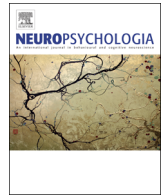




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Forget all that nonsense: The role of meaning during the forgetting of recollective and familiarity-based memories

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ABSTRACT

Memory can be divided into recollection and familiarity. Recollection is characterized as the ability to vividly re-experience past events, and is believed to be supported by the hippocampus, whereas familiarity is defined as an undifferentiated feeling of knowing or acquaintance, and is believed to be supported by extra-hippocampal regions, such as the perirhinal cortex. Recent evidence suggests that the neural architectures of the hippocampus and neocortex lead information in these regions being susceptible to different forgetting processes. We expand on these accounts and propose that the neocortex may be sensitive to the semantic content of a trace, with more meaningful traces being more easily retained. The hippocampus, in contrast, is not hypothesized to be influenced by semantics in the same way. To test this new account, we use a continuous-recognition paradigm to examine the forgetting rates words and nonwords that are either recollected or familiar. We find that words and nonwords that are recollected are equally likely to be forgotten over time. However, nonwords that are familiar are more likely to be forgotten over time than are words that are familiar. Our results support recent neuropsychologically-based forgetting theories of recollection and familiarity and provide new insight into how and why representations are forgotten over time.

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1. Introduction

Mental states of every kind, – sensations, feelings, ideas, – which were at one time present in consciousness and then have disappeared from it, have not with their disappearance absolutely ceased to exist.

– Hermann Ebbinghaus

Memory: A Contribution to Experimental Psychology, 1885.

Translated by Henry A. Ruger & Clara E. Bussenius, 1913.

The study of forgetting has been a mainstay of cognitive psychology since the time of Ebbinghaus and the earliest empirical studies of cognition. And as the quote above illustrates, forgetting is not a simple all-or-none process. Information can decay, decline, and fade to greater or lesser degrees. Decades of research examining the way in which information is forgotten has provided interesting insights into what it means to remember and how it is that individuals forget. Although this research has greatly enhanced our understanding of mnemonic processes, it has also sparked several debates about the specific processes that underlie

forgetting. Perhaps one of the more prominent of these debates pertains to whether forgetting is due to the decay of information (e.g., McGeoch, 1932; Underwood, 1957), or is instead the result of interference (see Wixted, 2004 for a review).¹ Recently, researchers have used neuropsychological evidence to argue that both interference and decay may typically contribute to forgetting, but that these processes affect different types of memories (Hardt et al., 2013; Sadeh et al., 2013). What these theories suggest, then, is the possibility that the processes that underlie forgetting vary as a function of the neuropsychological nature of the memory representation itself. In other words, how we forget may depend on how we remember.

1.1. The dual-process model of memory

Over the past few decades, an abundance of neuropsychological research has demonstrated that declarative memory can be divided into two distinct processes: recollection and familiarity

¹ Note that others have proposed active inhibition as well (Anderson et al., 1994). Although inhibition is a potential cause of forgetting, it is not focused on here as the present work follows up research that has been examining the differential role of interference vs. decay.

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(Diana et al., 2007; Eichenbaum et al., 2007; Yonelinas, 2002). Recollection is often described as the ability to vividly represent and re-experience past events such that one can remember the sights, sounds, feelings, and thoughts that transpired during those events. Familiarity, on the other hand, is often described as a feeling of knowing or acquaintance: it is the ability to “know” that something has been experienced before, even though one cannot report on where or when it was encountered.

Classically, recollection and familiarity have been measured using the *remember-know procedure* (Tulving, 1985). The remember-know procedure is a recognition task that requires participants to classify their responses based on the information they remember about each item. For example, after studying a list of words, participants may be presented with a new list of words that contains some items from the study list and some items that are new. They are then asked to identify a word as (1) “remembered” if they can recollect contextual details about what it was like when they originally studied the word, (2) “known” if they cannot recollect such contextual details but nonetheless feel as if the word was studied, or (3) “new” if they do not believe the word was studied. Because remember-know ratings are indirect and subjective indicators of recollection and familiarity, some researchers have raised concerns as to whether they provide accurate estimates of recollection and familiarity (e.g., Donaldson, 1996; Hirshman and Master, 1997; Inoue and Bellezza, 1998; Rotello and Zeng, 2008; Wixted and Stretch, 2004; Wixted, 2007). However, research suggests that remember-know ratings do reflect a qualitative distinction between memories (e.g., Yonelinas, 2002; Eichenbaum et al., 2007; Perfect and Dasgupta, 1997; Rajaram, 1993; Skinner and Fernandes, 2007) that converges with independent measures of recollection and familiarity when instructions on how to make remember-know responses are strict (see Rotello et al., 2005; Yonelinas, 2001; Yonelinas et al., 1996).

Beyond remember-know ratings, the dual-process view of memory has been supported by research that has shown that properties of recollected and familiar memories differ in a theoretically consistent manner. On the one hand, recollected items are often accompanied by specific contextual details (Perfect et al., 1996) and a subjective sense of mentally reliving those details (Eldridge et al., 2000; Hicks et al., 2002; Wixted, 2007). Moreover, researchers have found that during the process of recollection, secondary perceptual regions are re-activated (Khader et al., 2005; Nyberg et al., 2000). For example, it has been shown that, when people recollect face stimuli, there is a selective re-activation of the fusiform face area (Skinner et al., 2010), which has been shown to be extensively involved in face perception (e.g., Haxby et al., 1994). On the other hand, familiarity-based responses are not accompanied by a strong sense of contextual detail (Perfect et al., 1996), nor are they accompanied by a subjective sense of re-living or re-experiencing such details (Eldridge et al., 2005; Hicks et al., 2002; Wixted, 2007). Finally, although recollection and familiarity are not direct mappings of hippocampal and extra-hippocampal representations, respectively, recollection is typically closely tied to hippocampal involvement whereas familiarity typically is not (Eichenbaum et al., 2007; but see Ingram et al., 2012).

1.2. The neuropsychological basis of forgetting

Recently, researchers have begun to speculate on how the neural substrates that underlie recollection and familiarity may affect the ways in which these representations degrade and are forgotten with time. Building on the animal learning literature, Hardt et al. (2013) has proposed that although emphasis is often placed on interference in theories of forgetting, due to the unique structure and function of the hippocampus, decay (rather than interference) may play a prominent role in hippocampally-

represented traces. On the other hand, the neocortex represents information in such a way that overlapping representations are represented as overlapping neural codes (Norman and O'Reilly, 2003). As a result, when new information is acquired it would change the neural codes necessary for its own representation, but in doing so, alter the codes of similar or related representations as well. Hence, neocortical representations, and thus, familiarity-based representations, should be vulnerable to interference.

In contrast to the relative simplicity of the neocortex, the hippocampus is composed of several subfields (such as CA1, CA3, and the dentate gyrus) that interact to produce sparse coding. That is, representations in the hippocampus tend to use relatively few active neurons. Sparse coding results in an ability known as *pattern separation*, which is the hippocampus' ability to represent even related representations within relatively orthogonal, minimally overlapping neural patterns. A representation scheme that emphasized pattern separation should invariably produce representations that are protected against interference, as even related traces would likely not affect one another's neural representations. Hardt et al. (2013) therefore speculated that in the absence of strong interference effects, decay may be the primary mechanism through which forgetting occurs within the hippocampus. Specifically, they argued that regular decay may allow the hippocampus to selectively eliminate unneeded memories, while maintaining detailed and useful representations that are insulated against interference.

Sadeh et al. (2013) were similarly interested in how forgetting would vary as a function of memory representation. Examining the human literature on recollection and familiarity, Sadeh et al. (2013) found evidence that, consistent with the neuropsychological characterizations of the hippocampus and neocortex (Diana et al., 2007a; Eichenbaum et al., 2007; Yonelinas, 2002), recollections are indeed less prone to interference effects than are familiarity-based representations. For example, over a large number of published studies, Sadeh et al. (2013) observed that associative memory, which is often associated with recollection, tends to decline more rapidly over periods of one day to one week than does item memory, which is often associated with familiarity-based representation (e.g., Brubaker and Naveh-Benjamin, 2014; Hockley and Consoli, 1999). Moreover, studies that have used “remember” and “know” judgments as subjective measures of recollection and familiarity (Tulving, 1985) have found that recollection tends to decline significantly over a period of one day to three months, whereas familiarity declines much less over these time periods (e.g., Gardiner and Java, 1991; Gardiner, 1988; Viskontas et al., 2009). Sadeh et al. (2013) also found that event-related potential (ERP) measures of recollection tended to decline more with long delays than with short delays, whereas familiarity-based ERP signals often remained stable (Wolk et al., 2006). Hence, across a variety of measures, recollection appears to be sensitive to the length of the delay period after initial learning. In contrast to recollection's sensitivity to delay, across a number of studies that examined individuals with selective hippocampal damage, Sadeh et al. (2013) observed that individuals were especially sensitive to interference (e.g., Frisk and Milner, 1990; McKee and Squire, 1992).

Though Hardt et al. (2013) and Sadeh et al. (2013) present compelling cases for the idea that the neural substrates that support recollection and familiarity lead them to be differentially sensitive to decay and interference, at the time of their reviews, there existed no direct test of this hypothesis. Recently, however, Sadeh et al. (2016) have directly tested their hypothesis. In Sadeh et al.'s (2016) experiment, participants studied a series of words in a continuous recognition procedure (CRP), where participants were presented with a series of individual words, and for each word, they had to identify whether the word had been seen earlier in the list or was new. In this particular experiment, approximately

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