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# True and phantom recollection: An fMRI investigation of similar and distinct neural correlates and connectivity

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#### ARTICLE INFO

# ABSTRACT

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Although research suggests that most false memories are mediated by a sense of familiarity, behavioral evidence indicates that some are characterized by retrieval of item-specific details associated with recollection. However, neuroimaging studies have yet to isolate and analyze the neural correlates of false (or phantom) recollection, focusing instead on general recognition processes. In doing so, results are mixed with respect to the role of the medial temporal lobes (MTL) in distinguishing between true and false retrieval. The present study sought to investigate the neural basis of true and phantom recollection and clarify the role of the MTL in dissociating between the two processes. Results showed that true and phantom recollection were associated with a largely overlapping retrieval network including activity in bilateral anterior parahippocampal gyrus, fusiform gyrus, anterior cingulate cortex, and right superior parietal cortex. However, connectivity analyses using two common MTL seeds revealed a more inferior network (fusiform gyrus, hippocampus, middle temporal gyrus) associated with true recollection and a more superior network (superior parietal, superior frontal gyrus, posterior cingulate cortex) associated with false recollection. Finally, direct comparisons between true and phantom recollection showed greater activity in right hippocampus and early visual cortex for true recollection, whereas no region exhibited greater activity for false recollection. Results indicate that while both true and phantom recollection show similar patterns of activation, there are also distinctions in the neural networks contributing to the two recollection processes. Moreover, results conclude that within the MTL, the hippocampus proper can distinguish between true and phantom recollection.

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# Introduction

With regard to true memories, the dual process model of memory (Yonelinas, 2002) posits that recognition memory can be based on two distinct retrieval processes: recollection, or the retrieval of itemspecific details associated with a previous event, and familiarity, or a feeling that the event occurred previously, but absent of specific details of the episode. Research on false memories suggests that the majority of false memories are driven by increases in familiarity or gist-based processes (Brainerd and Reyna, 2002; Jacoby, 1991; Yonelinas et al., 1996) and are incorrectly endorsed as 'old events' based on their similarity to previously experienced true events. This similarity arises to the extent that the true prior event and the new event share common themes or properties (e.g., studying the words 'cow', 'sheep', and 'chicken' and falsely remembering the word 'pig' as being part of the studied list). The notion that false memories are based on such gist or familiarity is supported by evidence showing that, compared to true memories, false memories are associated with fewer perceptual

\* Corresponding author at: Department of Psychology, The Pennsylvania State University, 520 Moore Bldg. University Park, PA 16802, USA. Fax: +1 814 863 7002. *E-mail addresses*: nad12@psu.edu (N.A. Dennis), crb5303@psu.edu (C.R. Bowman), snv5004@psu.edu (S.N. Vandekar). details (Johnson and Raye, 1981; Norman and Schacter, 1997), greater reports of familiarity (Brainerd and Reyna, 2002; Roediger and McDermott, 1995), slower response times (Fabiani et al., 2000), and lower confidence (Mather et al., 1997; Miller and Wolford, 1999). However, like true memories, some false memories have been associated with fast response times (Loftus et al., 1989), high confidence (Dennis et al., 2008b; Kim and Cabeza, 2007; Loftus et al., 1995; Roediger and McDermott, 1995), and retrieval of itemspecific details (Geraci and McCabe, 2006; Payne et al., 1996; Schacter et al., 1998). This overlap in characteristics supporting both true and false memories challenges theories that all false memories are based solely upon above-criterion familiarity. Accordingly, such detaildriven false memories have been termed false or 'phantom' recollection (Brainerd et al., 2001). While phantom recollection has been observed in the behavioral literature (e.g., Gallo et al., 2001; Kensinger et al., 2007; Lampinen et al., 2001; Stahl and Klauer, 2009), no study to date has examined the neural correlates associated with phantom recollection. The goal of the current study is to examine the neural correlates mediating phantom recollection and to elucidate the neural basis associated with the overlap and distinction between true and phantom recollection.

Behavioral memory theories find that true recollection is a process in which memories are not mirror images of past events, but







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reconstructed from stored details (Roediger and McDermott, 1995; Schacter et al., 1998) via the medial temporal lobe (MTL) (Alvarez and Squire, 1994; Damasio, 1989; McClelland et al., 1995). In line with this theory, phantom recollection may be based on erroneous retrieval of details or faulty reconstructive processes that misattribute previously studied details to new, related items. Such retrieval is known as content borrowing and may occur when an encoding detail from one episode is incorrectly associated with a newly presented item at retrieval (e.g., related lure) in order to corroborate a feeling of oldness associated with the new item's presentation (and likely evoked by the similarity with previously presented items) (Lampinen et al., 1999, 2000; Odegard and Lampinen, 2004). Such details may include thoughts, and emotions, as well as perceptual and/or conceptual details associated with a previous memory. Thus, while the detail may itself be accurate in the sense that it was part of an encoding episode, it was never previously associated with the newly presented item.

Despite considerable behavioral evidence that false memories can be based on erroneous recollection, to date, our understanding of the neural correlates mediating phantom recollection has been limited by the type(s) of recognition tests and analyses performed during retrieval in false memory studies. While it has become relatively standard to isolate recollection and familiarity in behavioral and neuroimaging studies of true memories, the majority of studies investigating the neural correlates of false memories have not separated these processes, but used a yes/no recognition test to probe memory retrieval (Cabeza et al., 2001; Giovanello et al., 2009a; Gonsalves et al., 2004; Paz-Alonso et al., 2008; Schacter et al., 1997; Slotnick and Schacter, 2004). The binary nature of this testing method limits response options and does not allow for distinctions between recollection and familiarity processes to be made, combining both recognition judgments (as well as guessing) within a single 'yes' response.

Recent research in the domain of true memories has shown that such distinction between recollection and familiarity is critical - not only at the behavioral level (for a review see Yonelinas, 2002), but also at the neural level. For example, while true recollection has been associated with neural activity in the medial temporal lobe (MTL), medial prefrontal cortex (PFC), lateral parietal cortex, and posterior cingulate, familiarity has been associated with activity in lateral PFC regions, MTL, and superior parietal cortex (e.g., Daselaar et al., 2006a; Spaniol et al., 2009; Yonelinas et al., 2005). With regard to MTL activity, converging evidence from animal models, patient (e.g., amnesia) studies and neuroimaging studies shows the hippocampus and posterior parahipopcampal gyrus (PHG) are critical for recollection whereas the anterior PHG and rhinal cortex are critical for familiarity (for reviews see Diana et al., 2007; Eichenbaum et al., 2007, in press). Thus, any analysis collapsing across the two retrieval processes will not allow for specific conclusions regarding recollection and will underestimate the range of function subserved by the MTL. In addition, while a small number of studies have attempted to isolate recollection from familiarity-based false retrieval, the studies often do not elicit enough false alarms to isolate phantom recollection or perform direct contrasts between true and phantom recollection (Abe et al., 2008; Duarte et al., 2010; Garoff-Eaton et al., 2007).

Due to these methodological limitations, our understanding of the neural mechanisms mediating false retrieval, as well as our understanding of the similarities and distinctions between true and false retrieval, has largely focused on either more general components of retrieval or familiarity processes underlying false retrieval. For example, many studies conclude that overlap in neural processing of true and false memories is based on above-criterion familiarity (Duarte et al., 2010; Garoff-Eaton et al., 2006; Kahn et al., 2004; Kim and Cabeza, 2007). This overlap in activity includes frontal and parietal regions (Garoff-Eaton et al., 2006; Okado and Stark, 2003; Slotnick and Schacter, 2004), which mediate general decision making processes; late visual cortex (BA19/37) (Garoff-Eaton et al., 2006; Kuehnel et al., 2008; Slotnick and Schacter, 2004, 2006), which mediates retrieval processes associated with general object identity and meaning (Gonsalves and Paller, 2000); and the MTL (Cabeza et al., 2001; Garoff-Eaton et al., 2006; Kahn et al., 2004; Schacter et al., 1996, 1997; Stark et al., 2010), which mediates both recollection and familiarity-based retrieval. However, as noted above, familiarity and recollection are dissociable processes and while significant overlap in true and false retrieval has been linked primarily with familiarity processing, it is not clear whether, once isolated, true and phantom recollection also share similar neural networks.

Furthermore, overlapping activation in a given region across two different tasks (or retrieval responses – e.g., true and false recollection) does not necessarily indicate that the region is engaged in the same cognitive process across both tasks. Using functional connectivity analysis, recent studies have shown that even a commonly activated region may be engaged in different neural networks across the two tasks (e.g., Bollinger et al., 2010; Grady et al., 2003; Pugh et al., 2000; Rissman et al., 2004; St Jacques et al., 2009). For example, Bollinger et al. (2010) found that connectivity with the fusiform gyrus differed significantly for subsequent working and long-term memory. Specifically, the fusiform gyrus exhibited greater connectivity with the inferior frontal junction for working memory success and middle frontal gyrus for long-term memory success. Bollinger and colleagues concluded that this differential connectivity reflected the inferior frontal junction's role in expectancy-related sensory processing and the middle frontal gyrus' role in recognition memory. Results underscore the fact that even though a given brain region may be active across separate tasks, it may be involved in a different functional network in each of the tasks. The same may be true for different retrieval responses (e.g., true and false retrieval), such that the common overlap in MTL activation observed in previous studies may be associated with distinct cognitive processes and functional networks for each type of retrieval. While not utilized in previous false memory studies, the use of functional connectivity analyses can assess this possibility.

Moreover, despite the overlap in neural activation, studies also obtain dissociations between true and false neural activity. For example, several studies find that true, but not false retrieval is mediated by activity in sensory regions associated with its initial presentation such as primary auditory (Cabeza et al., 2001) and visual cortex (e.g., Brodmann's Area (BA) 17/18) (Okado and Stark, 2003; Slotnick and Schacter, 2004; Stark et al., 2010). Previous research suggests that this activity represents both the retrieval and sensory reactivation of perceptual and item-specific properties of studied items (Vaidya et al., 2002; Wheeler et al., 2000) and false memories, having never occurred previously, do not contain such details and thus are absent of this sensory reactivation signal. False retrieval, on the other hand, tends to elicit activation in late visual cortex (e.g., BA 19/37) and has been associated with conscious processing of an item as "old" regardless of response accuracy (Slotnick and Schacter, 2004; Stark et al., 2010). However, not all studies find this accuracy distinction in domain-specific regions (Duarte et al., 2010; Kahn et al., 2004; von Zerssen et al., 2001). It is unclear whether this lack of recapitulation differences is due to the fact that false recollection itself exhibits some form of sensory reactivation or, more likely, whether having collapsed across recollection and familiarity responding in previous studies, this difference between true and false recollection was masked by high rates of familiarity-based responding in both types of retrieval. If phantom recollection arises from contentborrowing (Lampinen et al., 2005) and reconstruction-based retrieval processing, then any new item should not elicit recapitulation in primary sensory cortices, but elicit retrieval of details from stored representations supported by activation in late visual cortex. However, if phantom recollection arises from weaker, albeit erroneous recapitulation (Kahn et al., 2004) then primary sensory cortex may mediate both types of recollection.

The MTL has also been shown to dissociate between true and false memories. However, mixed results across past studies leave several unanswered questions regarding the exact role of the MTL in false memory retrieval. While some studies find the MTL to be active for both true and false retrieval (Cabeza et al., 2001; Garoff-Eaton et al., 2006; Kahn et al., 2004; Schacter et al., 1996, 1997; Stark et al., 2010) other studies have found MTL activity only for retrieval of true, but not false memories (Dennis et al., 2008b; Giovanello et al., 2009a; Kim and Cabeza, 2007; Paz-Alonso et al., 2008). Furthermore, only a sub-set of the former studies find that MTL activity differentiates between true and false retrieval (Cabeza et al., 2001; Giovanello et al., 2009a; Kim and Cabeza, 2007; Paz-Alonso et al., 2008), whereas an equal number of studies find no basis for such a differentiation with the MTL (Okado and Stark, 2003; Schacter et al., 1997; Slotnick and Schacter, 2004; Stark et al., 2010). Noted previously, the discrepancies in MTL activity may stem from inconsistencies in testing procedures and the presence (or absence) of recollection-related responding within both true and false retrieval. When the two types of memory processes are combined in one response option (e.g., using yes/no recognition), a lack of MTL differences may be the result of collapsing across two separate and distinct cognitive and neural processes. In order to examine whether the MTL distinguishes between true and false recollection, we must isolate recollection from familiarity processing for both true and false memories.

The current study sought to resolve these previous limitations by using fMRI in conjunction with the Remember/Know/New paradigm to (1) isolate neural processes mediating recollection of both true and false memories and (2) directly compare neural activity associated each type of recollection. We hypothesize that true recollection will be associated with retrieval of perceptual and item-specific details of the encoding event, reflected in neural activity in both early and late visual cortex and the hippocampus, as well as other regions typically associated with recollection including the anterior cingulate (ACC) and superior parietal cortex. With regard to false retrieval, we hypothesize that phantom recollection will also be mediated by recollection-related activity in the ACC and superior parietal cortex as well as regions involved in reconstructive processes such as late visual cortex and the MTL. Second, the current study also sought to identify both common and distinct neural correlates associated with true and false recollection. While the initial analyses can identify neural correlates of each type of recollection, only through a conjunction analysis are we able to quantitatively assess the overlap in neural activity between true and false recollection. Based on previous evidence, we hypothesize that true and false recollection will show common activity in regions associated with decision making and reconstruction processes involved in retrieval of episodic details supporting recollection, including the ACC, the MTL, superior parietal cortex, and late visual cortex. Finally, dissociations between true and false recollection will be assessed using both functional connectivity analysis and direct contrasts between the two types of recollection-related activity. With regard to the functional connectivity analysis, we aim to explore accuracy-related differences in functional connectivity associated with commonly activated MTL regions. While exploratory in nature, we expect that even common MTL activity will result in dissociable neural networks for each type of retrieval. Finally, when directly assessing differences between true and false recollection, we hypothesize that, given that recapitulation is likely driven by the reoccurrence of a previously experienced sensory signal and an overall richness of details associated with veridical retrieval, true recollection will exhibit greater recollection-related activity in primary visual cortex and hippocampus as compared to phantom recollection. Based upon the theory that phantom recollection is mediated by similar (but erroneous) recollection-related processes as true recollection, we hypothesize that no brain region will exhibit greater activation for phantom compared to true recollection.

#### Methods

#### Participants

Twenty right-handed native English speakers were recruited from the Penn State University community. Participants were screened for history of neurological disorders and psychiatric illness, alcoholism, drug abuse, and learning disabilities. Two participants were excluded from the analysis due to head motion in excess of 4 mm and one was excluded for performing below chance, leaving data from 17 participants reported in all analyses [11 females; mean age=21.28 yrs (SD=1.79)]. All participants provided written informed consent and received financial compensation for their participation. All experimental procedures were approved by Penn State University's Institutional Review Board for the ethical treatment of human participants.

#### Stimuli

Stimuli consisted of 1092 color pictures of common objects. Images were obtained from an internet image search. All backgrounds were removed and pictures were cropped and resized to an approximate size of  $480 \times 480$  pixels (see Fig. 1). Images were presented focally and equated for resolution. Seven hundred twenty images were presented during encoding, including 90 categories of stimuli with 8 exemplars per category. Six hundred and forty two images were presented at retrieval including (a) 270 targets (3 of the 8 exemplars from each encoding category) (b) 270 related lures (3 novel images associated with each encoding category) and (c) 102 unrelated lures (including 3 novel images from each of 34 unrelated categories). Items selected as targets were counterbalanced between participants.

## Procedure

Encoding and retrieval both took place in the scanner with approximately 24 h separating the two memory phases. (Encoding data will be reported in a subsequent publication). Encoding was incidental and participants were instructed to make subjective pleasantness ratings of objects as they were presented. Encoding images were presented for 1 s and participants were given 2 s to make their pleasantness rating, followed by a variable interstimulus interval.

Images were projected onto a screen that participants viewed through a mirror attached to the head coil. All images were presented in the center of the screen with response options (e.g., Remember/ Know/New) displayed below each image. Behavioral responses were recorded using a 4 button response box. Images were displayed by COGENT in MATLAB (Math Works). Scanner noise was reduced with headphones and earplugs, and cushioning was used in the head coil to minimize head motion.

During retrieval, participants completed 6 runs each approximately 8 min in length. Each image was displayed for 2.5 s while participants made memory responses using the 'Remember-Know-New' paradigm (see Fig. 1). In accord with typical task instructions, participants were told to respond 'Remember' if they could recollect specific details about the object such as its shape, color, or their thoughts or feelings during its initial presentation. Participants were told to respond 'Know' if the picture looked familiar, but they could not recollect any specific details of its prior presentation. They were told to respond 'New' if they believed the picture was not presented during the encoding session. The images were pseudorandomly sorted, ensuring that no more than 3 images from any one category appeared in a row.

# Image acquisition

Images were acquired using a Seimens 3 T scanner equipped with a 12-channel head coil. A T1-weighted sagittal localizer was acquired



Fig. 1. Stimuli presentation. During encoding participants incidentally encoded 8 separate items from a given category (e.g., cats) and were asked to make pleasantness ratings for each item. At retrieval participants were told to identify which items were presented at encoding using the Remember–Know–New paradigm. Retrieval images included target items, related lures, and unrelated lures.

to locate the anterior (AC) and posterior (PC) comissures. Images were then prescribed parallel to the AC–PC plane. An MPRAGE was acquired with a 2300 ms TR, 3.41 ms TE, 230 mm field of view (FOV), 256<sup>2</sup> matrix, 160 axial slices, and 0.9 mm slice thickness for each participant. Echoplanar functional images were acquired using an interleaved acquisition, 2000 ms TR, 30 ms TE, 240 mm FOV, a 64<sup>2</sup> matrix, 34 axial slices with 3.8 mm slice thickness resulting in 3.8 mm isotropic voxels.

## Image processing

Functional data were preprocessed and analyzed with 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. Images were checked for movement artifacts using a time series diagnostic function TSDiffAna (Freiburg Brain Imaging) in MATLAB (MathWorks). Functional images were spatially normalized to a standard stereotaxic space using the Montreal Neurological Institute (MNI) templates implemented in SPM8 and resliced to a resolution of 3.8 mm<sup>3</sup>. The coordinates were later converted to Talairach space (Talairach and Tournoux, 1988). Finally, the volumes were spatially smoothed using an 8-mm isotropic Gaussian kernel.

# 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). Statistical Parametric Maps (SPMs) were identified for each participant by applying linear contrasts to the beta weights for the events of interest. Regressors associated with recollection and familiarity of targets and related lures were used in defining contrasts of interest (see below). Regressors for unrelated lures and 'no response' trials, as well as those for motion parameters were also included in the

model and treated as regressors of no interest. All individual SPMs were subjected to a random effects analysis for group analysis.

In order to obtain results that were corrected for multiple comparisons we used Monte Carlo simulations (http://www2.bc.edu/slotnics/ scripts.htm) to define individual voxel and cluster extent thresholds (e.g., Forman et al., 1995; Garoff-Eaton et al., 2007; Slotnick and Schacter, 2004, 2006; Slotnick et al., 2003). In this study, an individual voxel threshold of p < 0.01 was used in combination with a cluster extent threshold of 15 resampled voxels (823 mm<sup>3</sup>), which yielded results corrected for multiple comparisons at p < 0.05. In addition, we used the aal pickatlas (Maldjian et al., 2003; Tzourio-Mazoyer et al., 2002) to restrict all analyses to cortical and subcortical regions.

In order to identify neural correlates associated with true recollection we compared activity associated with 'Remember' responses to target items to activity associated with 'Know' responses to targets. A similar comparison was conducted for related lures in order to examine false recollection. This contrast allows us to control for identification of an item as 'old' while simultaneously isolating recollection-related activity. In order to assess similarities in neural processing between true and false recollection, a conjunction analysis was performed using the implicit masking procedure in SPM8. Specifically, an image mask was created for the false recollection contrast described above. The mask was then applied to the true recollection measure (with each contrast set to the previously described corrected threshold of p < 0.05). Finally, in order to examine regions that distinguished true and false recollection, we directly contrasted activation associated with true and false 'Remember' responses.

To assess MTL-based connectivity associated with true and false recollection, we used the common bilateral recollection-related activity in the PHG (see Table for coordinates) as a seed region and examined correlations in whole-brain activity separately for true and false recollection. This analysis was conducted to identify whether, despite exhibiting common recollection-related activity in the MTL, accuracy differences in recollection-related connectivity between the MTL and rest of the brain exist. A new model was created such that each trial in the model was uniquely coded as a separate event. This allowed us to extract individual beta values for each trial and sort by trial type. Given that the goal of this exploratory analysis was to assess connectivity for recollection, the analysis was constrained to true and false recollection trials (with the betas sorted into each trial type accordingly). We then correlated activity in the seed region for each form of recollection with that of the rest of the brain. The validity of this design has been confirmed in previous studies (e.g., Daselaar et al., 2006a; Dennis et al., 2008a; Rissman et al., 2004; Sadeh et al., 2011).

As a second step, average MTL connectivity for both true and false recollection trials was calculated by using a one-sample *t* test on the resulting correlation maps (random effects). Accuracy-related differences in connectivity were then calculated with a multiple contrast approach. The between-condition paired-sample *t* test was conducted at p<0.05 with a minimum cluster size of 30 voxels (1646 mm<sup>3</sup>), again, resulting in activation corrected at p<0.05(Slotnick et al., 2003), inclusively masking for effects of interest within each condition (p<0.05 and a minimal cluster size of 30 voxels).

# Results

# Behavioral

Participants' hit rates and false alarm rates are presented in Table 1. Participants made significantly more overall 'old' responses to targets than they did to related lures [t(16) = 8.30 p<0.001] and also significantly more recollection-related responses (i.e., 'remember' to targets than to related lures [t(16) = 10.15, p<0.001]). Recollection rates for hits and false alarms were not significantly correlated (r=0.116, p=0.66). Participants' overall false alarm rate to unrelated lures was significantly lower than that exhibited to related lures, [t(16) = 14.00, p<0.001], indicating that the high rate of false alarms to related lures was associated with the related nature of the stimuli and not simply a general tendency for participants to false alarm to all new items.

#### Imaging

Table 2 reports results associated with both true and false recollection, as well as activity common to both types of retrieval processes. True recollection was characterized by neural activity in a large network of regions including left hippocampus, posterior PHG, bilateral anterior PHG, left ventrolateral PFC, ACC, right superior parietal cortex and precuneus, left inferior temporal gyrus, early and late visual cortex, and fusiform gyrus. False recollection was also characterized by a large network of neural activity including left hippocampus and bilateral posterior PHG, bilateral anterior PHG, left inferior temporal gyrus, and late visual cortex including fusiform gyrus, middle occipital gyrus, and inferior parietal. A conjunction analysis of true and false recollection exhibited common neural activity in the ACC, bilateral anterior PHG, right late visual cortex, right occipitotemporal cortex, right superior parietal cortex, and precentral gyrus (see Fig. 2).

Table 3 reports results associated with accuracy-related differences in MTL-whole brain connectivity. Results indicate that, compared to false recollection, true recollection exhibited significantly greater connectivity between the left anterior PHG and several inferior regions including orbitofrontal cortex, ACC, bilateral hippocampus/anterior PHG,

Table 1	
Behavioral	results

	Targets	Related lures	Unrelated lures
Overall	0.80(0.11)	0.50(0.12)	0.08(0.08)
Recollection	0.48(0.10)	0.20(0.12)	0.04(0.06)
Familiarity	0.32(0.11)	0.30(0.14)	0.04(0.04)

The table reports mean response rates (and standard error) to targets, related lures and unrelated lures.

Tabl	e 2
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True and false recollection.

	BA	Н	Coord	Coordinates (T&T)			mm <sup>3</sup>
			X	Y	Ζ		
True recollection							
DLPFC	44/10	R	52	42	1	3.57	1055
ACC	32/10/11	М	4	33	-21	5.66	33,117
	24	М	0	10	23	4.81	2426
VLPFC	47/11	L	-26	30	-5	3.44	1266
MTL	/						
Anterior PHG	28/36	L	-19	0	-29	3.65	1371
	28/34	R	15	-3	-16	3.75	2320
Hippocampus/posterior PHG	-	L	-33	-28	-9	4.22	1055
Inferior temporal gyrus	21	L	-52	0	-20	3.49	2426
	20	Ē	22	0	-35	3.29	1688
	20	Ē	-37	-11	-28	4 91	2637
Fusiform gyrus/PHC	19/30/37	R	41	-46	-8	3 71	6275
Precentral gyrus	3/4/2	R	52	-3	51	4 55	15 135
Precupeus	7	M	-7	-33	46	2.96	1160
Superior parietal	7	R	30	-42	71	5.04	3111
Inferior/middle occiptial	, 18/19/37	I	-11	-76	_9	4 1 1	25 313
gyrus/fusiform gyrus	10/10/07	D	27	00	7	2.42	10.072
	18/19	к	37	-80	/	3.42	10,072
Occipital gyrus		T	22	50	17	4.40	7400
Cerebellum		L	-22	-58	-17	4.43	/488
Falsa recollection							
	32/10	м	0	45	_3	3 37	4006
Inforior tomporal gurus	20/28	IVI	20	45	26	1.10	2062
interior temporar gyrus	20/38	L I	-30	2	-30	4.40	2903
	20/21	L D	-45	-5	-23	4.02	200
MTI	20/21	ĸ	40	-,	-22	5.55	2140
Anterior DHC	34/28	R	10	0	_23	5.40	2680
Anterior DUC/	24/20 20/26/25	I	15	2	-23	2.40	2009
hippocampus	28/30/33	L	-15	-5	-20	5.17	5402
Postarior PHC /	27/20/25	T	26	20	0	5 40	2051
hippocompus	27/30/33	L	-20	-28	-9	5.45	2921
Destarior DLC	20/27/25	D	11	20	5	4.60	4445
Fusiform gurus	10	I	22	-39	-5	2.50	1966
Procentral gurus	19	L D	-22	-49	ے 1 د	4.00	10,000
Superior periotal	0/4/3/2	Л	32	-3	51	4.99	10,002
Superior parietal	/	ĸ	20	-43	20	4.42	3890
Middle essisitel munue	39/37	K D	45	-03	30	3.38	7243
Middle occipital gyrus	37/39/22	ĸ	45	-53	-1	3.97	2620
	19/39	L	-45	-/1	13	3.89	3676
Conjunction (true and false	recollection)						
	22/10	М	4	50	7	4 70	2050
ACC	52/10	IVI	-4	59	-7	4.70	2020
Aptorior DUC	20/26/24	т	22	0	22	262	2057
AIICHIUI PAG	20/00/04	L D	-22	0	-52	2.02	2037
Drocontrol gurss	34/2ð 4/2/2/C	К D	15	0	-20	5.01 4 FF	1213
Frecentral gyrus	4/3/2/0 7	K D	52	-3	51	4.33 2 / 1	938/
Superior parietal	/	ĸ	30	-46	6/	3.51 2.77	1213
Occupitotemporal cortex	3/ 10	ĸ	3/	-50	-1	3.//	1582
Superior occipital cortex	19	L	-33	-70	34	3.92	1002

The table reports areas distinctly activated for true recollection (Remember Hits>Know Hits) and false recollection (Remember FAs>Know FAs) and areas that are common to both true and false recollection.

DLPFC = Dorsolateral Prefrontal Cortex; ACC = Anterior Cingulate Cortex; VLPFC = Ventrolateral Prefrontal Cortex; MTL = Medial Temporal Lobe; PHG = Parahippocampal Gyrus; BA = Brodmann's Area; H = Hemisphere; t = statistical t value; T&T = Talairach and Tournix coordinates.

right inferior and superior temporal gyrus and right middle occipital gyrus. A similar pattern was observed when using the right anterior PHG as a seed — with greater connectivity between the right anterior PHG and the ACC, orbitofrontal cortex, bilateral hippocampus/anterior PHG, and left occipital cortex. In contrast, false recollection exhibited greater connectivity with several superior regions including right middle frontal gyrus, bilateral precental gyrus, super parietal and precuneus (left PHG seed) and right precentral gyrus, bilateral postcentral gyrus, right superior frontal gyrus, medial frontal gyrus, posterior cingulate, and right parietal cortex (right PHG seed) (see Fig. 3).



Fig. 2. Accuracy-independent recollection activity. Brain regions exhibiting common activity for True and False Recollection including the anterior cingulate cortex (ACC), right superior parietal cortex, and bilateral parahippocampal gyrus (PHG). Bar graphs display parameter estimates for 'remember' and 'know' hits as well as 'remember' and 'know' related false alarms (RFA) extracted for peak voxels within activated regions. See Table 1 for coordinates of peak activation. (R: right; L: left).

Table 4 reports results associated with accuracy-related differences in recollection: i.e., true>false and false>true remembering. Compared to false remembering, true remembering exhibited significantly greater activity in right hippocampus, right primary occipital cortex (BA 18), and the cerebellum (see Fig. 4). No region exhibited significantly greater activity for false compared to true remembering.

# Discussion

Using the Remember-Know-New paradigm, the current study investigated the neural correlates mediating true and false recollection. By isolating phantom recollection, the results yielded several novel findings. First, consistent with previous studies, true recollection was shown to activate a wide-spread network of regions traditionally associated with recollection-based retrieval, including left hippocampus and posterior PHG, bilateral anterior PHG, ACC, left ventrolateral PFC, parietal cortex, as well as both early and late visual cortex. False recollection activated a relatively similar network including left hippocampus and posterior PHG, bilateral anterior PHG, ACC, parietal cortex and late visual cortex. A conjunction analysis examined the overlap of these two processes and revealed common recollectionrelated activity in only bilateral anterior PHG, ACC, late visual cortex and superior parietal cortex. Despite this overlap, both MTL-based functional connectivity analyses and direct comparison between true and false remembering revealed dissociations in the neural correlates mediating each type of recollection. Specifically, functional connectivity analysis revealed greater connectivity with the MTL for true compared to false recollection with several ventral regions whereas false recollection was associated with greater MTL connectivity with more dorsal regions. Finally, when activation associated with the two remember responses were compared directly, true recollection was found to elicit significantly greater activation in right hippocampus and early visual cortex, while no region exhibited greater recollection-related activation for false memories. Each finding is discussed in depth, below.

# True and false recollection

Like previous studies of episodic memory, true recollection was found to be mediated by a large network of brain regions including dorsolateral and ventrolateral PFC, the ACC, bilateral hippocampus and PHG, inferior temporal gyrus, precuneus, right parietal cortex and primary and middle occipital cortex. These results support previous studies examining true recollection of semantic and perceptual stimuli (e.g., Henson et al., 1999a; Wheeler and Buckner, 2004; Woodruff et al., 2005; Yonelinas et al., 2005). Specifically, activation in the prefrontal cortex and the ACC has been shown to mediate retrieval of details critical to the process of recollection (Badre et al., 2005; Rugg et al., 1999) as well as post-retrieval monitoring processes associated with the evaluation of specific recollected details (Johnson et al., 1997; Mitchell et al., 2004; Rugg et al., 1999). Activity in regions sensitive to the encoding task, such as occipital cortex, have been associated with increased sensory reactivation and episodic reinstatement of the stimuli representations that were present during encoding (Kahn et al., 2004; Slotnick and Schacter, 2004; Woodruff et al., 2005). Finally, the hippocampus has been shown to be critical to the retrieval of item-specific details that form the basis of recollection as well as the recombination of multiple memories traces (Diana et al., 2007; Eldridge et al., 2000; Yonelinas et al., 2005). Taken together, results suggest that true recollection in the current study was mediated

# Table 3

Accuracy-related differences in MTL connectivity.

	BA	Н	Coordinates (T&T)			t	mm <sup>3</sup>
			x	у	Ζ		
True>false connectivity							
Right MTL seed							
Orbitofrontal cortex/ACC MTL	11	R	11	43	-18	4.1	3797
Hippocampus/anterior PHG	-	R	23	-1	-13	2.59	1212
	-	L	-15	-4	-13	3.54	1582
Occipital cortex	18	L	-23	-85	-12	3.78	4219
Cerebellum	-	М	0	-63	-3	3.26	1898
Left MTL seed							
ACC/Orbitofrontal cortex	25/11	Μ	4	25	-17	5.21	6802
Temporal pole	38	L	-30	6	-23	4.08	5801
MTL							
Hippocampus	-	L	-23	-23	-12	3.54	1898
Anterior PHG	28/34/36	R	19	$^{-1}$	-22	3.34	1107
	28/36	L	-23	-27	-15	2.98	1318
Inferior temporal/	20/37	R	64	-41	-14	3.14	5853
fusiform gyrus							
Superior temporal gyrus	22	R	64	-43	16	2.81	2742
Superior/middle	19/39	R	45	-72	28	3.52	2215
occipital gyrus							
Cerebellum	-	L	-45	-46	-36	3.65	5854
False>true connectivity							
Right MTL seed							
Medial frontal gyrus	10	М	-8	63	-3	2.69	2003
Superior frontal gyrus	6	R	15	-4	63	4.83	3797
Precentral gyrus	4	R	34	-23	50	3.14	2373
Post central gyrus	4/3/2/1	L	-64	-13	32	3.72	5748
	4/3/1	R	30	-23	50	3.56	3006
Posterior cingulate	31	Μ	8	-35	40	4.96	4746
Inferior parietal	40	R	56	-46	41	4.15	3586
Left MTL seed							
Middle frontal gyrus	8/9	R	23	24	34	2.86	1688
Precentral gyrus	4/6	L	-41	-9	46	3.33	7805
	4/6	R	34	-12	53	4.12	5221
Medial/superior frontal gyrus	6	L	-11	7	59	3.16	2426
Superior parietal/precuneus	5/7	R	11	-49	58	2.7	3059
Precuneus	7	L	-19	-67	56	2.76	4219
Cerebellum	-	L	-26	-57	-42	3.36	2689

The table reports right and left anterior MTL connectivity during recollection using seed voxels selected from true and false recollection conjunction L=(-22, 0, -32); R=(15, 0, -20).

MTL = Medial Temporal Lobe; PHG = Parahippocampal Gyrus; ACC = Anterior Cingulate Cortex; BA = Brodmann's Area; H = Hemisphere; t = statistical t value; T&T = Talairach and Tournix coordinates.

by the recapitulation, evaluation, and reconstruction of item-specific details of the encoding event.

Like true recollection, false recollection was found to be mediated by neural activity in the ACC, bilateral hippocampus and PHG, inferior temporal gyrus, right parietal cortex, and middle occipital cortex. While previous neuroimaging studies have examined false retrieval of semantic (e.g., Abe et al., 2008; Cabeza et al., 2001; Kim and Cabeza, 2007; Schacter et al., 1997) and perceptual stimuli (e.g., Okado and Stark, 2003; Slotnick and Schacter, 2004; Stark et al., 2010), none have isolated neural activity associated with false recollection (opposed to general familiarity processes). As such, previous studies have theorized that neural activity associated with false retrieval represents above threshold (or high levels of) familiarity processing. Having controlled for familiarity-based responding in the current analysis, the results challenge this interpretation.

Previous behavioral work has shown that memory retrieval is not an exact replay of prior experiences, but a constructive process, including the retrieval and combining of elements from past experiences (Roediger and McDermott, 1995; Schacter et al., 1998). On occasion, these processes are susceptible to error and distortions that lead us to endorse an event as 'old' when it is not (Schacter and Dodson, 2001; Schacter and Slotnick, 2004). Support for the reconstruction view of false memories comes from behavioral research examining semantic false memories and conjunction errors. For example, in the Deese-Roediger-McDermott (DRM) paradigm, intrusion of false memories associated with the recall of semantic associates are often found to occur at the ends of output sequences (i.e., the last responses made during free recall responding) (e.g., Brainerd, Reyna, Harnishfeger, and Howe, 1993; Payne et al., 1996; Roediger and McDermott, 1995). Accordingly, researchers conclude that these intrusions occur as a result of faulty reconstructions where individuals attribute properties and details associated with the retrieval of true memories to newly formed false memories. Also known as content borrowing (Lampinen et al., 2005), such faulty reconstruction produces detail-rich false memories by erroneously attributing aspects of one memory (such as the thoughts, emotions, perceptual and/or conceptual details associated with the previous memory) to another stimulus/memory such that the details are true but incorrectly bound. A similar type of faulty reconstruction occurs in the realm of conjunction errors where priorexperienced details are retrieved from memory, but erroneously recombined during retrieval to produce incorrect memories (Odegard and Lampinen, 2004; Reinitz et al., 1992).

Extending the theory of content borrowing to the current study, we propose that the observed neural mechanisms mediating phantom recollection are akin to the reconstructive processes underlying true recollection, but the basis for these outputs are retrieved details erroneously re-combined and attributed to related lure(s). This theory not only accounts for activation in recollection-related regions involved in evaluation and monitoring (i.e., ACC) and confidence judgments (i.e., parietal cortex), but also for the presence of PHG and specifically hippocampus activation during phantom recollection (regions involved in the retrieval and reconstruction of episodic details). Visual activation associated with false recollection was confined to regions in late visual cortex, which have previously been associated with conscious, but not veridical retrieval of memories (Slotnick and Schacter, 2004). This combined with the lack of early visual activation (seen in true recollection) is also consistent with the notion that the related lures did not reactivate fundamental sensory or perceptual traces associated with studied items (Slotnick and Schacter, 2004, 2006). Thus, the current results support the theory that details used in assessing related lures as 'remembered' were most likely those reconstructed from true events and not recapitulated with the presentation of the related lure image.

## Accuracy-independent recollection processes

In addition to examining the neural correlates of true and false recollection separately, we used a conjunction analysis to assess neural regions that exhibited common activation across both forms of recollection. Similar to the foregoing results, the conjunction analysis revealed common recollection-related activity in the ACC, anterior MTL, right parietal cortex and late visual cortex (see Fig. 2). Overlap of activity in these regions supports previous studies that have also identified these regions as participating in not only true recollection (e.g., Henson et al., 1999a,b; Rugg et al., 1999; Wheeler and Buckner, 2004; Woodruff et al., 2005; Yonelinas et al., 2005), but also both true and false retrieval (Cabeza et al., 2001; Kahn et al., 2004; Okado and Stark, 2003; Slotnick and Schacter, 2004). However, as noted previously, prior false memory studies have not examined phantom recollection and thus not measured common recollection-related activations. As such, the predominant interpretation of common activation has been in support of above threshold familiarity processing (e.g., Kahn et al., 2004). As noted above, the current results both contrast and extend these previous findings by showing that the ACC, anterior MTL, right parietal cortex and late visual cortex are also involved in processes supporting accuracy-independent



**Fig. 3.** Accuracy-specific connectivity. Accuracy-related differences in functional connectivity associated with common recollection-related activity in bilateral anterior PHG. (A) Functional connectivity to left MTL seed (Table 1: -22x, 0y, -32z). (B) Functional connectivity to right MTL seed (Table 1: 15x, 0y, -20z). See Table 2 for a description of clusters. (R: right; L: left).

recollection-related retrieval and not necessarily true recollection or above-criterion familiarity.

Of particular interest is the location of the accuracy-independent recollection activity within the MTL. Whereas recollection-related activity for true and false memories was found throughout the MTL, common overlap in recollection activity was confined to the anterior PHG. While previous studies have found that recollection-related activity is often associated with hippocampus and more posterior regions within the PHG, anterior MTL regions are often associated with familiarity-related processing (for a review see Diana et al., 2007). Thus, it is possible that this activity reflects above-threshold familiarity processing (e.g., Kahn et al., 2004) supporting both true and false recollection. This idea fits with evidence that recollection and familiarity are dissociable but not mutually exclusive (Yonelinas and Jacoby, 1995). Another possibility regarding the role of the anterior MTL in both true and false recollection is again one of reconstruction associated with content borrowing. Interestingly, anterior MTL activity has been observed for both the successful, yet flexible retrieval of associations in memory (Giovanello et al., 2004, 2009b) and imagining future events by recombining elements of prior experiences (Schacter and Addis, 2009). With regard to relational memory processing, Giovanello et al. (2009b) showed a dissociation along the axis of the hippocampus such that anterior hippocampus was associated with the flexible retrieval of previously bound details and the posterior hippocampus with the exact reinstatement of previous associations.

Table 4	
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Accuracy-related difference in recollection.

	BA	Н	Coordinates (T&T)			t	mm <sup>3</sup>
			x	у	Z		
True>false recollection							
Hippocampus	-	R	30	-18	-16	6.16	2162
Occipital cortex	18	R	26	-89	4	3.30	2953
Cerebellum	-	Μ	-4	-58	-29	4.28	1740
	-	R	19	-84	-25	3.44	1793
False>true recollection							
No significant areas of activation							

The table reports areas associated with the contrast Remember Hit>Remember False Alarm and the reverse contrast.

BA = Brodmann's Area; H = Hemisphere; t = statistical t value; T&T = Talairach and Tournix coordinates.

Consistent with the idea that the anterior MTL represents the flexible recombination of details during retrieval, Schacter and Addis (2009) found the anterior MTL to be active when individuals were instructed to recombine details of past experiences in the formation of a new future 'memory'. Based upon these previous findings, the activation in anterior MTL may represent neural activity associated with the retrieval of details from the encoding events, which in some cases (true recollection) are combined and associated with an actual past event and, in other cases (false recollection), combined to create a memory for an event that never occurred. This interpretation supports both the reconstruction theory of memory, its application to true and false retrieval, as well as behavioral theories of false memories that posit phantom recollection is mediated by the erroneous recombination of prior study details (Lampinen et al., 2005; Reinitz et al., 1992).

## Connectivity analysis

In order to further explore the role of the anterior MTL as it relates to true and false recollection, we assessed whole brain functional connectivity separately for the commonly activated MTL region for each type of recollection-based responding. Results indicate that, for true greater than false recollection, the anterior PHG showed significantly greater functional connectivity with inferior regions including bilateral hippocampus and anterior PHG, the ACC, orbitofrontal cortex, and occipital cortex. In contrast, false recollection showed greater functional connectivity with superior regions including bilateral preand post-central gyrus, superior PFC, and bilateral parietal cortex (see Fig. 3).

The inferior–superior dissociation supports a distinction between bottom–up and top–down control processes. Compared to false recollection, true recollection was associated with greater connectivity to several ventral regions including those associated with perceptual processing and sensory recapitulation (e.g., occipital cortex) (e.g., Allison et al., 1994; Prince et al., 2009; Puce et al., 1996; Vaidya et al., 2002), as well as memory-related regions within the bilateral hippocampus and PHG and decision–making regions within the ACC. Results suggests that, for true recollection, the anterior PHG may be involved in coordinating input from visual cortex and assessing the validity of this sensory recapitulation when determining oldness. False recollection, on the other hand, was associated with greater



Fig. 4. Accuracy-specific recollection activity. Regions showing greater activation for true compared to false remembering (primary visual cortex and hippocampus). Bar graphs display parameter estimates for true and false recollection extracted for peak voxels within activated regions. (R: right).

functional connectivity with dorsal regions, including those associated with top-down attentional components of retrieval and monitoring processes (e.g., parietal and PFC) (e.g., Cabeza, 2008; Corbetta et al., 1993; Henson et al., 1999b; Wagner et al., 2005). The results suggest that while true recollection is driven by relatively automatic processing of sensory signals, false recollection develops through a more controlled or directed cognitive process. This dichotomy is not incompatible with the reconstruction theory of memory proposed above, but merely suggests that the inputs to the anterior MTL, forming the basis of the reconstruction, may differ with respect to the type of recollection in which one is engaged. Specifically, while true recollection involves recombining veridical details invoked by the (re)presentation of the encoding episode, false recollection involves recombining details associated with potentially several different previously encountered episodes. Thus, in the absence of a raw sensory signal, phantom recollection may require greater directed attention and visuospatial processing in order to draw together previously experienced details in making a 'remember' decision.

This dichotomy is also supported by previous evidence that has shown the MTL to exhibit a similar ventral–dorsal dissociation in hippocampal-based functional connectivity between young and older adults in association with successful memory performance in each group. Specifically Grady et al. (2003) observed that young adults utilized a more ventral network, whereas older adults exhibited greater dorsal connectivity with the MTL. While this difference in connectivity between groups was associated with successful memory performance in each group, the authors concluded that the difference in connectivity reflected a similar difference in cognitive strategies to that proposed above: that ventral connectivity reflected a cognitive strategy utilizing perceptually-based processing in young adults and dorsal connectivity reflected a cognitive strategy utilizing visuospatial attentional processing in older adults. Given that false recollections are not associated with sensory reactivation, this activation may represent retrieval processing similar to that observed in older adults, who consistently show deficits in using item-specific information for memory processes (e.g., Daselaar et al., 2006b; Dennis et al., 2007; Duarte et al., 2010; Gutchess et al., 2005). The notion that false memories arise from higher-order or top-down attentional focus is consistent with this earlier work.

# Accuracy-specific recollection

Direct comparisons between true and false remembering also revealed significant accuracy-related differences in recollection activity. Specifically, the right hippocampus proper and right primary visual cortex exhibited significantly greater activation for true compared to false remembering (see Fig. 4). As noted previously, early visual cortex has been associated with recapitulation of a sensory signature (Buckner and Wheeler, 2001; Rugg and Wilding, 2000). Moreover, when present, this recapitulation in early visual cortex has only been observed for true, but not false perceptual retrieval (Slotnick and Schacter, 2004, 2006). As such, the current results support earlier findings that interpreted this activation difference as reflecting nonconscious memory processing (likely priming) of "old" items (Kim and Cabeza, 2007; Slotnick and Schacter, 2004, 2006). Moreover, the results expand upon previous work by showing that early visual cortex can specifically dissociate true and false *recollection*.

The hippocampus also showed this dissociation between true and false recollection. As noted, the hippocampus mediates recollection and the retrieval of item-specific details associated with prior encoding events (e.g., Daselaar et al., 2006a; Diana et al., 2007; Wheeler and Buckner, 2004). Prior false memory studies have disagreed regarding

the role of the hippocampus in supporting false memories and in whether the MTL distinguishes between the two types of retrieval processes (Dennis et al., 2008b; Giovanello et al., 2009a; Kensinger and Schacter, 2005; Kim and Cabeza, 2007; Paz-Alonso et al., 2008; von Zerssen et al., 2001). While the false recollection analysis presented above clearly indicates a role of the hippocampus in mediating phantom recollection, the direct contrast between true and false remembering further indicates that the hippocampus can also dissociate between the two types of recollection.

Studies that have failed to find MTL differences in true and false recognition have suggested that the null finding may stem from the fact that both processes are associated with reconstructive retrieval; and given its role in integrating information, MTL activity associated with faulty or misattributed memories may be indistinguishable from that supporting true memories (Okado and Stark, 2003). The current results argue against such a theory, showing that when neural processes supporting veridical and phantom recollection can be directly compared, the hippocampus is able to dissociate between the two forms of retrieval. This evidence supports previous work suggesting that regions within the MTL distinguish true memories independent of conscious awareness (Daselaar et al., 2006a).

No brain region exhibited more neural activity for false compared to true remembering. With the current results showing that true and false recollection are mediated by a large overlapping network, this finding suggests that false recollection is not associated with a distinct neural network, but is largely mediated by the same reconstructive processes that support true recollection. While the absence of regions exhibiting greater false activity has been observed previously (Giovanello et al., 2009a) a handful of studies have identified regions associated with increased activity for false compared to true memories (including left and right PFC, right precentral gyrus, left precuneus, bilateral parietal cortex, middle temporal gyrus, and ACC) (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kensinger and Schacter, 2005; Kim and Cabeza, 2007; Slotnick and Schacter, 2004). While differences between the current study and these previous findings may reflect familiarity-related differences in retrieval or differences that arise due to collapsing across retrieval responses, future work is necessary to fully investigate this possibility. However, it is noteworthy that regions associated with greater MTL connectivity for false recollection in the current study overlap with regions identified as more active for false memories in previous studies. As previously suggested, it may be the case that these regions are part of a network exercising topdown strategic control of retrieval processes in the absence of perceptual details (Grady et al., 2003). While we failed to identify increased false recollection activity in these regions in our direct contrasts, their presence in the connectivity analysis suggests that they are associated with false recollection, but may have been below threshold in the current analysis.

#### Conclusions

The current study sought to isolate the neural correlates of phantom recollection and examine both similarities and dissociations between true and phantom recollection. In doing so, the study overcame several methodological issues inherent in previous false memory studies by extracting recollection-related activity separate from familiarity processing. As such, this is the first study to identify neural correlates mediating phantom recollection and examine differences between true and phantom recollection using both direct contrasts and functional connectivity analyses. Results showed that both true and phantom recollection were mediated by a largely overlapping network, previously shown to support true recollection and memory-related reconstruction processes. Finding common activity associated with true and phantom recollection supports the theory that false retrieval can be based on erroneously triggered recollection processes (Kahn et al., 2004) and that recollection-related processing may occur

independent of the veridicality of the memory. Moreover, while accuracy-independent recollection activity was observed in the anterior PHG, connectivity analyses suggested that this region may be involved in utilizing differential inputs when assessing true compared to phantom recollection. Specifically, results suggested that true recollection may be driven by bottom-up information integrated from sensory input and item retrieval whereas false recollection may be driven by top-down attention control processes. Further dissociating the two types of recollection, direct comparisons found both primary visual cortex and the hippocampus showed significantly greater recollection-related activity for true compared to false remembering. Results suggest that despite the 'retrieval' of item-specific details associated with false memories, regions associated with recapitulation of the original sensory stimulus (early visual cortex) are able to dissociate between true and falsely recollected details. Results further clarify the role of the MTL with regard to its support of true and phantom recollection, showing that while phantom recollection is mediated by MTL-based reconstruction processes, the hippocampus proper is able to dissociate between true and phantom recollection.

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