What's the gist? The influence of schemas on the neural correlates underlying true and false memories

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A R T I C L E   I N F O

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A B S T R A C T

The current study used a novel scene paradigm to investigate the role of encoding schemas on memory. Specifically, the study examined the influence of a strong encoding schema on retrieval of both schematic and non-schematic information, as well as false memories for information associated with the schema. Additionally, the separate roles of recollection and familiarity in both veridical and false memory retrieval were examined. The study identified several novel results. First, while many common neural regions mediated both schematic and non-schematic retrieval success, schematic recollection exhibited greater activation in visual cortex and hippocampus, regions commonly shown to mediate detailed retrieval. More effortful cognitive control regions in the prefrontal and parietal cortices, on the other hand, supported non-schematic recollection, while lateral temporal cortices supported familiarity-based retrieval of non-schematic items. Second, both true and false recollection, as well as familiarity, were mediated by activity in left middle temporal gyrus, a region associated with semantic processing and retrieval of schematic gist. Moreover, activity in this region was greater for both false recollection and false familiarity, suggesting a greater reliance on lateral temporal cortices for retrieval of illusory memories, irrespective of memory strength. Consistent with previous false memory studies, visual cortex showed increased activity for true compared to false recollection, suggesting that visual cortices are critical for distinguishing between previously viewed targets and related lures at retrieval. Additionally, the absence of common visual activity between true and false retrieval suggests that, unlike previous studies utilizing visual stimuli, when false memories are predicated on schematic gist and not perceptual overlap, there is little reliance on visual processes during false memory retrieval. Finally, the medial temporal lobe exhibited an interesting dissociation, showing greater activity for true compared to false recollection, as well as for false compared to true familiarity. These results provided an indication as to how different types of items are retrieved when studied within a highly schematic context. Results both replicate and extend previous true and false memory findings, supporting the Fuzzy Trace Theory.

1. Introduction

Schemas are useful memory tools that allow information to be categorized according to a common concept or theme. In fact, schematic gist or the fundamental content about a scene can be extracted in less than 100 ms (Loftus and Mackworth, 1978; Potter, 1976; Torralba et al., 2006). With respect to memory, schematic gist has been shown to guide attention during scene processing and to facilitate memory for schema-consistent information versus schema-unrelated information (Brewer and Treyens, 1981; Hess and Slaughter, 1990; Miller and Gazzaniga, 1998). Despite this processing benefit, similar research has shown that schemas also contribute to false memories as individuals incorrectly identify new, but related, information as 'old'. This research has found high rates of false alarms for lures that include schema-

consistent information (Lampinen et al., 2001; Miller and Gazzaniga, 1998; Neuschatz et al., 2002; Pezdek et al., 1989), suggesting that schemas may also have a negative influence on verbatim memory. While behavioral and neuroimaging studies have investigated the influence of both semantic and perceptual gist on accurate and illusory memories (for review see Dennis et al. (2015); for meta-analysis see Kurkela and Dennis (2016)), it is unclear the extent to which highly schematic scenes elicit similar gist and how this gist supports schema memory, distinct from non-schema memory, nor is it clear the role that schemas play in supporting false distinct from true schematic memory. In addition, different memory processes, such as recollection and familiarity, have been shown to distinctly influence memory retrieval (see Yonelinas (2002) for review). Thus, an understanding of schema's influence on memory should also take into account both recollection

and familiarity. To investigate these questions, the current study aimed to: 1) identify the neural correlates of successful memory retrieval of both schematic and non-schematic items when studied within a highly schematic context, 2) investigate differences in retrieval processes between veridical and illusory memory stemming from schematic encoding, and 3) within each type of retrieval, examine the separate roles of recollection and familiarity. To do this, we utilized a novel scene paradigm extended from work from Brewer and Treyens (1981) and Miller and Gazzaniga (1998) in which memory was tested for targets and lures that are conceptually related or unrelated to a schematic scene.

Previous behavioral research has noted the benefits of schemas in facilitating both scene and object recognition. For example, Oliva and Torralba (2001) suggested that the global meaning (i.e., gist) of a scene can be extracted even in the absence of object shape or identity. It has also been shown that memory performance is influenced by the conceptual gist of a scene, leading to schema based expectations (Bower et al., 1979; Brewer and Treyens, 1981; Hannigan and Reinitz, 2003; Lampinen et al., 2001; Lampinen et al., 2000; Miller and Gazzaniga, 1998; Neuschatz et al., 2002; Pezdek et al., 1989). For example, in one of the original studies investigating the influence of scene gist on memory, Brewer and Treyens (1981) examined participants' memory for items within a schematic context (a graduate student office). Specifically, encoding items included those that were consistent with the schema (e.g., typewriter; hereafter referred to as *schematic* items), as well as items that would be unusual to find in that context (e.g., picnic basket; hereafter referred to as *schema-inconsistent* items) and items that were not specific to the schema, yet were not out of place or unusual (e.g., rug; hereafter referred to as *non-schematic* items). Researchers found that participants remembered more schematic items than schema-inconsistent or non-schematic items. Moreover, schema expectancy also contributed to false memories, wherein participants falsely remembered more non-presented schematic objects (e.g., books) than schema-inconsistent or non-schematic objects. Later studies have replicated and extended these initial findings, showing that the rate of false alarms is near equal to the hit rate for schematic objects (Lampinen et al., 2001; Miller and Gazzaniga, 1998; Pezdek et al., 1989).

While much of the previous research has compared schematic retrieval to retrieval of schema-inconsistent information (e.g., octopus on a farm; Brewer and Treyens, 1981; Loftus and Mackworth, 1978; Miller and Gazzaniga, 1998; Palmer, 1975), it is typically unrealistic to encounter anomalies such as these in everyday life. Rather, one is likely to encounter non-schematic items embedded within schematic scenes, such as a rug in the kitchen or a flowerpot on a farm. Neuroimaging research examining such comparisons is less common in the literature. Those that have find that retrieval of strongly-related (i.e., schematic) objects compared to weakly-related (i.e., non-schematic) objects is supported by activity in parahippocampal and retrosplenial complex (Bar and Aminoff, 2003; Bar et al., 2008), reflecting processing and evaluation of associations. In addition, results from encoding suggest a role of the medial PFC in reflecting the strength of relatedness between encoded items (van Kesteren et al., 2013); however results have been mixed at retrieval (e.g., van Buuren et al., 2014; van Kesteren et al., 2010b). With respect to schematic representations, prior work with semantic dementia and language processing has suggested that this strength in semantic relatedness, and in turn semantic and conceptual gist, is associated with activity in lateral temporal cortices, specifically the middle and superior temporal gyri (Noppeney et al., 2007; Price, 2000; see Saumier and Chertkow (2002) for review; Simons et al., 2005; Wise and Price, 2006). Thus, in line with this past work, we expect that retrieval of schematic (compared to non-schematic) true memories should be reliant on associative processing in the medial temporal lobe (MTL) and retrieval of conceptual gist, mediated by the lateral temporal cortices. Additionally, because the role of mPFC in mediating schematic compared to non-schematic retrieval is less clear,

any identified results will help further ascertain the function of this region at retrieval.

Compared to schematic true memory, successful memory for non-schematic items, which are only loosely associated with the schema, may not be afforded this same schematic processing advantage, as suggested by reduced retrieval rates observed in prior studies (see Alba and Hasher (1983) for review; e.g., Brewer and Treyens, 1981). Previous research has suggested that reduced memory for non-schematic items reflects both a deficiency in schema support and reduced attention to non-schematic items during encoding (Brewer and Treyens, 1981; Loftus and Mackworth, 1978; Owens et al., 1979; but see Pezdek et al. (1989) in relation to attention for schema-inconsistent items). As a result of reduced attention and weaker encoding, non-schematic retrieval is likely to be associated with more effortful retrieval and monitoring, mediated by activity in the anterior cingulate and parietal cortices (Cabeza et al., 2008; Ciaramelli et al., 2008; Fleck et al., 2006; Wheeler and Buckner, 2004). Furthermore, due to the small number of studies that have compared schematic to non-schematic memory, it was unclear whether the foregoing predictions would be observed in both recollection- and familiarity-based retrieval, or whether memory strength would have differential influences on the neural differences between trial types. Thus, it is important to explore both commonalities and differences in neural recruitment during successful retrieval of schematic and non-schematic items within the context of both recollection and familiarity.

As noted above, while schema processing and schematic gist may serve as useful mechanisms for supporting true memories, they have also been shown to lead to high rates of false memories for schematically-related lures (Aminoff et al., 2008; Intraub et al., 1996; Lampinen et al., 2001; Miller and Gazzaniga, 1998; Neuschatz et al., 2002; Roediger and Mcdermott, 1995a). Though examined behaviorally using scenes (e.g., Brewer and Treyens, 1981; Miller and Gazzaniga, 1998), it is unclear what specific cognitive and neural mechanisms support the retrieval of schematic false memories. Previous studies examining the neural basis of false retrieval have focused on either semantic false memories or perceptual false memories. Such studies have found substantial overlap in the neural mechanism supporting both true and false memories, including activity throughout the core retrieval network, including bilateral frontal and parietal regions (see Dennis et al. (2015); Kurkela and Dennis (2016) for reviews), bilateral caudate and insula (e.g., Cabeza et al., 2001; Garoff-Eaton, et al., 2006; Slotnick and Schacter, 2004), lateral temporal cortex (e.g., von Zerssen et al., 2001), occipital cortex (Cabeza et al., 2001; Dennis et al., 2014; Garoff-Eaton et al., 2006; Schacter et al., 1996; Stark et al., 2010) and hippocampus/parahippocampal gyrus (PHG) (Dennis et al., 2012; Garoff-Eaton et al., 2006; Iidaka et al., 2012; Schacter et al., 1997; Slotnick and Schacter, 2004; Stark et al., 2010; von Zerssen et al., 2001). While much of this activation has been attributed to engagement of similar reconstructive processes (Cabeza et al., 2001; Dennis et al., 2012; Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012; Kahn et al., 2004; Schacter et al., 1997, 1996; Slotnick and Schacter, 2004; von Zerssen et al., 2001), as well as retrieval-related evaluation and monitoring processes (Garoff-Eaton et al., 2006; Stark et al., 2010), basic stimulus-driven processes are also believed to account for the large amount of common neural activity.

For example, in perceptual relatedness paradigms, targets and lures share similar perceptual attributes, such as shape, color and/or size. This, in turn, is believed to result in similar perceptual processing in late visual cortices (BA 19 & 37) between targets and related lures (e.g., Atkins and Reuter-Lorenz, 2011), reflecting the conscious experience of memory, which is independent of true "oldness" (Dennis et al., 2012; Slotnick and Schacter, 2004). It is also thought to be indicative of successful retrieval of the general properties of originally studied items (e.g., shape, color; Slotnick and Schacter, 2004) or those involving the semantic label or general category (e.g., fruit, bird) to

which the item belongs. However, what is unique about the scene paradigm is that, unlike other visual false memory studies, the critical lures are not items perceptually related to that which was presented previously, but rather conceptually related to encoding items. For example, 'tractor' is schematically related to 'farm' and objects within a farm scene such as 'barn' and 'pig', but shares little perceptual similarity with these objects.

Therefore, it follows that schematic false memories, like those in the scene paradigm, arise not from activity in visual processing regions associated with perceptual overlap between lures and encoding information (Dennis et al., 2012; Goldmann et al., 2003; Gutchess and Schacter, 2012; Slotnick and Schacter, 2004), but from a shared conceptual or semantic gist between the encoding schema and the lures. In line with the influence of such semantic processing on memory retrieval, previous studies have highlighted the role of the lateral temporal cortices in mediating both true (as noted above) and illusory memories. Specifically, engagement of left lateral temporal cortex has been associated with semantic processing and retrieval of semantic gist across both true and false memory studies (Cabeza et al., 2001; Dennis et al., 2012, 2008b; Garoff-Eaton et al., 2007; Gutchess and Schacter, 2012; Kim and Cabeza, 2007b; Kubota et al., 2006). With respect to schematic true and false memory, given the schematic salience invoked in the scene paradigm, we hypothesize that both types of memory will be highly reliant on the retrieval of schematic gist. Importantly, given that schematic gist, as operationalized in the current scene paradigm, is inherently built on the semantic associations between items that are congruent with the presented schema at encoding (e.g., 'barn' and 'pig' with respect to 'farm'), we hypothesize that retrieval of both schematic targets and lures will be mediated by activity in bilateral temporal cortices, reflecting gist processing.

As noted above, MTL has also been shown to be a critical region, not just in supporting true, but also false memories (Dennis et al., 2014, 2008b, 2007b; Duarte et al., 2010; Garoff-Eaton et al., 2007; Norman and Schacter, 1997). However, the exact role of the MTL with respect to false memories remains unclear. One issue that may be contributing to this confusion is the fact that different MTL subregions have been shown to contribute differentially to recollection and familiarity in veridical memories (e.g., Daselaar et al., 2006; see Yonelinas (2002) for review), and thus, may also do so with respect to false memories. That is, while a wide breadth of behavioral research has shown that, like true memories, false memories can be retrieved in terms of both (phantom) recollection and familiarity (Brainerd et al., 2001; Lampinen et al., 2001; Mather et al., 1997; see also McCabe et al. (2009)) neuroimaging studies have just begun to investigate this dichotomy (Abe et al., 2013; Dennis et al., 2012; Duarte et al., 2010; Garoff-Eaton et al., 2007; Kim and Cabeza, 2007b; Stark et al., 2010). For example, Kim and Cabeza (2007b) compared high-confidence true recognition with high-confidence false recognition and found that true memory elicited increased activation in bilateral posterior hippocampus and PHG, indicating that high-confidence true recognition is mediated by recollection-related processes, whereas phantom recollection is not. Alternatively, recent work from our lab (Dennis et al., 2012) has shown that, compared to familiarity, both true and false recollection exhibited activity in the anterior hippocampus and PHG; yet true recollection showed greater hippocampal activity indicative of greater recovery of sensory details associated with past events.

Studies that have identified differences in familiarity-based true and false memories have told a slightly different story with respect to MTL activity. Specifically, recent work has suggested that false familiarity elicits greater activation in PHG due to a reliance on source retrieval in light of weak encoding of the item (Abe et al., 2013; Karanian and Slotnick, 2014; see also Kim and Cabeza (2007b)). Given the role of the PHG in source retrieval (Diana et al., 2007; Eichenbaum et al., 2012; Ranganath, 2010; Yonelinas et al., 2001), it has been posited that PHG activity reflects effortful contextual processing associated with attempts to relate the lure

with an encoding context (Karanian and Slotnick, 2014). The schematic encoding component of the current design allows for the examination of this theory of MTL activity and false memories. While a reliance on schematic gist of past presentations can easily lead to phantom recollection of schematic lures, it is also likely to result in high rates of familiarity-based false memories, as the strong schematic gist guides scene reinstatement and retrieval processes. To the extent that the encoding scenes elicit schematic contextual support during retrieval, we hypothesize that the hippocampus will show greater activation for true compared to false recollection and false familiarity will exhibit a greater reliance on the PHG than true familiarity.

To recap, the current study aims to expand upon previous false memory studies by investigating the influence of a schematic framework on memory retrieval utilizing a scene paradigm within the context of fMRI. To this end, we will extend the research on veridical memories to include an investigation of the neural basis of common and distinct mechanisms supporting schematic and non-schematic memories within the context of both recollection and familiarity. We will also extend the research on false memories to include an examination of the neural basis of visual false memories beyond previous work focusing on the role of perceptual relatedness. In addition to the foregoing investigation into veridical memories, we also aim to investigate both common and unique factors underlying true and false memories within the context of a schematic framework across both recollection and familiarity.

2. Materials and methods

2.1. Participants

Twenty-five right-handed native English speakers from the Penn State University community completed this experiment. Participants were screened for history of neurological disorders and psychiatric illness, alcoholism, drug abuse, and/or learning disabilities. One participant was excluded from the analysis due to head motion in excess of 4 mm. Two additional participants were also excluded for poor behavioral performance (greater than 50% miss rate for schematic targets), leaving data from 22 participants reported in all analyses [13 females; mean age=22.91 years (SD=3.01)]. All participants provided written informed consent and received financial compensation for their participation. All experimental procedures were approved by The Pennsylvania State University's Institutional Review Board for the ethical treatment of human participants.

2.2. Stimuli

Stimuli consisted of 26 schematic scenes (e.g., Bathroom, Farm), comprised of objects commonly associated with each schema (schematic targets: e.g., Farm: pig, barn; Bathroom: toilet, tub) as well as items unrelated to the schema (non-schematic targets: e.g., Farm: bush; flower pot; Bathroom: vase; spray bottle) (see Fig. 1). Lures also consisted of both items commonly associated with each schema (schematic lures: e.g., Farm: rooster, tractor; Bathroom: sink, plunger), as well as unrelated lures (e.g., purse, hammer). All backgrounds and images were obtained from an Internet image search. All items included in testing were normed for their association with each scene in a multi-step process. Specifically, all schematic scenes, along with their related schematic items, were verbally identified by both a group of individuals in the lab as well as an independent group of subject pool participants (N=20) in order to verify that each scene represented the intended schema. Furthermore, schematic items were identified as being related to the schema via a simple yes/no identification procedure. Items that were deemed as not related to the schema (i.e., that did not reach 100% consensus) were replaced with an appropriate alternative..
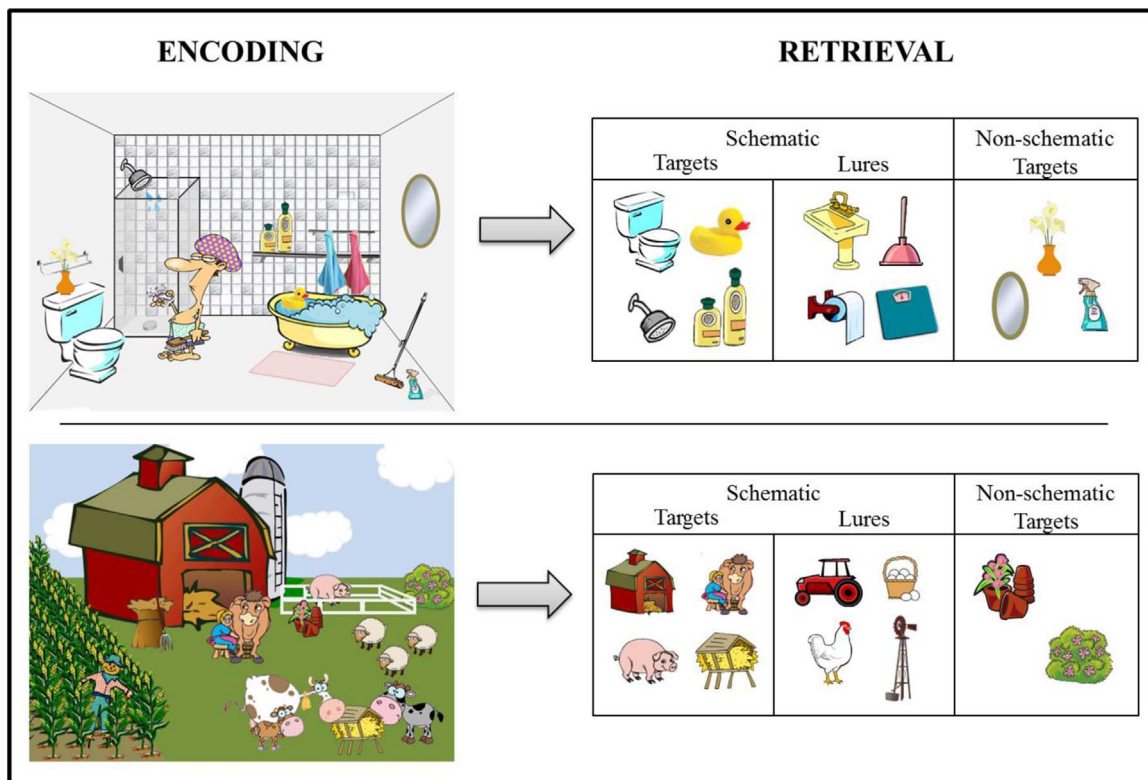
Fig. 1. Task design. During encoding, participants viewed schematic scenes (e.g., Bathroom, Farm). During retrieval, participants made 'Remember', 'Know', or 'New' responses to both schematically-related targets (e.g., toilet, pig) and schematically-related lures (e.g., sink, tractor), as well as non-schematic targets and lures.

Once the schematic targets and lures were finalized, non-schematic targets were then inserted in each scene. Non-schematic targets were defined as those that did not contribute to the schema of either the scene they were inserted into or any other scene in the study, yet still fit appropriately into the scene (i.e., such that at retrieval they did not stand out as schematic or schema-inconsistent to any given scene). Due to the difficulty of determining these non-schematic items, we transitioned to a rating scale. Specifically, non-schematic items were rated on an ordinal scale (1-unrelated to 4- related) by a unique group of subject pool participants (N=19) to ensure that non-schematic items were not schematically related to the scene in which they appeared, or any other scene. This rating process also included a random subsample of the schematic items, so that participants were not biased in their ratings of non-schematic items. As a first step in creating a division with respect to schema relatedness, only non-schematic items that met a rating of below 2.5 across all scenes were included as non-schematic targets. Items that failed to meet this criterion were replaced with appropriate alternatives. With respect to final relatedness ratings, while the subsample of schematic items had a mean relatedness rating of 3.70 (SD=.41; mode=3.89), non-schematic items had a mean rating of 1.48 (SD=.32; mode=1.14). This difference was statistically significant (t(269)=38.24; p < .001). To further investigate this issue, we examined the average ratings corresponding to each recollection and familiarity hit within both schematic and non-schematic items. Similar to the overall schema-relatedness ratings mentioned above, significant differences in relatedness were identified between schematic & non-schematic recollection, as well as familiarity, hits. A list of all items and scenes can be found in Appendix A. Scenes were presented focally and equated for resolution. Twenty-six scenes were presented during encoding in the same order for all participants. Three hundred individual items were presented at retrieval, including (a) 104 related targets (4 from each scene); (b) 62 unrelated targets (2–3 from each scene); (c) 104 related lures (4 associated with each scene); and (d) 30 unrelated lures.

2.3. Task and procedure

Encoding took place outside of the scanner while retrieval occurred in the scanner with approximately 30 min separating the two memory phases. Encoding was intentional; participants were asked to look at each scene and try to remember as much as they could for a later memory task. The 26 encoding scenes were presented for 10 s each across 2 runs, with 13 scenes presented in run one and the remaining 13 scenes presented in run two. During retrieval, all images (items from the scenes and new items) were presented in the center of the screen with three response options (Remember/Know/New) displayed below each image. Images were projected onto a screen that participants viewed through a mirror attached to the head coil. Behavioral responses were recorded with the participant's right hand on a 4-button response box. Images were displayed by COGENT in MATLAB (Mathworks Inc., Natick, MA, USA) and were displayed at a screen resolution of 1024 (H)×768 (V) at 75 Hz. At the viewing distance of 143 cm, the display area was 20° (H)×16° (V). Scanner noise was reduced with headphones, and cushioning was used in the head coil to minimize head motion.

During retrieval, participants completed 6 runs each approximately 7 min in length. Each image was displayed for 3 s while participants made memory responses using the 'Remember/Know/New' paradigm. The images were pseudorandomly sorted, ensuring that no more than 3 images from any one trial type appeared in a row and no 2 images associated with a given scene appeared in a row. In accord with typical Remember/Know/New task instructions, participants were told to respond 'Remember' if they could recollect specific details about the object such as its shape, color, placement in the scene 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.

2.4. Image acquisition

Structural and functional images were acquired using a Siemens 3T scanner equipped with a 12-channel head coil. A T1-weighted sagittal localizer was acquired to locate the anterior (AC) and posterior (PC) commissures. Images were then prescribed parallel to the AC–PC plane. An MPRAGE was acquired with a 1650 ms TR, 2.03 ms TE, 256 mm field of view (FOV), 256^2 matrix, 160 axial slices, and 1.0 mm slice thickness for each participant. Echo-planar functional images were acquired using a descending acquisition, 2500 ms TR, 25 ms TE, 240 mm FOV, a 80^2 matrix, 90° flip angle, 42 axial slices with 3.0 mm slice thickness resulting in 3.0 mm isotropic voxels.

2.5. Image processing

Pre-processing of all functional images was carried out in SPM8 (Wellcome Institute of Cognitive Neurology, London, UK. www.fil.ion.ucl.ac.uk), using MATLAB (Mathworks Inc., Natick, MA, USA). The functional time series were first corrected for differences in slice timing acquisition. EPI images were then realigned to the first image using a 6-parameter rigid body affine transformation. Next, the slice time corrected functional images were spatially normalized to the standard MNI (Montreal Neurological Institute) EPI template implemented in SPM8. To do this, the raw T1 MPRAGE images were co-registered to the mean realigned functional image, and then this co-registered T1MPRAGE image was segmented and registered to the MNI template. Lastly, the parameters from this registration process were applied to the slice time corrected and realigned functional images (3 mm isotropic voxels) to normalize them to the MNI template, with coordinates later converted into Talairach space (Talairach and Tournoux, 1988) for reporting. As a final preprocessing step, all of the normalized functional images were smoothed using a 6 mm full-width-half-maximum Gaussian smoothing kernel.

2.6. fMRI analyses

At the first level, trial-related activity was modeled using the general linear model (GLM) with a stick function corresponding to trial onset convolved with a canonical hemodynamic response function. A second-level random effects GLM was created treating subjects as a random effect. One sample *t*-tests were conducted to investigate contrasts of interest. The current analyses focused on 8 trial types of interest: 1) Schematic Recollection Hits, which were defined as 'Remember' responses to related targets; 2) Schematic Familiarity Hits, which were defined as 'Know' responses to related targets; 3) Schematic Misses, which were defined as 'New' responses to related targets; 4) Schematic Recollection False Alarms (FA), which were defined as 'Remember' responses to related lures; 5) Schematic Familiarity False Alarms, which were defined as 'Know' responses to related lures; 6) Schematic Correct Rejections (CR), which were defined as 'New' responses to related lures; 7) Non-schematic Recollection Hits, which were defined as 'Remember' responses to unrelated targets; 8) Non-schematic Familiarity Hits, which were defined as 'Know' responses to unrelated targets; and 9) Non-schematic Misses, which were defined as 'New' responses to unrelated targets. All other trial types, along with no response trials, were coded with their own regressors (as were movement parameters) and treated as regressors of no interest.

The first goal of the paper was to elucidate the neural mechanisms supporting memory for schematic and non-schematic items within both recollection and familiarity. To examine neural regions that were common to both schematic and non-schematic retrieval success we conducted a conjunction of schematic recollection hits > misses and non-schematic recollection hits > misses. The same analysis was subsequently conducted using familiarity hits. We then directly compared schematic recollection hits with non-schematic recollection hits, as well as schematic familiarity hits with non-schematic familiarity hits using

whole-brain maps to identify regions where successful retrieval processes differed between the two trial types. Unfortunately, a majority of participants did not make enough non-schematic false alarms within recollection or familiarity (< 10 trials) to allow for the investigation of non-schematic false memories. We therefore focused our false memory analyses on only schematic items.

Second, we aimed to elucidate the neural mechanisms supporting schematic false memories. In order to identify neural correlates supporting false recollection, we compared schematic recollection false alarms to schematic correct rejections. Next, a conjunction analysis of true and false recollection (Hit > Miss∩FA > CR) activity was constructed in SPM in order to identify neural activity that was common to both memory processes. In order to identify neural resources that were differentially recruited for each type of recollection response, we directly compared activity supporting recollected hits and recollected false alarms. To examine true and false familiarity, a similar conjunction analysis was conducted using schematic familiarity hits and schematic familiarity false alarms (in comparison to misses and correct rejections). We then again directly compared activity, this time supporting familiarity hits and familiarity false alarms.

In order to identify significant results in our contrasts of interest, we employed Monte Carlo simulations, implemented by 3dClustSim in AFNI version 16.0 (Cox and Hyde, 1997) to determine activation that was corrected for multiple comparisons at $p < .05$. The input to this simulation was the search space [grey matter mask using the Wake Forest University aal pickatlas (Lancaster et al., 2000; Maldjian et al., 2003)], across-subject average intrinsic smoothness in mm obtained from the residual time-series (11.15), and the uncorrected p threshold ($p < .005$). The results revealed a voxel extent of 66 required to correct for multiple comparisons at $p < .05$ at the whole brain level. An additional simulation was run to determine a correction specific to our a priori ROIs of interest, including the superior/middle temporal gyri (STG/MTG) and the MTL (bilateral hippocampus and parahippocampal gyrus). All ROIs were defined by using anatomical masks of each region (bilaterally) within the aal pickatlas toolbox in SPM8.

3. Results

3.1. Behavioral results

A 2×2 repeated measures ANOVA was conducted across all memory responses (combining recollection and familiarity) to examine the effects of stimulus type (target, lure) and relatedness (schematic, non-schematic) on proportion of 'old' responses (see Table 1 for

Table 1
Behavioral results.

	Schematic	Non-Schematic
Collapsed Response Rates		
Hit	.69 (.02)	.54 (.03)
FA	.54 (.03)	.24 (.04)
d′	.42 (.06)	.92 (.08)
Recollection Response Rates		
Hit	.44 (.03)	.25 (.02)
FA	.22 (.02)	.07 (.02)
Familiarity Response Rates		
Hit/Adjusted Hit	.25 (.02) / .45 (.03)	.30 (.04) / .39 (.04)
FA/Adjusted FA	.32 (.02) / .41 (.03)	.18 (.03) / .20 (.04)

The table reports the means and standard errors of the proportion of Collapsed (Recollection/'Remember' and Familiarity/'Know') response rates and for schematic and non-schematic targets (Hits) and lures (False Alarms; FA), as well as d′ values. Both raw and adjusted familiarity responses are reported. Adjusted familiarity hits are calculated as pKnow Hits/(1 - pRemember Hits) and adjusted familiarity FA are calculated as pKnow FA/(1 - pRemember FA).

means). This analysis revealed a significant main effect of stimulus type [$F(1, 21)=155.08$, $p < .001$], with participants making more 'old' responses to targets than to lures. There was also a significant main effect of relatedness, such that participants made more 'old' responses to schematic items than non-schematic items [$F(1, 21)=82.74$, $p < .001$], as well as a significant stimulus type by relatedness interaction [$F(1, 21)=24.35$, $p < .001$]. Follow up t-tests indicated that participants made more hits than false alarms for both schematic [$t(21)=6.49$, $p < .001$] and non-schematic [$t(21)=13.11$, $p < .001$] items. Participants also made more hits and false alarms to schematic targets than non-schematic targets [$t(21)=5.58$, $p < .001$; $t(21)=9.8$, $p < .001$; respectively].

A similar 2×2 ANOVA on recollection responses revealed a significant main effect of stimulus type [$F(1, 21)=92.39$, $p < .001$] and relatedness [$F(1, 21)=120.9$, $p < .001$]. Follow up t-tests indicated that participants made more recollection hits than recollection false alarms for both schematic and non-schematic items [$t(21)=8.45$, $p < .001$; $t(21)=9.3$, $p < .001$; respectively] and participants made significantly more schematic hits and schematic false alarms than non-schematic hits and false alarms [Hit: $t(21)=11.69$, $p < .001$; FA: $t(21)=7.64$, $p < .001$]. Finally, a 2×2 ANOVA on adjusted familiarity rates was conducted. Adjusted familiarity hits were calculated as pKnow Hits/(1 - pRemember Hits) and adjusted familiarity FA were calculated as pKnow FA/(1 - pRemember FA). This calculations takes into account the fact the recollection and familiarity are not mutually exclusive processes (Duarte et al., 2010, 2006; Yonelinas, 2002; Yonelinas and Jacoby, 1995). This ANOVA revealed a significant main effect of stimulus type [$F(1, 21)=47.9$, $p < .001$] and relatedness [$F(1, 21)=60.6$, $p < .001$], as well as a significant interaction [$F(1, 21)=26.9$, $p < .001$]. Follow up t-tests showed that adjusted familiarity hit rates were higher than adjusted familiarity false alarm rates in both schematic and non-schematic conditions [$t(21)=2.38$, $p < .05$; $t(21)=8.14$, $p < .001$; respectively], though much more so in the non-schematic condition. Results also indicated that participants made more adjusted familiarity hits and false alarms for schematic compared to non-schematic targets and lures [$t(21)=2.38$, $p < .05$; $t(21)=9.43$, $p < .001$ respectively]. A breakdown of the behavioral results is shown in Table 1.

3.2. Imaging results

3.2.1. Schematic and non-schematic retrieval success

With respect to true memories, a conjunction of schematic and non-schematic recollection success (Recollection Hit v Miss) revealed activation in regions within bilateral fronto-parietal cortices, bilateral middle temporal cortices, and left inferior frontal gyrus (IFG). A parallel conjunction examining familiarity success revealed activity in a more limited set of regions, including left middle and inferior frontal gyrus, left superior parietal cortex and left middle temporal gyrus (see Table 2; Fig. 2A).

The effect of schema on target recollection revealed greater activation in bilateral occipital cortex and left hippocampus for schematic target recollection, while non-schematic target recollection was supported by dorsal ACC and left supramarginal gyrus.[1] In regards to familiarity, no significant activity was observed for schematic greater than non-schematic target familiarity. The reverse contrast revealed activation only in bilateral middle temporal gyri (see Table 3; Fig. 2B).

3.2.2. True and and false schematic memory retrieval activity

A conjunction analysis between schematic true and false recollection revealed activation in the left middle frontal gyrus (MFG), left

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[1] It should be noted that the contrast of non-schematic recollection success (Hit v Miss) did reveal posterior parahippocampal gyrus at the corrected threshold, indicating that non-schematic targets utilized MTL for successful recollection.

Table 2
Common schematic and non-schematic retrieval success activity.

	BA	H	Coordinates (T & T)			t	mm^3
			X	Y	Z		
Recollection							
Middle Frontal Gyrus	10/11	L	−39	51	−7	5.34	5076
	46/9	L	−48	29	22	5.37	7749
	9	R	42	12	33	5.03	4320
Caudate	–	R	9	11	3	5.1	2619
	–	L	−9	11	0	5.23	4401
Middle Temporal Gyrus	21	L	−59	−36	−7	5.01	11718
		R	59	−36	−7	4.55	6264
Inferior/Superior Parietal Lobe	40/7	L	−33	−51	45	6.78	29646
		R	36	−60	48	6.02	14391
Familiarity							
Middle Frontal Gyrus	46/9	L	−45	35	21	4.18	3375
Inferior Frontal Gyrus	10	L	−45	46	4	4.38	3213
Middle Temporal Gyrus	21	L	−50	−36	3	4.13	1998
Superior Parietal Lobe	7	L	−30	−51	45	4.09	3105

Commonly activated regions for schematic and non-schematic recollection and familiarity retrieval success.
BA=Brodmann's Area; H=Hemisphere; L=Left; M=Medial; R=Right; t=statistical t-value; T & T=Talairach and Tournoux coordinates.
Italics represent a priori ROIs.

MTG, and bilateral inferior parietal lobe. Conjunction analyses between schematic true and false familiarity revealed activation in the left MFG and the left MTG (see Table 4; Fig. 3A).

Direct comparisons between schematic true and false recollection revealed greater activation in bilateral hippocampus, right MTG, and left occipital gyrus for true recollection, while false recollection was supported by greater activity in bilateral STG. No region showed greater activation for true greater than false familiarity; however false familiarity revealed greater activity in bilateral MTG/STG and left hippocampus, extending into PHG (see Table 5; Fig. 3B).

4. Discussion

Using a novel scene paradigm, the current study investigated the effect of schematic encoding on memory for schematic and non-schematic information, as well as schematic encoding on schematic false memories. The behavioral analyses showed that when a strong schematic context was present at encoding, memory for schematic items was better than for non-schematic items. While successful retrieval of both types of items was shown to rely on similar neural processes, differences between schematic and non-schematic retrieval revealed that schematic target recollection relied on the hippocampus and visual cortices, with no region showing greater activation for schematic target familiarity. Conversely, non-schematic target recollection was supported by regions in the prefrontal and parietal cortices, whereas non-schematic target familiarity was supported by greater activity in the lateral temporal cortices. While schematic encoding was shown to be beneficial to successful memory, it also significantly increased false memories for schematically-related lures. Neurally, schematic true and false recollection, as well as true and false familiarity, showed overlapping activation, suggesting that both types of memory processes recruit similar neural mechanisms regardless of the process supporting the memory decision. In particular, activity in left MFG and lateral temporal cortices was identified across all four memory responses, highlighting the ubiquitous role of these regions in the retrieval of schematic memories. Additionally, analyses identified several brain regions that distinguished between true and false retrieval. Specifically, visual cortex showed increased activity for true recollection, whereas bilateral MTG and STG showed increased activity
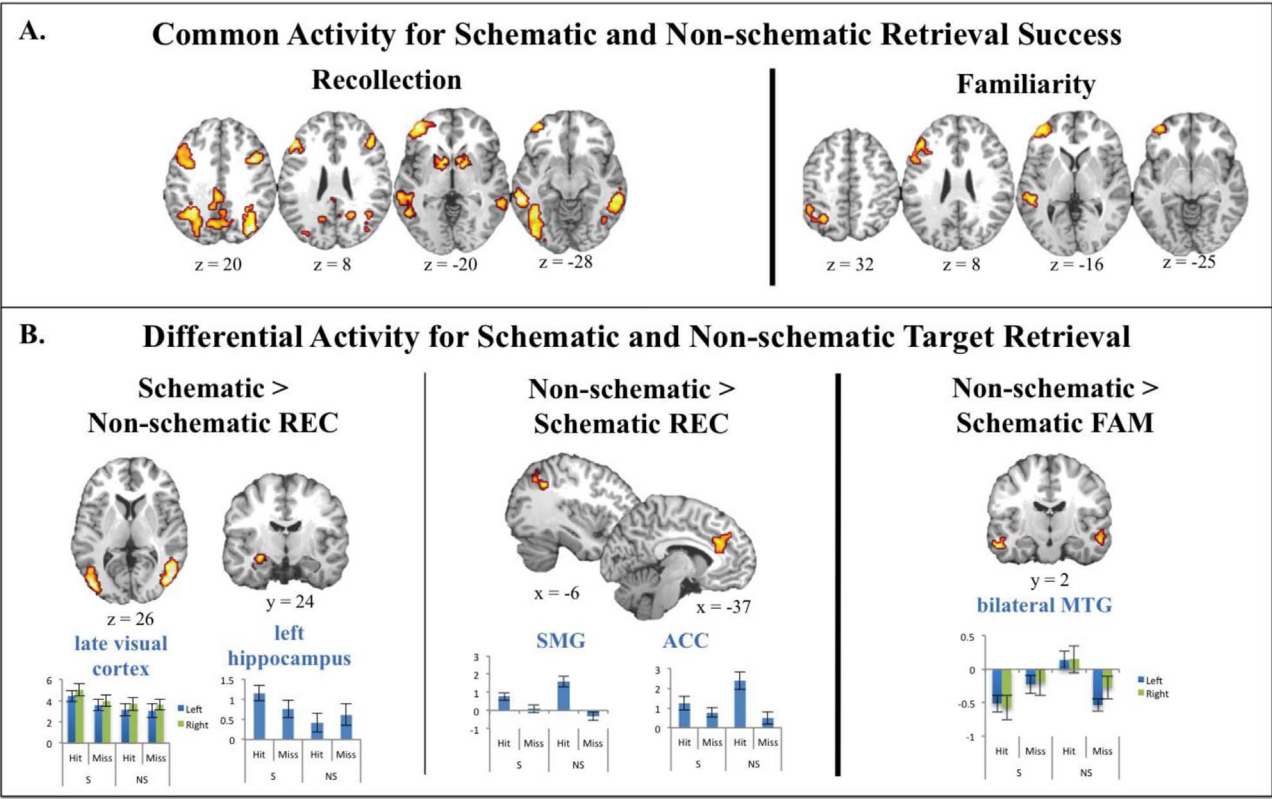
Fig. 2. Schematic and Non-schematic Memory. (A) Regions showing common activity for schematic and non-schematic recollection- and familiarity-based retrieval success (B) Regions showing differential activity for schematic and non-schematic recollection and familiarity. Y-axes represent beta estimates. REC=Recollection; FAM=Familiarity; S=Schematic; NS=Non-schematic; SMG=Supramarginal Gyrus; ACC=Anterior Cingulate Cortex; MTG=Middle Temporal Gyrus.

Table 3
Schema differences in target retrieval.

	BA	H	X	Y	Z	t	mm³
Schematic > Non-schematic							
Recollection							
Hippocampus	–	L	−27	−13	−9	4.28	648
Middle Occipital Gyrus	19	L	−48	−76	8	5.85	3807
	19/37	R	50	−71	4	5.75	6669
Familiarity							
No suprathreshold clusters							
Non-schematic > Schematic							
Recollection							
Anterior Cingulate	32	L	−6	30	27	3.75	2457
Supramarginal Gyrus	40	L	−42	−49	37	4.51	1971
Familiarity							
Middle Temporal Gyrus	21	L	−56	−16	−19	4.88	1296
		R	56	−19	−13	3.93	945

Areas exhibiting differential activation for schematic and non-schematic recollection and familiarity. BA=Brodmann's Area;
H=Hemisphere; L=Left; M=Medial; R=Right; t= statistical t-value; T & T=Talairach and Tournoux coordinates.
Italics represent a priori ROIs.

Table 4
Common true and false memory activity.

	BA	H	X	Y	Z	t	mm³
Recollection							
Middle Frontal Gyrus	10/46	L	−42	45	−4	4.57	2997
Middle Temporal Gyrus	21	L	−59	−33	−5	4.17	2241
Inferior Parietal Lobe	7/40	L	−33	−57	42	4.67	4428
Inferior Parietal Lobe/ Superior Occipital Gyrus	19/39	R	39	−72	35	5.22	2079
Familiarity							
Middle Frontal Gyrus	10	L	−45	51	−2	4.38	3294
Middle Temporal Gyrus	21	L	−50	−33	0	4.26	972

Commonly activated regions for true and false recollection and true and false familiarity.
BA=Brodmann's Area;
H=Hemisphere; L=Left; M=Medial; R=Right; t=statistical t-value; T & T=Talairach and Tournoux coordinates.
Italics represent a priori ROIs.

4.1. Common activity across schematic and non-schematic retrieval success

In line with previous studies that have found that schematic items are often better remembered than non-schematic items (see Alba and Hasher (1983) for review; e.g., Brewer and Treyens, 1981), results showed that schematic targets were remembered more often than non-schematic targets. This difference is reflective of the influence that the encoding schema has in supporting identification of and memory for information that is directly supportive of the schema. Despite this, successful retrieval of both schematic and non-schematic targets was
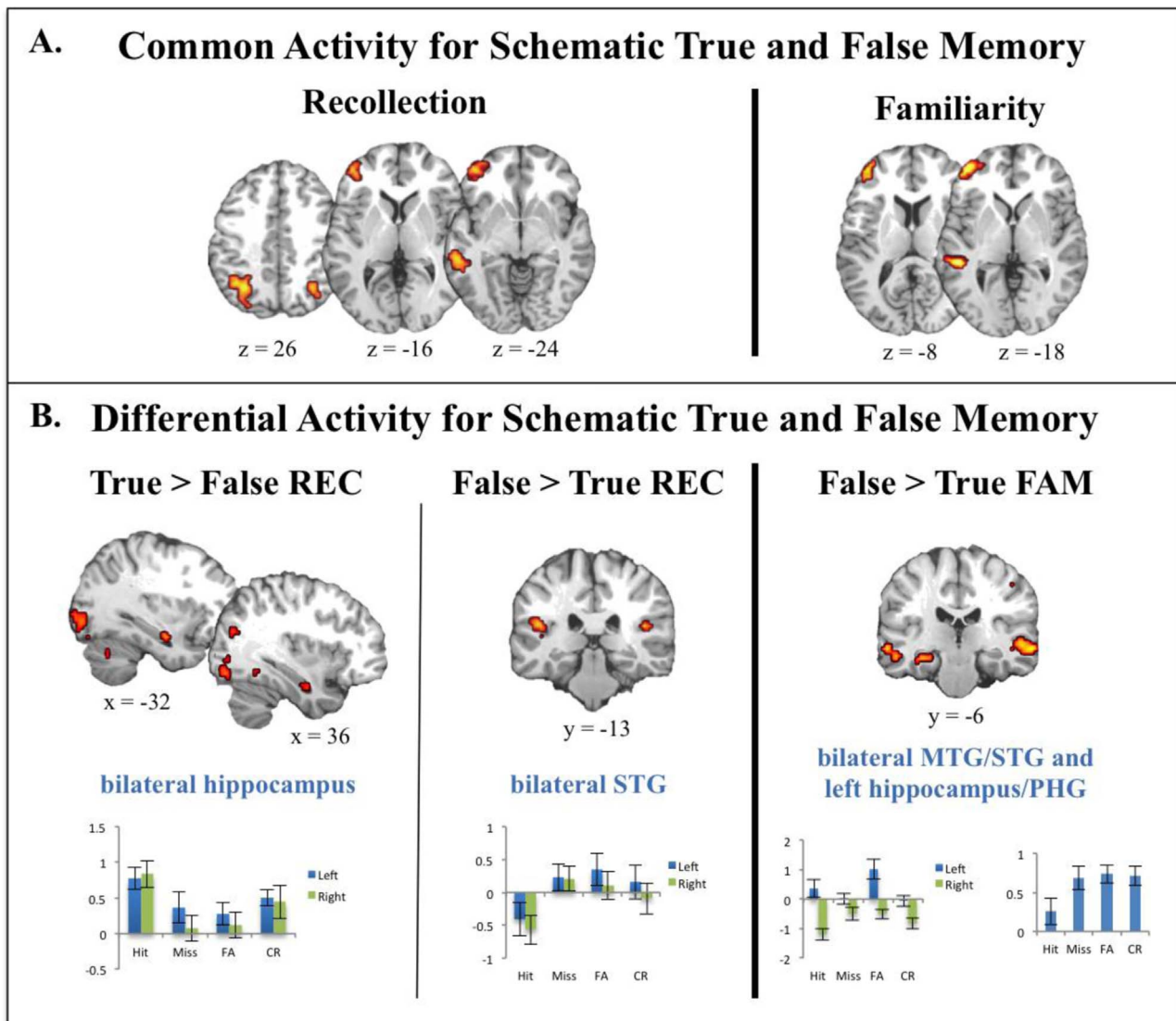
for false recollection and familiarity. Interestingly, the MTL showed increased activity for true compared to false recollection, but showed the opposite pattern for familiarity. Each finding is discussed in detail below.

Fig. 3. True and False Memory. (A) Regions showing common activity for true and false recollection and familiarity (B) Regions showing differential activity for true and false recollection and familiarity. Y-axis represents beta estimates. REC=Recollection; FAM=Familiarity; S=Schematic; NS=Non-schematic; FA=False Alarm; CR=Correct Rejection; STG=Superior Temporal Gyrus; MTG=Middle Temporal Gyrus; PHG=Parahippocampal Gyrus.

shown to rely on similar neural correlates across both recollection and familiarity. Specifically, retrieval success of both types of targets was mediated by activity in bilateral prefrontal and parietal cortices, including left IFG, regions consistently shown to support episodic recognition processes (Rugg and Vilberg, 2013; Spaniol et al., 2009).

Activation was also identified in lateral temporal cortices, which have been shown to support semantic processing and retrieval of verbal and semantic gist information (Saumier and Chertkow, 2002; Wise and Price, 2006). Moreover, we found a similar activation profile in lateral temporal cortices for both schematic *and* non-schematic retrieval success across recollection and familiarity. While initially counterintuitive, results suggest that the schematic context instantiated during encoding is a strong mediator of all retrieval processes, regardless of relatedness (schematic/non-schematic), memory strength (recollection/familiarity), and, as will be discussed later, veracity (true/false). Specifically, results suggest that once items are encoded in a highly schematic context, memory for both schematic and non-schematic items from that context is equally reliant on semantic gist processes. Importantly, this finding extends previous work by indicating that retrieval of items studied within a highly schematic context utilizes the schema for accurate retrieval support, even when these items are not directly supportive of the schema.

4.2. Differences in schematic and non-schematic target retrieval

Behavioral analyses found that schematic targets were better remembered than non-schematic targets. Furthermore, as predicted, schematic target recollection elicited greater activity in the hippocampus and visual cortex. The MTL, and specifically the hippocampus, has been consistently implicated in recollection success and in the retrieval of item-specific details, as well as source information (Diana et al., 2007; Eldridge et al., 2000; Yonelinas et al., 2005). Results support the notion that schematic compared to non-schematic hits are associated with the retrieval of greater encoding details, potentially due to enhanced encoding processes associated with identification and processing of the studied schema. In line with previous work, results suggest that schematic target recollection is reliant on greater contextual processing supported by the MTL (Bar and Aminoff, 2003; Bar et al., 2008).

Schematic target recollection was also supported by increased activity in late visual cortices (BA 19/37), compared with non-schematic target recollection. With respect to memory retrieval, activity in early visual cortex has been interpreted as reflecting recapitulation of item representations that were present at encoding, while activity in late visual cortex has been interpreted as reflecting memory for general

Table 5
Schematic true and false memory differences.

	BA	H	Coordinates (T & T)			t	mm³
			X	Y	Z		
True > False							
Recollection							
Hippocampus	–	R	24	–2	–17	4.06	1296
	–	L	–33	–11	–16	4.15	1296
Middle Temporal Gyrus	21	R	59	–28	–8	5.84	11151
Middle/Superior Temporal Gyrus	21/22	R	59	–48	1	3.60	729
Inferior/Middle Occipital Gyrus	18/19	L	–27	–79	5	4.34	7479
Cerebellum	–	L	–15	–61	–29	3.77	1971
Familiarity							
No suprathreshold voxels							
False > True							
Recollection							
Superior Temporal Gyrus	41/42	R	45	–29	16	4.66	1188
	41/42	L	–48	–32	19	4.25	1269
Familiarity							
Hippocampus/PHG	–	L	–33	–28	–10	4.2	1593
Middle/Superior Temporal Gyrus	21/ 20/22	R	59	–19	–8	5.22	5454
	21/ 20/22	L	–59	–39	–7	4.94	7911
Middle Temporal Gyrus	20	R	48	4	–27	3.82	675

Areas exhibiting differential activation for true and false recollection and familiarity.
BA=Brodmann's Area;
H=Hemisphere; L=Left; M=Medial; R=Right; t=statistical t-value; T & T=Talairach and Tournoux coordinates.
Italics represent a priori ROIs.

object identity and the conscious experience of identifying the item as 'old' (Slotnick and Schacter, 2004, 2006; Stark et al., 2010; Vaidya et al., 2002; Wheeler et al., 2000). To this end, results suggest that while lower level sensory reactivation of targets was consistent across schematic and non-schematic retrieval success (as evidenced by overlap in activity in early visual cortex), non-schematic target retrieval relied on conscious retrieval of the item and/or its context within the schema to support recollection. Interestingly, the foregoing differences were only observed for recollection and not familiarity responses, suggesting that neural differences in enhanced schema-related item accuracy may be supported by different mechanisms for familiarity.

Because non-schematic targets were not inherently tied to the encoding schema, it was predicted that participants would not be able to take full advantage of the encoding schema at retrieval, making these items more difficult to remember. This was reflected in both behavior and the neural results. Specifically, poorer recollection memory for non-schematic compared to schematic items was associated with increased activity within the ACC and left supramarginal gyrus. Previous memory research has implicated the ACC in supporting effortful cognitive control and conflict monitoring processes (Carter et al., 1998; Fleck et al., 2006), while the parietal cortex has been interpreted as mediating identification of old, or previously encountered, information. Additionally, the supramarginal gyrus, has been attributed to increases in attentional mechanisms, specifically within the context of recollection (Cabeza et al., 2008; Ciaramelli et al., 2010; Wheeler and Buckner, 2004), and may also direct a search for retrieval of general information that shares properties with a variety of contexts and is therefore more difficult to retrieve, as in the case of non-schematic items. Together, these results highlight the more difficult nature, and thus the increased cognitive effort, needed to retrieve non-schematic items when presented within a highly schematic context at encoding.

With respect to familiarity-based retrieval, no regions showed greater activation for schematic than non-schematic familiarity hits. Interestingly, non-schematic items relied on the lateral temporal cortices to a greater degree than did schematic retrieval. While counter-intuitive, we theorize that it may be the case that when presented with a weaker retrieval trace, retrieval of non-schematic items includes search and retrieval of the associated schema in which the items were presented in order to support item retrieval (see Tse et al. (2007), van Kesteren et al. (2012)). Future work is needed to examine this possibility with respect to non-schematic retrieval following schema-based encoding.

It should be noted that a handful of previous studies have identified a role for medial prefrontal cortex (mPFC) in supporting schema processing and schema memory retrieval (e.g., van Kesteren et al., 2013, 2010b). In the current study, however, we did not find evidence of mPFC in mediating retrieval of schematic compared to non-schematic memories (for a similar finding see, van Buuren et al. (2014)). While van Kesteren et al. (2013) also included analogous non-schematic items to those used in the current paradigm (identified as schema intermediate items in their study), the observed linear schema-congruency effect in mPFC does not appear to be due to differences in schematic and non-schematic retrieval, but instead appears to be due to a marked deactivation in mPFC associated with schema-incongruent retrieval. This may provide insight into the lack of mPFC observed in the current paradigm and may suggest that mPFC findings observed in other schema-based memory studies is either related to encoding-retrieval differences or is due to comparisons with schema-inconsistent memories. It is also possible that the mPFC plays a greater role in facilitation of knowledge integration at encoding and/or consolidation stages (Tse et al., 2011; van Kesteren et al., 2014, 2013, 2010a) as opposed to retrieval. To continue to clarify these issues, it is important that more studies be conducted to examine schema-relatedness on a continuous scale, as well as identifying neural differences between schema memory encoding and retrieval.

4.3. Common activity for true and false memory

In addition to its advantages to memory retrieval, schematic encoding has also been shown to have detrimental effects on memory, particularly with respect to an increased rate of false memories. Accordingly, while the schematic hit rate was greater than that of schematic false alarms, participants made significantly more schematic false alarms than non-schematic false alarms. In line with our predictions, the conjunction analysis of schematic true and false recollection (as well as that of familiarity) showed common retrieval activity in left MFG and left MTG (see Fig. 3A). As noted above, common activity in left MFG and left MTG highlights the influence of the encoding schema on memory retrieval, as both regions have been shown to be critical to semantic processing (Binder et al., 2009; Kircher et al., 2001; Noppeney and Price, 2002; Price, 2000; Wise and Price, 2006) and the retrieval of semantic gist (Buckner, 1996; Gabrieli et al., 1998; Noppeney et al., 2007; Price, 2000; Simons et al., 2005; Wise and Price, 2006). Additionally, within the context of false memory studies, the MTG has been shown to mediate retrieval of false memories based on semantic or conceptual similarity between lures and targets (Cabeza et al., 2001; Dennis et al., 2008b; Garoff-Eaton et al., 2007; Kim and Cabeza, 2007b; Kubota et al., 2006). Given that in the scene paradigm schematic gist is inherently built on the semantic associations between items that are congruent with the encoding schema, results suggest that recruitment of semantic processing regions underscores retrieval of the schema and the evaluation and integration of the congruent item (target or lure) to that schema. Moreover, the fact that left MFG and left MTG were identified in both the recollection and familiarity conjunction, speaks to the ubiquitous influence of semantic processing and schematic gist to schematic memory retrieval, in the current paradigm.

Interestingly, the results failed to show common activity in visual cortex, a region that has been identified in several previous false memory studies that have employed visual stimuli (Dennis et al., 2012; Gutchess and Schacter, 2012; Kurkela and Dennis, 2016; Slotnick and Schacter, 2004). As noted in the Introduction, while the scene paradigm is indeed visual by nature, is constitutes a relatively different paradigm than the perceptual relatedness paradigms used to date. A 'visual DRM' if you will, the scene paradigm examines memory for targets and lures that were related to a given schema (e.g., 'toilet' and 'sink' with respect to 'Bathroom') and are associated by means of common conceptual or schematic gist amongst the items. However, the items themselves share little perceptual similarity. Our current results suggest that, in the absence of perceptual overlap between targets and lures, there exists no overlapping processes within visual cortex that support recollection or familiarity of both true and false memories. This finding thus extends results from previous visual false memory studies and deepens our understanding of what processes may be common to false memories across a wide range of paradigms, as well as what processes underlie false retrieval with respect to the specific paradigm used.

4.4. Differential activation between schematic true and false memory

In addition to common activation, we sought to elucidate neural activity that differentially supported schematic true and false memories. Important differences between true and false schematic memory were identified in visual cortex, lateral temporal cortices, and MTL, with each discussed in turn below. Despite the lack of common visual activation, recollection results showed that true compared to false recollection showed increased activity across both early and late visual cortex (BA 18 & 19). As noted above, early visual activity has been attributed to the recapitulation of a sensory signature reflecting the retrieval of sensory details of the encoding event (c.f., the sensory reactivation hypothesis; Buckner and Wheeler, 2001; Rugg and Wilding, 2000), while late visual activity has been attributed to the retrieval of item identity (Slotnick and Schacter, 2004; Vaidya et al., 2002; Wheeler and Buckner, 2003; Wheeler et al., 2000). To this end, the results suggest that, compared to false recollection, true recollection is mediated by reactivation and reinstatement of perceptual details associated with the original encoding episode, as well as object labeling and general properties of the originally studied item (Garoff-Eaton et al., 2006; Slotnick and Schacter, 2004). Furthermore, given the fact that visual cortex activity failed to differentiate true and false familiarity, results suggest that familiarity responses may not retain the same perceptual details that are present for recollection.[2] Combined with the fact that no other region distinguished true from false familiarity, the results further suggest that, unlike recollection, subjective differences between familiarity decisions are less distinctive and are largely reliant on similar cognitive and neural processes.

Most interestingly, both recollection and familiarity false memories exhibited greater activity in bilateral lateral temporal cortices compared to true memories. Specifically, schematic false compared to true recollection exhibited increased activation in bilateral STG and schematic false compared to true familiarity exhibited increased activation in both bilateral MTG and STG (see Fig. 3B). Thus, results are consistent with our prediction that, given the salient schematic relationship between lures and the studied scenes, false memories would be largely reliant on retrieval of the schematic gist (Deese, 1959; Roediger and McDermott, 1995b). Additionally, combined with the absence of visual processes supporting false retrieval, results further suggest that false memories for visual stimuli that are schematically,

but not overtly perceptually related to information presented at encoding are mediated by the retrieval of schematic gist, regardless of memory strength. As such, the current results are consistent with the Fuzzy Trace Theory (Deese, 1959; Reyna and Brainerd, 1995; Roediger and McDermott, 1995b), which posits that gist traces support false memories, particularly in the absence of verbatim traces that offset the familiarity of the lure item.

As noted, prior false memory studies have disagreed about the role of the MTL in mediating false memories (see Dennis et al., 2015 for review). That is, 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., 1997, 1996; Stark et al., 2010), whereas others have found MTL activity only for retrieval of true, but not false, memories (Dennis et al., 2008b; Giovanello et al., 2009; Kim and Cabeza, 2007b; Paz-Alonso et al., 2008). In our earlier work (Dennis et al., 2012) we posited that this discrepancy might be due, in part, to inconsistencies in testing procedures and the tendency of past studies to collapse across recollection- and familiarity-related responses. Supporting this theory, as well as our predictions, the current findings showed the MTL elicited different patterns of activity when comparing true and false memories across recollection and familiarity. Specifically, bilateral anterior hippocampus showed greater activity for schematic true compared to false recollection, while schematic false compared to true familiarity exhibited greater activity in a more posterior region of left hippocampus/PHG (see Fig. 3B).

Regarding recollection, the current results support our earlier work, as well as that of others, who have separated out recollection processes with respect to true and false memories, identifying greater activity for true recollection in the hippocampus proper (Abe et al., 2013; Dennis et al., 2012; Kim and Cabeza, 2007b). Similar to the interpretation of greater MTL activity for schematic compared to non-schematic recollection above, current results suggest that true recollection is accompanied by greater recovery of item-specific episodic details from encoding, as well as the binding of multiple memory traces that is unique to recollection (Diana et al., 2007; Yonelinas et al., 2005).

While familiarity is generally defined as the absence of vivid retrieval for item-specific details, the current results showed false familiarity to be mediated by activity in left hippocampus/PHG. The current MTL results are consistent with recent false memory work that has broken down false recollection from that of familiarity, showing greater PHG activity for false compared to true familiarity (Abe et al., 2013; Karanian and Slotnick, 2014; see also Kim and Cabeza, 2007b). Despite the apparent dichotomy, a parsimonious explanation has been offered by Karanian and Slotnick (2014). Specifically, they suggest that within the context of false familiarity, PHG activity reflects a greater reliance on source processing in the face of a weak memory trace. That is, when only a weak retrieval trace is available, (such as only a low level of gist), false familiarity is supported by retrieval of the encoding source or surrounding details. For example, in the current study, participants may be recollecting the contextual event (i.e., gist of the scene), but are still lacking details of the item itself and are thus indicating a familiarity response. Interestingly, non-schematic familiarity also exhibited significantly greater recruitment of this region compared to schematic familiarity, and showed no difference with respect to schematic false familiarity. This result further supports the aforementioned conclusion that, when faced with a relatively weak item trace, enhanced retrieval of the encoding context may underlie a familiarity response for a given item. Further research should continue to build upon these theories of MTL involvement in true and false retrieval, specifically with respect to the separate contributions of recollection and familiarity processing.

4.5. Conclusions

Schemas have been shown to be both beneficial to memory, supporting encoding and retrieval success, but also detrimental when

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[2] This result should be interpreted with caution as true compared to false familiarity did show greater activation in late visual cortex (BA 19), though the cluster (51 voxels) fell shy of the corrected threshold (66 voxels).

novel information is highly related to the schema. The current study sought to investigate the influence that a schematic framework at encoding has on both veridical and false memories across different levels of memory strength. In doing so, the study built on recent work that has highlighted the need to examine the separate contributions of recollection and familiarity in the context of false memories (Abe et al., 2013; Dennis et al., 2012). Furthermore, the use of the scene paradigm allowed us to investigate the neural basis of false memory for pictorial items that have a conceptual, rather than a perceptual, relationship with encoded items. The study identified several novel results. In terms of memory success, while we identified a wealth of common regions supporting both schematic and non-schematic memory success, schematic recollection was supported by detailed retrieval mediated by the hippocampus and visual cortex. The more difficult non-schematic recollection, however, relied on regions supporting more effortful retrieval monitoring and evaluation strategies. With respect to false memories, common retrieval activity across veridical and illusory memory was found in lateral temporal regions that support semantic processing and retrieval of schematic gist. Moreover, activity in this region was greater for both false recollection and false familiarity suggesting that retrieval schematic information from encoding was a critical factor in mediating illusory memories, irrespective of memory strength. Importantly, the absence of common visual activity, suggests that, unlike previous studies utilizing visual stimuli, when false memories are predicated on schematic gist and not perceptual overlap, there is little reliance on visual processes during false memory retrieval. Furthermore, as visual activity was greater for true recollection, results suggest that visual cortices are critical for distinguishing true and false memories. Finally, the dissociation identified within the MTL suggests that memory strength is a critical factor to understanding the role of this region in supporting true and false memories. This study builds on past fMRI false memory research, clarifying and expanding our knowledge of the neural mechanisms supporting memory.

Acknowledgements

Appendix A

Scene	Schematic Targets	Lures	Non-schematic Targets
Airport	Car rental sign	Airline pilot	End table
	Departure gate sign	Gate sign	Restroom sign
	Man holding suitcases	Luggage rack	TV
	Man picking luggage	Security guard	
Bathroom	Rubber duck	Bathroom floor scale	Flower vase
	Shampoo bottles	Sink	Mirror
	Shower head	Toilet paper roll	Spray bottle
	Toilet	Toilet plunger	
Beach	Beach ball	Flip flops	Red wagon
	Beach umbrella	Sand pail/shovel	Sun
	Sand castle	Snorkling goggles	
	Surfboard	Suntan lotion bottle	
Birthday	Balloon	Birthday cake	Ice cream cone
	Birthday clown	Happy Birthday sign	Rug
	Birthday presents	Party hat	Scenic picture frame
	Piñata	Party noise-maker	
Camping	Campfire	Fishing pole	Folding chair
	Canoe	Food cooler	Lightening bug

	Lantern	Oar	Squirrel
	Tent	Sleeping bag roll	
Christmas	Christmas train	Candy cane	Cat
	Christmas tree	Christmas stocking	Family photo
	Holiday wreath	Mistletoe	
	Santa sleigh decoration	Nutcracker	
Church	Altar	Bible	Flower arrangement
	Baptismal font	Jeweled chalice	Wooden stand
	Crucifix	Organ	
	Stained glass nativity	Rosary	
Cinderella	Cinderella & Prince Charming	Glass slipper	Lamp post
	Cinderella carriage	Magic horses	Topiary
	Clock tower	Mouse friend (Mary)	
	Fairy godmother	The Grand Duke	
Circus	Circus elephant	Cannon stunt man	Light
	Ring leader	Circus juggler	Umbrella
	Ring of fire stunt	Seal balancing ball	
	Trapeze artist	Unicycling clown	
Doctor Office	Blood pressure cuff	Doctor bag & stethoscope	Newspaper
	Examination table	IV bag	Rolling stool
	Medical tools	Nurse	
	Medicine rack	Physician scale	
Farm	Barn	Basket of eggs	Flower bush
	Cow being milked	Rooster	Flower pots
	Hay bale	Tractor	
	Pig	Windmill	
Football	Cheerleaders	Foam finger	Bench
	Coach	Football	Duffel bag
	Gatorade dispenser	Goal posts	
	Referee	Scoreboard	
Fourth of July	American flag	Eagle	Bicycle
	Kid playing baseball	Patriotic chef	Hamburger
	Patriotic themed pie	Sparkler	
	Small grill	Uncle Sam hat	
Golf	Golf ball	Golf bag	Hot air balloon
	Golf cart sign	Golf cart	Rabbit
	Golfer	Hole information sign	Table & chairs set
	Hole flag	Tee	
Gym	Hand weights	Dumbbell holder	Coat rack
	Man exercising	Gym sneakers	Portable boombox
	Treadmill	Man doing yoga	Window
	Weightlifting duo	Weight bench	
Halloween	Black arched cat	Frankenstein	Moon
	Ghost	Jack-o-lantern	Paper bag
	Human skull	Witch's cauldron	
	Witch	Zombie	
Kitchen	Coffee pot	Dishwasher	Pet bowls
	Microwave	Refrigerator	Wine bottle
	Oven mitt	Rolling pin	
	Stove	Toaster	

Scene			
Child's Nursery	Alphabet blocks	Baby booties	Lamp
	Child playpen	Baby bottle	Laundry
	Rattle	Pram stroller	
	Teddy bear	Toy rocking horse	
Office	Computer monitor	Briefcase	Tissue box
	Filing cabinet	Calculator	Trash can
	Memo pad	Desk phone	Wall clock
	Office worker	Mouse & mouse pad	
Park	Kid catching frisbee	Ride-on horse rocker	Bird
	Park bench	Playground merry-go-round	Butterfly
	Playground jungle-gym	Slide	Kite
	Sandbox	Soccer ball	
Pool	Boy swimming	No running sign	First aid kit
	Diving board	Pool skimmer	Girl with ball
	Inner tube	Swimming sign	
	Life preserver	Towel	
Safari	Roaring lion	Binoculars	Tree
	Safari jeep	Bison skull	Well
	Wildlife photographer	Ostrich	
	Zebra	Rhinoceros	
School/Classroom	Alphabet sign	Composition notebook	Bookshelf
	Apple	Overhead projector	Recycling bin
	Child's backpack	School bell	Speaker
	Pencil sharpener & pencils	Scissors	
Ski Slope	Ski lodge	Gondola	Beaver
	Ski sign	Skier	Dog
	Snowboarder	Skis	Helicopter
	Snowman	Snowmobile	
Thanksgiving	Cornucopia	Cooked turkey	Log
	Male pilgrim	Harvest food basket	Table
	Native American	Hunting rifle	
	Turkey	Pilgrim hat	
Underwater	Octopus	Dolphin	Boot
	Puffer fish	Eel	Glass bottle
	Seahorse	Lobster	
	Treasure chest	Starfish	
Unrelated Lures (not associated with any scene)	Astronaut, Bride and groom, Chessboard, Convertible, Cowboy boot, Cupid, Detour sign, Dump truck, Film reel, Flower bouquet, Game controller, Gavel, Grocery cart, Hammer, Handcuffs, High heels, Hockey player, Magnifying glass, Money, Nail polish bottle, Needle and thread, Paint palette , Piano, Pot of gold, Remote controller, Rocket ship, Saxophone, Sombrero, Sword, Test tubes		

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