



Neural correlates underlying true and false associative memories



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ABSTRACT

Despite the fact that associative memory studies produce a large number of false memories, neuroimaging analyses utilizing this paradigm typically focus only on neural activity mediating successful retrieval. The current study sought to expand on this prior research by examining the neural basis of both true and false associative memories. Though associative false memories are substantially different than those found in semantic or perceptual false memory paradigms, results suggest that associative false memories are mediated by similar neural mechanisms. Specifically, we found increased frontal activity that likely represents enhanced monitoring and evaluation compared to that needed for true memories and correct rejections. Results also indicated that true, and not false associative memories, are mediated by neural activity in the MTL, specifically the hippocampus. Finally, while activity in early visual cortex distinguished true from false memories, a lack of neural differences between hits and correct rejections failed to support previous findings suggesting that activity in early visual cortex represents sensory reactivation of encoding-related processing.

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1. Introduction

Successful recognition memory is a critical part of everyday life. For example, the need to remember faces of people we have previously met or places we have visited in the past is critical to social interactions. More challenging than remembering individual pieces of information from our past is remembering which individual items were part of a single past episode. For example, you may have met three different people: Anne in the library, Eileen in the post office, and Marie in the grocery store. While you may remember the individual places you visited and names of those you met, you may have difficulty remembering in which context you met each person. When meeting Anne for a second time it may be embarrassing to inadvertently misremember her as a postal worker, not a librarian. Failures of associative memory can range from minor (mistaking someone as a postal worker instead of a librarian) to severe (mistaking someone as the criminal you saw rob a bank instead of the customer who you saw at the supermarket checkout). To examine the cognitive and neural basis underlying these memory errors, the current study uses an associative

memory paradigm to investigate both true and false associative memories.

In the lab, associative memories are examined by presenting two items together during a single encoding trial. Retrieval success is determined not by memory for the individual items, but by memory for which two items were presented together. False associative memories occur when a recombination of items is incorrectly endorsed as having been presented together at study. What makes these recombinations particularly vulnerable to memory errors is the fact that both individual items constituting the recombined lure were presented during study, albeit not as part of the same episode (i.e., not paired together). While several neuroimaging studies have used the associative memory paradigm to study true memories (Bunge, Burrows, & Wagner, 2004; Ford, Verfaellie, & Giovanello, 2010; Giovanello & Schacter, 2012; Giovanello, Schnyer, & Verfaellie, 2004, 2009; Kohler, Danckert, Gati, & Menon, 2005; McCormick, Moscovitch, Protzner, Huber, & McAndrews, 2010; Prince, Daselaar, & Cabeza, 2005; Stark & Squire, 2003; van Kesteren, Rijpkema, Ruiters, & Fernandez, 2010), only one previous study has used it to investigate the neural basis of false memories (Giovanello, Kensinger, Wong, & Schacter, 2009).

The neural basis of false memories has most often been studied using semantic or perceptual false memory paradigms, such as the Deese–Roediger McDermott (DRM) paradigm, perceptual relatedness paradigms, or source memory paradigms. One of the most

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ubiquitous findings generated from false memory studies is the considerable overlap in the neural networks mediating both true and false memories (Dennis, Bowman, & Turney, *in press*). Specifically, both true and false memories have been shown to exhibit similar activation in bilateral frontal and parietal cortex, lateral temporal cortex, occipital cortex, and regions within the medial temporal lobes (MTL), including the hippocampus and parahippocampal gyrus (Atkins & Reuter-Lorenz, 2011; Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Dennis, Bowman, & Vandekar, 2012; Garoff-Eaton, Kensinger, & Schacter, 2007; Garoff-Eaton, Slotnick, & Schacter, 2006; Iidaka, Harada, Kawaguchi, & Sadato, 2012; Kahn, Davachi, & Wagner, 2004; Okado & Stark, 2003; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; Schacter, Koutstaal, Johnson, Gross, & Angell, 1997; Schacter et al., 1996; Slotnick & Schacter, 2004; von Zerssen, Mecklinger, Opitz, & von Cramon, 2001). Such widespread overlap has been attributed to several factors, including the fact that targets and related lures share similar properties (e.g., Garoff-Eaton et al., 2006), the engagement of highly similar retrieval-related evaluation and monitoring processes (e.g., Atkins & Reuter-Lorenz, 2011), retrieval of contextual information (e.g., Okado & Stark, 2003), and evidence that both types of memories are supported by above-threshold familiarity processing (e.g., Kahn et al., 2004).

Despite this overlap, neural differences between true and false memories have also been observed. For example, both perceptual and source false memory studies have found increased activations in early visual regions for true compared to false memories, and have attributed this increase to the retrieval of perceptual details (Abe et al., 2008; Dennis et al., 2012; Fabiani, Stadler, & Wessels, 2000; Okado & Stark, 2003; Slotnick & Schacter, 2004; Stark, Okado, & Loftus, 2010). Such findings have been interpreted within the framework of the sensory reactivation hypothesis (e.g., Marche, Brainerd, & Reyna, 2010; Mather, Henkel, & Johnson, 1997; Norman & Schacter, 1997). Specifically, researchers posit that, by virtue of having been presented previously, true memories elicit reactivation of the neural activity in sensory regions that was involved in their initial encoding (e.g., Vaidya, Zhao, Desmond, & Gabrieli, 2002; Wheeler, Petersen, & Buckner, 2000). Having never been presented previously, false memories, however, will not be accompanied by this heightened sensory signal. Increased MTL activity has also been observed for true compared to false memories across several studies and is posited to reflect retrieval of sensory details associated with the original encoding event (Cabeza et al., 2001; Kahn et al., 2004; Okado & Stark, 2003; Stark & Okado, 2003). On the other hand, prefrontal cortex (PFC) activity is often found when comparing false to true memories and has been attributed to monitoring, reconstructive processes, and semantic elaboration given the lack of a strong sensory signature on which to base memory retrieval (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kensinger & Schacter, 2006; Kim & Cabeza, 2007; Kubota et al., 2006; Okado & Stark, 2003; Schacter, Buckner, et al., 1997; Schacter et al., 1996; Slotnick & Schacter, 2004).

Associative false memories are, in some ways, different from other types of false memories in that all components of the associative lure were previously encountered during the study phase. Specifically, they are different from perceptual and semantic false memories where only close associates of the lure (but not the lure itself) were present at encoding; and are also different from source monitoring false memories where the attributed source is often based on mental imagery or the lure is presented in a different modality than what is provided at test. Given this distinction, it is unclear whether the neural correlates leading to associative false memories are similar to those identified in previous false memory studies. For example, with respect to the sensory reactivation findings in early visual cortex, it is unclear whether associative false memories would exhibit a similar decrease compared to true

memories. The sensory reactivation theory might predict that true associative memories would exhibit a greater sensory signal in early visual cortex because only targets would depict the exact re-presentation of item–item associations from encoding. However, if early visual cortex is sensitive only to the content of information, irrespective of exact re-representation, then recombined lures may elicit heightened activity in visual regions as well.

A similar question surrounds the role of the MTL in processing both true and false associative memories. Given the critical role of item–item binding in associative memories, the hippocampus has consistently emerged as one of the most critical regions when examining associative memory success (Giovanello, Schnyer, et al., 2009; Giovanello et al., 2004; Kirwan & Stark, 2004; Prince et al., 2005; Ranganath, Cohen, Dam, & D'Esposito, 2004). However, support for the role of the hippocampus in associative memories is mainly identified by comparing associative retrieval to item retrieval (Cansino, Maquet, Dolan, & Rugg, 2002; Giovanello & Schacter, 2012; Giovanello et al., 2004; Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001). This contrast confounds memory type (associative/item) with differences in the amount of information required to be processed (two items/a single item). A more accurate assessment of associative memory success compares associative hits to correctly rejected associative lures. While only a handful of studies have used correct rejections as a control condition, those that do also support previous results showing a role for the hippocampus in mediating associative memory retrieval (Chen, Olsen, Preston, Glover, & Wagner, 2011; Ford et al., 2010). Additionally, Ford et al. (2010) found that the MTL, specifically the perirhinal cortex, only responded to accurate memory for related word pairs (e.g., fireman) and not false recombinations or intact unrelated word pairs (e.g., dog-couch). Results suggest that the response of the MTL to accurate associative memories may occur only when items are meaningfully related. While the foregoing studies support the role of the MTL in successful associative memories, the neural basis for false associative memories was not similarly explored (see also Achim & Lepage, 2005).

The only previous study to examine the neural basis of associative false memories (Giovanello, Kensinger, et al., 2009) used compound words and word pairs (e.g., check-list). Results of Giovanello, Kensinger, et al., 2009 suggest that semantic associative memories are mediated by a frontal–parietal network that includes the anterior cingulate cortex, left middle frontal gyrus, inferior parietal lobule, and posterior cingulate. However, a comparison of true and false associative memories revealed no neural differences in the MTL or early visual cortex. One reason for the absence of differential neural activity may be attributed to the stimuli used. That is, in using compound words (e.g., checklist; needlepoint) and recombining the word stems at retrieval to form a novel compound word (e.g., checkpoint), the participants may not have viewed the compound words as two discrete items requiring binding. Furthermore, while the study used words as stimuli, both MTL and sensory reactivation differences are most common when stimuli are complex visual images such as photographs or abstract shapes (Dennis et al., 2012; Kahn et al., 2004; Kensinger & Schacter, 2006; Slotnick & Schacter, 2004). As such, rich perceptual stimuli may be needed to fully explore the role of sensory reactivation in true and false associative memories.

In order to overcome the foregoing limitations, the current study used rich visual stimuli that were not related prior to testing (i.e., novel faces and scenes). In doing so the study ensured that activity related to true and false associative memory could be attributed to the success or failure of binding unique and unrelated perceptual information. We predicted that, in accord with the sensory reactivation hypothesis, true associative retrieval will be mediated by greater activity in early visual cortices compared to both false associative memories and correct rejections of recombined

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