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Elucidating the neural correlates of related false memories using a systematic measure of perceptual relatedness

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ABSTRACT

Previous memory research has exploited the perceptual similarities between lures and targets in order to evoke false memories. Nevertheless, while some studies have attempted to use lures that are objectively more similar than others, no study has systematically controlled for perceptual overlap between target and lure items and its role in accounting for false alarm rates or the neural processes underlying such perceptual false memories. The current study looked to fill this gap in the literature by using a face-morphing program to systematically control for the amount of perceptual overlap between lures and targets. Our results converge with previous studies in finding a pattern of differences between true and false memories. Most importantly, expanding upon this work, parametric analyses showed false memory activity increases with respect to the similarity between lures and targets within bilateral middle temporal gyri and right medial prefrontal cortex (mPFC). Moreover, this pattern of activation was unique to false memories and could not be accounted for by relatedness alone. Connectivity analyses further find that activity in the mPFC and left middle temporal gyrus co-vary, suggestive of gist-based monitoring within the context of false memories. Interestingly, neither the MTL nor the fusiform face area exhibited modulation as a function of target-lure relatedness. Overall, these results provide insight into the processes underlying false memories and further enhance our understanding of the role perceptual similarity plays in supporting false memories.

Introduction

The ability to accurately remember previous experiences and differentiate between previously encountered information and new information is critical to maintaining accurate memory. However, several factors make this distinction difficult, including the amount of perceptual similarity shared between old and new information. In the field of memory, the inaccurate identification of a new item, irrespective of its similarity to a studied item, is known as a false memory. In the domain of false memories, perceptual overlap between targets and lures has shown to result in an increased rate of false memories through the influence of gist-based processes (i.e., memory for general features of an episodic event) (Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012; Slotnick and Schacter, 2004; Stark et al., 2010). While perceptual false memories have been widely studied in the literature, research has only taken a cursory investigation into the role of perceptual overlap between lures and targets in false memories. Specifically, previous false memory studies have not systematically controlled how the specific degree of perceptual overlap between lures and targets influences the neural mechanisms underlying false memories. To address this issue, the current study aimed to expand upon previous perceptual false memory studies by systematically varying the degree of perceptual relatedness between lures and targets.

One prominent theory of false memories, the Fuzzy Trace Theory, suggests false memory errors result as a consequence of an overreliance on gist traces of the encoding event at the expense of a reliance on item-specific details from encoding at the time of memory retrieval (Brainerd and Reyna, 1990). Furthermore, the amount of false memories to lure items is suggested to be a function of the amount of perceptual similarity or gist overlap between targets and lures. Previous research suggests that the sharing of gist traces between targets and lures is a critical factor in accounting for the rate of false memories (e.g., Gutchess and Schacter, 2012; Koutstaal and Schacter, 1997; Roediger and Mcdermott, 1995). Specifically, individuals make more false alarms to lures that share perceptual properties (i.e., via shape or color) with targets than to items that do not. Yet, prior neuroimaging studies have failed to systematically control for the degree of perceptual overlap or relatedness between targets and lures (but see Gutchess and Schacter (2012) for parametric increases in gist

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encoding).

In general, perceptual false memory paradigms exploit the perceptual overlap in features between target and lure items to induce false memories (e.g., Gutchess and Schacter, 2012; Koutstaal and Schacter, 1997; Slotnick and Schacter, 2004). Specifically, participants are presented with pictures of one or more exemplars from various categories during encoding (e.g., 'chair'; 'dog'). During retrieval target items are intermixed with related lures (category exemplars that were not presented at encoding) and unrelated lures (new items whose category was not presented during encoding, e.g., Dennis et al., 2012; Koutstaal and Schacter, 1997; Slotnick and Schacter, 2004). False alarm rates to such related lures often mirror or closely approximate hit rates to target items. That is, perceptually related lures are likely to be classified as "old" at a similar rate as targets (Glanzer and Adams, 1985; Hockley, 2008; Nosofsky et al., 2011) as participants have difficulty in distinguishing between the two related items, while unrelated lures are relatively easily rejected. While some studies have attempted to use lures that are objectively more similar than others (Bowman and Dennis, 2016), no study has systematically controlled for the degree of perceptual overlap between targets and lures in order to investigate the influence of perceptual similarity on false memories.

Coinciding with this behavioral findings, neuroimaging studies examining perceptual based false memories have found differences in neural activation supporting true and false memories (for review, see Dennis et al. (2015)). For example, studies have shown that perceptual false memory retrieval in which there was a shared semantic component (e.g., similar category membership between targets and lures) and shared perceptual features, rely on processing within left middle and superior temporal gyri and late visual cortices (e.g., Dennis et al., 2012; Garoff-Eaton et al., 2006; Slotnick and Schacter, 2004). Researchers have interpreted this activation as evidence of an overreliance on perceptual gist and general processing of object identity supporting memory retrieval. Furthermore, as increased activation in lateral temporal cortex is also found to support false compared to true memories, researchers have suggested it reflects increased reliance on gist information, in the absence of a detailed or item-based retrieval signal (for review, see Dennis et al. (2015)).

Activity in the prefrontal cortex (PFC) has also been shown to differentiate between false memories to perceptually related lures and true memories (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kensinger and Schacter, 2006; Kim and Cabeza, 2007b; Kubota et al., 2006; Okado and Stark, 2003; Schacter et al., 1996). Studies have attributed this increased PFC activity to an increased need for monitoring, reconstructive processes, and semantic elaboration supporting false memories—with the specific interpretation dependent upon the precise locus of PFC activation. A recent meta-analysis found the most consistently activated frontal region underlying false memories is the medial PFC (mPFC) (Kurkela and Dennis, 2016), which has been associated with greater reliance on retrieval monitoring and evaluation processes necessary when making difficult memory decisions related to critical lures (e.g., Hofer et al., 2007; Iidaka et al., 2012).

Another notable difference between true and false retrieval is the finding of increased activity in early visual processing regions (i.e., BA 17 & 18) for true compared to false memories. This has been interpreted within the context of the '*sensory reactivation hypothesis,*' (e.g., Marche et al., 2010; Mather et al., 1997; Norman and Schacter, 1997). Specifically, the sensory reactivation hypothesis postulates that, by virtue of having been presented previously, target items will elicit retrieval-related reactivation of the encoding episode in sensory regions that were involved in their initial encoding (e.g., Vaidya et al., 2002; Wheeler et al., 2000). This is in contrast to related lures, which on the other hand, were not previously presented and thus are not accompanied by this heightened sensory signal at retrieval. However, despite strong evidence supporting the sensory reactivation hypothesis, not all perceptual false memory studies find this dissociation (e.g., Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012). For example, using categorized pictures, Gutchess and Schacter (2012) found that false memories associated with a stronger semantic gist representation (which was manipulated by presenting groupings of either 4, 8, or 14 exemplars per category of stimuli at encoding), resulted in increased activation in both the hippocampus and visual processing regions (BA 17 and 37). One explanation for this difference across studies may be related to the properties of the lure stimuli in relation to the target stimuli. That is, perhaps when related lures and targets share significant perceptual overlap with one another, the presentation of the lure at retrieval is sufficient to reactivate the perceptual experience from encoding (Gutchess and Schacter, 2012), compared to when they share less overlap. However, no study has investigated this by systematically controlling for the perceptual similarity between targets and lures.

Further still, another region that has shown varied findings with respect to distinguishing true and false memories is the medial temporal lobe (MTL). While some studies have found the hippocampus/parahippocampal gyrus (PHG) to support both true and false retrieval (e.g., Dennis et al., 2012; Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012; Kahn et al., 2004; Slotnick and Schacter, 2004; Stark et al., 2010; von Zerssen et al., 2001), others find greater MTL involvement associated with true compared to false memories (e.g., Cabeza et al., 2001; Dennis et al., 2012', 2008b; Giovanello et al., 2009; Kahn et al., 2004; Kensinger and Schacter, 2006; Kim and Cabeza, 2007b; Paz-Alonso et al., 2008). Studies suggest that greater MTL activation for true memories reflects greater recovery of sensory details associated with targets (Cabeza et al., 2001; Kahn et al., 2004; Okado and Stark, 2003), while others suggested this neural increase reflects the role of the hippocampus in binding together true details from past events (Kensinger and Schacter, 2006), or recollection processes (Dennis et al., 2012; Kim and Cabeza, 2007b). Interestingly, despite the foregoing findings, a recent meta-analysis found no consistent role for the MTL in supporting false memories (for review, see Kurkela and Dennis (2016)).

Such varied results may reflect several factors including methodological differences across studies and/or the measured degree of overlap between the related lure and the target item from the same category. With respect to item relatedness, research shows that the anterior portions of the MTL track relatedness (Bowman and Dennis, 2015; Daselaar et al., 2006; Kirchhoff et al., 2000; Tulving et al., 1996) and reflects bottom-up novelty signals, triggered by less related items. Furthermore, researchers posit that this increase in activation reflects a mismatch or recall-to-reject signal within the MTL (Bowman and Dennis, 2015; Kumaran and Maguire, 2009), beyond that found for item novelty alone (Brown and Aggleton, 2001) or unrelated novelty. However, given that previous studies have not systematically controlled the perceptual relatedness between targets and lures, it remains unclear whether varying the perceptual overlap between the two stimuli would influence the strength of the MTL's novelty signal with respect to false memories.

One critical issue in the aforementioned perceptual false memory studies is that 'relatedness', has typically been defined as membership within a given category of stimuli (e.g., chairs, dogs). Despite overlap in category membership, there likely exists a fair degree of variance amongst related lures with respect to perceptual overlap with the target(s). We posit that this variance may be a critical factor in elucidating the neural components mediating false memories. To that end we aim to clarify and extend previous findings with regards to the neural correlates underlying false

memories to perceptually related lures by controlling for the amount of perceptual overlap between the lures and targets, and elucidating neural activity that supports false memories as a function of this increase in perceptual similarity. As such, we posit that, though several neural regions have shown overlap between true and false memories, there may only be a subset of regions that are increasingly engaged as relatedness is strengthened. Specifically, activity within the lateral temporal cortex, PFC, and MTL, as well as stimulus-specific processing regions, such as visual cortex, may show systematic increases in activity as a function of target/lure similarity. Such increases in activity would reflect the influence of gist and perceptual relatedness on the cognitive and neural mechanisms supporting false memories.

A category of stimuli that is well suited to investigating perceptual overlap between targets and lures is faces. That is, given the common structural organization amongst facial features, face stimuli present a unique means by which to examine the role of perceptual relatedness in false memories. Specifically, a given face can be morphed with a second, distinct face to form a unique face that shares perceptual properties with the original face. As a result, we can obtain a systematic measure of similarity between a target and lure (e.g., a morphed face can include features that are 70% from one face and 30% from another). To this end, the current study utilized both target faces at retrieval (Parent X) and lure faces consisting of morphed faces that incorporated varying degrees of Parent X and a new face (Parent Y), as well as unmorphed, Parent Y faces. Specifically, morphed faces were created by varying the percentage of perceptual overlap between a target face (Parent X) and another face, not used in the experiment (Parent Y) to obtain multiple levels of lure relatedness [70:30 (target:new face), 50:50 (target:new face), 30:70 (target:new face)] (see Table 1). Additionally, given that all targets and lures were generated from a single category (faces), we were able to reduce the influence of semantic processing to false memories more generally.

We anticipate differences in true and false memory retrieval to be consistent with previous studies of false memory for related information (for review, seeKurkela and Dennis, 2016). Critical to our investigation of the effect of target-lure relatedness, we used a parametric modulation analysis with respect to false memories at each morph step in order to elucidate neural activity underlying false memories as a function of target-lure relatedness. Thus, we predict an increase rate of false alarms as a linear function of increased relatedness between related lures and targets. Additionally, we predict that systematic increases in perceptual relatedness will be associated with increased activation in regions within the PFC, reflecting monitoring and evaluation processes and in the MTL, reflecting tracking of relatedness and overlap between target and lures. Additionally, we predict that systematic increases in perceptual relatedness will also be associated with increased activation within the visual cortex, including fusiform face area (FFA), (which has been shown to support the perceptual processing of faces; Hoffman and Haxby (2000) and Kanwisher and Yovel (2006)), reflecting the increased familiarity of the related face lure to that of the target. Finally, we predict that systematic increases in perceptual relatedness will be associated with increased activity within the lateral and medial temporal cortices, reflecting the involvement of gist processing and processing of related information, respectively.

Material and methods

Participants

Twenty-five right-handed young adults (17 female) between the ages of 18–31 years old [mean age = 23 years, (SD = 3.74)] were recruited from The Pennsylvania State University community and received monetary compensation for their participation. All participants were screened for history of neurological disorders and psychiatric illness, alcoholism, drug abuse, and learning disabilities. All participants provided written informed consent and all procedures were approved by The Pennsylvania State University's Institutional Review Board. Prior to participation in the study, all participants successfully completed the Mars Letter Contrast Sensitivity Test (Arditi, 2005), which examines peak visual contrast. This test was included to assess processing of relatively low retinal spatial frequencies, confirming that participants could perceptually notice the difference between items, especially at relatively low relatedness levels. The average log contrast sensitivity (CS) score for both eyes was 1.86 (.04), which fell in the

Table 1
Study stimuli and behavioral results.

% of Parent Faces	(100:0)	(70:30)	(50:50)	(30:70)	(0:100)
Trial Type	Target	Morphed Lure	Morphed Lure	Morphed Lure	Unmorphed Lure
Percentage Old	0.74 (0.14)	0.56 (0.14)	.30 (.13)	.25 (.15)	.10 (.10)
Response Times (ms)					
Hits	4151.54 (1041.21)	-	-	-	-
Misses	3970.19 (646.08)	-	-	-	-
False Alarms	-	3871.06 (877.72)	3436.06 (1076.64)	3299.05 (1557.56)	2120 (1200)
Correct Rejections	-	4243.31 (966.05)	3995.13 (852.83)	4007.69 (660.72)	3740.59 (1163.21)

This table shows the study stimuli and behavioral results. Presented is an exemplar of a target face and its corresponding lure faces, given the various degrees of morphing in the current study. Note, at retrieval, participants only saw one of the faces from each category, i.e., participants saw either the target face or one of the lures at retrieval. Below each exemplar face are indices of behavioral performance across each category. All responses are collapsed across confidence ratings and the inverse of response rates (percentage old) for hits and false alarms corresponds to the miss and correct rejection rates, respectively.

normal range of 1.72–.92 for middle-age/young adults. Additionally, in a subsequent perceptual discrimination task, paired sample t-tests assessing performance revealed that participants were able to correctly discriminate between targets and all levels of morphed lures (all p's $< .001$).

Stimuli

Experimental task

The stimuli consisted of 228 pictures of adult faces (ages 18–39). Faces were evenly divided by gender and presented with neutral expressions. Half of the faces were Caucasian and the other half were an even mixture of minority races (African Americans, Indians, Asians, and Hispanics). Faces were chosen from The Color Facial Recognition Technology (FERET) database (Phillips et al., 1998) and the AR Face database (Martinez and Benavente, 1998). The background of each image was removed and pictures were cropped and resized to an approximate size of 384×514 pixels. Images were presented focally and equated for resolution and were displayed at a screen resolution of 1024 (H) $\times$ 768 (V) at 75 Hz. At the viewing distance of 143 cm, the display area was 20° (H) ° 16° (V) with experimental stimuli subtending 5° (H) $\times$ 4° (V).

Face morphing was done using Abrosoft Fantamorph software version 5.0 (http://www.fantamorph.com/overview.html). Each face was marked with key identification points (referred to as nodes) that identified key features of each face. While the total number of nodes on each face varied to allow for precision of morphing within a pair. Across faces, on average, this included 50 nodes for the face outline, 40 for hair outline, 10 for the nose, 30 for the lips, and 6 for the neck area. Aside from considerations for race and gender, all morph pairs were randomly selected. While we did not control for visual properties of the faces (i.e., symmetry, specific facial characteristics) per se, we utilized faces with a neutral expression from the identified face databases and we also ensured that none of the faces had any distinct marks (e.g., tattoos), jewelry (e.g., earrings), or other identifying features (e.g., glasses).

During encoding, participants viewed 96 original unmorphed faces (parent X; Table 1). Of the 96 study faces, 48 were brought to retrieval as target faces. The remaining encoding faces (48) were morphed with a unique new face (using one of 48 parent Y faces) to create 16 morphed/blended faces in each of the following categories—70:30, 50:50, and 30:70—where the first number represents the percentage of the 'parent X' face and the latter represents the percentage of the 'Parent Y' face used to create the blended image (note that parent Y face was never seen during encoding). An additional 16 uniquely, unmorphed Parent Y faces (0:100) were also used as lures during retrieval.

Furthermore, in order to ensure that each related lure was perceptually distinguishable from its target parent face we piloted all morphed and parent faces prior to testing in a perceptual discrimination task in an independent group of participants (N=30). Each parent face was presented focally on the computer next to the corresponding morphed face to be used during retrieval. Face pairs were presented for 4 s and participants were asked to respond 'identical' or 'different'. Morphed faces that could not be distinguished from the parent face (rated as identical more than 20% of the time) were replaced such that all faces used in the experimental paradigm were rated as 'different' with a rate of at least 80%. Participants in the current study also completed this perceptual discrimination task after retrieval to verify perceptual discriminability between targets and morphs.

Procedure

Participants first performed the contrast sensitivity task to ensure eligibility to participate in the study. Once participants performed above criteria, they were given a brief overview of the study, along with task instructions. Encoding, retrieval, and a dynamic face localizer (see below for details and rationale) then took place in the scanner. Images were displayed by COGENT in MATLAB (Mathworks). Images were projected onto a screen and viewed by participants through a mirror attached to the head coil. All images were presented in the center of the screen with response options displayed below each image. Behavioral responses were recorded using a 4-bottom-response box. Scanner noise was reduced with headphones and earplugs, and additional cushioning was used in the head coil to minimize head motion.

Encoding was evenly divided into 4 runs, each lasting approximately 4 min. During each run, participants were presented with 24 faces, each face presented for a total of 4 s. During the face presentation, participants were asked to rate each face, on a scale of 1–4, based on how typical (difficult to spot in a crowd) or atypical (distinct or easy to spot in a crowd) the face appeared. The presentation of each face was followed by a variable interstimulus interval (1–5 s). Following encoding, there was a 20-min delay period during which structural images (MPRAGE & DTI) were acquired and the instructions of the retrieval task were given.

During retrieval (also in the scanner), participants were shown 112 faces including 48 targets, 48 related lures (morphed faces), and 16 unmorphed lures, evenly distributed across 4 runs. The images were pseudorandomly sorted to ensure that no more than 3 images from any one trial type appeared in a row. Each face was displayed for 4 s followed by a variable inter trial interval (ITI) ranging between 1000 and 5000 ms. During retrieval, participants made old/new recognition memory responses using confidence ratings (old-high confidence; old-low confidence; new-low confidence; new-high confidence). Participants were instructed that some faces might seem similar to that which was presented during the study phase, but only to respond 'old' if the exact face was presented at study. Immediately following retrieval, the dynamic face localizer was presented, which included a silent, fluid concatenation of short (15 s) movie vignettes (32 in total), lasting approximately 9 min. No responses were required; participants were instructed to simply pay attention to each of the short vignettes. Subsequently, outside of the scanner, all participants completed the perceptual discrimination task to verify differentiation between parent faces and their respective morphs used during retrieval. Only data from retrieval are analyzed in the current study. Encoding data will be presented in a subsequent manuscript.

Image acquisition

Images were acquired using a Siemens Prisma Fit 3T scanner equipped with a 32-channel head coil. Functional EPI images were then prescribed approximately parallel to the AC-PC plane with a 30° steep angle. Echo-planar functional images for encoding and retrieval were acquired using a descending acquisition, 2500 ms TR, 25 ms TE, 240 mm FOV, a 80^2 matrix, 42 axial slices with 3 mm slice thickness resulting in 3 mm isotropic voxels. For the functional dynamic face localizer, Echo-planar functional images were acquired using a descending acquisition, 3000 ms TR, 30 ms TE, 240 mm FOV, a 80^2 matrix, 42 axial slices with 3 mm slice thickness resulting in 3 mm isotropic voxels. 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 mm slice thickness for each participant.

fMRI analysis

Functional data were preprocessed and analyzed with SPM8

(Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). Images were first checked for scanner and movement artifacts using a time-series diagnostic function TSDiffAna (Freiburg Brain Imaging) in MATLAB. Time-series data were realigned and images were then co-registered to the individual's T1 image. Functional data were then spatially normalized into a standard stereotaxic space using the Montreal Neurological Institute (MNI) EPI template implemented in SPM8, including resampling to the original voxel size of $3 \times 3 \times 3$ mm. A high-pass filter (128 s) was included in the model to correct for scanner drift. Finally, the volumes were spatially smoothed using a 6-mm isotropic Gaussian kernel.

We utilized both the traditional contrast approach and a parametric modulation analysis at the whole-brain level to assess the neural correlates mediating false memories a) overall and b) systematically as a function of relatedness between targets and lures. Trial-related activity was modeled with a general linear model (GLM) using a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function (hrf). In order to increase power in all analyses, we collapsed across confidence levels in order to create four regressors of interest: hits, misses, false alarms, and correct rejections. 'No response' trials and motion parameters were also modeled as regressors of no interest. Direct comparisons between the two trial types (hits and false alarms) allowed us to investigate unique neural activity associated with each memory type. In order to examine the linear trends across relatedness for false memories, a linear parametric analysis was conducted. Specifically, we modeled a linear increase in false alarms as a function of relatedness (70:30 = 4; 50:50 = 3, 30:70 = 2, 0:100 = 1). This regressor allowed for the identification of regions whose activity correlated linearly (i.e., increasing as relatedness increased) with respect to the different levels of target/lure relatedness. We included unmorphed Parent Y faces (faces that were not morphed with target faces) in the parametric analysis because a) they were perceptually less similar to the target faces than the 30:70 faces and yet b) they were still items from the same category (faces). Thus, we felt that they continued to reflect a measurable difference in relatedness between lure and target items.

In order to ensure activity in our parametric false memory contrast was not associated with relatedness more generally, but was specific to false memory activity, we also examined activity that parametrically modulated correct rejections as relatedness to targets increased and used that activation as an exclusive mask ($p < .05$ uncorrected) in the false memory parametric analysis. All individual statistical parametric maps were subjected to a random effects analysis and subsequently submitted to a second-level group analysis.

Finally, in order to further clarify results from the parametric analysis, we conducted a connectivity analysis using generalized psychological interaction analysis (gPPI; McLaren et al., 2012) in SPM8. Specifically we used the mPFC region identified in the parametric analysis as a seed and investigated connectivity between the PFC and the lateral temporal cortex in order to determine whether increased activity across both regions were correlated with respect to neural recruitment supporting false memories. Specifically, a spherical mask with an 8 mm radius was generated around the peak-activated voxel (MNI coordinates: 6, 53, 10) from the mPFC cluster identified in the false memory parametric contrast. This mask was used to define individual seed regions within the gPPI analysis framework adapted from the Generalized PPI Toolbox (McLaren et al., 2012; https://www.nitrc.org/projects/gppi). PPI contrasts directly compared connectivity of all false memories. We then ran a one-sample t-test at the group level in order to examine group effects within a mask of the lateral temporal activation also identified in the false parametric contrast. By focusing on connectivity between these two regions we were able to investigate whether increases in monitoring activity were brought online with respect to increases in gist activity within the context of false memories.

In order to identify significant results in all 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 $p < 0.05$. The input to this simulation was the search space from a grey matter mask derived from the Wake Forest University Automated Anatomical Labeling (AAL) PickAtlas, available within SPM. It utilizes an automated anatomical parcellation of the spatially normalized single-subject high-resolution T1 volume provided by the Montreal Neurological Institute (Collins et al., 1998) and is available as a commonly used software toolbox (Lancaster et al., 2000; Maldjian et al., 2003; Tzourio-Mazoyer et al., 2002), intrinsic smoothness in mm (x y z = 11.21) and $p < 0.005$. Results indicated a cluster extent of 61 resampled voxels was required to correct for multiple comparisons at $p < 0.05$ at the whole brain level. Additional simulations were run to determine a correction specific to a priori regions of interest (ROIs) in the MTL and the superior/middle temporal gyri (see details below on defining ROIs used for creating the following masks). Results indicated that, within the MTL mask an extent threshold of 10 voxels in association with an uncorrected $p < 0.005$, resulted in a corrected threshold of $p < 0.05$, as did 17 voxels extent in the superior temporal/middle temporal gyri (STG/MTG) mask.

Defining regions of interest

Based on our a priori predictions regarding the FFA, MTL, and superior and middle temporal gyri, we created ROI maps defining each region for ROI analyses (in addition to the full brain analyses conducted for each contrast of interest). The MTL and lateral temporal cortices were defined using anatomically defined regions identified by the AAL pickatlas. More specifically, the MTL ROI included the left and right parahippocampal gyrus, amygdala and hippocampus. The lateral temporal cortex included the left and right middle and superior temporal gyri.

Finally, because the FFA is defined functionally and not anatomically, it is typical to use a face localizer to identify an independent measure of FFA from that of the experimental stimuli. Thus, similar to face processing studies (Scherf et al., 2010; Avidan et al., 2005), the FFA was functionally defined using a dynamic face localizer task (Adapted from Hasson et al. (2004)) that mapped face-sensitive regions in each participant. Stimuli consisted of silent, fluid blocks of short (15-s) movie vignettes (32 in total). Each block contained video clips of people and faces (e.g., individuals laughing, angry, neutral), buildings (e.g., skyscrapers, houses in residential and business areas, etc.), navigation through natural landscapes (e.g., plains, meadows, mountains, oceans, etc.), and miscellaneous common objects (e.g., moving cars, running faucets, etc.). In order to isolate face processing, beta weights were generated at the subject levels for each condition (faces, places, buildings, navigation). Next, faces were contrasted against all other categories in order to compute face selectivity. Then, a one-sample t-test was conducted across subjects in order to create a group-level contrast map that isolated FFA bilaterally. Overall, unlike commonly used face localizers that utilize static photographs, this dynamic face localizer allowed for a natural exploration of the visual environment. It also provides robust category-selective activation in ventral temporal regions (Avidan et al., 2005).

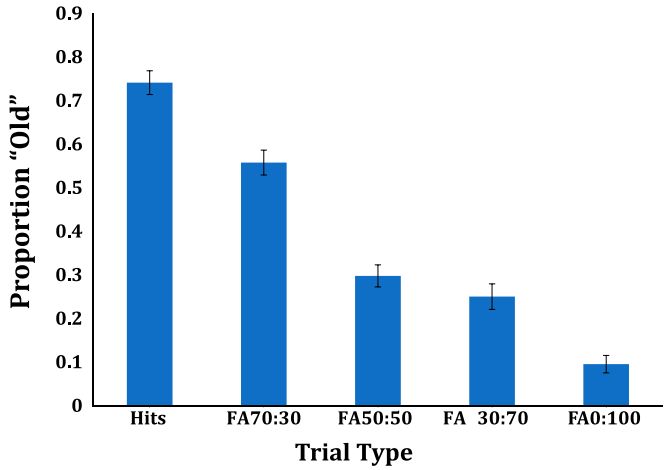

Fig. 1. Results revealed a main effect of relatedness in which the rate of false alarms increased linearly, as target/lure relatedness increased. FA=False Alarms.

Results

Behavioral

In order to examine the effects of stimulus type (targets, lures) on the proportion of 'old' responses, a paired sample t-test across 'old' responses to targets and lures (collapsed across relatedness) was performed. Results showed that participants made significantly more 'old' responses to targets than to lures [$t(24)=15.39$, $p<.001$]. In order to more specifically investigate the effects of levels of relatedness on false memories, a repeated measure ANOVA was conducted on false alarm rates across the differing levels of relatedness. Results revealed a main effect of relatedness in which the rate of false alarms increased linearly, as relatedness increased, [$F(1, 24)=112.20$ $p<0.001$]. Fig. 1 provides a visual display of this finding. Post-hoc pairwise Bonferroni corrected comparisons showed that false alarm rates for the 70:30 related lures significantly differed from all the other lures, 50:50 significantly differed from 70:30 and 0:100 lures, but not from 30:70 lures, and 30:70 significantly differed from 70:30 and 0:100 lures (see Table 1). Using reaction time as the dependent variable, another repeated measures ANOVA revealed a significant linear effect of relatedness on reaction time when making false alarms [$F(1, 24)=19.44$, $p<.001$], such that reaction increased as relatedness between targets and lures increased (see Table 1).

Imaging

True and false retrieval

Analysis of neural differences between true and false retrieval showed that true, compared to false memories, elicited greater activity in bilateral early visual cortex (BA 18) and right PHG. In contrast, false memories elicited greater activity in right superior frontal gyrus and left STG (see Table 2).

Parametric modulation

Table 3 reports neural activity associated with false memories as a function of the target/lure perceptual relatedness, including activity in right mPFC (BA 10) and bilateral MTG (BA 21).[1] In order to confirm that the regions identified in the parametric analysis were uniquely associated with false alarm activity and not due to relatedness more generally, we explicitly masked the false memory analysis with a similar parametric analysis on correction rejections (exclusive masking was carried out using a liberal uncorrected threshold of $p<0.05$ for the mask).[2] No region exhibited overlap between the two analyses, confirming that the foregoing activity is specific to false memories.

Table 2
True and false retrieval.

	BA	H	Coordinates (T&T)			t	mm^3
			X	Y	Z		
True > false retrieval							
Parahippocampal Gyrus	–	R	21	−4	−9	5.75	837
Inferior Occipital Gyrus	18	R	30	−85	3	5.32	3861
Lingual Gyrus	17/18	L	−21	−89	−7	4.42	10341
False > true retrieval							
Superior Frontal Gyrus	10	R	33	57	4	4.63	3564
Superior Temporal Gyrus	42	L	−62	−32	19	3.86	783

The table reports regions activated for true compared to false retrieval and false compared to true retrieval. 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 3
False alarm parametric modulation.

	BA	H	Coordinates (T&T)			t	mm^3
			X	Y	Z		
Medial Prefrontal Cortex (mPFC)	10	R	6	52	7	6.03	6318
Middle Temporal Gyrus	21	L	−53	−25	−8	4.75	1539
Middle Temporal Gyrus	21	R	53	−36	−7	4.21	837

The table reports regions activated for false memory as a function of the similarity between the lure and target item. 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.

mPFC connectivity

Connectivity analyses revealed a significant correlation between mPFC and left, but not right, middle temporal gyrus with respect to neural recruitment supporting the above-mentioned perceptually related false alarms.

ROI results

Our a priori hypotheses predicted modulation of false alarms as a function of relatedness in PFC and lateral temporal cortex, as well as FFA and MTL. While our whole brain results exhibited modulation of activity in PFC and lateral temporal cortices, we did not observe the predicted increases in FFA or MTL. In order to fully interrogate the response pattern within these regions, we used an ROI approach to take a closer look at activation within each region. Using a liberal threshold of $p<.05$ within each ROI, neither the FFA nor MTL exhibited any effect of relatedness supporting false memories. Additionally, we investigated whether activation in each region might be better characterized by any non-parametric response pattern by creating a non-parametric model consisting of hits, misses, false alarms and correct rejections where false alarm and correct rejection regressors were further broken down by the relatedness condition (i.e., 70:30; 50:50; 30:70; 0:100). This model allowed us to explore, in greater detail, the pattern of activity

[1] An identical analysis conducted on the morphed faces alone resulted in a similar pattern of activation as reported above with small reductions in cluster extent and the absence of right MTG activity.

[2] A liberal threshold for an exclusive mask is more conservative in excluding regions from the masked SPM. The procedure of exclusively masking main effects by their interaction is formally equivalent to the original definition of a "cognitive conjunction" (Price and Friston, 1997).

within the FFA and MTL. We obtained and plotted the mean activity within the functionally defined FFA ROI and the anatomically defined MTL ROI, for each trial type of interest within false alarms. A repeated measure ANOVA revealed no significant differences amongst false alarm regressors in any ROI. Hence, activity within both the FFA and MTL does not appear to be modulated by the systematic degree of relatedness in false alarms (see Supplementary Fig. 1).

Discussion

Expanding upon previous paradigms used to study false memories of perceptually related items, the current study investigated the neural circuitry that supported false memory retrieval as a function of the perceptual relatedness between the lures and the targets. Similar to previous studies, while true memories elicited greater activity in right PHG and early visual cortex (BA 18) bilaterally, false memories elicited increased activity in right superior frontal gyrus and left STG. Unique to the current study, analyses investigated the relationship between neural activity supporting false memories as a function of the perceptual overlap between lures and targets. With regard to the manipulation of lure relatedness, our behavioral finding indicated that, as perceptual relatedness to the target increased, false alarm rates also linearly increased. Imaging results converged with our behavioral findings, identifying several regions that exhibited increased false memory activation as a function of relatedness, including right mPFC (BA 10) and bilateral middle temporal gyri (BA 21). Together, our findings further clarify the roles of monitoring and perceptual processes in false memories. Each finding is discussed further, below.

Overall differences in true and false retrieval

Similar to previous studies examining differences between true and false memories using perceptually related stimuli, true compared to false memories, were supported by increased activity in bilateral early visual cortices (BA 18) and MTL (right PHG) (see Fig. 2A)). In line with the sensory reactivation hypothesis, activity within early visual cortex has been proposed to reflect episodic reinstatement of the perceptual representations supporting the encoding episode (Garoff-Eaton et al., 2006; Kahn et al., 2004; Okado and Stark, 2003; Slotnick and Schacter, 2004, 2006). Similarly, activity within the MTL, and specifically within the PHG, has also been shown to reflect accurate retrieval of item-specific details of the encoding episode (e.g., Cabeza et al., 2001; Dennis et al., 2012; Kim and Cabeza, 2007). Together, the observed activity within these regions supports previous work showing that true recognition is supported by the recapitulation and reconstruction of item-specific details of the encoding event (e.g., Slotnick and Schacter, 2004; Wheeler and Buckner, 2004; Yonelinas et al., 2005).

With respect to false retrieval, results are consistent with our predictions that false memories stemming from perceptual overlap between targets and lures require greater evaluation and monitoring processes than true memories, which are accompanied by the recapitulation of sensory details of the encoding episode. Specifically, false compared to true retrieval was accompanied by increased activity in right superior frontal gyrus and left STG (see Fig. 2B)). Increased frontal activity for false memories has been found across numerous studies (for review, see Dennis et al. (2015) and Kurkela and Dennis (2016)) and interpreted as reflecting a reliance on frontally mediated retrieval processes, including monitoring and evaluation (e.g., Cabeza et al., 2001; Garoff-Eaton et al., 2007; Schacter et al., 1997; Slotnick and Schacter, 2004; Yonelinas et al., 2005). Also in line with our predictions, false compared to true retrieval exhibited activation in the left STG, which has been associated with semantic processing and retrieval of semantic gist (Noppeney et al., 2007; Price, 2000; Simons et al., 2005; Wise and Price, 2006). Taken together, activation in the STG observed in the current study supports the notion that lateral temporal regions support false memories through the involvement of semantic gist, along with perceptual relatedness between lures and targets.

Interestingly, while the role of the lateral temporal cortex has previously been observed in studies that utilize a strong semantic/categorical component to the study of false memories, the current study found that activity in this region was associated with false memory within a single category of stimuli, faces. As such, the results represent an interesting extension of previous work suggesting that (1) this region may represent gist processing more generally and/or (2) false memories for faces involves semantic processing. With respect to the latter interpretation, it may be the case that false retrieval for faces relies in part on semantic labeling of a given face, such as “the girl with the freckles”. Such a label may have been generated at encoding and reactivated at retrieval when individuals are presented with the related lure that matches the label to any extent. This is especially relevant to the retrieval of these false memories, as they are not accompanied by the recapitulation of sensory details. Thus, individuals are likely using gist and not verbatim traces in their memory evaluation.

Modulation of activity for false memories as a function of relatedness

One of the main goals of the current study was to examine the role of systematic increases in perceptual relatedness in false memories on both behavioral rates of false memories and neural recruitment supporting false memories. Behaviorally, we found that the rate of false memories was dependent on the systematic degree of target/lure similarity. Specifically, there was a significant linear effect in the false memory rate and reaction times as a function of increasing perceptual relatedness between lures and targets. As noted in the results, the only pairwise comparison that failed to reach significance was the false alarm rate difference between 30:70 and 50:50 lures. Given this significant linear trend we speculate that this single insignificant pairwise comparison may reflect a lack of power (especially as there is a numerical increase in false memories from 30:70 to 50:50). This finding is largely consistent with previous studies that find both semantic and perceptual similarity to be a key factor in eliciting false memories (e.g., Deese, 1959; Gallo and Roediger, 2003; Garoff-Eaton et al., 2007; Koutstaal and Schacter, 1997; McEvoy et al., 1999; Roediger and Mcdermott, 1995). Moreover, we extend previous research to show that discrete increases in perceptual relatedness between lures and targets also increased false memories. In other words, the perceptual gist of the lure is a strong factor in predicting whether the lure will be mistakenly identified as ‘old’ at test.

With respect to the neural results, as predicted, we observed that as the similarity between the related lure and the target increased, activity within bilateral MTG and right mPFC also increased (see Fig. 3). Extending our interpretation of lateral temporal activation supporting overall false memories to perceptually related lures (see above), the parametric results suggest a greater reliance on general gist processing and/or semantic gist as perceptual similarity between targets and lures increased. To this end results are consistent with the Fuzzy Trace Theory of memory, which posits that false recognition is mediated by a strong sense of familiarity and often predicated on retrieval of the gist traces (Deese, 1959; Reyna and Brainerd, 1995; for review, see Reyna and Brainerd (2011)). The current analysis suggests an increased

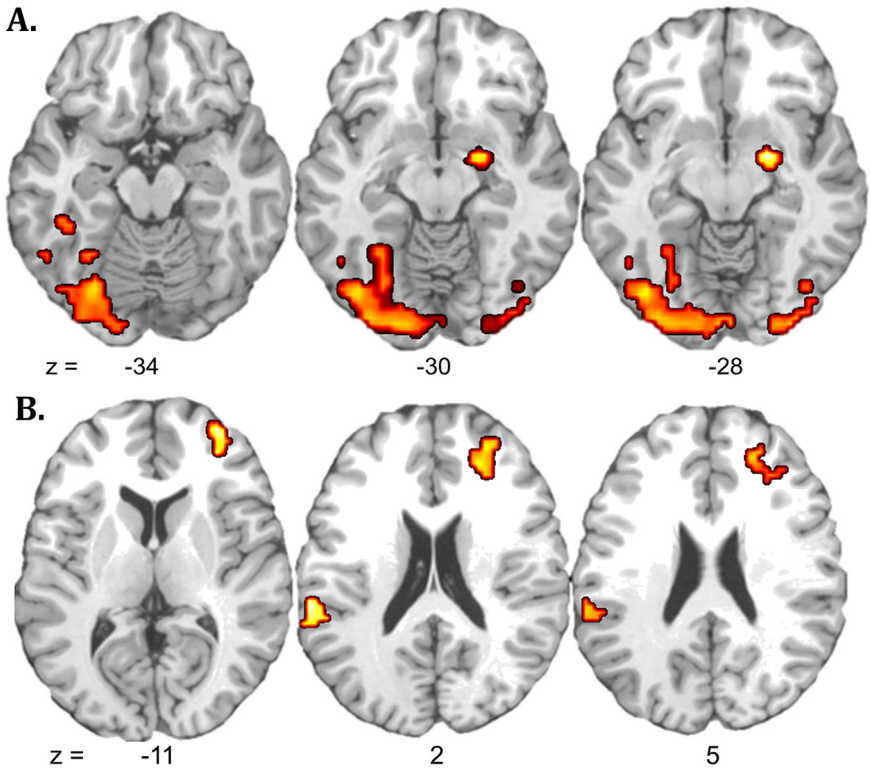

Fig. 2. A) Regions showing greater activity for true compared to false retrieval, including early and late visual cortices (bilaterally) and right parahippocampal gyrus. **B)** Regions showing greater activity for false compared to true retrieval, including left superior temporal gyrus and medial prefrontal cortex.

contribution of gist traces in support of false memories, as a function of the strength of the gist trace (see also Gutchess and Schacter (2012)). This also supports previous false memories studies that conclude that the reliance on familiarity and relatedness traces are fundamental to supporting false memories (Brainerd and Reyna, 2002; Dennis et al., 2008; Dennis et al., 2008b; Koutstaal and Schacter, 1997).

Interestingly, the lateral temporal activation identified in the parametric analysis differed from that identified in the foregoing analysis that collapsed across levels of relatedness for false memories. Specifically, the parametric analysis yielded bilateral activation in lateral temporal regions that were more superior and posterior to that observed in the collapsed relatedness false memories analysis. Investigations across previous studies revealed that there has been little consistency in the foci of activity within the lateral temporal cortices (e.g., Dennis et al., 2014', 2014; Duarte et al., 2010; Garoff-Eaton et al., 2006). A closer investigation of false memory activation in lateral temporal cortex found in previous studies that collapsed across degrees of relatedness across both semantic and perceptual stimuli (Dennis et al., 2014) showed relative consistency in spatial overlap (with respect to the z dimension: −59, −31, 8 and 45, −9, 17) with the current study's collapsed false memory relatedness contrast (−62, −32, 19). The peak of activity in the parametric analysis from the current study (−53, −25, −8) on the other hand, was relatively aligned with a false memory cluster from a study in which lures were re-combinations of encoding pairs (Dennis et al. (2008): −38, −26, −8; Dennis et al. (2014): −48, −1, −6), and thus incurred a higher amount of perceptual overlap between studied items and lures than is encountered in more traditional false memory studies. Thus, the difference in location within the lateral temporal cortex may reflect or be dependent upon the amount of perceptual

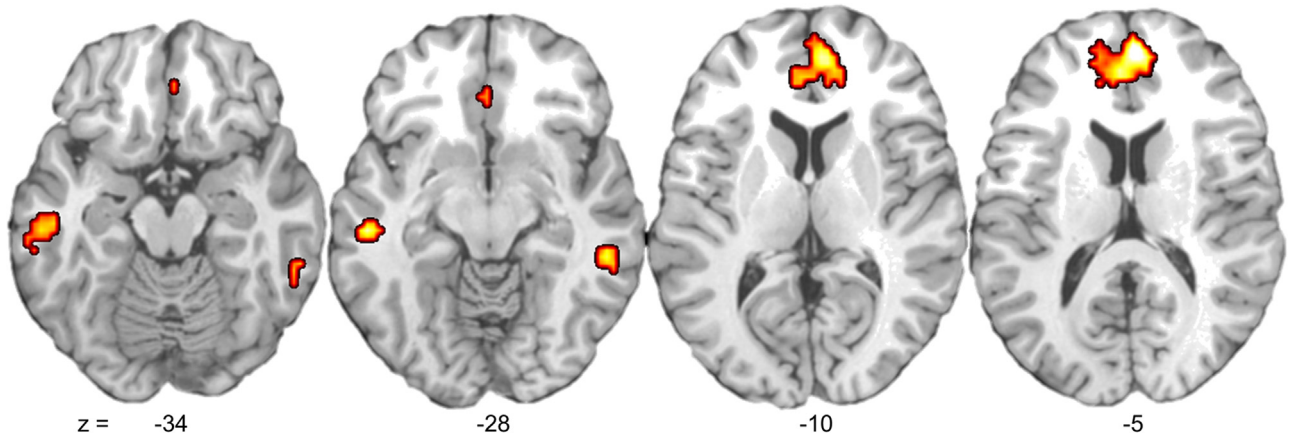

Fig. 3. Regions showing parametric increase in false memory activity as function of the similarity between the lure and target item, including bilateral middle temporal gyrus and medial prefrontal cortex.

overlap or gist incurred across lure stimuli.

As predicted, the right mPFC also showed increased activation with respect to target/lure similarity. Previous studies have related activity within this region to task difficulty in decision-making (e.g., Volz et al., 2005; Zysset et al., 2006). False memory studies have also consistently seen activity in mPFC, associating it with greater reliance on evaluation and monitoring processes necessary when making memory decisions related to critical lures (Atkins and Reuter-Lorenz, 2011; Dennis et al., 2014, 2012; Garoff-Eaton et al., 2007; Iidaka et al., 2012; von Zerssen et al., 2001). Furthermore, results of the connectivity analysis showed that activity in the right mPFC was correlated with activity in the left MTG region that was also found active in the parametric analysis. As such, results suggest that increased monitoring and evaluation processes are necessary to deal with increases in gist activity within the context of false memories.

This interpretation of the data is consistent with previous false memory studies in which activity in mPFC, has been attributed to increased monitoring (Garoff-Eaton et al., 2006; Okado and Stark, 2003; Slotnick and Schacter, 2004), difficulty of evaluating a response decision (Maril et al., 2001), as well as greater mnemonic processing of the related lures (Iidaka et al., 2012; Okado and Stark, 2003; von Zerssen et al., 2001). Other studies examining conflict between competing representations (Barch et al., 2001; van Veen and Carter, 2002) and competing mnemonic representations (Kuhl et al., 2007) also attribute increased mPFC activity to the handling of such increasing cognitive demands. Our results extend this interpretation of mPFC activity within false memories by showing that mPFC activity supporting false memories is modulated by the systematic degree of relatedness between lures and targets. Connectivity results also support the notion that as similarity between target and lure items increased, connectivity between mPFC and left lateral temporal cortex increased, suggesting an increased need for evaluation and monitoring as gist-activity increased. Furthermore, results suggest an increase in conflict and difficulty in decision-making as the similarity between lures and targets increased. This was also supported by our behavioral data, showing increases in reaction time for lures.

One could speculate that the foregoing findings reflect activity associated with relatedness more generally, and are not specific to false memory activity. In order to explore this hypothesis, we also examined activity that parametrically modulated correct rejections as relatedness to targets increased. At the corrected threshold used in the current study, results revealed no significant activity. As a second step, we masked the false memory activity with the correct rejection activity using an exclusive mask of $p < .05$ uncorrected (note that while $p < .05$ is liberal with respect to inclusion of activation, as an exclusive mask, this actually represents a relatively conservative exclusion threshold). No region exhibited overlap between the two analyses. Thus, we concluded that none of the regions evident in the false memory parametric contrast resulted from general increases in relatedness, but instead reflected increases in activity that are specific to false memories.

Though contrary to our predictions, the lack of parametric modulation in FFA and MTL should be considered, as these regions play vital roles in the retrieval of faces and item-specific details, respectively. The FFA is known to be involved in the recognition of familiar faces (Haxby et al., 2000). Nevertheless, within the context of false memories, this region does not appear to modulate systematic increases in relatedness. Furthermore, this FFA ROI was evident for true greater than false memories and not for false greater than true memories. Taken together, this can be interpreted as the FFA having preference for true old faces. In this case, it would appear that the lure face, even if very related to the target face, was not sufficient to elicit activity from the FFA region. This provides further support for the specific involvement of the FFA in retrieving item-specific details, supporting true, not false memories.

As for MTL activity, this region has been implicated as a region that tracks relatedness to support true memories (Cabeza et al., 2001; Dennis et al., 2012, 2008b; Giovanello et al., 2009; Kahn et al., 2004; Kensinger and Schacter, 2006; Kim and Cabeza, 2007b; Paz-Alonso et al., 2008). We originally hypothesized that the inconsistency of MTL findings for false memories may have been due to the lack of a systematic measure of the relatedness of lures used across studies. Yet, even in our study, MTL still did not appear to modulate activity of false memories to perceptually related lures. This could be interpreted similarly to that of the visual (FFA) activity above in showing that, though the MTL may be involved in the reconstruction and retrieval of sensory details, in the case of false memories, unless the details are truly old, they are not tracked by this region. In saying so, it is also possible that only parts of the MTL track relatedness (i.e., PHG, anterior vs. posterior parts of the hippocampus, etc.). Future studies should examine the role of sub-regions within the MTL or utilize multivariate pattern analyses as it can provide greater specificity in elucidating the involvement of MTL sub-regions in false memory retrieval.

Limitations and future directions

The present study was able to replicate previous findings of distinct activity of true and false memories, as well as provide novel insight into the neural basis of false memories that arise due to perceptual overlap between lure and target stimuli. Nevertheless, we note limitations to our approach that should be taken into consideration. First, because we wanted to investigate false memories as a function of perceptual relatedness to the target image, the current design necessitated using a limited number of lure trials at each relatedness level in order to have a balance between total targets and total lures. Thus, this resulted in a limited numbered of false memories at each relatedness level. While this was anticipated and was included as a planned parametric analysis, it limited our ability to assess neural activity at each level of relatedness separately.

Future studies may attempt to adjust the task design to better account for this issue. Increasing the overall number of lure trials will also allow for an examination of neural mechanisms underlying systematic differences in confidence, which we were unable to investigate here, due to insufficient trial counts. Second, while we discuss the results in terms of perceptual relatedness in false memories, we recognize that replication across varied stimuli-types beyond faces (e.g., objects) is necessary to extend these results to the field more generally. Third, we identified two findings contrary to our predictions (e.g., the lack of early visual cortex and MTL activity associated with our false memory parametric analysis). The null results reported in the MTL and FFA ROIs may be due to the collapsing of confidence across memories. Increasing the number of lure trials overall in future studies, may allow for further examination of the involvement of these regions isolating the effect of relatedness on high confidence false memories.

Conclusion

The current study aimed to elucidate the cognitive and neural mechanisms underlying both true and false retrieval, as well as the influence of the perceptual overlap between targets and lures on false retrieval. Behaviorally, our results showed as the perceptual similarity between a lure and a studied face increased, so too did the false alarm rate and reaction time to lures. As such, results provide evidence for the notion that false memories result, in part,

due to the amount of perceptual overlap between lures and studied items. With respect to the neuroimaging results, our results converge with previous studies showing distinct neural activity supporting true and false memories. Specifically, supporting previous false memory studies, true compared to false memories showed increased activity in bilateral early visual cortex (BA 18), reflecting the recapitulation of item-specific details of the encoding event and in right PHG, reflecting accurate reconstruction of item-specific details. On the other hand, false greater than true memories elicited increased activity in the right superior frontal gyrus and the left STG, suggestive of a need for greater monitoring and increased reliance on gist traces associated with the related lure.

Unique to our study, we examined the role of systematic increases in perceptual relatedness between lures and targets on the neural recruitment supporting false memories. Extending results from prior studies, the current findings highlight the role of the mPFC, and bilateral MTG in modulating false memories as a function of relatedness. Additionally, connectivity analyses showed a significant relationship between activity in mPFC and left MTG. Taken together, results indicate an increased need for monitoring as gist increased when making false memories. Overall, these results provide insight into the processes underlying false memories and further enhance our understanding of the role perceptual similarity plays in supporting false memories.

Conflict of interest

The experimental protocol employed in the present study was approved for ethical treatment of human participants by the Institutional Review Board at Penn State University, and the experimental data were collected with the understanding and written consent of each participant. We have no conflicts of interest, financial or otherwise, that would preclude a fair review or publication of this manuscript. We have no contracts relating to this research and no financial interest in this work. This manuscript is not submitted for publication elsewhere, nor have the results been previously published. All contents of this manuscript have been reviewed by all authors.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuroimage.2016.09.005.

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