The influence of perceptual similarity and individual differences on false memories in aging

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ABSTRACT

Previous false memory research has suggested that older adults' false memories are based on an over-reliance on gist processing in the absence of item-specific details. Yet, false memory studies have rarely taken into consideration the precise role of item-item similarity on the cognitive and neural mechanisms underlying perceptual false memories in older adults. In addition, work in our laboratory has suggested that when investigating the neural basis of false memories in older adults, it is equally as critical to take into account interindividual variability in behavior. With both factors in mind, the present study was the first to examine how both controlled, systematic differences in perceptual relatedness between targets and lures and individual differences in true and false recognition contribute to the neural basis of both true and false memories in older adults. Results suggest that between-subject variability in memory performance modulates neural activity in key regions associated with false memories in aging, whereas systematic differences in perceptual similarity did not modulate neural activity associated with false memories.

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1. Introduction

Age-related memory dysfunction has been shown to stem from both increases in forgetting and increases in false memories (McCabe et al., 2009). The latter is often more pronounced in memory studies where there is a high degree of similarity between studied targets and lures presented at retrieval (Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Tun et al., 1998). Although research regarding perceptual processing suggests that older adults have difficulty in differentiating between 2 similar items (e.g., Park et al., 2004; Yassa et al., 2011), false memory studies have not investigated the precise role of item-item similarity on the cognitive and neural mechanisms underlying perceptual false memories in older adults. In addition, several lines of research have suggested that age-related variability in cognitive performance, particularly in memory (Christensen et al., 1994, 1999; Lindenberger and Baltes, 1997; Nelson and Dannefer, 1992), has a significant influence on the neural basis of behavior (e.g., Davis et al., 2008; Gazzaley et al., 2005; Grady et al., 2005), including false memories (Dennis et al., 2007, 2014a). Furthermore, although previous studies investigating false memories in aging have focused on age differences in neural recruitment, there has been little focus on identifying what neural activity independently supports false memories in older adults, as well as what differentiates the true and false memory processes in aging. To address these issues, the present study aimed to expand upon previous research investigating perceptual false memories in aging by investigating how both systematic differences in perceptual similarity between targets and lures and individual differences in memory performance contribute to the neural basis of both true and false memories in older adults.

Perceptual false memories arise when perceptual similarity between targets and lures causes individuals to incorrectly endorse a new item, or lure, as a target during memory retrieval (e.g., Gutchess and Schacter, 2012; Koutstaal and Schacter, 1997; Slotnick and Schacter, 2004). Owing to this overlap, perceptually related lures are often classified as "old" at a similar rate as targets (Glanzer and Adams, 1985; Hockley, 2008; Nosofsky et al., 2011), whereas unrelated lures are relatively easily rejected. With respect to aging, research suggests that although older adults may successfully encode details necessary for making accurate memory decisions, they fail to make use of these details at retrieval (Bowman and Dennis, 2015; Bulevich and Thomas, 2012; Cohn et al., 2008; Koutstaal, 2003; Mitchell et al., 2013; Multhaup, 1995; Park et al., 1984; Pezdek, 1987; Rahhal et al., 2002), leading to high rates of false memories. This may stem from their reduced ability to differentiate between similar representations in the visual cortex (e.g., Bowman and Dennis, 2015; Park et al., 2004). Although

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perceptual relatedness appears to be a critical factor in accounting for perceptual false memories, the precise relationship between perceptual similarity and neural activation underlying false memories in aging has yet to be examined.

In the presence of target-lure similarity, research has suggested that older adults tend to employ gist-based strategies during retrieval and underutilize item-specific memory traces (e.g., Dennis et al., 2007, 2008; Koutstaal and Schacter, 1997; Koutstaal et al., 1999). That is, according to the fuzzy-trace theory, memory can be based on both item-specific (verbatim) and gist traces (Brainerd and Reyna, 2002). Whereas item-specific traces include distinctive features of the individual items, gist traces include the general meaning of the event but lack perceptual details of individual items. Although both traces can support true memories, it is posited that false memories arise in aging from a reduced reliance on item-specific traces combined with an overreliance on gist traces. Thus, older adults will often endorse a lure as old because it matches the gist trace associated with a given study item (or items) (Balota et al., 1999; Tun et al., 1998).

Supporting this, previous work from our laboratory shows that older adults do not effectively use early occipital cortex, a region shown to support retrieval of item-specific or sensory traces (Buckner and Wheeler, 2001; Rugg and Wilding, 2000), when discriminating between studied items and perceptually related lures (Bowman and Dennis, 2015; Dennis et al., 2014a). In addition, our work shows that older adults use lateral middle temporal gyrus and superior temporal gyrus (MTG and STG, respectively), regions shown to support semantic gist processing (Simons et al., 2005; Wise and Price, 2006), when making false memories (Dennis et al., 2007, 2008, 2014a). In addition to semantic false memories, activity in STG and MTG has also been shown to support familiarity-based false memories (Duarte et al., 2010) and highly confident perceptual false memories (Dennis et al., 2014b). Thus, taken together, results suggest that the lateral temporal cortex may represent not just semantic gist, but gist-based processing more generally, with respect to false memories in aging. Furthermore, older adults' reliance on gist memory and overlapping perceptual details from encoding may lie at the heart of age-related increases in false memories.

To the extent that such perceptual overlap represents shared gist, older adults may be more prone to false memories for lures that share a higher degree of overlapping features than lures that share less featural overlap with targets. In line with this, we recently showed that the amount of perceptual overlap between the lures and targets was a critical factor in accounting for false memory activation in the bilateral MTG and right medial prefrontal cortex (mPFC) in young adults (Turney and Dennis, 2017). The mPFC has been shown to support cognitive control in memory decisions (e.g., Iidaka et al., 2006; Jacques et al., 2011; Johnson et al., 1993; Kim, 2010, 2013) and is consistently activated in support of false memories (see Kurkela and Dennis, 2016 for results from a recent meta-analysis). Critical to the current design, false memory studies have ascribed the need for enhanced evaluation and monitoring processes when making memory decisions concerning related lures, linking this processing to increased recruitment of the mPFC (Atkins and Reuter-Lorenz, 2011; Dennis et al., 2012, 2014a, 2014b; Garoff-Eaton et al., 2007; Iidaka et al., 2012; von Zerssen et al., 2001). In addition, prior results found that activity in the mPFC was correlated with activity in the left MTG, suggesting that, with respect to false memories, increased monitoring and evaluation processes are engaged as a function of increases in gist activity (Turney and Dennis, 2017). Given older adults' reliance on gist processing, it is critical to examine this relationship in older adults so to fully understand the processes underlying high rates of false memories in aging.

In addition to the role of gist, previous work in our laboratory has also identified a critical role of individual differences in accounting for neural activity supporting memory in older adults. Specifically, our research has shown sizeable variability in rates of both true and false memories within our older cohorts (Dennis et al., 2007, 2014a). Moreover, this variability has been directly related to neural activity supporting both true and false memory performance. For example, neural recruitment during encoding of semantic information was found to be parametrically modulated by the rate of subsequent true memories in occipitotemporal and occipitoparietal cortices, bilateral MTG, and right ventrolateral prefrontal cortex. Similarly, false memory rates were shown to correlate with activity in left STG and bilateral MTG in older adults (Dennis et al., 2007). A similar pattern of activity was observed during retrieval of visual false memories, such that activity in the right superior frontal gyrus (SFG) and left superior parietal cortex was predicted by higher rates of true recollection, whereas activity in bilateral MTG and STG was predicted by higher rates of false recollection (Dennis et al., 2014a). Taken together, results suggest that individual differences in both true and false recognition are critical metrics to consider when evaluating the neural basis of cognitive performance in older adults.

Based on older adults' propensity to both encode and use gist traces during memory retrieval, the foregoing results may serve as a model for how gist operates in older adults. To that end, the present study examines the effect of perceptual relatedness on false memories in older adults. Specifically, we investigated whether perceptual similarity between targets and lures modulates the neural systems that mediate false memories in older adults. To do so we performed a memory test that used faces as targets and included retrieval lures consisting of morphed faces that incorporated varying degrees of the target face and a new face (Turney and Dennis, 2017). Given the structural organization of faces as a category of stimuli, the use of face morphs to investigate similarity effects on false memories has several advantages. For example, a lure face can be created by morphing a studied face with a novel face to form a unique face that shares a measured degree of perceptual overlap with the original face. As such, we can obtain a controlled, systematic measure of perceptual relatedness between a target and lure and be in a position of examining the false memories as a function of that relatedness.

Precisely, morphed faces were created by varying the percentage of perceptual overlap between a target face and another face, not used in the experiment, to obtain specific levels of target/lure similarity. In addition, given that all targets and lures were generated from a single category (faces), we were able to largely eliminate the influence of semantic processing to false memories more

Table 1
Participant demographics

	M (SD)
Age	67.78 (5.83)
Years of education	19.73 (3.71)
Cognitive assessment tasks	
MMSE	29.26 (1.21)
WAIS-III	
Symbol Search	13.74 (3.39)
Digit Symbol Encoding	13.87 (2.83)
Symbol Copy	114.52 (23.82)
Digit Span	12.96 (3.51)
Arithmetic	11.91 (3.45)
Letter Number Sequencing	12.48 (3.07)
Vocabulary	12.91 (3.70)
Beck Depression Inventory	1.61 (2.06)

Key: M, mean; MMSE, Mini–Mental State Examination; SD, standard deviation; WAIS-III, Wechsler Adult Intelligence Scale-III.

Table 2
Study stimuli and behavioral results

Percentage of parent faces	(100:0)	(70:30)	(50:50)	(30:70)	(0:100)
Stimuli type	Parent X	Morph	Morph	Morph	Parent Y
Trial type	Target	Lure	Lure	Lure	New
Percentage old	0.73 (0.10)	0.59 (0.13)	0.45 (0.17)	0.36 (0.16)	0.18 (0.12)
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 are an exemplar of a target face and lure faces, given the various degrees of morphing in the present study. 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. Response times (in milliseconds) and standard deviations for all trial types are also reported.

generally, focusing mainly on memory errors stemming from perceptual factors. This is critical to understand the influence of perceptual factors in false memories, particularly in aging, where semantic influences on cognition and false memories are widely documented (e.g., Dehon and Bredart, 2004; Schacter et al., 1997b; Tun et al., 1998). Furthermore, based on previous work in our laboratory indicating that neural recruitment supporting false memories in aging is related to both within- and between-subject variability (Dennis et al., 2007, 2014a), we aimed to examine the relationship between individual differences in memory performance and the neural correlates underlying veridical and false memories in older adults.

Consistent with previous perceptual memory studies in aging, we posit that true memories (hits > misses) will be associated with neural activity in the occipital cortex, the medial temporal lobe (MTL), and frontal cortices, and false memories (false alarms > correct rejections) will be associated with neural activity in frontal, parietal, and occipital cortices. Given the foregoing evidence regarding the role of gist and individual differences supporting false memories and corresponding neural activity, we posit that both increases in perceptual similarity between targets and lures and increased rates of true and false memories in older adults should modulate neural activity in brain regions shown to support true and false memories. Specifically, we predict that systematic increases in perceptual relatedness between targets and lures will be associated with increased activity within the mPFC and MTG/STG. In addition, using memory performance in a regression analysis, we predict that individual differences in true memories will be associated with recruitment of mPFC and hippocampal activity, whereas individual differences in false memories will be associated with recruitment of both mPFC activity and bilateral MTG/STG activity, as higher error rates reflect increased reliance on gist processing.

2. Material and methods

2.1. Participants

Twenty-five right-handed older adults (16 females) between the ages of 60 and 81 years (mean age = 68 years, SD = 5.83) were recruited from Centre County community and received monetary compensation for their participation. All participants were screened for history of neurological disorders and psychiatric illness, dementia, and contraindications to magnetic resonance imaging (Table 1). All participants provided written informed consent, and all procedures were approved by the Pennsylvania State University's Institutional Review Board. Before 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 score for both eyes was 1.68 (0.03), which fell in the normal range of 1.52–1.76 for older adults over the age of 60 years. In addition, 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 < 0.05).

2.2. Stimuli

2.2.1. 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 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) × 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) × 4° (V). Face morphing was done using Abrosoft FantaMorph software, version 5.0 (http://www.fantamorph.com/overview.html).

During encoding, participants viewed 96 original unmorphed faces (parent X). 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 1 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 unrelated lures during retrieval. (For additional details regarding stimuli and the morphing procedure, see Turney and Dennis, 2017).

2.3. 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 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-button-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 minutes. During each run, participants were presented with 24 faces, each face presented for a total of 4 seconds. 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 seconds). Following encoding, there was a 20-minute delay period during which structural images (T1 and diffusion tensor images) 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 1 trial type appeared in a row. Each face was displayed for 4 seconds followed by a variable intertrial interval 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 those which were presented during the study phase, but only to respond "old" if the exact face was presented at study.

Immediately following retrieval, a dynamic face localizer was presented. This task was used to map face-sensitive regions. The task included a silent, fluid concatenation of short (15 seconds) movie vignettes (32 in total), lasting approximately 9 minutes. Vignettes included 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.). No responses were required; participants were instructed to simply pay attention to each of the short vignettes. Similar to previous face-processing studies (Scherf et al., 2010; Avidan et al., 2005), the use of this passive viewing task employs rich visual inputs that successfully map face-selective activation in individual participants (see below for details regarding the analysis). Finally, 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 present study. Encoding and diffusion tensor imaging data will be analyzed at a future date and presented in a subsequent manuscript(s).

2.4. Image acquisition

Images were acquired using the Siemens Prisma Fit 3T scanner equipped with a 32-channel head coil. Functional images were then prescribed approximately parallel to the anterior commissure-posterior commissure line plane with a 30-degree steep angle. Echo-planar functional images for encoding and retrieval were acquired using a descending acquisition, 2500-ms repetition time (TR), 25-ms echo time (TE), 240-mm field of view (FOV), an 80^2 matrix, and 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, an 80^2 matrix, and 42 axial slices with 3-mm slice thickness resulting in 3-mm isotropic voxels. A T1 scan was acquired with a 1650-ms TR, 2.03-ms TE, 256-mm FOV, 256^2 matrix, 160 axial slices, and 1 mm slice thickness for each participant.

2.5. Functional magnetic resonance imaging 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 coregistered to the individual's T1 image. Functional data were then spatially normalized into a standard stereotaxic space using the Montreal Neurological Institute EPI template implemented in SPM8, including resampling to the original voxel size of $3 \times 3 \times 3$ mm. A high-pass filter (128 seconds) was included in the model to correct for scanner drift. Finally, the volumes were spatially smoothed using a 6-mm isotropic gaussian kernel.

We used both the traditional contrast approach and a parametric modulation analysis at the whole-brain level to assess the neural correlates mediating false memories. In addition, to investigate a priori predictions with regard to individual differences in aging, we used regression analyses within SPM, incorporating in both hit rate and false alarm rates across participants. Specifically, trial-related activity was modeled with a general linear model using a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function. To increase power in all analyses, we collapsed across confidence levels to create 4 regressors of interest: hits, misses, false alarms, and correct rejections. Mean (and range) trial counts for the 4 trial types of interest were as follows: hits: 35(24–44); misses: 13(4–24); false alarms: 26(12–42); and correct rejections: 38(22–52). As is typical of most false memory studies, memory errors are relatively lower than correct responses. Trial counts, however, fall within the range of previous false memory studies and thus present no issue with respect to analysis or interpretation of data. "No response" trials and motion parameters were also modeled as regressors of no interest.

True memories were analyzed by direct comparisons between hits and misses, whereas comparisons between false alarms and correct rejections allowed us to investigate neural activity supporting false memories. Individual difference analyses were conducted to identify neural activity associated with variability in older adults' behavioral performance supporting both true and false retrieval. Specifically, we regressed the contrast of false alarms > correct rejections on false alarm rates to identify regions in which behavioral performance predicted the magnitude of activation for false recognition. A similar analysis was conducted for true memories in which hits > misses contrast was regressed with hit rates to identify regions in which behavioral performance predicted the magnitude of activation for true recognition. Direct comparisons between hits and false alarms allowed us to investigate unique neural activity associated with each memory type. Finally, to examine the linear trends across relatedness for false memories, a

linear parametric analysis was conducted by modeling 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 (1) they were perceptually less similar to the target faces than the 30:70 faces and yet (2) they were still items from the same category (faces). Thus, we felt that they continued to reflect a measurable difference in similarity between lure and target items.

2.5.1. Defining regions of interest

Based on our a priori predictions regarding the mPFC, MTL, and STG and MTG, we created region-of-interest (ROI) maps defining each region for ROI analyses (in addition to the whole-brain analyses conducted for each contrast of interest). All 3 regions were defined using anatomically defined regions identified by the automated anatomical labeling (AAL) PickAtlas. More specifically, the mPFC included the bilateral anterior and middle cingulum; the MTL ROI included the left and right parahippocampal gyri and hippocampus; and the lateral temporal cortex included the left and right MTG and STG. In addition, based on the stimulus used in the present study we were also interested in exploring activity with the fusiform face area (FFA). 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. Specifically, face processing was isolated by contrasting face activity against that of all other categories within each participant (i.e., buildings, navigation through natural landscapes, and miscellaneous common objects). A 1-sample t-test was then conducted across subjects to create a group-level contrast map that isolated FFA bilaterally at the group level.

All analyses were conducted both within the foregoing ROIs and the whole brain so as to obtain a comprehensive understanding of neural processes supporting true and false memories in aging. 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 $p < 0.05$. For the whole-brain analysis, the input to this simulation was the search space from a gray matter mask derived from the Wake Forest University AAL PickAtlas, available within SPM, intrinsic smoothness in millimeters (x y z = 11.47), and $p < 0.005$. Results indicated a cluster extent of 63 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 ROIs in the MTL, mPFC, and the STG/MTG (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 18 voxels in the mPFC and 20 voxels in the STG/MTG mask.

3. Results

3.1. Behavioral

To examine the effects of stimulus type (targets, lures) on the proportion of "old" responses, we performed a paired sample t-test across "old" responses to targets and lures (collapsed across relatedness). Results showed that participants made significantly more "old" responses to targets (hits) than to lures (false alarms) [$t(24) = 15.56$, $p < 0.001$; for means see Table 2]. To more specifically investigate the effects of levels of relatedness on false memories, we conducted a repeated measure analysis-of-variance (ANOVA) 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 [$F(1, 24) = 330.64$, $p < 0.001$] (see Table 2 and Fig. 1). Post hoc t-tests 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 (all p's < 0.05 Bonferroni corrected), but not from 30:70 lures, and 30:70 significantly differed from 70:30 and 0:100 lures. A second repeated measure ANOVA using reaction time as the dependent variable also revealed a significant linear effect of relatedness on reaction time when making false alarms [$F(1, 25) = 8.57$, $p = 0.007$], such that reaction time also increased as relatedness between targets and lures increased.

3.2. Imaging

3.2.1. True and false memories

Whole-brain analyses revealed that successful true memories elicited activity throughout the traditional retrieval network, including widespread occipital cortex activity encompassing bilateral early (Brodmann area [BA] 17/18) and late (BA 19/37/39) visual cortex, bilateral MTL including hippocampus and parahippocampal gyrus (PHG), bilateral precentral gyrus, left middle frontal gyrus (MFG), and posterior cingulate (Table 3).

No region reached significance when examining false memories compared with correct rejections.

When directly compared, true compared with false memories exhibited greater activity in the bilateral occipital cortex (BA 17/18), left inferior frontal gyrus (BA 45/46), left PHG, and posterior cingulate. No region showed greater activity for false compared with true memories.

3.2.2. False alarm activity modulated by similarity

No region reached significance when assessing false memories as a function of perceptual similarity.

3.2.3. Individual differences

Individual differences in hit rate modulated activity in several frontal regions including the mPFC and medial SFG as well as bilateral PHG. Individual differences in false alarm rate also modulated activity in the mPFC as well as bilateral MTG, bilateral caudate, left hippocampus, right superior parietal cortex, and precuneus (see Table 4; Fig. 2).

3.2.4. Exploratory results

One of our a priori predictions was the modulation of false alarm activity as a function of similarity in the mPFC and lateral temporal cortex (similar to young adults). Having not observed the predicted increases, we further investigated the response pattern within these regions using a liberal threshold of $p < 0.05$ within each ROI. This investigation revealed activity in bilateral STG [left peak: −59, −32, 15; t = 3.3; k = 67]; [right peak: 65, −24, 13; t = 3.07; k = 28]; and the mPFC [peak: 0,31,−8; t = 3.50; k = 46] (see Supplemental Fig. 1). Finally, we also explored the pattern of activity within the FFA and MTL with respect to false memories and perceptual similarity. To fully examine the response pattern within these regions, we plotted the mean activity within the functionally defined FFA ROI (left only) and the anatomically defined MTL ROIs, for each trial type of interest within false alarms. A repeated measure ANOVA revealed no significant differences among false alarm regressors in any ROI. Hence, similar to results obtained in young
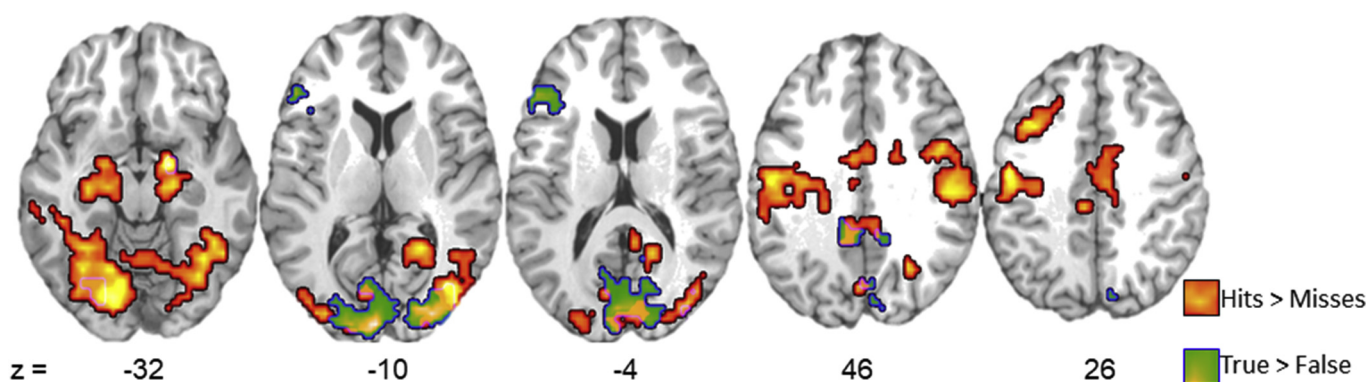
Fig. 1. True memory activity. Regions showing greater activity for hits compared with misses (true memories; shown in "hot" color), including bilateral early and late visual cortices, bilateral medial temporal lobe including hippocampus and parahippocampal gyrus, bilateral precentral gyrus, left middle frontal gyrus, and posterior cingulate. When directly compared, true compared with false memories (shown in "blue-green" color) exhibited a subset of the above mentioned activity, including bilateral occipital cortex, left inferior frontal gyrus, left parahippocampal gyrus, and posterior cingulate. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

adults (Turney and Dennis, 2017), there is some evidence that activity in bilateral temporal cortex and mPFC is sensitive to target-lure similarity, whereas activity within both the FFA and MTL does not appear to be modulated by the systematic degree of relatedness in false alarms (see Supplemental Fig. 2).

4. Discussion

The present study investigated the neural basis of false memory retrieval as a function of the perceptual similarity between lures and targets in a group of older adults. Similar to previous studies in older adults, successful memory retrieval elicited activity throughout the occipital cortex as well as bilateral hippocampus and PHG, left MFG, and cingulate gyrus. Moreover, recruitment of activity in bilateral occipital cortex, left inferior frontal gyrus, right PHG, and posterior cingulate was significantly greater for true compared with false memories. Although no region exhibited overall group effects for false memories, either in general or with regard to similarity, we did observe significant effects when accounting for individual differences. Specifically, hit rates predicted increased neural activity in

frontal regions, including the mPFC and medial SFG as well as bilateral PHG, and false alarm rates predicted activity in the mPFC, bilateral MTG, bilateral caudate, left hippocampus, right superior parietal cortex, and precuneus. Together, our findings further clarify the neural basis supporting both true and false memories in older adults, pointing strongly to a role of individual differences in behavior accounting for neural recruitment. Results and further interpretation are discussed in the following sections.

4.1. True memories

Replicating results from previous studies investigating memory retrieval in older adults, results showed that true memories were supported by activity in bilateral early and late visual cortices, bilateral MTL including hippocampus and PHG, and MFG. Novel to the present study, we also showed that much of this activity was greater for true compared with false memory retrieval. As such, results suggest that the foregoing regions are not only critical to

Table 3
Activation supporting true and false memories

			T&T coordinates				
	H	BA	x	y	z	t	mm³
Hit > miss							
Precentral gyrus	L	4/6	−50	−11	37	5.41	8721
	R	6	53	−17	29	4.84	6399
Middle frontal gyrus	L	8/9	−24	27	44	4.82	3186
Cingulate gyrus	M	24/31	−6	−2	34	4.07	4509
Hippocampus/PHG	R	34/37	18	−4	−9	6.48	2916
Hippocampus/PHG	L	34/37	−30	−19	−11	4.09	3159
IOG/MOG	R/L	17/18/19/37/39	36	−80	2	6.45	63,558
FA > CR	n/a						
Hit > FA							
Inferior frontal gyrus	L	45/46	−50	31	8	4.3	2025
PHG	*R*	*34*	*18*	*−7*	*−11*	*4.61*	*297*
Posterior cingulate	L	31/23	−9	−43	31	4.23	4131
IOG/MOG	R	18/19/17	30	−85	5	6.34	24,462
FA > hit	n/a						

The table reports regions activated for true and false memories. Italics represent regions identified with ROI analyses.
Key: BA, Brodmann's area; CR, correct rejection; FA, false alarm; H, hemisphere; IOG, inferior occipital gyrus; L, left; M, medial; MOG, middle occipital gyrus; PHG, parahippocampal gyrus; R, right; ROI, region of interest; t, statistical t-value; T&T, Talairach and Tournoux coordinates.

Table 4
Regression analysis for true and false memories

			T&T coordinates				
	H	BA	x	y	z	t	mm³
Hits > miss regression with hit rate							
Anterior cingulate cortex	R	32/(25)	12	28	−8	5.81	6912
Putamen			24	10	−10	4.24	648
Superior frontal gyrus	M	6	0	17	61	4.86	3348
Parahippocampal gyrus	*L*	*34*	*−15*	*−10*	*−11*	*4.78*	*378*
Parahippocampal gyrus	R	34	21	−16	−13	4.28	2187
FA > CR regression with FA rate							
Medial prefrontal cortex	M	10	−6	57	−5	5.03	2538
Striatum							
Caudate/putamen	R		21	20	8	5.14	3753
Caudate	L		−12	22	3		1836
Putamen/lentiform nucleus	L		−18	0	20	4.11	2808
Hippocampus	*L*		*−30*	*−22*	*−13*	*3.55*	*405*
Middle temporal gyrus	L	21	−59	−16	−19	4.74	1701
Middle/superior temporal gyrus	R	22/42	56	−9	10	4.55	2943
Superior temporal gyrus	*L*	*22*	*−53*	*5*	*−2*	*4.15*	*702*
Superior temporal gyrus	*L*	*42*	*−48*	*−24*	*5*	*3.59*	*567*
Superior parietal cortex	R	7	53	−39	50	5.29	2727
Precuneus	M	7	−6	−36	58	4.76	7074

The table reports neural activity predicted by rate of true and false recollection. Italics represent regions identified with ROI analyses.
Key: BA, Brodmann's area; CR, correct rejection; FA, false alarm; H, hemisphere; L, left; M, medial; R, right; ROI, region of interest; t, statistical t-value; T&T, Talairach and Tournoux coordinates.
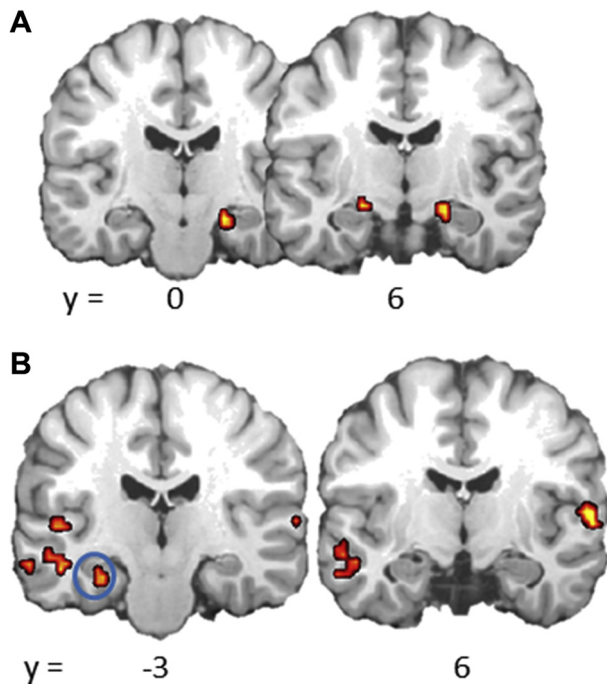
Fig. 2. True and false regression activity. (A) Activity in the bilateral parahippocampal gyrus associated with individual differences in hit rates. (B) Activity in bilateral middle and superior temporal gyri and left hippocampus (circled) associated with individual differences in false alarm rate. The anatomical masks were applied to whole-brain data to isolate activity in the aforementioned regions for display purposes.

memory success but also differentiate between veracity in memory retrieval in aging. With respect to retrieval-related activity in the occipital cortex, previous studies have connected activity in the early visual cortex (BA 17 and 18) with the recapitulation of sensory details from an encoded episode that is re-experienced at retrieval (Kahn et al., 2004; Slotnick and Schacter, 2004; Woodruff et al., 2005) and activity in late visual cortex (BA 19 & 37) with retrieval of more general aspects of the encoded episode and the conscious retrieval of information (Slotnick and Schacter, 2004, 2006; Stark et al., 2010; Vaidya et al., 2002). Given that both regions differentiate hits from misses and false alarms, the current results suggest that both the recapitulation of early sensory details and higher order visual processing are critical to memory success in older adults. Interestingly, occipital activity was not present in the true memory regression analysis and thus was not modulated by behavior. Taken together, results suggest that activity in the early visual cortex represents a nonconscious sensory signal (Slotnick and Schacter, 2004, 2006) that is not recruited by way of strategic processing in older adults who show higher levels of memory performance.

Furthermore, the bilateral anterior hippocampus and PHG were also shown to support successful memory retrieval for faces. As a key component in the memory network, the hippocampus is posited to reflect retrieval of item-specific details from encoding that support recollection and highly accurate memories (see Rugg and Vilberg, 2013), whereas the PHG has been shown to support contextual information and familiarity (e.g., Davachi, 2006; Diana et al., 2007; Ranganath et al., 2004). The results suggest that older adults rely on both types of memory when correctly identifying studied faces. Interestingly, despite widespread recruitment of both MTL regions for true memories, the PHG, and not the hippocampus proper, was found to both distinguish hits from false alarms and be predictive of hit rates in the regression analysis. The lack of

distinction between veridical and false retrieval in the hippocampus suggests that the hippocampus may contribute to false memories in a manner that univariate analyses are not sensitive enough to detect. This conclusion is supported by the finding that hippocampal activity was associated with increased false alarm rates in the regression analysis (for further discussion on this point, see below). Taken together, results suggest that, in aging, the hippocampus may not be able to adequately differentiate between targets and lures in a manner needed to accurately classify related lures as "new" and this failure has a direct impact on performance measures.

4.2. False memories

The absence of activation for false alarms compared with both correct rejections and hits is noteworthy, yet not without precedence. While previous false memory studies have consistently identified regions that are more active for both hits and correct rejections compared with false alarms, the opposite contrasts have yielded far fewer significant results. A common interpretation of this pattern has been that both true and false memory retrieval are based on a highly similar retrieval network (e.g., Atkins and Reuter-Lorenz, 2011; Cabeza et al., 2001; Dennis et al., 2012; Schacter et al., 1997a), yet false retrieval does not engage the network to the extent that true retrieval does (Dennis et al., 2012). This difference in processing can be attributed to that fact that by virtue of its original presentation at encoding, true retrieval of targets is accompanied by a larger number of memory traces than that of false retrieval.

The present study also investigated the neural basis of false memories in aging by examining the relationship between cognitive performance and neural recruitment in older adults. Consistent with previous false memory studies in older adults (Dennis et al., 2007, 2014a), the present study found that false alarm rates predicted activity in several regions including the bilateral MTG and STG, mPFC, precuneus, and hippocampus. Noted above, activity in lateral temporal cortices has been implicated in semantic gist processing (Simons et al., 2005; Wise and Price, 2006) and the integration of semantic information (e.g., Mashal et al., 2007; Mason and Just, 2004; St George et al., 1999). Combined with its role in category-based processing of perceptual stimuli (e.g., Haxby et al., 2001; Sheinberg and Logothetis, 1997), we have posited that this activity reflects a role of the lateral temporal cortex in gist processing more generally (Dennis et al., 2014a; Turney and Dennis, 2017). Alternatively, it is possible that this activity represents retrieval of a semantic label (e.g., girl with red hair) that may have been applied to the corresponding target face during encoding and acts as general retrieval trace, supporting false identification of the related face. Although additional research is needed to distinguish between the foregoing possibilities, the results are consistent with our predictions, showing that gist processing is a key contributor to increased rates of false memories in older adults.

Like the lateral temporal gyri, the mPFC and precuneus are often implicated in false memories, showing greater activity for false compared with true retrieval (for a meta-analysis see Kurkela and Dennis, 2016). Such an increase has been interpreted as reflecting the need for additional cognitive control processes needed for the evaluation and monitoring of related lures during memory retrieval (Atkins and Reuter-Lorenz, 2011; Dennis et al., 2012, 2014a, 2014b; Garoff-Eaton et al., 2007; Iidaka et al., 2012; von Zerssen et al., 2001). Consistent with previous analyses from our laboratory (Dennis et al., 2007; 2014a; Webb and Dennis, under review), activation across both gist and control regions suggests that older adults who generate the highest rates of false alarms do so by monitoring and relying upon gist activity when

making their erroneous memory choices. Interestingly, false alarm rates also predicted increased neural recruitment in the hippocampus, a region typically associated with veridical recollection. As such, results suggest that high false alarm rates may also be based on recollection of studied details associated with the related target, misattributed to the related lure at retrieval (Dennis et al., 2014a; Webb and Dennis, under review; Gutchess and Schacter, 2012).

Interestingly, unlike young in the same task (Turney and Dennis, 2017), and counter to our predictions, older adults did not exhibit increased recruitment in any brain region as a function of target-lure similarity. This is an interesting finding as it is widely theorized that older adults are directly influenced by gist processing in (false) memory tasks (Koustaal and Schacter, 1997; Paige et al., 2016; Tun et al., 1998). Within the current paradigm, the degree of perceptual similarity between the lure and its corresponding target was proposed to reflect the shared gist between the lure and its corresponding target. While behavioral results supported this preposition (i.e., showing an increased rate of false memories as a function of target-lure similarity), the absence of neural modulation in older adults suggests that the 2 factors are not related in the same way they are in young (Turney and Dennis, 2017).[1] The absence of neural modulation as a function of gist mirrors recent findings from Paige et al. (2016). Taken together, results may suggest that despite higher false alarms rates in older compared with younger adults,[2] there is a threshold above which false memories are not differentially influenced by factors that modulate the relationship between targets and lures (e.g., perceptual relatedness, gist). Alternatively, high variability in behavior among the older adults may have also been a contributing factor to the absence of a group effect at our corrected threshold.

4.3. Limitations and future directions

The present study supported previous findings in showing that neural activity across several regions is able to distinguish true compared with false memories, as well as novel findings showing the role of perceptual relatedness and the relationship between individual differences in false memory performance and modulation of lateral temporal activity in aging. Nevertheless, we note limitations to the current design that should be considered. Second, to have a balance between total targets and total lures, the current design included a limited number of lure trials (and hence false alarms) at each relatedness level. Although this was anticipated in our planned parametric analysis, it did not allow for the assessment of neural activity at each level of lure relatedness.

5. Conclusions

The present study investigated the effect of perceptual similarity and individual differences on the neural basis of true and false memories in older adults. With respect to true memories, results replicate prior studies showing that memory success in aging is supported by processing in the typical retrieval network, including bilateral early and late visual cortices, bilateral MTL, and PFC. Moreover, as a large portion of this network also showed greater activation for hits compared with false alarms, results suggest that this activation mainly reflects successful retrieval and evaluation of encoding-related memory traces that distinguish not just between hits and misses but also between veridical and erroneous memories. No region exhibited increased activation for false memories nor did older adults modulate neural activity as a function of similarity between lures and target faces. Thus, while behavioral results suggest that systematic increases in perceptual similarity significantly contributes to false memory rates, neural evidence suggests that these perceptual effects do not have an effect on neural functioning supporting false memories. Finally, an analysis including individual differences in behavior showed that false alarm rates predicted false memory activity in several regions, including the mPFC, bilateral STG and MTG, right superior parietal cortex, precuneus, and hippocampus. Results converge with previous findings suggesting that variability in performance within the older adults sample is a significant contributor to the neural basis of false memories (Dennis et al., 2007; 2014a; Webb and Dennis, under review).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.neurobiolaging.2017.10.020.

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[1] It may be of interest to note that when activity in our a priori ROIs were investigated at a lenient threshold ($p < 0.05$), older adults did exhibit modulation of neural activity in bilateral STG and mPFC (see Supplemental Fig. 1), but not MTL and FFA (see Supplemental Fig. 2), as a function of target-lure similarity. This pattern, across all 4 regions, mirrored that found in young adults (Turney and Dennis, 2017). Hence, there is some evidence that like young adults older adults are sensitive to target-lure similarity.

[2] When comparing between older adults in the present study and younger adults from the same paradigm (Turney and Dennis, 2017), older adults exhibited a significantly higher rate of false alarms (0.40) compared with younger adults [0.30; t(41) = 3.37, $p = 0.001$].

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