

Scale-invariant Characteristics of Forgetting: Toward a Unifying Account of Hippocampal Forgetting across Short and Long Timescales

Talya Sadeh¹ and Yoni Pertzov²

Abstract

■ After over 100 years of relative silence in the cognitive literature, recent advances in the study of the neural underpinnings of memory—specifically, the hippocampus—have led to a resurgence of interest in the topic of forgetting. This review draws a theoretically driven picture of the effects of time on forgetting of hippocampus-dependent memories. We review evidence indicating that time-dependent forgetting across short and long timescales is reflected in progressive degradation of hippocampal-dependent relational information.

This evidence provides an important extension to a growing body of research accumulated in recent years, showing that—in contrast to the once prevailing view that the hippocampus is exclusively involved in memory and forgetting over long timescales—the role of the hippocampus also extends to memory and forgetting over short timescales. Thus, we maintain that similar rules govern not only remembering but also forgetting of hippocampus-dependent information over short and long timescales. ■

INTRODUCTION

Recent years have seen a resurgence of interest in the topic of forgetting—a topic that had been relatively neglected in the memory literature since the 1970s (Wixted, 2004). There is an increasing acknowledgment in the field that understanding why information is forgotten is at least as important as understanding how information is encoded and retained (e.g., Davis & Zhong, 2017; Richards & Frankland, 2017; Nørby, 2015; Sadeh, Ozubko, Winocur, & Moscovitch, 2014). Perhaps most obviously, it is essential to elucidate the causes of memory failures to alleviate them in cases of abnormal forgetting (e.g., Butler & Zeman, 2008) as well as in cases of normative, but maladaptive, forgetting. Notwithstanding the downsides of forgetting, it also has some important beneficial functions. These functions have been enumerated in previous reviews, which highlight the adaptive role of forgetting in both cognitive and emotional aspects (Richards & Frankland, 2017; Nørby, 2015; Hardt, Nader, & Nadel, 2013). On the cognitive level, it is essential to forget details of memories over time to generalize across exemplars and create concepts and schemas. On the emotional level, forgetting of negative experiences is crucial for one's psychological well-being, emotional regulation, and maintenance of a positive self-concept. Indeed, negative experiences are much less likely to be remembered than positive experiences (Berntsen & Rubin, 2002). Further-

more, the inability to forget negative experiences or the disproportionate focus on such experiences is associated with psychopathologies such as posttraumatic stress disorder and depression (Nørby, 2015).

The revived interest in the study of forgetting brings with it a renewed focus on the passage of time as a significant cause of memory loss (e.g., Davis & Zhong, 2017; Miguez et al., 2016; Sadeh et al., 2014; Hardt et al., 2013). This focus on time as an important determinant of forgetting comes in contrast to the more traditional view, which focused on interference as the major cause of forgetting (Underwood, 1957). Interference theories, however, reached a dead end in their attempt to provide a comprehensive account of forgetting, and as John Wixted noted, “by 1970, the field had clearly lost its patience with increasingly complicated interference theories of forgetting” (Wixted, 2004). A few decades later, the mere passage of time has now re-emerged as a possible inducer of forgetting, alongside interference as an additional factor—rather than the sole factor (see Appendix A).

This is not a comprehensive review of forgetting, but rather a more selective review with the goal of drawing the readers' attention to some striking similarities between time-dependent forgetting of information over short and long timescales. By “short timescales,” we refer to cases in which an interval of a few seconds is employed between study and test—sometimes described as STM or working memory paradigms (e.g., Baddeley, 1992). By “long timescales,” we refer to cases in which the study–test intervals are of several minutes to days, weeks, and even months.

¹Ben-Gurion University of the Negev, Beer Sheva, Israel, ²The Hebrew University of Jerusalem

The similarities between forgetting patterns across these two timescales provide novel evidence in support of the increasingly popular idea that a single, hippocampus-based, mechanism underlies memory at both short and long timescales (for a discussion of potential mechanisms, see Appendix A). Importantly, our focus on the role of time in forgetting does not entail that we disregard interference as a potent inducer of forgetting (see Appendix B for an elaboration regarding studies examining forgetting due to interference, which are not within the focus of the current manuscript). Rather, as we discuss in the Directions for Future Research section, possible parallels between the contribution of interference to forgetting across short and long timescales is an exciting topic for future research. In addition, this review focuses only on forgetting occurring spontaneously, which is not induced by external manipulations. This is in contrast to forgetting induced by experimental manipulations, such as retrieval-induced forgetting and directed forgetting (Anderson & Huddleston, 2012).

We begin by briefly reviewing evidence for the idea that the hippocampus plays a similar role in supporting memories across short and long timescales. This idea is at the premise of our claim that hippocampal representations are particularly sensitive to time-dependent forgetting over both timescales. We then review the empirical evidence supporting our claim. We point to some striking similarities between forgetting characteristics across timescales, including the type of the memory representation sensitive to forgetting, as well as the effects of encoding duration and of top-down processes on forgetting. We then discuss other characteristics of forgetting that are shared across timescales and specifically the question of whether information is lost gradually or in an all-or-none fashion. Finally, we raise some intriguing open questions for future research.

THE HIPPOCAMPUS SUPPORTS MEMORY OVER SHORT AND LONG TIMESCALES

Our proposal that a similar mechanism underlies forgetting over short and long timescales is closely linked to and extends accumulating evidence that the medial-temporal lobe (MTL) and the hippocampus, in particular, support memory across these two timescales. This evidence comes in contrast to traditional accounts (Alvarez, Zola-Morgan, & Squire, 1994; Cave & Squire, 1992; Atkinson & Shiffrin, 1971; Baddeley & Warrington, 1970, and more recent ones: Davelaar, Goshen-Gottstein, Ashkenazi, Haarmann, & Usher, 2005; Talmi, Grady, Goshen-Gottstein, & Moscovitch, 2005), which regarded short- and long-term memory as two distinct systems or memory stores that are supported by distinct brain regions. The idea that remembering over short and long timescales is driven by a single mechanism has been extensively reviewed elsewhere (e.g., Yonelinas, 2013; Cashdollar, Duncan, & Duzel, 2011; Ranganath & Blumenfeld, 2005; Nairne, 2002). Here, we give a short

summary of the main findings supporting this idea, with emphasis on those with relevance to the similarities in forgetting patterns across timescales.

According to traditional accounts, information maintained over short timescales is stored in a temporary buffer, distinct from the long-term memory store. Studies of patients with long-term memory impairments following damage to the MTL provided compelling evidence for these accounts, showing that these patients were not impaired in memory tasks with retention intervals of several seconds (Milner, Squire, & Kandel, 1998; Cave & Squire, 1992; Baddeley & Warrington, 1970; Wickelgren, 1968). Perhaps the first piece of evidence for this notion came from the famous study of patient H. M. (Scoville & Milner, 1957). H. M., as well as two additional patients with psychiatric conditions, had pronounced long-term memory deficits as a result of removal of a large portion of their MTL (Scoville & Milner, 1957). Strikingly, however, these patients performed normally when asked to retain a three figure number or two words for several minutes, as long as they were not distracted during this time. Another study (Wickelgren, 1968) of patient H. M. examined his yes/no recognition memory for single items over short timescales. It was found that the rate of decay of memory traces over short intervals (0.25–8 sec) was within the normal range. Similarly, Cave and Squire (1992) examined a group of patients with hippocampal damage and deficits in long-term memory in standard memory tests probing memory over intervals of several minutes. Notably, these patients performed within the range of controls on standard verbal and nonverbal STM tests (e.g., digit span). Evidence along similar lines has also been reported in nonhuman primates. For example, Alvarez et al. (1994) found that monkeys with lesions to the hippocampus were not impaired in a delayed matching-to-sample with a very short delay (0.5 sec) but were impaired at longer delays (>30 sec). Based on such evidence, the predominant view at the time was that the hippocampus and its surrounding MTL structures support long-term memory but are not necessary for remembering information across short timescales.

However, a growing body of research from recent years has begun questioning this view, with accumulating evidence implicating the MTL in memory across short timescales of several seconds (Ezzyat & Olson, 2008; Olson, Moore, Stark, & Chatterjee, 2006; Holdstock, Gutnikov, Gaffan, & Mayes, 2000; Buffalo, Reber, & Squire, 1998; Holdstock, Shaw, & Aggleton, 1995; Owen, Sahakian, Semple, Polkey, & Robbins, 1995; Aggleton, Shaw, & Gaffan, 1992). Recent patient studies have provided specific evidence for the involvement of the hippocampus (rather than the MTL more generally) in memory over short timescales (Finke et al., 2008; Hannula, Tranel, & Cohen, 2006). This evidence is complemented by fMRI studies showing activation in the MTL and the hippocampus, in particular, during STM tasks across a wide variety of stimulus domains (Öztekin, Davachi, & McElree, 2010;

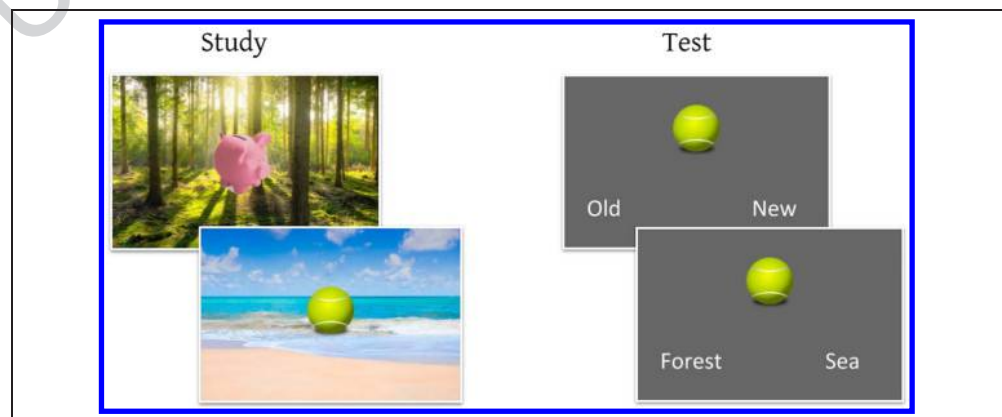
Ranganath, Cohen, & Brozinsky, 2005; Ranganath & D'Esposito, 2001; Stern, Sherman, Kirchhoff, & Hasselmo, 2001; Elliott & Dolan, 1999). Interestingly, two studies from the 1970s, which have been relatively unnoticed in this body of research, already hinted to the possible necessity of the hippocampus to memory across short timescales. Thus, the idea that the role of the hippocampus extends beyond long-term memory has its roots in earlier research. In one study, amnesic patients showed impaired memory for faces over retention intervals of 30 sec (Warrington & Taylor, 1973). Another study found that monkeys with impairments in the hippocampal system due to fornix lesions were impaired in an equivalent of a yes/no recognition paradigm for short lists of colors or spatial positions with a retention interval of 3 sec (Gaffan, 1977).

What is the role of the hippocampus in memory over short retention intervals? Why did early studies suggest that it is not necessary for short-term retention of information? The idea that the hippocampus supports the process of relational binding may provide an answer to both of these questions. "Relational binding" refers to the process of encoding representations regarding relations between two (or more) entities or pieces of information (Ryan, Moses, Barense, & Rosenbaum, 2013; Figure 1). Encoding relational bindings is a ubiquitous memory process, which underlies much of our information acquisition. To mention just a few examples, relational binding is required to represent the link between a certain item and its location, the association between two items (e.g., two words), and the relation between an item (e.g., a sentence) and the context in which it was experienced (e.g., where we heard that sentence).

Mounting evidence has suggested that the MTLs and specifically the hippocampus play a crucial role in learning novel associations—namely, in relational binding (for reviews, see Olsen, Moses, Riggs, & Ryan, 2012; Ranganath, 2010). Most importantly to the current context, it has been

claimed that this role is not limited to long-term memory. Rather, the hippocampus supports mnemonic functions relying on relational binding regardless of the durations of the study–test interval (Yonelinas, 2013). Both imaging and patient studies have provided evidence for the role of MTL and hippocampus in supporting memory for relational information over short timescales (Libby, Hannula, & Ranganath, 2014; Yee, Hannula, Tranel, & Cohen, 2014; Aly, Ranganath, & Yonelinas, 2013; Pertzov, Miller, et al., 2013; Race, LaRocque, Keane, & Verfaellie, 2013; Watson, Voss, Warren, Tranel, & Cohen, 2013; Cashdollar et al., 2009; Hannula & Ranganath, 2008; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006; for a review, see Yonelinas, 2013; but also see Jeneson & Squire, 2012; Baddeley, Allen, & Vargha-Khadem, 2010). To give just a few examples, patients with MTL damage were found to be impaired in memory for object–location associations after an 8-sec delay (Olson, Moore, et al., 2006). The patients were not impaired, however, in their memory for objects or locations over these delays; thus, their impairment was only apparent when the task involved relational binding. Hippocampal volume was found to predict the number of object–location binding errors following a 4-sec delay in familial Alzheimer's patients (Liang et al., 2016). Along similar lines, a study examining patients with hippocampal amnesia found that they were impaired in a yes/no continuous recognition task for face-scenes relations even when the recognition test immediately followed presentation of the corresponding study trial (Hannula et al., 2006). Finally, results from imaging studies further support the involvement of the hippocampus in relational memory over short timescales. For instance, in one study, participants were required to detect changes in the layout of four objects presented on a 3 × 3 grid following an 11-sec delay (Hannula & Ranganath, 2008). Hippocampal activation both at encoding and at retrieval predicted performance in the task. Thus, an impressive body of evidence has been accumulated in support of

Figure 1. A common paradigm for assessing relational binding of information. In the illustrated example, participants are required to maintain relational binding between an object (e.g., tennis ball) and its background image (e.g., beach). During learning, objects are overlaid on a specific background (e.g., forest or beach), and the relation between each object and its specific background is encoded. At retrieval, typically two possible memory tests are given: (1) an old/new recognition test, probing memory for the object, and (2) a source memory test, probing memory for the relation between the object and its background.



the notion that the MTL and the hippocampus, in particular, support memory for relational information not only over long timescales but over short timescales, as well.

With regard to the second question, “Why did earlier studies suggest that the hippocampus is not necessary for memory across short durations?” An analysis of some of the earlier patient studies suggests that the memory tasks employed in those studies did not rely on relational binding. Retention intervals were indeed short, but the information submitted to memory did not involve creation of novel associations between entities (for reviews, see Yonelinas, 2013; Ranganath & Blumenfeld, 2005). Rather, as evident from our review of earlier studies above, the study materials were nonrelational (item-only), simple, and overlearned. For instance, an often-used task in these studies was the digit span task (e.g., Cave & Squire, 1992; Penfield & Milner, 1958). Other studies probed memory for single items (e.g., digits) using a yes/no recognition test (Wickelgren, 1968). Finally, in the famous study of patient H. M. (Scoville & Milner, 1957), digits and words were used as well.

TIME-DEPENDENT FORGETTING OF HIPPOCAMPUS-BASED RELATIONAL INFORMATION

Having briefly reviewed the common underlying neural mechanisms of memory over short and long timescales, we now turn to discuss the similarities between their patterns of time-dependent forgetting. The most striking commonality between time-dependent forgetting patterns over short and long timescales is that it is manifested in the weakening of hippocampus-based relational memory. In contrast, memory of distinct items or pieces of information is less sensitive to forgetting over time (see Appendix A).

Long Timescales

Forgetting of relational and item information over long timescales has been examined using a wide variety of paradigms. Perhaps the most straightforward method for contrasting these two types of representations is the comparison of associative versus item memory. In associative memory paradigms, pairs of items are presented at study. At test, memory for the association between the item pairs is probed by asking participants to distinguish between “intact” pairs—two items that appeared within the same pair—and “recombined” pairs—two items that appeared at study but were not paired with one another. Using such paradigms, it has been found that associative memory shows substantial forgetting over timescales of a few days to 3 months (Sweegers & Talamini, 2014; Brubaker & Naveh-Benjamin, 2013; Talamini & Gorree, 2012; Hockley & Consoli, 1999, Experiment 2¹). Item information, in contrast, shows less forgetting over these timescales or no forgetting at all. For instance, a greater decline in associative versus item information was reported by

Brubaker and Naveh-Benjamin (2013) when examining forgetting rates over 10 min (Experiment 1) and over 24 hr (Experiment 2). In addition, higher forgetting rates of associative compared with item memories have been reported among individuals with amnesic mild cognitive impairment (Wang, Li, Li, & Zhang, 2013).

In a somewhat similar paradigm, item memory is compared with source memory—the relation between an item and its external source or context (Figure 1). For instance, the source of an item can be operationalized as the voice (e.g., male or female voice) in which a word is spoken (Bornstein & Lecompte, 1995). One of the first studies along these lines (Brown & Halliday, 1991) found that item memory declined to a lesser extent than source memory when comparing immediate versus 1-week delay (but see Bornstein & Lecompte, 1995). Another study that used the source memory paradigm found that, although memory for single objects ceased to decline after 30 days and remained stable even after 3 months, memory for the association between an object and its location continued to decline over these timescales (Talamini & Gorree, 2012). A recent study (Lew, Pashler, & Vul, 2016) also examined associations between objects and their locations and found that these associations are forgotten over a delay of up to a week. In contrast, memory for the locations themselves is almost unharmed over these timescales.

A very common paradigm that can be construed as one that contrasts item memory versus relational memory is the remember/know (R/K) procedure; Sadeh, Moran, & Goshen-Gottstein, 2015; Mickes, Seale-Carlisle, & Wixted, 2013; Gardiner & Richardson-Klavehn, 2000; Gardiner & Java, 1990; Tulving, 1985). In this paradigm, participants are instructed to make a subjective judgment regarding each item they retrieve from memory. A “remember” (R) judgment is given if the item is retrieved via the process of recollection—namely, its retrieval is accompanied by contextual information (e.g., a thought or feeling that was associated with the item at study, a sound or smell that accompanied presentation of the item at study). In contrast, a “know” (K) judgment is given if the item is retrieved via the process of familiarity—namely, its retrieval is not accompanied by additional contextual details, but the item merely feels familiar. Thus, although recollection reflects retrieval of relational information (the relation between an item and its contextual details), familiarity reflects retrieval of item information alone. Numerous studies that used the R/K procedure found a significant decline in the probability of making R judgments over various periods of time (from 15 min to 3 months). In contrast, there is a less pronounced decline in the probability of making K judgments or no decline at all (Sadeh, Moran, Stern, & Goshen-Gottstein, 2018; Sadeh, Ozubko, Winocur, & Moscovitch, 2016; Yang et al., 2016; Petrican et al., 2010; Sharot & Yonelinas, 2008; Wolk et al., 2006; Gardiner, 1988). In many cases, the probability of K responses increases with time—reflecting conversion of responses from R to K, presumably due to the loss of relational, contextual details over time (Carr, Viskontas, Engel,

& Knowlton, 2010; Tunney, 2010; Viskontas, Carr, Engel, & Knowlton, 2009; Barber, Rajaram, & Marsh, 2008; Dudukovic & Knowlton, 2006; Uncapher & Rugg, 2005; Hockley & Consoli, 1999; Conway, Gardiner, Perfect, Anderson, & Cohen, 1997).

An additional procedure often used to distinguish between recollection and familiarity relies on receiver operating characteristics—a plot depicting the hit rate versus the false alarm rate for varying confidence levels. The shape of the receiver operating characteristic plot is considered to reflect the degree to which recognition memory relies on recollection or familiarity (Yonelinas, 1997, 2002). Thus, like the R/K procedure, this procedure may be construed as one which distinguishes between retrieval relying on relational binding (recollection) versus retrieval of item-only information (familiarity). Two studies used this procedure to examine the effects of retention interval length on these retrieval processes. In one of these studies, it was found that relational memory (i.e., the recollection measure) declined more than item memory (i.e., the familiarity measure) over periods of weeks (Wais, Wixted, Hopkins, & Squire, 2006). The other study found that relational memory decreased after 1 week, whereas the measure reflecting item memory increased (Tunney, 2010).

Additional evidence for the greater forgetting of relational information (compared with item information) over time may be found in studies examining forgetting of central details versus peripheral (or surface) details (Sekeres, Winocur, Moscovitch, et al., 2018; Sekeres et al., 2016; Murphy & Shapiro, 1994; for reviews, see Sekeres, Winocur, & Moscovitch, 2018; Sekeres, Moscovitch, & Winocur, 2017). Such studies examined memory for rich stimuli (stories and movie clips) in which central details—namely, the story line—can be clearly distinguished from peripheral details, pertaining to contextual details such as the exact wording of the story or the perceptual properties of the movie clips. The peripheral details may be regarded as relational information, in that they represent the contextual details that are associated with an item. Thus, retrieval of peripheral details entails reinstating the relation between an item and its contextual details. Furthermore, mnemonic processing of peripheral details, as other relational information, relies on the hippocampus (Sekeres, Winocur, & Moscovitch, 2018; Sekeres, Winocur, Moscovitch, et al., 2018). In line with the notion that relational information is particularly sensitive to time-dependent forgetting, it has been found that peripheral details show faster time-dependent forgetting than central details (Sekeres, Winocur, Moscovitch, et al., 2018; Sekeres et al., 2016; Murphy & Shapiro, 1994). Furthermore, the forgetting of peripheral details was associated with a decrease of activation in the hippocampus (Sekeres, Winocur, Moscovitch, et al., 2018).

Short Timescales

Several recent studies of time-dependent forgetting over timescales of several seconds have used a task coined the

“delayed estimation task” (Pertzov, Manohar, & Husain, 2017; Pertzov, Bays, Joseph, & Husain, 2013; Pertzov, Dong, Peich, & Husain, 2012; Zhang & Luck, 2009). One of the advantages of this task is that it can be used to quantify errors due to impaired relational memory. Such errors were found to increase with the length of the retention intervals (Pertzov et al., 2017; Pertzov, Miller, et al., 2013). Unlike in traditional memory tasks that use discrete scales of reports (e.g., familiar/unfamiliar, change occurred/did not occur), delayed estimation tasks require the participants to reproduce a feature of an item out of a continuous scale. For example, several patches of color are displayed, and after a short delay, the position of a patch is cued, and participants are required to report its color out of a color wheel with hundreds of colors that change gradually across its perimeter. Interestingly, a significant amount of the reports in such tasks cluster not only around the feature of the cued item but also around the values of the other items that were displayed in the array (Bays, Wu, & Husain, 2011). Thus, somewhat similar to transposition errors in serial recall (Henson, Norris, Page, & Baddeley, 1996), participants “swap” between the cued and uncued items and mistakenly report the feature of the wrong item. Such “swap” errors are often considered to be a result of a failure in binding the memory of items to their correct context and especially location (Manohar, Pertzov, & Husain, 2017; Schneegans & Bays, 2017; Pertzov & Husain, 2014), thus reflecting weak relational memory. Swap errors increase with the length of the retention interval (from 1- to 4-sec delay) and explain a significant proportion of forgetting errors, both when object–location (Pertzov et al., 2012) and orientation–location (Pertzov et al., 2017) information is relevant to the task. Thus, when instructed to report the location of a recently displayed object, participants often report the correct location of another object that was displayed in the memory array, more so following extended delay (Pertzov et al., 2012; Figure 2). Similarly, when instructed to report the orientation of a recently seen bar, participants often report the exact orientation of one of the unprobed bars, more so following longer delays (Pertzov et al., 2017). Swap errors were found to be more frequent following MTL damage due to antibody-associated limbic encephalitis (Pertzov, Miller, et al., 2013), as well as during early stages of familial Alzheimer’s disease (Liang et al., 2016).

ENCODING DURATION AND THE RATE OF FORGETTING

One intriguing question regards the relationship between the duration of encoding (or the number of repetitions during encoding) and the rate in which information is forgotten; in other words, whether forgetting rate is a function of the amount of time dedicated to encoding. Intuitively, it seems plausible that memories that benefited from longer encoding time should be forgotten more slowly, but—most

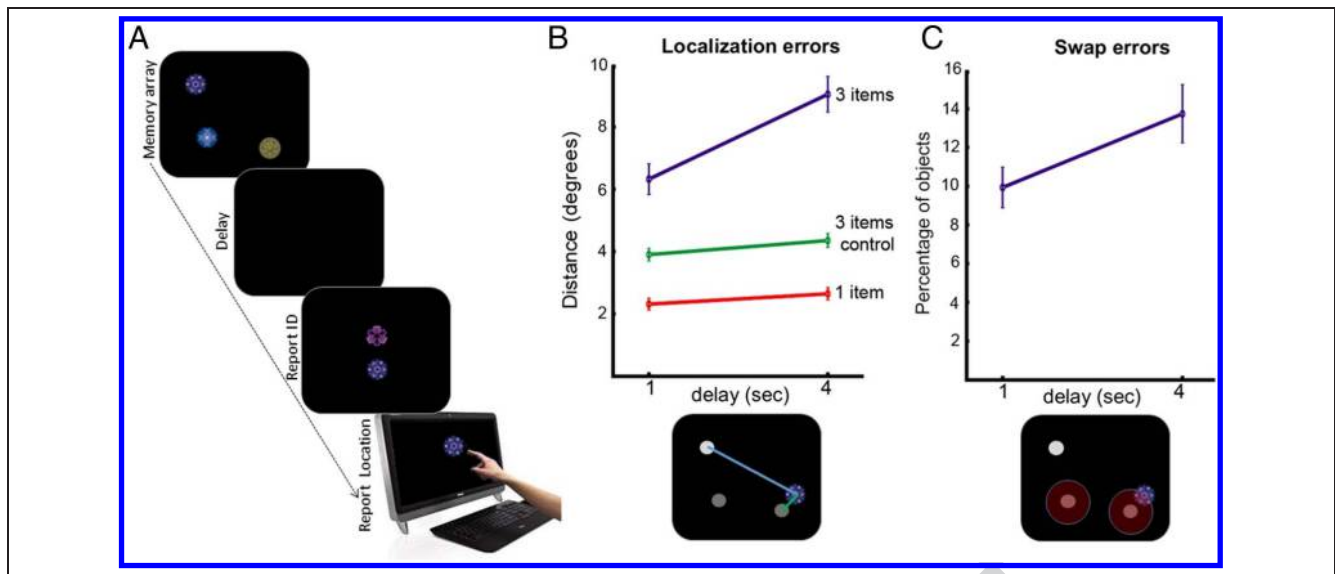


Figure 2. Object location binding errors increase with delay length. (A) A typical trial in a delayed localization task. One or three fractals are simultaneously presented in pseudorandom locations. Following a delay of 1 or 4 sec, a two alternative forced-choice between one of the displayed fractals and a foil is presented. Participants are required to drag the previously presented fractal on the touch screen to its remembered, original location on the screen. (B) Localization errors in trials with one (red) and three (blue) fractals. The “nearest neighbor” control error (green) was calculated as the minimal distance between a reported location and any one of the previously presented items (in three item displays). The image at the bottom depicts a specific example for distance calculation. The bright circle and the two darker circles represent the locations of the target and the two other fractals in the memory array, respectively. The blue line illustrates the localization error to the target and the green line the “nearest item control” distance. (C) Percentage of swap errors in which the fractal was localized within a predefined threshold around of the original location of nontarget objects. Adapted with permission from Pertsov et al. (2012).

interestingly—encoding time does not seem to have a strong influence on the rate of forgetting both at the long and short timescales. Note that, unlike encoding duration, the level of semantic processing (Craik & Tulving, 1975) or whether the stimuli were tested or not (Roediger & Karpicke, 2006) do seem to influence forgetting rate.

Long Timescales

Slamecka and McElree (1983) asked participants to study a list of words while varying the number of study trials (one or three) and the retention interval (immediate, 1 day, and 5 days). They found strong effects of retention interval and number of study trials on performance, but no interaction. Thus, the rate of forgetting between the short and long retention intervals was not significantly different following one or three study trials. The authors concluded that long-term forgetting of verbal lists is unaffected by their extent of learning. However, another study of verbal memory across shorter timescales (Hellyer, 1962) found conflicting results. In that study, the number of presentations (1, 2, 4, or 8) of consonants and the length of the retention intervals (up to 27 sec) were manipulated. When considering the proportion of correctly recalled consonants, consecutive repetitions during encoding led to slower forgetting over time. These results initiated an intense debate emphasizing the effect of different monotonic scalings of the dependent measure on such conclusions. Thus, considering the

proportion of correct responses could lead to one conclusion, but performing monotonic scaling of the measure (e.g., squared root of correct responses) might lead to a different conclusion. Loftus (1985) suggested a novel method for assessing the similarity of forgetting rates that is invariant to monotonic scaling of the dependent variable. This method quantifies the retention interval length that is required for memory performance to fall from any given level to some lower level; “If this time is the same for different degrees of original learning, then forgetting is not affected by degree of original learning. If this time is greater for higher degrees of original learning, then forgetting is slower with higher original learning.” (Loftus, 1985). This method led to the conclusion that forgetting rate is actually dependent on initial encoding time.

In an effort to resolve this conundrum, Bogartz (1990) noted that the values that represent the length of the retention interval and accuracy should also be monotonically scaled to fit the psychological value of time and accuracy. He reanalyzed the two empirical studies above and came to the conclusion that both data sets—Hellyer (1962) in shorter timescales and Slamecka and McElree (1983) in longer timescales—support the notion that the rate of forgetting does not depend on the time allotted to learning (but see Wixted, 1990). Notwithstanding the scaling complexity, when using the most standard measures of errors (e.g., percent correct in recognition tests), the rate of forgetting is not found to be modulated

by the initial encoding duration (Hintzman & Stern, 1984). For example, when observing percent correct performance in a recognition task, forgetting rates between 10 (or 30) min and 1 (or 2) week were independent of the number of repetitions during encoding (Hintzman & Stern, 1984).

Short Timescales

A recent study examined the effects of encoding duration on the rate of short-term forgetting using two well-established measures of memory performance in a delayed estimation task: the average raw errors and the precision of recall (Cohen-Dallal, Fradkin, & Pertzov, 2018). In three experiments, the two established measures yielded qualitatively similar forgetting slopes regardless of the initial encoding duration. The initial encoding duration was determined by the number of direct fixations on the items and by pre-defining different display durations. Both direct fixations and increased display duration led to strong enhancement of memory performance but did not change the rate of forgetting.

TOP-DOWN PROCESSES REDUCE FORGETTING OVER TIME

Encoding duration does not necessarily influence the rate of forgetting; however, this does not mean that the rate of forgetting is fixed. In fact, top-down, strategic allocation of attention toward selected memory representations can counteract forgetting, both in the long and short timescales. For instance, motivation and goal relevance can lead to slower rates of forgetting in long and short timescales, respectively. When participants are motivated to “save” a selected memory from forgetting they are able to protect it, but at times with a cost to other memory representations. In this section, we will describe the behavioral evidence for high-level, voluntary influence on forgetting at both timescales. We refer to these high-level factors collectively as top-down processes.

Long Timescales

Several studies in the long-term memory literature have shown that when individuals are motivated to pay attention to study items their memory for these items declines at a slower rate, as compared with cases in which motivation is not induced externally (Miendlarzewska, Bavelier, & Schwartz, 2016). Motivation is typically manipulated by giving participants monetary rewards during learning. Strikingly, differences in forgetting rates between rewarded and nonrewarded conditions are found even in the absence of initial differences in memory—namely, when memory in an immediate test is comparable across the two conditions (Figure 3). Thus, the effects of motivation on memory cannot be attributed merely to differences in encoding,

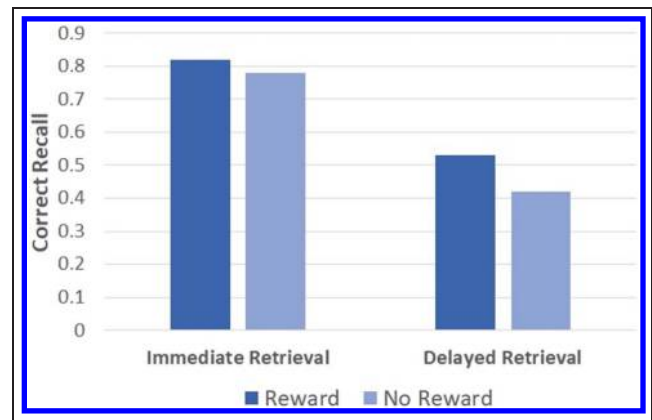


Figure 3. Illustration of the effects of motivation on forgetting based on data from Murayama and Kuhbandner (2011). Motivation is typically manipulated by giving participants monetary rewards during learning. Immediately following study, memory performance for both rewarded and nonrewarded items is similar. However, at delayed retrieval (e.g., one week or three following study), memory performance is significantly better in the reward versus no reward condition. Thus, motivation decreases forgetting rates.

but rather to differences in maintenance processes and forgetting over time. Importantly, as we elaborate in our review of the studies below, several studies (Chowdhury, Guitart-Masip, Bunzeck, Dolan, & Düzel, 2012; Abe et al., 2011; Wittmann et al., 2005) rule out the possibility that the effect of motivation on forgetting rates is merely a result of ceiling effects at immediate testing.

In an incidental encoding experiment, pictures from one category predicted a monetary reward and pictures from a second category did not (Wittmann et al., 2005). No differences were found in recognition memory performance between rewarded and nonrewarded pictures in an immediate memory test. Importantly, corrected recognition in this immediate memory test was not at ceiling (mean = 63% across conditions). Slower forgetting of rewarded information was demonstrated by significant differences between the rewarded and nonrewarded conditions in a delayed memory test 3 weeks later. A similar pattern of results was reported in another study (Murayama & Kuhbandner, 2011) that employed an incidental encoding task to examine effects of reward on time-dependent forgetting. Motivation was manipulated between participants, with a “Money” group receiving a monetary award for each item (trivia question) answered correctly during the study phase and a “No-money” group receiving no monetary rewards. Although both groups’ memory performance was equivalent in an immediate memory test given 10 min after study, a week later, the “Money” group outperformed the “No-money” group. Another study showed that reward enhances memory even after a 24-hr delay; however, it did not include a comparison to a short delay condition (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006). Therefore, the effect might be a result of enhanced encoding of the

rewarded information and not necessarily to decreased forgetting.

Although external motivation is typically induced by monetary rewards, it can also be induced by pharmacological manipulation of the reward system. Such a manipulation was employed in a study examining memory performance among older adults (Chowdhury et al., 2012). In that study, the rewarded group received L-DOPA, and the non-rewarded group received placebo. Compared with placebo, L-DOPA affected memory performance primarily in the long-delay test (6 hr after study), rather than in the short-delay test (2 hr after study). Thus, it mainly affected forgetting rate. No ceiling effect was observed in the short-delay test, with corrected recognition around 20%. Finally, specific effects of reward on delayed versus immediate memory performance have also been reported in motor learning. Monetary rewards did not influence performance in the initial test but abolished forgetting over 6 hr, 24 hr, and 30 days (Abe et al., 2011). Results of this study too cannot be attributed to ceiling effects at the immediate test nor to a scaling confound, as the mean error rate for that test was, in fact, higher than after 24 hr. Thus, although the nonrewarded group showed forgetting over time, the rewarded group showed post-training improvement.

Short Timescales

The idea that high-level strategic control can counteract short-term forgetting is an integral part in many theories of short-term and working memory. In their influential model of working memory, Baddeley and Hitch incorporated the “phonological loop” and “visual sketch pad” that are part of the executive control system. The role of these parts is to refresh memories to counteract forgetting (Baddeley & Hitch, 1974). Camos and Barrouillet include refreshing as an integral part of the time-based resource-sharing model in which memory traces are forgotten with time, but they “can be refreshed by bringing them back into the focus of attention” (Barrouillet & Camos, 2012). According to a related model (Ricker & Cowan, 2010), attention-related processing “assists in the retention” of refreshable memory representations. These theories rely on several lines of empirical evidence regarding available refreshing time and memory performance. Unfortunately, none of these studies addressed top-down influence on forgetting directly, but only indirectly. A recent study tested more directly how forgetting rate could be modulated by high-level control. High-level control was manipulated by varying the probability of probing an item in a specific color, therefore manipulating task relevance. Unlike the previous studies that tested performance following a fixed retention interval (see Appendix B), forgetting rate was assessed by measuring recall following several lengths of retention intervals. Importantly, the cue that signaled the item that is most likely to be probed was provided after the display vanished (i.e., retro-cue)

and therefore could not influence perceptual and encoding processes. The cued, goal-relevant item was forgotten more slowly than the other items, as if it was a single item in memory (Pertzov et al., 2017; Pertzov, Miller, et al., 2013). Notably, the decreased rate of forgetting came with a cost to the other representations, as they were forgotten faster than in conditions in which no item was cued.

DOES FORGETTING OF INFORMATION OVER TIME OCCUR GRADUALLY OR IN AN ALL-OR-NONE FASHION?

This section focuses on the pattern of forgetting over long and short timescales. For both timescales, time-dependent forgetting may follow one of two patterns. One possibility is that memories gradually lose their fidelity over time. Alternatively, it may be the case that the information that is forgotten after a certain duration can no longer be accessed—namely, forgetting occurs in an all-or-none fashion.

This line of research in long-term forgetting has been studied independently from short-term forgetting. Interestingly, the evidence from both avenues of research has converged, demonstrating that, in most cases, forgetting occurs gradually due to information becoming noisier with time or due to graded loss of details and vividness of the mnemonic representations. Note, however, that these findings do not preclude the possibility that some mnemonic representations degrade to the point that their traces can no longer be accessed (or are completely lost).

Long Timescales

Given that the similarities between forgetting patterns over short and long timescales pertain primarily to memories dependent on the hippocampus, we focus on the characteristics of forgetting of relational, hippocampal-dependent information. That is, our discussion focuses on cases in which the materials submitted to memory consist not only of a single item but rather of an item bound to its context (e.g., an object appearing in a certain location). We ask whether, over time, the contextual information associated with the item is forgotten gradually or shows an all-or-none pattern of forgetting.

The vast majority of studies examining forgetting over long timescales probed memory using tests of recall or recognition, which provide only a binary measure—that is, memories are assumed to be either remembered or forgotten. A recent study, however, examined forgetting using graded (rather than binary) measures (Lew et al., 2016). In that study, memory for the context of an object (its location) was examined by having participants mark the location in which the object was presented at study on the screen, such that a continuous measure reflecting the exact deviation from the studied location could be extracted. Memory was tested on the same day, a week, 2 weeks, and 4 weeks after encoding. Over these periods,

localization errors were not distributed uniformly on the screen but rather the precision of localization performance gradually declined. These results are thus in line with a degradation in the fidelity of contextual information over time, rather than a complete loss of access. An additional study also examined a graded measure of contextual precision in memory, as well as in perception (Brady, Konkle, Gill, Oliva, & Alvarez, 2013) by having participants select the color of a perceived or of a memorized object on a continuous color scale. Though that study did not directly examine forgetting by comparing two retention intervals (see Appendices A and B), support for gradual decline in memory fidelity may be gained from comparing the memory condition to the perception condition. The precision of responses in the long-term memory condition was reduced compared with the condition that incorporated no delay.

Additional support for gradual loss of hippocampus-dependent relational memory may be found in studies examining forgetting of peripheral details over time (Sekeres, Winocur, & Moscovitch, 2018; Sekeres, Winocur, Moscovitch, et al., 2018; Sekeres et al., 2016, 2017). As mentioned previously, peripheral details are regarded as contextual, hippocampal-dependent information. Forgetting of peripheral details is manifested in a decrease in the number of details over time, thus showing a graded pattern of forgetting. In further support of a graded pattern of forgetting are findings from these studies showing that the subjective ratings of vividness decrease with time.

Interestingly, a recent study provided evidence for all-or-none forgetting of episodic events, which are dependent on the hippocampus (Joensen, Gaskell, & Horner, 2019). The study examined forgetting of dependencies between three elements of an event (person, location, and object). It was found that, across various study–test intervals (immediate test, 12-hr delay, and 1-week delay), dependencies between the three elements constituting the event remained stable. These results were taken as evidence that forgetting of these events occurs in an all-or-none manner, such that the complex relation between the elements is either maintained or is completely lost. The results of this study appear inconsistent with the pattern of gradual forgetting of hippocampus-dependent information we have reviewed above. However, this seeming inconsistency may be accounted for by an important distinction between the memoranda in this study as compared with the memoranda in other studies we review in this section. Although Joensen et al. (2019) examined the links between several elements, the other studies examined the contextual information associated with the item. Indeed, as also suggested by Joensen et al., although the links between elements of an event remain constant over time (referred to there as “central details”), memory for the contextual information associated with each element (referred to there as “peripheral details”) may gradually decline.

Turning back to evidence for gradual forgetting of hippocampus-based representation, a widely used approach to examine such representations is by measuring estimates of recollection and familiarity, with the idea that recollection-based representations reflect relational memory of an item bound to its contextual representation (e.g., Sadeh et al., 2016; Diana, Yonelinas, Ranganath, 2007). In contrast, familiarity-based representations reflect item-only information and are supported by extrahippocampal (Sadeh et al., 2014; Diana et al., 2007; but see Squire, Wixted, & Clark, 2007). The question of whether recollection-based representations reflect graded versus all-or-none memory signals has sparked a heated debate in the literature (Elfman, Aly, & Yonelinas, 2014; Ingram, Mickes, & Wixted, 2012; Onyper, Zhang, & Howard, 2010; Wixted & Mickes, 2010; Mickes, Wais, & Wixted, 2009; Parks & Yonelinas, 2009; Yonelinas, 2002; Yonelinas, Dobbins, Szymanski, Dhaliwal, & King, 1996). Although this question has only been discussed in the context of successful memory, insights onto forgetting can be deduced from this extensive literature.

For both recollection-based and non-recollection-based representations, mnemonic performance is predominantly indexed by binary accuracy measures—reflecting an often implicit assumption that an item is either remembered alongside its full contextual detail or forgotten. However, recent studies have sought to distinguish between the success and the precision of recollection (Harlow & Yonelinas, 2016; Harlow & Donaldson, 2013). Along similar lines to previous graded measures applied (Lew et al., 2016; Brady et al., 2013), precision was examined by having participants select the location of the remembered item on an analog scale. Most importantly, it was found that, when recollection succeeds, it is graded—namely, can occur with varying degrees of precision. Unfortunately, however, these studies did not examine whether forgetting over time results in a decrease in precision, which is an interesting direction for future research.

In addition, in some studies measuring recollection and familiarity, confidence measures are obtained in addition to recollection and familiarity measures, thus enabling a more analog measure of memory fidelity. Typically, when measuring confidence levels in combination with R/K judgments—reflecting recollection-based (R) and non-recollection-based (K) representations—the vast majority of R judgments are given the highest confidence rating. The number of lower confidence R judgments is negligible (Ingram et al., 2012; Wixted & Mickes, 2010). However, it has recently been suggested that R judgments are predominantly accompanied by the highest confidence rating due to a bias induced by the typically used instructions (rather than the possibility that contextual retrieval either succeeds or completely fails). Indeed, it was shown that, by using different instructions that emphasize that confidence ratings can be made on both recollection and familiarity scales, a nontrivial proportion of R judgments were reported with

lower confidence ratings (Ingram et al., 2012). This finding shifts the balance toward the idea that graded, rather than all-or-none representations, underlie recollection-based memories.

To our knowledge, very few studies have examined changes in confidence ratings or other graded measures of performance in recollection-based memory representations as a function of time (see Appendix B). In Experiment 2 of Tulving's seminal study (Tulving, 1985), which introduced the R/K paradigm, memory performance and confidence ratings were assessed following a delay of 1 and 8 days. The probability of making an R response decreased with time, and the majority of R responses (75%) were made with the highest confidence rating. Unfortunately, however, the breakdown of R and K responses' confidence ratings by delay interval was not reported. Therefore, it is unclear whether R responses were judged with lower confidence ratings after a long delay than after a short delay—a finding that would have entailed gradual memory decline. Still, given that a nonnegligible proportion (25%) of the R responses were judged with lower confidence, it is feasible that the proportion of these responses was higher after the long delay than after the short delay. Another study that collected both R/K and confidence ratings compared memory immediately after study versus 7 days later (Brezis, Bronfman, Yovel, & Goshen-Gottstein, 2017). At the immediate test, the vast majority of R responses were given with the highest confidence ratings. Following a week's delay, many of those R responses shifted to K responses. Importantly, however, a nonnegligible proportion of R responses shifted from the highest confidence rating to a lower confidence rating. This study thus suggests that hippocampal-based memory representations, captured via R judgments, show gradual memory degradation. A potential caveat to our interpretation is the uncertainty as to whether low confidence recollected memories are different from memories judged as familiar. It has been claimed that R and K items only differ with regard to the strength of their corresponding memory traces (Dunn, 2004). Thus, K items might merely represent weak R items, and so low-confidence R items may be indistinguishable from K items. However, this claim has been questioned by findings showing that low-confidence R items differ qualitatively from K items in that the former's source accuracy is higher than that of the latter (Ingram et al., 2012).

On a theoretical viewpoint, Tulving's ideas regarding the availability versus accessibility of memories (Tulving & Pearlstone, 1966) also appear to support the idea of graded memory decline. According to these ideas, items might not be accessible at a certain point in time and hence are not retrieved, but their memory traces still exist. The availability of inaccessible traces is manifested by the finding that the corresponding items may be retrieved at a later occasion, given different cues or memory tests. Thus, the memory traces of previously inaccessible items are not completely lost, a notion that seems inconsistent with the idea of all-or-none forgetting.

Taken together, it appears that most of the evidence from the long-term memory literature supports a graded pattern of forgetting of hippocampal-based representations, which can at times lead to a complete loss of access to the memory trace.

Short Timescales

As in long-term forgetting, early studies of short-term forgetting used binary reports—hampering an assessment of gradual decline of memories due to forgetting (e.g., Phillips, 1974). The recent increase in the use of analog scales of report in STM studies, which is sensitive to the fidelity of memory (Ma, Husain, & Bays, 2014), has been applied only seldom in forgetting research.

One study assessed delayed reproduction of color and simple shapes using a semianalog reporting cycle (Zhang & Luck, 2009). Errors were larger following a 10-sec delay compared with 4 sec, and this increase was attributed to random guessing spread on the whole report scale. Random guessing is presumed to reflect an all-or-none memory loss as “no memory” or more precisely no access to memory is expected to lead to random guesses. The proxy for gradual loss, the width of the cluster of reports around the correct value, also broadened with delay length, but this broadening was not significant in this study. Based on these findings, the authors claimed that memory representations “suddenly die” rather than slowly degrade with time.

A later study used a wider variety of memory loads and delays and showed that not only random guessing increases with the retention interval. Precision of recall, which is inversely related to the width of memory reports distribution around the correct value, also degrades with time. Such time-dependent degradation of precision was stronger when multiple items were remembered, but it was still observed even when a single item was in memory (Pertzov et al., 2017). A recent study used similar methods to demonstrate that even when remembering one item, either complex (face) or simple, its fidelity becomes gradually noisier with time (Rademaker, Park, Sack, & Tong, 2018). Note that such degradation in precision seems to be less prominent when memorizing a single inverted face, as well as multiple faces (Krill, Avidan, & Pertzov, 2018). More theoretical studies have shown how such gradual loss could be explained by a time-dependent drift in a ring attractor neural model (Schneegans & Bays, 2018; Koyluoglu, Pertzov, Manohar, Husain, & Fiete, 2017).

We conclude that converging evidence has accumulated showing that time-dependent loss of information across short and long timescales is usually reflected in gradual loss of fidelity, but at times also in complete loss of accessibility.

DIRECTIONS FOR FUTURE RESEARCH

Research on forgetting of hippocampal-based representations is still at its infancy and thus gives rise to a fertile

line of exploration. In particular, many open questions remain with regard to the commonalities in the characteristics of forgetting across short and long timescales.

One intriguing question regards the effects of emotion on forgetting. Evidence suggests that emotional memories are forgotten at a slower rate than neutral memories over long timescales (e.g., 24 hr vs. 5 min; Sharot & Yonelinas, 2008). It has recently been suggested that the slower forgetting of emotional memories is due to their dependence on the amygdala and its interaction with nonhippocampal MTL structures, rather than on the hippocampus (Yonelinas & Ritchey, 2015). This hypothesis aligns well with the notion, promoted in the current review, that hippocampal representations are more prone to temporal degradation than nonhippocampal representations. An open question for future research is whether slower forgetting of emotional memories can be found over short timescales as well.²

An additional question for future research concerns the effects of reward on forgetting rates over short timescales. In the section regarding top-down influences on forgetting rates, we reviewed some compelling evidence showing that inducing motivation via monetary reward decreases forgetting rates over long timescales. Preliminary evidence suggests that similar results may also be obtained when examining forgetting rates over short timescales (Pertsov, Bays, et al., 2013). This evidence, reviewed above, reveals slower forgetting over short timescales for items that are more likely to be probed. Presumably, these items were assigned higher values, as selectively focusing attention on them benefitted performance in the task. Thus, motivation was intrinsic to the mnemonic task. It remains to be examined whether similar results may be obtained when some of the items are assigned higher value through external motivations such as monetary reward.

As mentioned at the outset of this review, degradation over time is only one, albeit important, cause of forgetting. An additional, no less potent, cause of forgetting is interference from similar information (Wixted, 2004; Underwood, 1957). Current theories of forgetting (Sadeh et al., 2014; Hardt et al., 2013) suggest that the cause of forgetting is determined by the properties of underlying memory representations. Memories dependent on the hippocampus are relatively immune to interference since even similar memories are represented in distinct neural codes—a characteristic coined pattern separation. As we have highlighted throughout this review, these memories are forgotten mostly due to degradation over time. Contrary to the hippocampus, in nonhippocampal regions, similar pieces of information are represented in largely overlapping patterns. Therefore, mnemonic representations that are less dependent on the hippocampus are hypothesized to be forgotten primarily due to interference from similar information. Predictions based on these theories were tested—and confirmed—in a recent empirical study that directly compared the effects of delay and interference on hippocampal and nonhippocampal mnemonic repre-

sentations (Sadeh et al., 2016). In that study, forgetting rates were examined over relatively long timescales (several minutes). An intriguing question for future research is whether similar results will be obtained over short timescales as well.

Conclusions

In this review, we described several striking parallels between time-dependent forgetting across short and long timescales. We highlighted four major patterns of similarity. First, relational information that relies on the hippocampus is especially prone to forgetting over time. Second, the rate in which information is forgotten is not necessarily influenced by initial encoding duration. Third, the rate of forgetting can be modulated by top-down processes, such as motivation and selective attention. Finally, forgetting does not inevitably lead to a complete loss of information but rather also to more gradual degradation. Together, the great similarity between time-dependent forgetting across short and long timescales contributes to evidence from recent years showing that memory functions over both these timescales are mediated by a hippocampal-based mechanism. We thus conclude that, like remembering, the mechanisms involved in forgetting across short and long timescales are at least partially overlapping.

APPENDIX A: WHAT CAUSES FORGETTING OVER TIME?

Time-dependent forgetting of hippocampal-based, relational representations is readily accounted for by the notion of contextual drift (Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019; Sadeh et al., 2014, 2018; Sederberg, Howard, & Kahana, 2008). The hippocampus binds item information (e.g., a face, word, picture) with the context in which the item was encountered (Sadeh, Maril, Bitan, & Goshen-Gottstein, 2012; Diana et al., 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Davachi, Mitchell, & Wagner, 2003). Context refers to any information peripheral to the study item, including external information (e.g., the spatial location) and internal information, such as an individual's mood and her thoughts and associations. The bound item-context entity constitutes the memory trace. Successful retrieval of an item depends on the degree to which the study context is reinstated during retrieval (Tulving, 1974, 1983; Tulving & Thomson, 1973). Therefore, according to the contextual drift notion, forgetting is the result of a change or drift in context between study and test. Indeed, models of episodic memory, such as the temporal context model (Polyn, Norman, & Kahana, 2009; Sederberg et al., 2008), highlight the short-lived nature of context, such that contextual information continuously fluctuates over time (Sederberg et al., 2008; Estes, 1955). Relatedly, forgetting may be further advanced by

contextual interference, such as intervening activities or physical changes (Yonelinas et al., 2019).

An additional, not necessarily contradicting explanation for forgetting has originated in research of memory over short timescales. According to this account, memory encoding depends on rapid plasticity in flexibly coding neurons that may reside in the hippocampus (Manohar, Zokaei, Fallon, Vogels, & Husain, 2019). Such plasticity allows distinct representations (e.g., items and context) to be bound together into a coherent memory representation. Time-dependent volatility of the synaptic weights is expected to lead to forgetting of relational or conjunctive information over time. Such forgetting does not occur “because of any specific decay rule, but rather because the plasticity rule operates continuously to alter all synaptic weights, and this ‘erodes’ the representations that are not currently active” (Manohar et al., 2019).

APPENDIX B: ASSESSING TIME-DEPENDENT FORGETTING

Many studies have assessed memory performance following a fixed retention interval. In such cases, errors cannot necessarily be attributed to forgetting. Thus, it is impossible to know if memory was not encoded properly, was lost during maintenance (forgotten), or was not properly accessed during retrieval. A useful method to circumvent this attribution problem is to use at least two different lengths of retention interval. When assessing memory over a few seconds, the different retention interval conditions can be interleaved within the same block of trials. In such cases, all processes that occur before or after the maintenance stage are equivalent in all conditions, as participants cannot know what the length of the retention interval will be when they encode the items into memory. Therefore, any increase in reporting errors following a relatively longer retention interval can only be attributed to the extended interval (i.e., forgetting) and not to other processes related to encoding or retrieval. When we discuss forgetting over the short term, we focus on studies that used interleaved retention interval conditions within blocks.

Isolating forgetting processes when considering longer timescales is more challenging as the long timescales often preclude a single session procedure. Researchers deal with this in several ways. One option is to invite participants to two or more sessions: Typically, the first session includes encoding of a long list of items and retrieval of a portion of those items. The next sessions only include retrieval phases, each time of a different portion of items that had not been tested in earlier sessions (e.g., Tunney, 2010; Hockley & Consoli, 1999; Bornstein & Lecompte, 1995). Alternatively, the first session includes only an encoding phase, and the second session includes retrieval of items from the first session as well as encoding and retrieval of new items (e.g., Sharot & Yonelinas, 2008). Another option is to conduct the entire experiment in a single session, with two study–test blocks:

one in which the test immediately follows the study phase, and one in which a retention interval of several minutes is interposed between study and test (e.g., Brubaker & Naveh-Benjamin, 2013). Finally, some studies manipulate the length of retention interval between participants, such that one group receives a memory test immediately following the study and the other after a certain retention interval (e.g., Sadeh et al., 2016; Wolk et al., 2006; Brown & Halliday, 1991; Gardiner, 1988).

In summary, forgetting should not be regarded as the flip side of remembering. Rather, forgetting refers to the loss of information that was remembered at some point in time. Therefore, to tap forgetting, it is essential to determine that the forgotten information was encoded into memory in the first place. This is typically done by employing multiple retention intervals and examining the decrease of memory performance as a function of the duration of the study–test interval.

An additional, crucial point with regard to assessing time-dependent forgetting is teasing apart the effects of delay from interference. This is particularly challenging as delay is inherently entangled with interference: Retention intervals necessarily involve interference, either from external stimuli or from internal thoughts. To disentangle delay from interference, an exact definition of the concept of interference is needed. Here, we embrace the approach that considers interference as processing of additional information that is similar to the information submitted to memory (Sadeh et al., 2014, 2016; Hardt et al., 2013). Thus, studies manipulating interference would include paradigms such as continuous recognition paradigms in which longer study–test lags also entail presentation of more interfering materials (Yonelinas & Levy, 2002; Hockley, 1992; Murdock & Hockley, 1989), additional study–test sessions that followed the encoded list (Hockley, 1992), manipulations of list length (Cary & Reder, 2003), and displaying stimuli during the retention interval (Sun et al., 2017; see Sadeh et al., 2014, for a full review of studies manipulating delay vs. interference over long timescales). As we mention in the main text, according to recent theoretical accounts (Sadeh et al., 2014; Hardt et al., 2013), interference is the major cause of forgetting for nonhippocampal, item-based representations. In line with this notion, studies manipulating interference, as those mentioned above, found that item information was forgotten to a larger extent than relational information (Sadeh et al., 2014, 2016). Furthermore, interference may differ with regard to the pattern of forgetting it induces: Rather than being gradual (as is the case for delay), forgetting due to interference may show an all-or-none pattern, as observed when interfering stimuli are displayed after the memory array (Sun et al., 2017).

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Reprint requests should be sent to Talya Sadeh, Department of Brain and Cognitive Sciences, Ben-Gurion University of the Negev, Beer Sheva, Israel, 8410501, or via e-mail: tsadeh@bgu.ac.il.

Notes

1. Note, however, that most other results reported in that article did not find significantly different levels of forgetting for item and associative memory.
2. The evidence presented in this section refers to cases in which emotionally charged items, rather than associations, are submitted to memory. Thus, it stands to reason that indeed memory for these items depends on nonhippocampal structures and, therefore, shows slower temporal degradation. Interestingly, a recent study has shown that when memory for an association between a negative element and a neutral element is probed, the association between the elements is weaker than when the association is between two neutral elements (Bisby, Horner, Bush, & Burgess, 2018). This study did not examine forgetting as it did not compare memory performance across at least two time points. Still, an interesting question for future research is whether the forgetting patterns of associations between negative and neutral elements differ from those of associations between several neutral elements.

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