

# 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, Ruiter, & 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

lures. In all three instances, the individual items constitute ‘old’ items that have been studied at encoding, but only in the true memory condition are the items presented in the exact manner (i.e., combination) in which they were previously encountered. Based on the role of the MTL in mediating memory success and the particular role of the hippocampus in mediating associative memory processing, we also predicted greater MTL and specifically hippocampal activity for true compared to false associative memories. Finally, we predicted that, in the absence of sensory reactivation and a strong MTL signal, associative false memories will be mediated by similar top-down, reconstructive processing that mediates other types of false memories and thus will be associated with increased PFC activity.

## 2. Methods

### 2.1. Participants

Nineteen healthy, right-handed participants (11 female) between the ages of 18–29 years old [mean age = 23 yrs, ( $SD = 2.92$ )], were recruited from The Pennsylvania State University community and were paid for their participation. One participant was excluded for insufficient number of false alarm trials ( $<10$ ). Participants were screened for history of neurological and psychiatric illness, learning disability, and drug/substance abuse. All participants provided written informed consent and all procedures were approved by The Pennsylvania State University Institutional Review Board.

### 2.2. Stimuli

Stimuli consisted of 220 color photographs of faces and 220 color photographs of scenes. Face stimuli consisted of both male and females faces, each exhibiting a neutral expression, taken from the following online databases: the Color FERET database (Phillips, Moon, Rizvi, & Rauss, 2000), adult face database from Dr. Denise Park’s lab (Minear & Park, 2004), the AR face database (Martinez & Benavente, 1998), and the FRI CVL Face Database (Solina, Peer, Batageli, Juvan, & Kovac, 2003). Scene stimuli consisted of outdoor and indoor scenes collected from an Internet image search. Using Adobe Photoshop CS2 version 9.0.2 and Irfanview 4.0 (<http://www.irfanview.com/>), we edited face stimuli to a uniform size ( $320 \times 240$  pixels) and background (black), and scene stimuli were standardized to  $576 \times 432$  pixels. During the associative encoding task, 195 face-scene pairs were presented with the face positioned

to left of center and the scene to the right (see Fig. 1). All stimuli were presented against a black background. At retrieval, 130 encoding pairs were presented as targets (exact face-scene pairing) and the remaining 65 were randomly recombined as related lures (new face-scene pairing). Twenty-five completely novel face-scene combinations were also presented during retrieval, serving as novel lures.

### 2.3. Procedure

During both associative encoding and retrieval participants lay supine in the scanner and images were projected onto a screen which was viewed through a mirror mounted on the head coil. Behavioral responses were made with the right hand and recorded using a four key standard button box controller. Associative encoding consisted of 5 four-minute runs. Half of the faces and scenes had been previously studied by the participants in an item encoding phase in an attempt to facilitate associative encoding of familiarized items. All trials pertaining to this manipulation were collapsed for the purpose of the current analysis. During encoding each face-scene combination was presented for 3000 ms, during which time participants were asked to rate on a scale of 1–4 how well the face fit with the scene. Participants were also informed that a memory test would follow. Encoding data will be presented in a subsequent publication.

During retrieval, targets, recombined lures, and novel lures were randomly intermixed and displayed for 4000 ms, during which time participants made memory responses using the ‘Remember/Know/New’ paradigm. Participants were specifically alerted to the inclusion of the three different trial types and were further instructed to respond ‘Remember’ if they were certain that the exact pairing was presented in the previous task, and can remember specific details about the association and pairings’ presentation from the study phase. In addition, participants were instructed to respond ‘Know’ if the exact face-scene pair looked familiar, but their memory was lacking any specific details of its prior presentation/association. Finally, participants were told to respond ‘New’ if they believe that the exact face-scene pair was not presented together during the encoding session (even if the individual items were presented during the encoding phase). It was further made clear that a rating of ‘New’ should be made even if participants remembered having seen a particular face or scene before, but did not see them in that specific combination before. Retrieval lasted approximately 25 minutes and consisted of 5 five-minute runs.

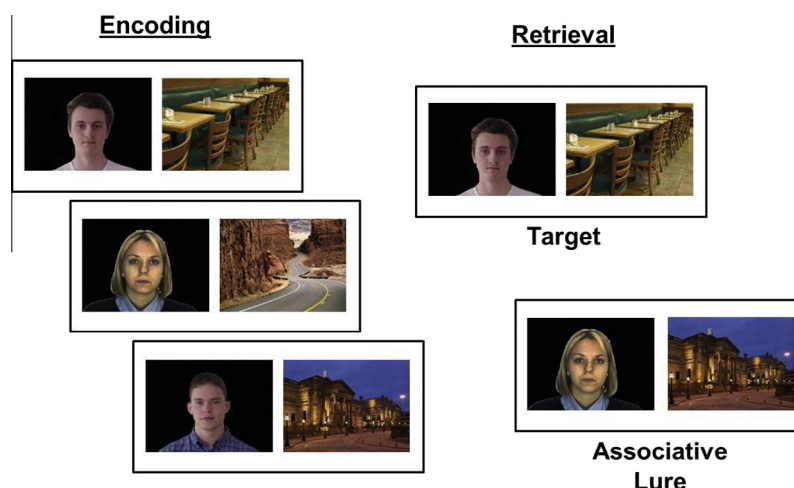


Fig. 1. Study design and examples of stimuli.

## 2.4. Image acquisition

Images were collected using a Siemens 3T scanner and a 12-channel head coil. Images were acquired using a T1 weighted sagittal localizer to align scans to the AC-PC line. High resolution anatomical images were acquired with a 1650 ms repetition time (TR), 2.03 ms echo time (TE), 240 mm field of view (FOV),  $256 \times 256$  matrix, 160 axial slices, and 1 mm slice thickness for each participant. Echoplanar functional images were acquired using an interleaved acquisition, 2500 ms TR, 25 ms TE, 240 mm FOV, a  $80 \times 80$  matrix, 48 axial slices with 3.0 mm slice thickness resulting in 3.0 mm isotropic voxels. The angle of acquisition was set approximately perpendicular to the hippocampus, without sacrificing coverage of the frontal lobes.

## 2.5. Image processing

Processing of fMRI data was carried out using SPM8 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, <http://www.fil.ion.ucl.ac.uk/spm>). Time-series data were corrected for differences in slice acquisition times and realigned. Slice time correction and realignment were carried out using the first volume of the first run as the reference slice. With regard to co-registration, as a first step structural images were co-registered to the standardized Montreal Neurological Institute (MNI) space. As a second step information from this step was applied to all functional images during normalization in order to transform individual images to standard MNI space. No resampling of voxels was conducted. Processed data were then spatially smoothed using an 8 mm isotropic Gaussian kernel.

## 2.6. fMRI analyses

Trial-related activity was modeled in the General Linear Model (GLM) with a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function (HRF). The current analyses focused on three trial types of interest: Hits, which were defined as both 'Remember' and 'Know' responses to targets; false alarms, which were defined as both 'Remember' and 'Know' responses to recombined lures; and correct rejections, which were defined as 'New' responses to recombined lures. Misses, correct rejections to novel lures, and no response trials were also coded with their own regressor (as were movement parameters) and treated as regressors of no interest. In order to identify neural correlates supporting both true and false associative memory, we compared each memory response to a common baseline of correct rejections of related lures. By using correct rejections as a baseline, we were able to control for general stimuli presentation and decision making involved in associative memory judgments, yet isolate neural activity that specifically supports the memory decision of interest. Direct comparisons between associative hits and false memories allowed for the identification of neural resources that were differentially recruited for each type of memory response.

For all contrasts, in order to obtain results that are corrected for multiple comparisons, we used Monte Carlo simulations (<https://www2.bc.edu/sd-slotnick/scripts.htm>) to define individual voxel and cluster extent thresholds (e.g. Forman et al., 1995; Garoff-Eaton et al., 2007; Quadflieg et al., 2008; Slotnick & Schacter, 2004). This procedure takes into account the acquisition matrix ( $80 \times 80$ ), number of slices (48), voxel dimensions ( $3.0 \text{ mm}^3$ ), intrinsic smoothness (13.3 mm), and resampling of voxels (none) in order to simulate data and estimate the rate of Type I error given the protocol parameters. In this study, an individual voxel threshold of  $p < 0.01$  was used in combination with a cluster extent

threshold of 18 voxels ( $486 \text{ mm}^3$ ) in order to identify results corrected for multiple comparisons at  $p < 0.05$ .

## 3. Results

### 3.1. Behavioral

As noted above, hits and false alarms were identified by combining all 'old' responses (i.e., Remember and Know responses) to targets and lures respectively. A one-way repeated measures ANOVA examining the effect of trial type (targets, recombined lures, novel lures) revealed a significant effect of trial type [ $F(2,36) = 202.7$ ,  $p < 0.001$ ]. Post-hoc tests were carried out using a Bonferroni correction for multiple comparisons. Results showed that participants made significantly more overall 'old' responses to targets ( $M = 0.80$ ,  $SD = 0.11$ ) than they did to recombined lures ( $M = 0.44$ ,  $SD = 0.14$ ) [ $t(18) = 11.124$ ,  $p < 0.001$ ] and novel lures ( $M = 0.10$ ,  $SD = 0.12$ ) [ $t(18) = 17.462$ ,  $p < 0.001$ ]. In addition, participants' overall false alarm rate to recombined lures was significantly higher than that exhibited to novel lures, [ $t(18) = 10.9$ ,  $p < .001$ ], indicating that the high rate of false alarms to recombined lures was associated with the history of the stimuli and not simply a general tendency for participants to false alarm to all new face-scene combinations.

### 3.2. Imaging

Neural activity associated with both true and false associative recognition compared to the correct rejection baseline condition is reported in Table 1 and differential activity between true and false retrieval is reported in Table 2. Compared to correct rejections, true associative memory showed increased neural activity in a number of regions including the left hippocampus (see Fig. 2a), left inferior frontal gyrus and bilateral inferior parietal cortex. False associative memories showed increased neural activity across several regions within the PFC including anterior cingulate cortex (ACC) and bilateral inferior, middle and superior frontal gyri (see Fig. 2b). (see Table 1 for a complete list of regions) Direct contrasts between true and false associative recognition showed greater activity in left hippocampus and PHG, anterior cingulate cortex, left superior parietal cortex and several regions within both early and late visual cortex for true associative recognition (see Fig. 3a). In contrast, greater activity for false associative recognition was found in left superior temporal gyrus, right inferior parietal and several regions within the PFC including ACC, bilateral middle frontal gyrus and right inferior frontal gyrus (see Fig. 3b). (see Table 2 for a complete list of regions).

## 4. Discussion

The current study examined the neural basis underlying both true and false associative memories. Results suggest that the MTL, specifically the hippocampus, supports true associative memories. Consistent with the sensory reactivation theory, the visual cortex exhibited greater activity for true compared to false memories. However, a lack of differential activity in this region for true memories compared to correct rejections suggests that the foregoing difference could not be explained by sensory reactivation alone. Finally, consistent with many previous false memory studies, false associative memories were mediated by neural activity in the PFC. Discussed in more detail below, the results broaden our understanding of the cognitive and neural basis underlying false memories by extending research into the domain of associative memory.



**Table 1**

This table reports areas distinctly activated for hits and false alarms compared with correct rejections.

	BA	H	Coordinates (T&T)			<i>t</i>	mm <sup>3</sup>
			X	Y	Z		
<i>Hit &gt; CR</i>							
Inferior frontal gyrus	11/47	L	−45	36	−13	4.75	2673
Precentral gyrus	4	L	−48	−13	49	3.56	702
Postcentral gyrus	2	R	30	−39	54	3.23	1026
Pre/postcentral gyrus	1/2/3/4	R	53	−16	52	3.86	5832
Caudate	−	L	−6	8	1	3.60	864
Hippocampus	−	L	−33	−16	−10	3.92	756
Inferior parietal	40	R	68	−40	29	3.38	594
	40	L	−59	−46	32	3.32	864
<i>FA &gt; CR</i>							
Inferior frontal gyrus	47/45	R	45	22	1	3.3	594
Middle frontal gyrus	6/9	L	−42	−2	41	3.29	1215
	10/46	R	33	46	16	4.06	3969
	10	R	45	45	−3	4.16	810
Middle/inferior frontal gyrus	46/44/47/10	L	−36	46	5	4.42	8802
Superior frontal gyrus	8/6	R	15	19	59	3.72	1242
	8/6	L	−6	13	51	3.71	1053
Anterior cingulate cortex	32	L	−12	32	20	5.22	1701
Pre/post central gyrus	1/2/3/4	L	−30	−31	37	4.68	594
Postcentral gyrus	1/2/40	R	42	−28	36	4.06	1890
Inferior parietal	40	R	51	−33	51	3.53	540
Cerebellum	−	L	−39	−55	−31	4.03	513

BA = Brodmann's Area; H = Hemisphere; L = left; R = right; *t* = statistical *t*-value; T&T = Talairach and Tournoux coordinates.

#### 4.1. Neural correlates supporting true associative memories

##### 4.1.1. MTL

The majority of association memory studies identify the MTL, in particular the hippocampus, as a key region supporting successful memory performance (Giovanello, Schnyer, et al., 2009; Giovanello et al., 2004; Kirwan & Stark, 2004; Prince et al., 2005; Ranganath, Cohen, Dam, & D'Esposito, 2004). However, the research supporting this conclusion is often one that contrasts association memory with item memory (in which the former involves successful retrieval of two items as well as their association, whereas the latter involves successful retrieval of a single item). The current study controlled for this imbalance in the amount and type of information being retrieved when assessing the neural correlates of successful associative retrieval by contrasting associative hits with associative correct rejections. In doing so, the results support and extend earlier work, showing greater hippocampal involvement in associative retrieval compared to correct rejections (see Fig. 2a). Furthermore, the results support the hypothesis that the hippocampus is critical to successful retrieval of item–item associations, and hippocampal activity observed in previous associative memory studies was not driven by the difference in complexity between associative memory and item memory.

Both the lack of hippocampal activation for false associative memories compared to correct rejections and the activation of this region in true compared to false retrieval further suggests that the MTL, including the hippocampus, is uniquely involved in the *accurate* retrieval of complex associative memories. As previously noted, within the current study, false associative memories occurred when two encoding items were rearranged to form a new pair during retrieval and the participant incorrectly identified the new pair as having previously been presented. Like true associative memories, false associative memories involved correct retrieval of one or both of the individual items, but they also represented a failure to retrieve the correct context or association among the items. As such, the two retrieval processes engaged many of the same cognitive operations, but differed with respect

**Table 2**

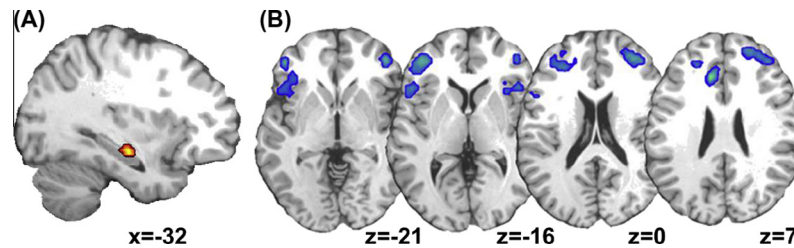
This table reports areas distinctly activated for true (Hit > FA) and false (FA > Hit) memory.

	BA	H	Coordinates (T&T)			<i>t</i>	mm <sup>3</sup>
			X	Y	Z		
<i>Hit &gt; FA</i>							
Medial frontal gyrus	10	M	−3	63	7	3.38	702
Anterior cingulate cortex	11/25	M	−3	36	−23	5.59	8235
Inferior frontal gyrus	47	L	−24	27	−15	3.63	756
	11/47	R	21	25	−12	4.36	513
Precentral gyrus	4	R	53	−4	49	3.84	729
	4	L	−21	−25	50	3.97	1107
	6	R	30	−9	66	3.29	513
Striatum	−	M	−3	8	−4	4.98	1647
	−	M	6	7	−9	4.22	702
	−	R	30	2	10	3.75	1053
	−	L	−21	3	13	4.03	810
Hypothalamus	−	M	0	−4	−8	4.19	486
Amygdala	−	L	−27	−7	−11	4.4	594
Anterior PHG/hippocampus	34	L	−12	1	−16	4.36	891
Hippocampus/PHG	28	L	−21	−28	−7	3.86	486
Superior temporal gyrus	42	R	50	−26	20	3.79	5859
Paracentral lobule	5	M	−6	−28	50	4.71	2997
Superior parietal cortex	7	L	−21	−44	62	4.46	1620
Fusiform gyrus	19	L	−30	−63	−13	3.61	1107
Middle occipital cortex	19/37	R	42	−54	−6	3.74	2889
	37	R	30	−62	5	3.88	675
Occipitoparietal cortex	19/39	L	−48	−70	22	3.81	2133
Superior occipital gyrus	19	R	21	−80	42	3.39	945
Primary occipital cortex	18/17	L	−6	−83	−2	5.47	7992
	17/18	R	21	−88	4	4.37	4671
Cerebellum	−	L	−30	−63	−13	3.61	729
	−	L	−24	−80	−14	4.07	1026
	−	R	15	−78	−25	4.11	2700
<i>FA &gt; Hit</i>							
Superior/middle/inferior frontal gyrus	6/8/9/10/46/11	R	24	22	48	5.79	26973
Inferior frontal gyrus	47	R	36	19	−9	4.65	2214
Middle frontal gyrus	8	L	−48	7	35	4.20	3159
	10/46	L	−33	46	8	3.70	2079
Anterior/middle cingulate	32	R	9	21	31	4.69	3942
Superior temporal gyrus	22	L	−48	−1	−6	2.96	810
Pre/post central gyrus	1/2/3/4	L	−30	−34	34	5.16	1323
Inferior parietal	40	R	48	−39	51	5.82	3753
Cerebellum/brainstem	−	R	12	−38	−42	3.89	594
Brainstem	−	M	−6	−25	−10	4.37	1539

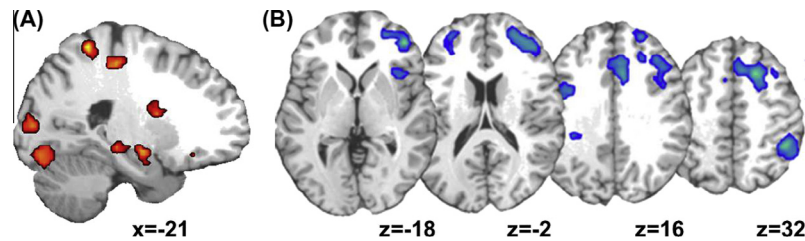
BA = Brodmann's Area; H = Hemisphere; L = left; R = right; *t* = statistical *t*-value; T&T = Talairach and Tournoux coordinates.

to retrieval of the association that connected the items. While many previous studies have identified a role of the MTL and specifically the hippocampus in associative memory (Giovanello, Schnyer, et al., 2009; Giovanello et al., 2004; Kirwan & Stark, 2004; Prince et al., 2005; Ranganath, Cohen, Dam, & D'Esposito, 2004), this study extends those findings by showing that hippocampal activity does not support false associative retrieval.

The current results also support previous studies investigating semantic and perceptual false memories, which have found that the MTL is preferentially active for true compared to false retrieval (Cabeza et al., 2001; Dennis, Kim, & Cabeza, 2008; Dennis et al., 2012; Giovanello, Kensinger, et al., 2009; Kahn et al., 2004; Kensinger & Schacter, 2006; Kim & Cabeza, 2007; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008). In several of the foregoing studies, researchers have suggested that greater MTL



**Fig. 2.** (a) Neural activity supporting true memories compared to correct rejections and (b) neural activity supporting false memories compared to correct rejections.



**Fig. 3.** Direct comparisons of neural activity supporting (a) true memories compared to false memories and (b) false memories compared to true memories.

activation for true compared to false memories reflects recovery of sensory details (Cabeza et al., 2001; Kahn et al., 2004; Okado & Stark, 2003), whereas others have suggested this neural increase reflects the role of the hippocampus in either binding together true details from past events (Kensinger & Schacter, 2006) or recollection of studied details (Dennis et al., 2012; Kim & Cabeza, 2007). With regard to the theory that MTL activity reflects the recovery of sensory details, we feel our results are less compatible with this theory given that both the targets and related lures included stimuli that had been presented previously and thus should be in a position to evoke similar recovery of sensory details. The sole difference between the two trial types was the presence or absence of the exact pairing. As such, we feel our results are most consistent with the binding theory. Specifically, the differential hippocampal activation observed in the current study may reflect the retrieval of associative details linking the two items for hits, whereas false associative memories reflect retrieval of the individual items, but, like correct rejections, lacks retrieval of the binding link between items. Moreover, these MTL results suggest that false associative memories are not driven by retrieval of inaccurate links between items studied.

#### 4.1.2. Visual cortex

As noted above, there was a substantial difference between the related lures presented in the current study and that of previous false memory studies. Specifically, in the current study both targets and related lures were comprised of items that had been presented during encoding, with the only difference being whether they were presented as the same item pair (targets) or recombined to form a new pair (lures). Previous false memory studies have observed significantly greater neural activity in early visual cortex for true compared to false memories, positing that this difference reflects activity associated with retrieval of perceptual properties of the original encoding episode (the sensory reactivation hypothesis) (e.g., Dennis et al., 2012; Slotnick & Schacter, 2004). We posited that if the visual cortex was simply sensitive to the presentation of old items (and not the exact association), then no differences between targets and lures would be found. Yet, if early visual cortex was sensitive to the exact arrangement of the earlier item–item presentation than it would elicit greater engagement for true compared to false associative retrieval. Evidence supporting this prediction was mixed.

The current results showed greater activity in occipital cortex for true compared to false associative memories (see Fig. 3a). That is, despite the subjective experience of identifying a face–scene pair as ‘old’, only the accurate assessment of oldness and exact arrangement of previous item–item pairs resulted in recapitulation of the original sensory signal. At first glance, these results are consistent with previous false memory studies, which interpret similar differences in occipital activation within the framework of the sensory reactivation hypothesis (e.g., Dennis et al., 2012; Slotnick & Schacter, 2004). However, expanding upon that notion, true retrieval should also elicit greater activation in occipital cortices compared to related lures that were correctly rejected as ‘new’. This was not the case in the current study. Thus, it is difficult to conclude that the visual activity reported in the current study represents a sensory signal that is generated in response to the exact presentation of prior information (see Slotnick & Schacter, 2004). An alternative explanation is that, in order to accurately detect a new association as novel, retrieval of the correct association (for at least one of the items) needs to occur. While the physical stimulus is not presented at the time, imagery-based retrieval of this extra information may be mediated by occipital cortices and thus negates any difference in the region between true associative retrieval and novelty detection. Future research is needed in order to test this theory and elucidate the cognitive operation driving the difference between true and false associative memories in visual cortex.

#### 4.2. Neural correlates supporting false associative memories

##### 4.2.1. PFC

Like many false memory studies in other domains (semantic, perceptual, misinformation) (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), false associative memories were also found to elicit greater activity in the PFC compared to true memories. Specifically, increased activity was observed in bilateral inferior and middle frontal gyri and right superior frontal gyrus (see Figs. 2b and 3b). Greater frontal recruitment for false memories has been attributed to the need for increased monitoring and evaluation associated with the more effortful memory decision required for lures, which is made in

the absence of a sensory-related signal emanating from visual cortex and/or MTL (Kim & Cabeza, 2007; Nessler & Mecklinger, 2003; Schacter et al., 1996). Studies investigating neural differences between correct rejections and hits have also found increased PFC activity for correct rejections (Achim & Lepage, 2005; Duzel, Habib, Guderian, & Heinze, 2004; Giovanello & Schacter, 2012; Lepage, Brodeur, & Bourgooin, 2003). Specifically, greater frontal activation for correct identification of rearranged pairs compared to intact pairs has been observed in right dorsolateral PFC, supporting an increased role of monitoring in the evaluation of lures compared to target items. The current study extends this previous work by showing increased PFC activity for false compared to both true associative memories and correct rejections. In doing so, the data support the view that monitoring and conflict resolution are not only recruited for the evaluation of related lures, but are recruited to a greater extent when the ultimate decision regarding such stimuli is incorrect, perhaps due to the need for a more robust retrieval process or evaluation of a memory decision in the absence of a strong sensory signal.

It should be noted that while the current results are consistent with a large number of false memory studies across several domains, the only other study to investigate false associative memories did not find greater PFC activity for false compared to true associative memories (Giovanello, Kensinger, et al., 2009). The difference between the two studies may be due to reduced power in the former study. That is, participants in the previous study made, on average, less than ten associative false memories, reducing power to detect significant activation effects for false greater than true memories. However, when the threshold was lowered the results showed greater activity in bilateral inferior and medial PFC for false associative memories, consistent with that observed in the current study.

Together with a lack of MTL or sensory processing activity for false memories, the current results suggest that the basis for making a false associative memory decision is primarily mediated by cognitive processing within frontal regions. As such, the current results contribute to a growing body of literature that asserts false memories arise from a reliance on top-down decision making processes that occur in the absence of a sensory signal for the related lure. In the case of associative lures this signal may be that of the associative link connecting previously encountered items. In addition, taken together with results from previous false memory studies the current results further support the notion that failures in monitoring mediate false memories across a wide range of paradigms and memory types.

## 5. Conclusions

The current results support previous false memory studies but also expand findings to include associative false memories. While similar to perceptual, semantic, and source monitoring errors, associative false memories represent a substantively different type of false memory in that all items in the recombined lure were presented during encoding. Despite this difference in the composition of associative lures, the current results suggest that associative false memories are mediated by similar neural mechanisms as those identified in previous false memory studies. Specifically, results support the conclusion that associative false memories are driven by frontally mediated mechanisms that likely represent increased monitoring and evaluation associated with the more effortful memory decision regarding recognition of rearranged pairs. The lack of MTL activity for false retrieval further supports the conclusion that false associative retrieval is not driven by retrieval of an inaccurate association or link between studied items. Taken together results contribute to a growing body of

literature suggesting that despite differences across false memory paradigms, frontal and MTL differences between true and false memories are ubiquitous.

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