et al., 2017). If acetylcholine shifts the balance between internal and external attentional states in the hippocampus, then high levels of acetylcholine should improve behavior on externally oriented attention tasks that require the hippocampus. Conversely, low levels of acetylcholine should improve behavior on internally oriented attention tasks that require the hippocampus. This remains to be examined in future work: Few pharmacological studies in humans have directly tested the proposal that acetylcholine can modulate hippocampal attention processes (see Ruiz and Aly (2019), for an example).

Acetylcholine is therefore strongly implicated in encoding vs. retrieval states as well as in attention (Newman et al., 2012). This suggests that the neuromodulatory mechanisms involved in attention and memory are inherently related: Acetylcholine may modulate the balance between externally vs. internally oriented attention in the hippocampus, in the service of encoding vs. retrieval.

5.2. *Retrieval and encoding modes: competition or cooperation?*

We have discussed evidence that internal states may prioritize memory retrieval, often at the cost of encoding (Duncan et al., 2012b). These findings imply competition between these mnemonic processes. For example, memory retrieval is poorer when performing a concurrent encoding or attention task (Fernandes and Moscovitch, 2000; Wais et al., 2010; Aly and Turk-Browne, 2017). Additionally, performance on an ongoing working memory task is slower and poorer when holding a (non-focal) prospective memory intention in mind (Anderson and McDaniel, 2019). Finally, familiar information in our environment can bias us toward memory retrieval at the cost of encoding (Duncan et al., 2012b; Duncan and Shohamy, 2016). Such trade-offs support the notion that encoding and retrieval may operate in distinct states in the hippocampus (see Section 4), as well as across larger cortical networks (Huijbers et al., 2013; Long and Kuhl, 2019). This trade-off can be adaptive: It can help protect memories against interference because the influence of the external world can be minimized when one is attending to a retrieved memory.

However, the relationship between encoding and retrieval may be more complex than pure competition. For example, one illustrative study found that suppression of memory retrieval is associated with a reduction in hippocampal activity and results in worse memory encoding for events occurring around the time of suppression (Hulbert et al., 2016). Thus, suppressing retrieval is followed by a period of diminished encoding. These findings point to a non-competitive interaction between retrieval and encoding: if they always competed, encoding should improve when retrieval is impaired.

One caveat to this interpretation is that simultaneous suppression of retrieval and encoding may be a result of overall downregulation of hippocampal function, as evidenced by decreased hippocampal activity (Hulbert et al., 2016). If the hippocampus is not actively processing information, both encoding and retrieval would be downregulated regardless of whether a trade-off between them usually exists. However, this interpretation must be treated cautiously because decreased BOLD activity as measured with fMRI does not necessarily mean that a brain region's function is suppressed. For example, the relationship between BOLD signals and local field potentials, a measure of neural activity, is less consistent in the hippocampus than in the cortex (Ekstrom, 2010); this makes it difficult to relate the magnitude or even the sign of the BOLD signal in hippocampus to the magnitude of neural activity. Furthermore, decreased univariate activity in the hippocampus has been observed along with enhanced multivariate pattern similarity signals — multivariate signals that correlate with behavior (Aly and Turk-Browne, 2016a, 2016b; Cordova et al., 2019). In fact, reduced hippocampal activity has been observed in a task that requires intact hippocampal function for accurate performance (2016b; Ruiz et al., 2019). Together, this suggests that decreased BOLD activity cannot be interpreted as suppression of a brain region's function (2016b). Therefore, the mechanisms underlying the joint downregulation of encoding and retrieval during memory suppression, as well as other factors that affect when and how encoding and retrieval compete, deserve further investigation.

If encoding and retrieval sometimes both decline together, can they also both come online together in a way that facilities cognition? Indeed, encoding and retrieval sometimes cooperate. One such example is integrative encoding, in which a current experience is linked to a prior memory (Schlichting and Preston, 2015). This process involves retrieving memories while concurrently encoding the current moment (Zeithamova et al., 2012; Richter et al., 2016). Such cooperation between encoding and retrieval can lead to memory updating, which is adaptive when one wants to form integrated memory traces that preserve important relationships between individual memories (Zeithamova et al., 2012; Richter et al., 2016).

Indeed, whether encoding and retrieval cooperate or compete may depend partly on our intention to integrate memories vs. retrieve or encode them in isolation (Richter et al., 2016): The intention to integrate memories may facilitate cooperation between encoding and retrieval. Neural signatures of memory integration are distinct from those for encoding or retrieval (Richter et al., 2016), further illustrating that competition vs. cooperation of encoding and retrieval may be separable internal states.

Neurotransmitters may also be key to understanding when encoding and retrieval states compete or cooperate. Acetylcholine may trigger competition between encoding and retrieval: Acetylcholine levels switch the hippocampus between states optimized for encoding and those optimized for retrieval (Hasselmo and Schnell, 1994; Hasselmo, 1995; Hasselmo and Barkai, 1995; Hasselmo et al., 1995, 1996; Meeter et al., 2004). Conversely, dopamine may facilitate cooperation between encoding and retrieval. Dopamine enhances plasticity in CA3-CA1 connections (Li et al., 2003) — which are important for memory retrieval — but dopamine is also thought to enhance memory encoding (Lisman and Grace, 2005). Thus, dopamine may modulate the encoding of current experiences, which can then be directly linked to past experiences retrieved via CA3. This is consistent with theoretical models proposing that dopamine may bias the hippocampus toward memory integration (for reviews, see Shohamy and Adcock, 2010; Duncan and Schlichting, 2018; Clewett and Murty, 2019).

The role of dopamine may differ between the hippocampus and other regions. In prefrontal cortex, dopamine plays a role in switching between external and internal states. For example, activation of D1 vs D2 receptors in prefrontal cortex is important for modulating online maintenance of existing information vs. encoding new information (O'Reilly, 2006; Durstewitz and Seamans, 2008). Additionally, dopaminergic modulation in prefrontal cortex may play a role in attentional

Box 1
Future Directions:

How might the cognitive and neural mechanisms of retrieval mode differ for episodic vs. semantic memory?

Tulving suggested that retrieval mode involves holding a subset of a specific memory in mind. In what way does retrieval mode depend on, vs. operate independently from, memory accessibility?

Does retrieval mode modulate the strength with which memories are reactivated or only the probability of remembering?

How does the intention to forget differ from the intention to remember? Might some neurological conditions (e.g., *post-traumatic stress disorder) affect one process more than the other?*

How does retrieval mode interact with the contents of the memory? Are emotional or salient memories, vs. neutral memories, more likely to come to mind even without a retrieval mode?

suppression (e.g., van Schouwenburg et al., 2010). In line with this, higher levels of dopamine in prefrontal cortex predict greater suppression of competing memories, as reflected in larger retrieval-induced forgetting (Wimber et al., 2011).

Thus, although the role of dopamine differs across brain regions, in the hippocampus it may promote cooperation between encoding and retrieval. Although it is tempting to propose that cholinergic states promote competition between encoding and retrieval while dopamine promotes cooperation, this would be an oversimplification. Cholinergic states can also sometimes facilitate cooperation between these mnemonic processes. For example, states of low acetylcholine increase integrative encoding (Schlichting and Preston, 2015), which requires both encoding current experiences and retrieving related prior experiences. When and how cholinergic states support competition vs. cooperation between encoding and retrieval is an important area for future work.

In sum, our internal state can prioritize memory retrieval, but this does not always need to be at the cost of encoding. Whether encoding and retrieval compete or cooperate may be determined by our intentions and the balance of neurotransmitters in the brain.

5.3. Concluding remarks

While the focus of this review has been on internal states, internal states are often altered by our external environment. For example, the intention to forget can change one's internal context (Manning et al., 2016), but the intention itself is often triggered by an external cue to remember vs. forget — at least in typical laboratory studies. Similarly, the presence of novel vs. familiar information in our external environment can change the levels of acetylcholine in the brain, biasing our internal state toward memory encoding vs. retrieval (Duncan et al., 2012b). Therefore, although we have emphasized the influence of internal states on memory retrieval, external and internal context are inherently intertwined.

To conclude, Tulving's retrieval mode hypothesis (1983) emphasized the rememberer's internal, neurocognitive state as an important factor influencing successful retrieval. However, the internal factors that influence retrieval mode are still being elucidated. We elaborated on Tulving's hypothesis by specifying some neural mechanisms and differentiable states that could bias individuals toward successful remembering. Intention, attention, and neuromodulatory states can — in isolation or synergistically — contribute to retrieval mode. We propose that intention and attention are inherently and hierarchically related: Intentions to retrieve or suppress a memory can guide our attention toward internal representations. This hierarchy is sometimes reversed, such as when attention facilitates the spontaneous retrieval of a stored prospective intention. Neuromodulatory states, such as acetylcholine, set the neural background on which cognitive states (e.g., intention or attention) can operate. Future work examining this proposal and other open questions (Box 1) will help further characterize when and how intention, attention, and neuromodulatory states interact. In that way, we will gain new insights into the dynamic factors that gate access to our memories.

Acknowledgements

This work was supported by a National Science Foundation CAREER Award from the Division of Behavioral and Cognitive Sciences (BCS-1844241) to M. Aly. We would like to thank Peter Sanfilippo for creating the illustrations in Fig. 1, Dr. Katherine Duncan for helpful discussions, and Dr. Maureen Ritchey and Natalie Biderman for helpful feedback and comments on an earlier version of this manuscript.

References

Addante, R.J., Watrous, A.J., Yonelinas, A.P., Ekstrom, A.D., Ranganath, C., 2011. Prestimulus theta activity predicts correct source memory retrieval. Proc. Natl. Acad. Sci. 108 (26), 10702–10707. https://doi.org/10.1073/pnas.1014528108.

Aly, M., Turk-Browne, N.B., 2016a. Attention promotes episodic encoding by stabilizing hippocampal representations. Proc. Natl. Acad. Sci. 113 (4), E420–E429. https://doi.org/10.1073/pnas.1518931113.

Aly, M., Turk-Browne, N.B., 2016. Attention stabilizes representations in the human hippocampus. Cerebr. Cortex 26 (2), 783–796. https://doi.org/10.1093/cercor/bhv041.

Aly, M., Turk-Browne, N.B., 2017. How hippocampal memory shapes, and is shaped by, attention. In: Hannula, D.E., Duff, M.C. (Eds.), The Hippocampus from Cells to Systems: Structure, Connectivity, and Functional Contributions to Memory and Flexible Cognition, pp. 369–403. https://doi.org/10.1007/978-3-319-50406-3_12.

Aly, M., Yonelinas, A.P., Kishiyama, M.M., Knight, R.T., 2011. Damage to the lateral prefrontal cortex impairs familiarity but not recollection. Behav. Brain Res. 225 (1), 297–304. https://doi.org/10.1016/j.bbr.2011.07.043.

Anderson, B.A., Jacoby, L.L., Thomas, R.C., Balota, D.A., 2011. The effects of age and divided attention on spontaneous recognition. Mem. Cogn. 39 (4), 725–735.

Anderson, J.R., 1974. Retrieval of propositional information from long-term memory. Cogn. Psychol. 6 (4), 451–474. https://doi.org/10.1016/0010-0285(74)90021-8.

Anderson, M.C., Bjork, R.A., Bjork, E.L., 1994. Remembering can cause forgetting: retrieval dynamics in long-term memory. J. Exp. Psychol. Learn. Mem. Cogn. 20 (5), 1063.

Anderson, M.C., Bunce, J.G., Barbas, H., 2016. Prefrontal–hippocampal pathways underlying inhibitory control over memory. Hippocampal interactions with brain networks that influence learning & memory. Neurobiol. Learn. Mem. 134, 145–161. https://doi.org/10.1016/j.nlm.2015.11.008.

Anderson, M.C., Green, C., 2001. Suppressing unwanted memories by executive control. Nature 410 (6826), 366. https://doi.org/10.1038/35066572.

Anderson, M.C., Hanslmayr, S., 2014. Neural mechanisms of motivated forgetting. Trends Cogn. Sci. 18 (6), 279–292. https://doi.org/10.1016/j.tics.2014.03.002.

Anderson, M.C., Huddleston, E., 2012. Towards a cognitive and neurobiological model of motivated forgetting. In: Belli, R.F. (Ed.), True and False Recovered Memories: toward a Reconciliation of the Debate, pp. 53–120. https://doi.org/10.1007/978-1-4614-1195-6_3.

Anderson, M.C., Ochsner, K.N., Kuhl, B.A., Cooper, J., Robertson, E., Gabrieli, S.W., Gabrieli, J.D.E., 2004. Neural systems underlying the suppression of unwanted memories. Science 303 (5655), 232–235. https://doi.org/10.1126/science.1089504.

Anderson, McDaniel, M.A., 2019. Retrieval in prospective memory: multiple processes or just delay? Q. J. Exp. Psychol. https://doi.org/10.1177/1747021819845622, 174702181984562.

Ardila, A., Rosselli, M., 1989. Neuropsychological characteristics of normal aging. Dev. Neuropsychol. 5 (4), 307–320. https://doi.org/10.1080/87565648909540441.

Aslan, A., Bäuml, K.-H.T., 2011. Individual differences in working memory capacity predict retrieval-induced forgetting. J. Exp. Psychol. Learn. Mem. Cogn. 37 (1), 264–269. https://doi.org/10.1037/a0021324.

Asplund, C.L., Todd, J.J., Snyder, A.P., Marois, R., 2010. A central role for the lateral prefrontal cortex in goal-directed and stimulus-driven attention. Nat. Neurosci. 13 (4), 507–512. https://doi.org/10.1038/nn.2509.

Baddeley, A., Lewis, V., Eldridge, M., Thomson, N., 1984. Attention and retrieval from long-term memory. J. Exp. Psychol. Gen. 113 (4), 518–540. https://doi.org/10.1037/0096-3445.113.4.518.

Badre, D., Wagner, A.D., 2007. Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia 45 (13), 2883–2901. https://doi.org/10.1016/j.neuropsychologia.2007.06.015.

Bahrick, H.P., Bahrick, L.E., Bahrick, A.S., Bahrick, P.E., 1993. Maintenance of foreign language vocabulary and the spacing effect. Psychol. Sci. 4 (5), 316–321. https://doi.org/10.1111/j.1467-9280.1993.tb00571.x.

Bakker, A., Kirwan, C.B., Miller, M., Stark, C.E.L., 2008. Pattern separation in the human hippocampal CA3 and dentate gyrus. Science (New York, N.Y.) 319 (5870), 1640–1642. https://doi.org/10.1126/science.1152882.

Baldo, J.V., Shimamura, A.P., 2002. Frontal Lobes and Memory. The Handbook of Memory Disorders, 2nd. John Wiley & Sons, pp. 363–379.

Baxter, M.G., Bucci, D.J., Gorman, L.K., Wiley, R.G., Gallagher, M., 2013. Selective immunotoxic lesions of basal forebrain cholinergic cells: effects on learning and memory in rats. Behav. Neurosci. 127 (5), 619–627. https://doi.org/10.1037/a0033939.

Bein, O., Duncan, K., Davachi, L., 2019. Mnemonic prediction errors bias hippocampal states. BioRxiv 740563. https://doi.org/10.1101/740563.

Bengtsson, S.L., Haynes, J.-D., Sakai, K., Buckley, M.J., Passingham, R.E., 2009. The representation of abstract task rules in the human prefrontal cortex. Cerebr. Cortex 19 (8), 1929–1936. https://doi.org/10.1093/cercor/bhn222.

Benoit, R.G., Anderson, M.C., 2012. Opposing mechanisms support the voluntary forgetting of unwanted memories. Neuron 76 (2), 450–460.

Benoit, R.G., Gilbert, S.J., Frith, C.D., Burgess, P.W., 2012. Rostral prefrontal cortex and the focus of attention in prospective memory. Cerebr. Cortex 22 (8), 1876–1886. https://doi.org/10.1093/cercor/bhr264.

Benoit, R.G., Hulbert, J.C., Huddleston, E., Anderson, M.C., 2015. Adaptive top–down suppression of hippocampal activity and the purging of intrusive memories from consciousness. J. Cogn. Neurosci. 27 (1), 96–111.

Berron, D., Schütze, H., Maass, A., Cardenas-Blanco, A., Kuijf, H.J., Kumaran, D., Düzel, E., 2016. Strong evidence for pattern separation in human dentate gyrus. J. Neurosci.: Off. J. Soc. Neurosci. 36 (29), 7569–7579. https://doi.org/10.1523/JNEUROSCI.0518-16.2016.

Berryhill, M.E., 2012. Insights from neuropsychology: pinpointing the role of the posterior parietal cortex in episodic and working memory. Front. Integr. Neurosci. 6 https://doi.org/10.3389/fnint.2012.00031.

Bird, C.M., Keidel, J.L., Ing, L.P., Horner, A.J., Burgess, N., 2015. Consolidation of complex events via reinstatement in posterior cingulate cortex. J. Neurosci. 35 (43), 14426–14434. https://doi.org/10.1523/JNEUROSCI.1774-15.2015.

Bjork, R.A., 1988. Retrieval practice and the maintenance of knowledge. Pract. Aspects Memory: Curr. Res. Issues 1, 396–401.

Block, L.G., Morwitz, V.G., 1999. Shopping lists as an external memory aid for grocery shopping: influences on list writing and list fulfillment. J. Consum. Psychol. 8 (4), 343–375. https://doi.org/10.1207/s15327663jcp0804_01.

Bonnici, H.M., Richter, F.R., Yazar, Y., Simons, J.S., 2016. Multimodal feature integration in the angular gyrus during episodic and semantic retrieval. J. Neurosci. 36 (20), 5462–5471. https://doi.org/10.1523/JNEUROSCI.4310-15.2016.

Bornstein, A.M., Khaw, M.W., Shohamy, D., Daw, N.D., 2017. Reminders of past choices bias decisions for reward in humans. Nat. Commun. 8, 15958. https://doi.org/10.1038/ncomms15958.

Braver, T.S., Barch, D.M., 2002. A theory of cognitive control, aging cognition, and neuromodulation. Neurosci. Biobehav. Rev. 26 (7), 809–817. https://doi.org/10.1016/S0149-7634(02)00067-2.

Braver, T.S., Bongiolatti, S.R., 2002. The role of frontopolar cortex in subgoal processing during working memory. Neuroimage 15 (3), 523–536. https://doi.org/10.1006/nimg.2001.1019.

Brody, A.L., Mandelkern, M.A., London, E.D., Olmstead, R.E., Farahi, J., Scheibal, D., Mukhin, A.G., 2006. Cigarette smoking saturates brain α4β2 nicotinic acetylcholine receptors. Arch. Gen. Psychiatr. 63 (8), 907–915. https://doi.org/10.1001/archpsyc.63.8.907.

Brown, T.I., Carr, V.A., LaRocque, K.F., Favila, S.E., Gordon, A.M., Bowles, B., Wagner, A.D., 2016. Prospective representation of navigational goals in the human hippocampus. Science 352 (6291), 1323–1326. https://doi.org/10.1126/science.aaf0784.

Burgess Gonen-Yaacovi, G., Volle, E., 2011. Functional neuroimaging studies of prospective memory: what have we learnt so far? Neuropsychologia 49 (8), 2246–2257. https://doi.org/10.1016/j.neuropsychologia.2011.02.014.

Burgess, P.W., Veitch, E., de Lacy Costello, A., Shallice, T., 2000. The cognitive and neuroanatomical correlates of multitasking. Neuropsychologia 38 (6), 848–863.

Burgess, Scott, S.K., Frith, C.D., 2003. The role of the rostral frontal cortex (area 10) in prospective memory: a lateral versus medial dissociation. Neuropsychologia 41 (8), 906–918.

Butler, A.J., James, K.H., 2010. The neural correlates of attempting to suppress negative versus neutral memories. Cognit. Affect Behav. Neurosci. 10 (2), 182–194. https://doi.org/10.3758/CABN.10.2.182.

Cabeza, R., Ciaramelli, E., Moscovitch, M., 2012. Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. Trends Cogn. Sci. 16 (6), 338–352. https://doi.org/10.1016/j.tics.2012.04.008.

Cabeza, R., Ciaramelli, E., Olson, I.R., Moscovitch, M., 2008. The parietal cortex and episodic memory: an attentional account. Nat. Rev. Neurosci. 9 (8), 613–625. https://doi.org/10.1038/nrn2459.

Cabeza, R., Mazuz, Y.S., Stokes, J., Kragel, J.E., Woldorff, M.G., Ciaramelli, E., Moscovitch, M., 2011. Overlapping parietal activity in memory and perception: evidence for the attention to memory model. J. Cogn. Neurosci. 23 (11), 3209–3217. https://doi.org/10.1162/jocn_a_00065.

Carr, M.F., Frank, L.M., 2012. A single microcircuit with multiple functions: state dependent information processing in the hippocampus. Curr. Opin. Neurobiol. 22 (4), 704–708. https://doi.org/10.1016/j.conb.2012.03.007.

Carr, V.A., Engel, S.A., Knowlton, B.J., 2013. Top-down modulation of hippocampal encoding activity as measured by high-resolution functional MRI. Neuropsychologia 51 (10), 1829–1837.

Chen, J., Cook, P.A., Wagner, A.D., 2015. Prediction strength modulates responses in human area CA1 to sequence violations. J. Neurophysiol. 114 (2), 1227–1238. https://doi.org/10.1152/jn.00149.2015.

Cheong, M.Y., Yun, S.H., Mook-Jung, I., Joo, I., Huh, K., Jung, M.W., 2001. Cholinergic modulation of synaptic physiology in deep layer entorhinal cortex of the rat. J. Neurosci. Res. 66 (1), 117–121. https://doi.org/10.1002/jnr.1203.

Chua, E.F., Schacter, D.L., Rand-Giovannetti, E., Sperling, R.A., 2006. Understanding metamemory: neural correlates of the cognitive process and subjective level of confidence in recognition memory. Neuroimage 29 (4), 1150–1160. https://doi.org/10.1016/j.neuroimage.2005.09.058.

Ciaramelli, E., Grady, C.L., Moscovitch, M., 2008. Top-down and bottom-up attention to memory: a hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. Neuropsychologia 46 (7), 1828–1851. https://doi.org/10.1016/j.neuropsychologia.2008.03.022.

Ciaramelli, E., Grady, C., Levine, B., Ween, J., Moscovitch, M., 2010. Top-down and bottom-up attention to memory are dissociated in posterior parietal cortex: neuroimaging and neuropsychological evidence. J. Neurosci. 30 (14), 4943. https://doi.org/10.1523/JNEUROSCI.1209-09.2010.

Clarke, A.J.B., Butler, L.T., 2008. Dissociating word stem completion and cued recall as a function of divided attention at retrieval. Memory 16 (7), 763–772. https://doi.org/10.1080/09658210802261116.

Clewett, D., Murty, V.P., 2019. Echoes of emotions past: how neuromodulators determine what we recollect. ENeuro 6 (2). https://doi.org/10.1523/ENEURO.0108-18.2019. ENEURO.0108-18.2019.

Colgin, L.L., 2016. Rhythms of the hippocampal network. Nat. Rev. Neurosci. 17 (4), 239–249. https://doi.org/10.1038/nrn.2016.21.

Cooper, R.A., Ritchey, M., 2019. Cortico-hippocampal network connections support the multidimensional quality of episodic memory. ELife 8, e45591.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215. https://doi.org/10.1038/nrn755.

Cordova, N.I., Turk-Browne, N.B., Aly, M., 2019. Focusing on what Matters: Modulation of the Human hippocampus by Relational Attention. Hippocampus.

Craik, F.I., Govoni, R., Naveh-Benjamin, M., Anderson, N.D., 1996. The effects of divided attention on encoding and retrieval processes in human memory. J. Exp. Psychol. Gen. 125 (2), 159.

Davachi, L., Mitchell, J.P., Wagner, A.D., 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. Proc. Natl. Acad. Sci. 100 (4), 2157–2162. https://doi.org/10.1073/pnas.0337195100.

Davachi, Lila, Wagner, A.D., 2002. Hippocampal contributions to episodic encoding: insights from relational and item-based learning. J. Neurophysiol. 88 (2), 982–990.

Dempster, F.N., 1992. The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. Dev. Rev. 12 (1), 45–75. https://doi.org/10.1016/0273-2297(92)90003-K.

Depue, B.E., Curran, T., Banich, M.T., 2007. Prefrontal regions orchestrate suppression of emotional memories via a two-phase process. Science 317 (5835), 215–219. https://doi.org/10.1126/science.1139560.

Douchamps, V., Jeewajee, A., Blundell, P., Burgess, N., Lever, C., 2013. Evidence for encoding versus retrieval scheduling in the Hippocampus by theta phase and acetylcholine. J. Neurosci. 33 (20), 8689–8704. https://doi.org/10.1523/JNEUROSCI.4483-12.2013.

Dudukovic, N.M., DuBrow, S., Wagner, A.D., 2009. Attention during memory retrieval enhances future remembering. Mem. Cogn. 37 (7), 953–961.

Dudukovic, N.M., Wagner, A.D., 2007. Goal-dependent modulation of declarative memory: neural correlates of temporal recency decisions and novelty detection. Neuropsychologia 45 (11), 2608–2620. https://doi.org/10.1016/j.neuropsychologia.2007.02.025.

Duncan, K., Curtis, C., Davachi, L., 2009. Distinct memory signatures in the Hippocampus: intentional states distinguish match and mismatch enhancement signals. J. Neurosci. 29 (1), 131–139. https://doi.org/10.1523/JNEUROSCI.2998-08.2009.

Duncan, K., Ketz, N., Inati, S.J., Davachi, L., 2012a. Evidence for area CA1 as a match/mismatch detector: a high-resolution fMRI study of the human hippocampus. Hippocampus 22 (3), 389–398. https://doi.org/10.1002/hipo.20933.

Duncan, K., Sadanand, A., Davachi, L., 2012b. Memory's penumbra: episodic memory decisions induce lingering mnemonic biases. Science 337 (6093), 485–487. https://doi.org/10.1126/science.1221936.

Duncan, K., Schlichting, M.L., 2018. Hippocampal representations as a function of time, subregion, and brain state. Neurobiol. Learn. Mem. 153, 40–56. https://doi.org/10.1016/j.nlm.2018.03.006.

Duncan, K., Shohamy, D., 2016. Memory states influence value-based decisions. J. Exp. Psychol. Gen. 145 (11), 1420–1426. https://doi.org/10.1037/xge0000231.

Duncan, K., Tompary, A., Davachi, L., 2014. Associative encoding and retrieval are predicted by functional connectivity in distinct hippocampal area CA1 pathways. J. Neurosci. 34 (34), 11188–11198. https://doi.org/10.1523/JNEUROSCI.0521-14.2014.

Durstewitz, D., Seamans, J.K., 2008. The dual-state theory of prefrontal cortex dopamine function with relevance to catechol-O-methyltransferase genotypes and schizophrenia. Biol. Psychiatry 64 (9), 739–749. https://doi.org/10.1016/j.biopsych.2008.05.015.

Eichenbaum, H., 2017. Prefrontal-hippocampal interactions in episodic memory. Nat. Rev. Neurosci. 18 (9), 547–558. https://doi.org/10.1038/nrn.2017.74.

Einstein, G.O., McDaniel, M.A., 2005. Prospective memory: multiple retrieval processes. Curr. Dir. Psychol. Sci. 14 (6), 286–290. https://doi.org/10.1111/j.0963-7214.2005.00382.x.

Einstein, G.O., McDaniel, M.A., 2010. Prospective memory and what costs do not reveal about retrieval processes: a commentary on Smith, Hunt, McVay, and McConnell (2007). J. Exp. Psychol. Learn. Mem. Cogn. 36 (4), 1082–1088. https://doi.org/10.1037/a0019184.

Ekstrom, A., 2010. How and when the fMRI BOLD signal relates to underlying neural activity: the danger in dissociation. Brain Res. Rev. 62 (2), 233–244. https://doi.org/10.1016/j.brainresrev.2009.12.004.

Favila, S.E., Samide, R., Sweigart, S.C., Kuhl, B.A., 2018. Parietal representations of stimulus features are amplified during memory retrieval and flexibly aligned with top-down goals. J. Neurosci. 38 (36), 7809–7821. https://doi.org/10.1523/JNEUROSCI.0564-18.2018.

Felleman, D.J., Van Essen, D.C., 1991. Distributed hierarchical processing in the primate cerebral cortex. Cerebr. Cortex 1 (1), 1–47. https://doi.org/10.1093/cercor/1.1.1.

Fernandes, M.A., Moscovitch, M., 2000. Divided attention and memory: evidence of substantial interference effects at retrieval and encoding. J. Exp. Psychol. Gen. 129 (2), 155.

Fernandes, M.A., Moscovitch, M., Ziegler, M., Grady, C., 2005. Brain regions associated with successful and unsuccessful retrieval of verbal episodic memory as revealed by divided attention. Neuropsychologia 43 (8), 1115–1127. https://doi.org/10.1016/j.neuropsychologia.2004.11.026.

Gagnepain, P., Henson, R.N., Anderson, M.C., 2014. Suppressing unwanted memories reduces their unconscious influence via targeted cortical inhibition. Proc. Natl. Acad. Sci. 111 (13), E1310–E1319. https://doi.org/10.1073/pnas.1311468111.

Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R.T., D'Esposito, M., 2008. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. Proc. Natl. Acad. Sci. 105 (35), 13122–13126. https://doi.org/10.1073/pnas.0806074105.

Gazzaley, A., Cooney, J.W., Rissman, J., D'Esposito, M., 2005. Top-down suppression deficit underlies working memory impairment in normal aging. Nat. Neurosci. 8 (10), 1298. https://doi.org/10.1038/nn1543.

Gilbert, S.J., 2011. Decoding the content of delayed intentions. J. Neurosci. 31 (8), 2888–2894. https://doi.org/10.1523/JNEUROSCI.5336-10.2011.

Gilbert, S.J., Frith, C.D., Burgess, P.W., 2005. Involvement of rostral prefrontal cortex in selection between stimulus-oriented and stimulus-independent thought. Eur. J. Neurosci. 21 (5), 1423–1431. https://doi.org/10.1111/j.1460-9568.2005.03981.x.

Gilbert, S.J., Gollwitzer, P.M., Cohen, A.-L., Oettingen, G., Burgess, P.W., 2009. Separable brain systems supporting cued versus self-initiated realization of delayed intentions. J. Exp. Psychol. Learn. Mem. Cogn. 35 (4), 905–915. https://doi.org/10.1037/a0015535.

Giovannini, M.G., Rakovska, A., Benton, R.S., Pazzagli, M., Bianchi, L., Pepeu, G., 2001. Effects of novelty and habituation on acetylcholine, GABA, and glutamate release from the frontal cortex and hippocampus of freely moving rats. Neuroscience 106 (1), 43–53.

Greve, A., Cooper, E., Kaula, A., Anderson, M.C., Henson, R., 2017. Does prediction error drive one-shot declarative learning? J. Mem. Lang. 94, 149–165. https://doi.org/10.1016/j.jml.2016.11.001.

Günseli, E., Aly, M., 2019, October. Memory-guided Attentional States Are Established by the hippocampus and Medial Prefrontal Cortex. Poster presented at the Society for Neuroscience Meeting, Chicago, IL.

Harrison, T.L., Mullet, H.G., Whiffen, K.N., Ousterhout, H., Einstein, G.O., 2014. Prospective memory: effects of divided attention on spontaneous retrieval. Mem. Cogn. 42 (2), 212–224. https://doi.org/10.3758/s13421-013-0357-y.

Hasher, L., Zacks, R.T., 1988. Working memory, comprehension, and aging: a review and a new view. In: Bower, G.H. (Ed.), Psychology of Learning and Motivation, vol. 22, pp. 193–225. https://doi.org/10.1016/S0079-7421(08)60041-9.

Hasher, L., Zacks, R.T., May, C.P., 1999. Inhibitory control, circadian arousal, and age. In: Attention and Performance. Attention and Performance XVII: Cognitive Regulation of Performance: Interaction of Theory and Application. The MIT Press, Cambridge, MA, US, pp. 653–675.

Hashimoto, R., Abe, N., Ueno, A., Fujii, T., Takahashi, S., Mori, E., 2012. Changing the criteria for old/new recognition judgments can modulate activity in the anterior hippocampus. Hippocampus 22 (2), 141–148. https://doi.org/10.1002/hipo.20878.

Hasselmo, M.E., 1995. Neuromodulation and cortical function: modeling the physiological basis of behavior. Behav. Brain Res. 67 (1), 1–27.

Hasselmo, M.E., 2006. The role of acetylcholine in learning and memory. Curr. Opin. Neurobiol. 16 (6), 710–715. https://doi.org/10.1016/j.conb.2006.09.002.

Hasselmo, M.E., Barkai, E., 1995. Cholinergic modulation of activity-dependent synaptic plasticity in the piriform cortex and associative memory function in a network biophysical simulation. J. Neurosci.: Off. J. Soc. Neurosci. 15 (10), 6592–6604.

Hasselmo, M.E., Bodelón, C., Wyble, B.P., 2002. A proposed function for hippocampal theta rhythm: separate phases of encoding and retrieval enhance reversal of prior learning. Neural Comput. 14 (4), 793–817. https://doi.org/10.1162/089976602317318965.

Hasselmo, M.E., Fehlau, B.P., 2001. Differences in time course of ACh and GABA modulation of excitatory synaptic potentials in slices of rat hippocampus. J. Neurophysiol. 86 (4), 1792–1802. https://doi.org/10.1152/jn.2001.86.4.1792.

Hasselmo, M.E., Schnell, E., 1994. Laminar selectivity of the cholinergic suppression of synaptic transmission in rat hippocampal region CA1: computational modeling and brain slice physiology. J. Neurosci.: Off. J. Soc. Neurosci. 14 (6), 3898–3914.

Hasselmo, M.E., Schnell, E., Barkai, E., 1995. Dynamics of learning and recall at excitatory recurrent synapses and cholinergic modulation in rat hippocampal region CA3. J. Neurosci. 15 (7), 5249–5262. https://doi.org/10.1523/JNEUROSCI.15-07-05249.1995.

Hasselmo, M.E., Stern, C.E., 2014. Theta rhythm and the encoding and retrieval of space and time. Neuroimage 85 (Pt 2), 656–666. https://doi.org/10.1016/j.neuroimage.2013.06.022.

Hasselmo, M.E., Wyble, B.P., Wallenstein, G.V., 1996. Encoding and retrieval of episodic memories: role of cholinergic and GABAergic modulation in the hippocampus. Hippocampus 6 (6), 693–708. https://doi.org/10.1002/(SICI)1098-1063(1996)6:6<693::AID-HIPO12>3.0.CO;2-W.

Haynes, J.D., Sakai, K., Rees, G., Gilbert, S., Frith, C., Passingham, R.E., 2007. Reading hidden intentions in the human brain. Curr. Biol. 17 (4), 323–328. https://doi.org/10.1016/j.cub.2006.11.072.

Heathcote, A., Loft, S., Remington, R.W., 2015. Slow down and remember to remember! A delay theory of prospective memory costs. Psychol. Rev. 122 (2), 376. https://doi.org/10.1037/a0038952.

Herron, J.E., Wilding, E.L., 2004. An electrophysiological dissociation of retrieval mode and retrieval orientation. Neuroimage 22 (4), 1554–1562. https://doi.org/10.1016/j.neuroimage.2004.04.011.

Hertel, P.T., Calcaterra, G., 2005. Intentional forgetting benefits from thought substitution. Psychon. Bull. Rev. 12 (3), 484–489. https://doi.org/10.3758/BF03193792.

Honey, C.J., Newman, E.L., Schapiro, A.C., 2017. Switching between internal and external modes: a multiscale learning principle. Netw. Neurosci. 1 (4), 339–356. https://doi.org/10.1162/NETN_a_00024.

Huerta, P.T., Lisman, J.E., 1993. Heightened synaptic plasticity of hippocampal CA1 neurons during a cholinergically induced rhythmic state. Nature 364 (6439), 723–725. https://doi.org/10.1038/364723a0.

Huerta, P.T., Lisman, J.E., 1995. Bidirectional synaptic plasticity induced by a single burst during cholinergic theta oscillation in CA1 in vitro. Neuron 15 (5), 1053–1063.

Huijbers, W., Schultz, A.P., Vannini, P., McLaren, D.G., Wigman, S.E., Ward, A.M., Sperling, R.A., 2013. The encoding/retrieval flip: interactions between memory performance and memory stage and relationship to intrinsic cortical networks. J. Cogn. Neurosci. 25 (7), 1163–1179. https://doi.org/10.1162/jocn_a_00366.

Hulbert, J.C., Henson, R.N., Anderson, M.C., 2016. Inducing amnesia through systemic suppression. Nat. Commun. 7, 11003. https://doi.org/10.1038/ncomms11003.

Hutchinson, J.B., Uncapher, M.R., Wagner, A.D., 2009. Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. Learn. Mem. 16 (6), 343–356. https://doi.org/10.1101/lm.919109.

Iidaka, T., Anderson, N.D., Kapur, S., Cabez, R., Craik, F.I., 2000. The effect of divided attention on encoding and retrieval in episodic memory revealed by positron emission tomography. J. Cogn. Neurosci. 12 (2), 267–280.

Jacoby, L.L., Woloshyn, V., Kelley, C., 1989. Becoming famous without being recognized: unconscious influences of memory produced by dividing attention. J. Exp. Psychol. Gen. 118 (2), 115.

Johnson, A., van der Meer, M.A., Redish, A.D., 2007. Integrating hippocampus and striatum in decision-making. Curr. Opin. Neurobiol. 17 (6), 692–697. https://doi.org/10.1016/j.conb.2008.01.003.

Jonker, T.R., Seli, P., MacLeod, C.M., 2013. Putting retrieval-induced forgetting in context: an inhibition-free, context-based account. Psychol. Rev. 120 (4), 852–872. https://doi.org/10.1037/a0034246.

Kensinger, E.A., Garoff-Eaton, R.J., Schacter, D.L., 2007. How negative emotion enhances the visual specificity of a memory. J. Cogn. Neurosci. 19 (11), 1872–1887.

Kerrén, C., Linde-Domingo, J., Hanslmayr, S., Wimber, M., 2018. An optimal oscillatory phase for pattern reactivation during memory retrieval. Curr. Biol.: CB 28 (21), 3383–3392. https://doi.org/10.1016/j.cub.2018.08.065 e6.

Kesner, R.P., Rolls, E.T., 2015. A computational theory of hippocampal function, and tests of the theory: new developments. Neurosci. Biobehav. Rev. 48, 92–147. https://doi.org/10.1016/j.neubiorev.2014.11.009.

Kim, Hongkeun, Cabeza, R., 2007. Trusting our memories: dissociating the neural correlates of confidence in veridical versus illusory memories. J. Neurosci. 27 (45), 12190–12197. https://doi.org/10.1523/JNEUROSCI.3408-07.2007.

Kim, Hoseok, Ährlund-Richter, S., Wang, X., Deisseroth, K., Carlén, M., 2016. Prefrontal parvalbumin neurons in control of attention. Cell 164 (1), 208–218. https://doi.org/10.1016/j.cell.2015.11.038.

Koechlin, E., Basso, G., Pietrini, P., Panzer, S., Grafman, J., 1999. The role of the anterior prefrontal cortex in human cognition. Nature 399 (6732), 148–151. https://doi.org/10.1038/20178.

Kopelman, M.D., Stanhope, N., Kingsley, D., 1999. Retrograde amnesia in patients with diencephalic,temporal lobe or frontal lesions. Neuropsychologia 37 (8), 939–958. https://doi.org/10.1016/S0028-3932(98)00143-2.

Kremin, T., Hasselmo, M.E., 2007. Cholinergic suppression of glutamatergic synaptic transmission in hippocampal region CA3 exhibits laminar selectivity: implication for hippocampal network dynamics. Neuroscience 149 (4), 760–767. https://doi.org/10.1016/j.neuroscience.2007.07.007.

Kuhl, B.A., Chun, M.M., 2014. Successful remembering elicits event-specific activity patterns in lateral parietal cortex. J. Neurosci. 34 (23), 8051–8060. https://doi.org/10.1523/JNEUROSCI.4328-13.2014.

Kuhl, B.A., Dudukovic, N.M., Kahn, I., Wagner, A.D., 2007. Decreased demands on cognitive control reveal the neural processing benefits of forgetting. Nat. Neurosci. 10, 908.

Kuhl, B.A., Johnson, M.K., Chun, M.M., 2013. Dissociable neural mechanisms for goal-directed versus incidental memory reactivation. J. Neurosci. 33 (41), 16099–16109. https://doi.org/10.1523/JNEUROSCI.0207-13.2013.

Kuhl, B.A., Wagner, A.D., 2009. Forgetting and retrieval. In: Berntson, G.G., Cacioppo, J. T. (Eds.), Handbook of Neuroscience for the Behavioral Sciences, neubb001031. https://doi.org/10.1002/9780470478509.neubb001031.

Lau, H.C., Rogers, R.D., Haggard, P., Passingham, R.E., 2004. Attention to intention. Science (New York, N.Y.) 303 (5661), 1208–1210. https://doi.org/10.1126/science.1090973.

Lavenex, P., Amaral, D.G., 2000. Hippocampal-neocortical interaction: a hierarchy of associativity. Hippocampus 10 (4), 420–430. https://doi.org/10.1002/1098-1063(2000)10:4<420::AID-HIPO8>3.0.CO;2-5.

Lee, H., Kuhl, B.A., 2016. Reconstructing perceived and retrieved faces from activity patterns in lateral parietal cortex. J. Neurosci. 36 (22), 6069–6082. https://doi.org/10.1523/JNEUROSCI.4286-15.2016.

Lee, H., Samide, R., Richter, F.R., Kuhl, B.A., 2019. Decomposing parietal memory reactivation to predict consequences of remembering. Cerebr. Cortex 29 (8), 3305–3318. https://doi.org/10.1093/cercor/bhy200.

LeMoult, J., Hertel, P.T., Joormann, J., 2010. Training the forgetting of negative words: the role of direct suppression and the relation to stress reactivity. Appl. Cognit. Psychol. 24 (3), 365–375. https://doi.org/10.1002/acp.1682.

Lepage, M., Ghaffar, O., Nyberg, L., Tulving, E., 2000. Prefrontal cortex and episodic memory retrieval mode. Proc. Natl. Acad. Sci. 97 (1), 506–511.

Leutgeb, J.K., Leutgeb, S., Moser, M.-B., Moser, E.I., 2007. Pattern separation in the dentate gyrus and CA3 of the hippocampus. Science (New York, N.Y.) 315 (5814), 961–966. https://doi.org/10.1126/science.1135801.

Levy, B.J., Anderson, M.C., 2002. Inhibitory processes and the control of memory retrieval. Trends Cogn. Sci. 6 (7), 299–305. https://doi.org/10.1016/S1364-6613(02)01923-X.

Levy, B.J., Anderson, M.C., 2012. Purging of memories from conscious awareness tracked in the human brain. J. Neurosci. 32 (47), 16785–16794. https://doi.org/10.1523/JNEUROSCI.2640-12.2012.

Li, S., Cullen, W.K., Anwyl, R., Rowan, M.J., 2003. Dopamine-dependent facilitation of LTP induction in hippocampal CA1 by exposure to spatial novelty. Nat. Neurosci. 6 (5), 526. https://doi.org/10.1038/nn1049.

Lisman, J.E., Grace, A.A., 2005. The hippocampal-VTA loop: controlling the entry of information into long-term memory. Neuron 46 (5), 703–713. https://doi.org/10.1016/j.neuron.2005.05.002.

Loft, S., Remington, R.W., 2013. Wait a second: brief delays in responding reduce focality effects in event-based prospective memory. Q. J. Exp. Psychol. 66 (7), 1432–1447. https://doi.org/10.1080/17470218.2012.750677.

Logan, G.D., Gordon, R.D., 2001. Executive control of visual attention in dual-task situations. Psychol. Rev. 108 (2), 393–434. https://doi.org/10.1037/0033-295X.108.2.393.

Long, N.M., Kuhl, B.A., 2019. Decoding the tradeoff between encoding and retrieval to predict memory for overlapping events. Neuroimage 201, 116001. https://doi.org/10.1016/j.neuroimage.2019.07.014.

Long, N.M., Lee, H., Kuhl, B.A., 2016. Hippocampal mismatch signals are modulated by the strength of neural predictions and their similarity to outcomes. J. Neurosci. 36 (50), 12677–12687. https://doi.org/10.1523/JNEUROSCI.1850-16.2016.

Luo, L., Craik, F.I., 2008. Aging and memory: a cognitive approach. Can. J. Psychiatr. 53 (6), 346–353. https://doi.org/10.1177/070674370805300603.

Mack, A., Rock, I., 1998. Inattentional Blindness. MIT press.

Mangels, J.A., Gershberg, F.B., Shimamura, A.P., Knight, R.T., 1996. Impaired retrieval from remote memory in patients with frontal lobe damage. Neuropsychology 10 (1), 32–41. https://doi.org/10.1037/0894-4105.10.1.32.

Manning, J.R., Hulbert, J.C., Williams, J., Piloto, L., Sahakyan, L., Norman, K.A., 2016. A neural signature of contextually mediated intentional forgetting. Psychon. Bull. Rev. 23 (5), 1534–1542. https://doi.org/10.3758/s13423-016-1024-7.

McCormick, C., St-Laurent, M., Ty, A., Valiante, T.A., McAndrews, M.P., 2013. Functional and effective hippocampal–neocortical connectivity during construction and elaboration of autobiographical memory retrieval. Cerebr. Cortex 25 (5), 1297–1305.

McDaniel, M.A., Einstein, G.O., 2000. Strategic and automatic processes in prospective memory retrieval: a multiprocess framework. Appl. Cognit. Psychol. 14 (7), S127–S144. https://doi.org/10.1002/acp.775.

McDaniel, M.A., Umanath, S., Einstein, G.O., Waldum, E.R., 2015. Dual pathways to prospective remembering. Front. Hum. Neurosci. 9 https://doi.org/10.3389/fnhum.2015.00392.

McHugh, S.B., Francis, A., McAuley, J.D., Stewart, A.L., Baxter, M.G., Bannerman, D.M., 2015. Hippocampal acetylcholine depletion has No effect on anxiety, spatial novelty preference, or differential reward for low rates of responding (DRL) performance in rats. Behav. Neurosci. 129 (4), 491–501. https://doi.org/10.1037/bne0000072.

Meeter, M., Murre, J.M.J., Talamini, L.M., 2004. Mode shifting between storage and recall based on novelty detection in oscillating hippocampal circuits. Hippocampus 14 (6), 722–741. https://doi.org/10.1002/hipo.10214.

Meier, B., Graf, P., 2000. Transfer appropriate processing for prospective memory tests. Appl. Cognit. Psychol. 14 (7), S11–S27. https://doi.org/10.1002/acp.768.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24 (1), 167–202. https://doi.org/10.1146/annurev.neuro.24.1.167.

Momennejad, I., Haynes, J.-D., 2012. Human anterior prefrontal cortex encodes the ‘what’ and ‘when’ of future intentions. Neuroimage 61 (1), 139–148. https://doi.org/10.1016/j.neuroimage.2012.02.079.

Momennejad, I., Haynes, J.-D., 2013. Encoding of prospective tasks in the human prefrontal cortex under varying task loads. J. Neurosci. 33 (44), 17342–17349. https://doi.org/10.1523/JNEUROSCI.0492-13.2013.

Montgomery, S.M., Buzsáki, G., 2007. Gamma oscillations dynamically couple hippocampal CA3 and CA1 regions during memory task performance. Proc. Natl. Acad. Sci. U. S. A 104 (36), 14495–14500. https://doi.org/10.1073/pnas.0701826104.

Moritz, S., Gläscher, J., Sommer, T., Büchel, C., Braus, D.F., 2006. Neural correlates of memory confidence. Neuroimage 33 (4), 1188–1193. https://doi.org/10.1016/j.neuroimage.2006.08.003.

Morris, C.D., Bransford, J.D., Franks, J.J., 1977. Levels of processing versus transfer appropriate processing. J. Verb. Learn. Verb. Behav. 16 (5), 519–533. https://doi.org/10.1016/S0022-5371(77)80016-9.

Moscovitch, M., 2008. The hippocampus as a “stupid,” domain-specific module: implications for theories of recent and remote memory, and of imagination. Can. J. Exp. Psychol. Revue. Canadienne de Psychologie Expérimentale 62 (1), 62–79. https://doi.org/10.1037/1196-1961.62.1.62.

Mullet, H.G., Scullin, M.K., Hess, T.J., Scullin, R.B., Arnold, K.M., Einstein, G.O., 2013. Prospective memory and aging: evidence for preserved spontaneous retrieval with exact but not related cues. Psychol. Aging 28 (4), 910–922. https://doi.org/10.1037/a0034347.

Neunuebel, J.P., Knierim, J.J., 2014. CA3 retrieves coherent representations from degraded input: direct evidence for CA3 pattern completion and dentate gyrus pattern separation. Neuron 81 (2), 416–427. https://doi.org/10.1016/j.neuron.2013.11.017.

Newman, E.L., Gillet, S.N., Climer, J.R., Hasselmo, M.E., 2013. Cholinergic blockade reduces theta-gamma phase Amplitude coupling and speed modulation of theta frequency consistent with behavioral effects on encoding. J. Neurosci. 33 (50), 19635–19646. https://doi.org/10.1523/JNEUROSCI.2586-13.2013.

Newman, E.L., Gupta, K., Climer, J.R., Monaghan, C.K., Hasselmo, M.E., 2012. Cholinergic modulation of cognitive processing: insights drawn from computational models. Front. Behav. Neurosci. 6 https://doi.org/10.3389/fnbeh.2012.00024.

Norman, K.A., 2010. How hippocampus and cortex contribute to recognition memory: revisiting the Complementary Learning Systems model. Hippocampus 20 (11), 1217–1227. https://doi.org/10.1002/hipo.20855.

Okuda, J., Fujii, T., Ohtake, H., Tsukiura, T., Yamadori, A., Frith, C.D., Burgess, P.W., 2007. Differential involvement of regions of rostral prefrontal cortex (Brodmann area 10) in time- and event-based prospective memory. Int. J. Psychophysiol.: Off. J. Int. Org. Psychophysiol. 64 (3), 233–246. https://doi.org/10.1016/j.ijpsycho.2006.09.009.

Okuda, J., Fujii, T., Yamadori, A., Kawashima, R., Tsukiura, T., Fukatsu, R., Fukuda, H., 1998. Participation of the prefrontal cortices in prospective memory: evidence from a PET study in humans. Neurosci. Lett. 253 (2), 127–130. https://doi.org/10.1016/S0304-3940(98)00628-4.

O'Reilly, R.C., McClelland, J.L., 1994. Hippocampal conjunctive encoding, storage, and recall: avoiding a trade-off. Hippocampus 4 (6), 661–682. https://doi.org/10.1002/hipo.450040605.

O'Reilly, Randall C., 2006. Biologically based computational models of high-level cognition. Science 314 (5796), 91–94. https://doi.org/10.1126/science.1127242.

Ortega, A., Gómez-Ariza, C.J., Román, P., Bajo, M.T., 2012. Memory inhibition, aging, and the executive deficit hypothesis. J. Exp. Psychol. Learn. Mem. Cogn. 38 (1), 178–186. https://doi.org/10.1037/a0024510.

Parent, M.B., Baxter, M.G., 2004. Septohippocampal acetylcholine: involved in but not necessary for learning and memory? Learn. Mem. 11 (1), 9–20. https://doi.org/10.1101/lm.69104.

Patil, A., Duncan, K., 2018. Lingering cognitive states shape fundamental mnemonic abilities. Psychol. Sci. 29 (1), 45–55. https://doi.org/10.1177/0956797617728592.

Paz-Alonso, P.M., Bunge, S.A., Anderson, M.C., Ghetti, S., 2013. Strength of coupling within a mnemonic control network differentiates those who can and cannot suppress memory retrieval. J. Neurosci. 33 (11), 5017–5026. https://doi.org/10.1523/JNEUROSCI.3459-12.2013.

Potter, K.W., Huszar, L.D., Huber, D.E., 2018. Does inhibition cause forgetting after selective retrieval? A reanalysis and failure to replicate. *Cortex*; J. Devoted Study Nerv. Syst. Behav. 104, 26–45. https://doi.org/10.1016/j.cortex.2018.03.026.

Prete, F. del, Hanczakowski, M., Bajo, M.T., Mazzoni, G., 2015. Inhibitory effects of thought substitution in the think/no-think task: evidence from independent cues. Memory 23 (4), 507–517. https://doi.org/10.1080/09658211.2014.907429.

Quamme, J.R., Weiss, D.J., Norman, K.A., 2010. Listening for recollection: a multi-voxel pattern analysis of recognition memory retrieval strategies. Front. Hum. Neurosci. 4 https://doi.org/10.3389/fnhum.2010.00061.

Raaijmakers, J.G.W., 2018. Inhibition in memory. In: Wixted, J.T. (Ed.), Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience, pp. 1–34. https://doi.org/10.1002/9781119170174.epcn108.

Rajaram, S., Pereira-Pasarin, L.P., 2007. Collaboration can improve individual recognition memory: evidence from immediate and delayed tests. Psychon. Bull. Rev. 14 (1), 95–100. https://doi.org/10.3758/BF03194034.

Reynolds, J.R., West, R., Braver, T., 2009. Distinct neural circuits support transient and sustained processes in prospective memory and working memory. Cerebr. Cortex 19 (5), 1208–1221. https://doi.org/10.1093/cercor/bhn164.

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 (Pt A), 323–335. https://doi.org/10.1016/j.neuroimage.2015.08.051.

Robin, J., Garzon, L., Moscovitch, M., 2019. Spontaneous memory retrieval varies based on familiarity with a spatial context. Cognition 190, 81–92. https://doi.org/10.1016/j.cognition.2019.04.018.

Robin, J., Moscovitch, M., 2014. The effects of spatial contextual familiarity on remembered scenes, episodic memories, and imagined future events. J. Exp. Psychol. Learn. Mem. Cogn. 40 (2), 459–475. https://doi.org/10.1037/a0034886.

Robin, J., Moscovitch, M., 2017. Familiar real-world spatial cues provide memory benefits in older and younger adults. Psychol. Aging 32 (3), 210–219. https://doi.org/10.1037/pag0000162.

Robin, J., Wynn, J., Moscovitch, M., 2016. The spatial scaffold: the effects of spatial context on memory for events. J. Exp. Psychol. Learn. Mem. Cogn. 42 (2), 308–315. https://doi.org/10.1037/xlm0000167.

Roediger, H.L., Karpicke, J.D., 2006. Test-enhanced learning: taking memory tests improves long-term retention. Psychol. Sci. 17 (3), 249–255. https://doi.org/10.1111/j.1467-9280.2006.01693.x.

Roediger, H.L., McDermott, K.B., 1995. Creating false memories: remembering words not presented in lists. J. Exp. Psychol. Learn. Mem. Cogn. 21 (4), 803–814. https://doi.org/10.1037/0278-7393.21.4.803.

Román, P., Soriano, M.F., Gómez-Ariza, C.J., Bajo, M.T., 2009. Retrieval-induced forgetting and executive control. Psychol. Sci. 20 (9), 1053–1058. https://doi.org/10.1111/j.1467-9280.2009.02415.x.

Rowe, J.B., Sakai, K., Lund, T.E., Ramsoy, T., Christensen, M.S., Baare, W.F.C., Passingham, R.E., 2007. Is the prefrontal cortex necessary for establishing cognitive sets? J. Neurosci. 27 (48), 13303–13310. https://doi.org/10.1523/JNEUROSCI.2349-07.2007.

Rugg, M.D., Wilding, E.L., 2000. Retrieval processing and episodic memory. Trends Cogn. Sci. 4 (3), 108–115. https://doi.org/10.1016/S1364-6613(00)01445-5.

Ruiz, N.A., Meager, M.R., Agarwal, S., Aly, M., 2019. The hippocampus is critical for spatial relational attention. BioRxiv 765222. https://doi.org/10.1101/765222.

Ruiz, N., Aly, M., 2019, October. Cholinergic Modulation Enhances Hippocampally-dependent Spatial Relational Attention. Poster presented at the Society for Neuroscience Meeting, Chicago, IL.

Sakai, K., 2008. Task set and prefrontal cortex. Annu. Rev. Neurosci. 31 (1), 219–245. https://doi.org/10.1146/annurev.neuro.31.060407.125642.

Sakai, K., Passingham, R.E., 2003. Prefrontal interactions reflect future task operations. Nat. Neurosci. 6 (1), 75. https://doi.org/10.1038/nn987.

Schlichting, M.L., Preston, A.R., 2015. Memory integration: neural mechanisms and implications for behavior. Curr. Opin. Behav. Sci. 1, 1–8. https://doi.org/10.1016/j.cobeha.2014.07.005.

Schmitz, T.W., Correia, M.M., Ferreira, C.S., Prescot, A.P., Anderson, M.C., 2017. Hippocampal GABA enables inhibitory control over unwanted thoughts. Nat. Commun. 8 (1), 1311. https://doi.org/10.1038/s41467-017-00956-z.

Scullin, M.K., McDaniel, M.A., Shelton, J.T., Lee, J.H., 2010. Focal/nonfocal cue effects in prospective memory: monitoring difficulty or different retrieval processes? J. Exp. Psychol. Learn. Mem. Cogn. 36 (3), 736–749. https://doi.org/10.1037/a0018971.

Sederberg, P.B., Kahana, M.J., Howard, M.W., Donner, E.J., Madsen, J.R., 2003. Theta and gamma oscillations during encoding predict subsequent recall. J. Neurosci.: Off. J. Soc. Neurosci. 23 (34), 10809–10814.

Sestieri, C., Shulman, G.L., Corbetta, M., 2010. Attention to memory and the environment: functional specialization and dynamic competition in human posterior parietal cortex. J. Neurosci. 30 (25), 8445. https://doi.org/10.1523/JNEUROSCI.4719-09.2010.

Shapiro, M.L., Riceberg, J.S., Seip-Cammack, K., Guise, K.G., 2014. Functional interactions of prefrontal cortex and the Hippocampus in learning and memory. In: Derdikman, D., Knierim, J.J. (Eds.), Space,Time and Memory in the Hippocampal Formation, pp. 517–560. https://doi.org/10.1007/978-3-7091-1292-2_19.

Sherman, B.E., Turk-Browne, N.B., 2018. November). *How Does the hippocampus Simultaneously Process Instances and Regularities?* Poster Presented at the Society for Neuroscience Meeting (San Diego, CA).

Shohamy, D., Adcock, R.A., 2010. Dopamine and adaptive memory. Trends Cogn. Sci. 14 (10), 464–472. https://doi.org/10.1016/j.tics.2010.08.002.

Simons, J.S., Gilbert, S.J., Owen, A.M., Fletcher, P.C., Burgess, P.W., 2005. Distinct roles for lateral and medial anterior prefrontal cortex in contextual recollection. J. Neurophysiol. 94 (1) https://doi.org/10.1152/jn.01200.2004.

Simons, J.S., Peers, P.V., Mazuz, Y.S., Berryhill, M.E., Olson, I.R., 2010. Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. Cerebr. Cortex 20 (2), 479–485. https://doi.org/10.1093/cercor/bhp116.

Simons, J.S., Schölvinck, M.L., Gilbert, S.J., Frith, C.D., Burgess, P.W., 2006. Differential components of prospective memory?: evidence from fMRI. Neuropsychologia 44 (8), 1388–1397. https://doi.org/10.1016/j.neuropsychologia.2006.01.005.

Simons, J.S., Spiers, H.J., 2003. Prefrontal and medial temporal lobe interactions in long-term memory. Nat. Rev. Neurosci. 4 (8), 637–648. https://doi.org/10.1038/nrn1178.

Sinclair, A.H., Barense, M.D., 2018. Surprise and destabilize: prediction error influences episodic memory reconsolidation. Learn. Mem. 25 (8), 369–381. https://doi.org/10.1101/lm.046912.117.

Smith, R.E., 2003. The cost of remembering to remember in event-based prospective memory: investigating the capacity demands of delayed intention performance. J. Exp. Psychol. Learn. Mem. Cogn. 29 (3), 347–361. https://doi.org/10.1037/0278-7393.29.3.347.

Sohn, M.H., Goode, A., Stenger, V.A., Carter, C.S., Anderson, J.R., 2003. Competition and representation during memory retrieval: roles of the prefrontal cortex and the posterior parietal cortex. Proc. Natl. Acad. Sci. 100 (12), 7412. https://doi.org/10.1073/pnas.0832374100.

St Peters, M., Demeter, E., Lustig, C., Bruno, J.P., Sarter, M., 2011. Enhanced control of attention by stimulating mesolimbic-corticopetal cholinergic circuitry. J. Neurosci.: Off. J. Soc. Neurosci. 31 (26), 9760–9771. https://doi.org/10.1523/JNEUROSCI.1902-11.2011.

Staudigl, T., Hanslmayr, S., 2013. Theta oscillations at encoding mediate the context-dependent nature of human episodic memory. Curr. Biol. 23 (12), 1101–1106. https://doi.org/10.1016/j.cub.2013.04.074.

Staudigl, T., Hanslmayr, S., Bäuml, K.-H.T., 2010. Theta oscillations reflect the dynamics of interference in episodic memory retrieval. J. Neurosci.: Off. J. Soc. Neurosci. 30 (34), 11356–11362. https://doi.org/10.1523/JNEUROSCI.0637-10.2010.

St-Laurent, M., Abdi, H., Buchsbaum, B.R., 2015. Distributed patterns of reactivation predict vividness of recollection. J. Cogn. Neurosci. 27 (10), 2000–2018. https://doi.org/10.1162/jocn_a_00839.

Summerfield, C., Egner, T., 2009. Expectation (and attention) in visual cognition. Trends Cogn. Sci. 13 (9), 403–409. https://doi.org/10.1016/j.tics.2009.06.003.

Tomlinson, T.D., Huber, D.E., Rieth, C.A., Davelaar, E.J., 2009. An interference account of cue-independent forgetting in the no-think paradigm. Proc. Natl. Acad. Sci. 106 (37), 15588–15593. https://doi.org/10.1073/pnas.0813370106.

Treves, A., Rolls, E.T., 1992. Computational constraints suggest the need for two distinct input systems to the hippocampal CA3 network. Hippocampus 2 (2), 189–199. https://doi.org/10.1002/hipo.450020209.

Tulving, E., 1983. Elements of Episodic Memory. Oxford University Press, New York.

Tulving, E., 1985. Memory and consciousness. Can. Psychol. Psychologie Canadienne 26 (1), 1–12. https://doi.org/10.1037/h0080017.

Tulving, E., Schacter, D.L., 1990. Priming and human memory systems. Science 247 (4940), 301–306. https://doi.org/10.1126/science.2296719.

Tulving, E., Thomson, D.M., 1971. Retrieval processes in recognition memory: effects of associative context. J. Exp. Psychol. 87 (1), 116–124. https://doi.org/10.1037/h0030186.

Turchi, J., Sarter, M., 1997. Cortical acetylcholine and processing capacity: effects of cortical cholinergic deafferentation on crossmodal divided attention in rats. Brain Res. Cognit. Brain Res. 6 (2), 147–158.

Uncapher, M.R., Rugg, M.D., 2009. Selecting for memory? The influence of selective attention on the mnemonic binding of contextual information. J. Neurosci. 29 (25), 8270–8279.

Uttl, B., 2011. Transparent meta-analysis: does aging spare prospective memory with focal vs. Non-focal cues? PLoS One 6 (2). https://doi.org/10.1371/journal.pone.0016618.

van Schouwenburg, M., Aarts, E., Cools, R., 2010. Dopaminergic modulation of cognitive control: distinct roles for the prefrontal cortex and the basal ganglia. Curr. Pharmaceut. Des. 16 (18), 2026–2032.

van Strien, N.M., Cappaert, N.L.M., Witter, M.P., 2009. The anatomy of memory: an interactive overview of the parahippocampal–hippocampal network. Nat. Rev. Neurosci. 10 (4), 272–282. https://doi.org/10.1038/nrn2614.

Vogel, E.K., McCollough, A.W., Machizawa, M.G., 2005. Neural measures reveal individual differences in controlling access to working memory. Nature 438 (7067), 500. https://doi.org/10.1038/nature04171.

Vogt, K.E., Regehr, W.G., 2001. Cholinergic modulation of excitatory synaptic transmission in the CA3 area of the Hippocampus. J. Neurosci. 21 (1), 75–83. https://doi.org/10.1523/JNEUROSCI.21-01-00075.2001.

Volle, E., Gonen-Yaacovi, G., de Lacy Costello, A., Gilbert, S.J., Burgess, P.W., 2011. The role of rostral prefrontal cortex in prospective memory: a voxel-based lesion study. Neuropsychologia 49 (8), 2185–2198. https://doi.org/10.1016/j.neuropsychologia.2011.02.045.

Vortac, O.U., Edwards, M.B., Manning, C.A., 1995. Functions of external cues in prospective memory. Memory 3 (2), 201–219. https://doi.org/10.1080/09658219508258966.

Vredeveldt, A., Hitch, G.J., Baddeley, A.D., 2011. Eyeclosure helps memory by reducing cognitive load and enhancing visualisation. Mem. Cogn. 39 (7), 1253–1263. https://doi.org/10.3758/s13421-011-0098-8.

Wagner, A.D., Shannon, B.J., Kahn, I., Buckner, R.L., 2005. Parietal lobe contributions to episodic memory retrieval. Trends Cogn. Sci. 9 (9), 445–453. https://doi.org/10.1016/j.tics.2005.07.001.

Wais, P.E., Kim, O.Y., Gazzaley, A., 2012a. Distractibility during episodic retrieval is exacerbated by perturbation of left ventrolateral prefrontal cortex. Cerebral Cortex (New York, N.Y.: 1991) 22 (3), 717–724. https://doi.org/10.1093/cercor/bhr160.

Wais, P.E., Martin, G.M., Gazzaley, A., 2012b. The impact of visual distraction on episodic retrieval in older adults. Brain Res. 1430, 78–85. https://doi.org/10.1016/j.brainres.2011.10.048.

Wais, P.E., Rubens, M.T., Boccanfuso, J., Gazzaley, A., 2010. Neural mechanisms underlying the impact of visual distraction on retrieval of long-term memory. J. Neurosci. 30 (25), 8541. https://doi.org/10.1523/JNEUROSCI.1478-10.2010.

West, R.L., 1996. An application of prefrontal cortex function theory to cognitive aging. Psychol. Bull. 120 (2), 272–292. https://doi.org/10.1037/0033-2909.120.2.272.

Wheeler, M.A., Stuss, D.T., Tulving, E., 1995. Frontal lobe damage produces episodic memory impairment. J. Int. Neuropsychol. Soc. 1 (6), 525–536. https://doi.org/10.1017/S1355617700000655.

Whelihan, W.M., Lesher, E.L., 1985. Neuropsychological changes in frontal functions with aging. Dev. Neuropsychol. 1 (4), 371–380. https://doi.org/10.1080/87565648509540321.

Wimber, M., Schott, B.H., Wendler, F., Seidenbecher, C.I., Behnisch, G., Macharadze, T., Bäuml, K.T, Richardson-Klavehn, A., 2011. Prefrontal dopamine and the dynamic control of human long-term memory. Transl. Psychiatry 1 (7). https://doi.org/10.1038/tp.2011.15 e15.

Wimber, Maria, Alink, A., Charest, I., Kriegeskorte, N., Anderson, M.C., 2015. Retrieval induces adaptive forgetting of competing memories via cortical pattern suppression. Nat. Neurosci. 18 (4), 582–589. https://doi.org/10.1038/nn.3973.

Yassa, M.A., Stark, C.E.L., 2011. Pattern separation in the hippocampus. Trends Neurosci. 34 (10), 515–525. https://doi.org/10.1016/j.tins.2011.06.006.

Yonelinas, A.P., Aly, M., Wang, W.-C., Koen, J.D., 2010. Recollection and familiarity: examining controversial assumptions and new directions. Hippocampus 20 (11), 1178–1194. https://doi.org/10.1002/hipo.20864.

Zeithamova, D., Dominick, A.L., Preston, A.R., 2012. Hippocampal and ventral medial prefrontal activation during retrieval-mediated learning supports novel inference. Neuron 75 (1), 168–179. https://doi.org/10.1016/j.neuron.2012.05.010.