Understanding associative false memories in aging using multivariate analyses

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ABSTRACT

Associative memory declines in aging arise, in part, from age-related increases in false memories to recombined lures. Studies have shown that there is a benefit to associative memory if the configural context of associative pairs is maintained from encoding to retrieval. The current study aimed to examine whether this benefit of contextual congruency is reduced in aging, and whether the neural similarity of memory representations between targets and lures underlies age-related increases in false memories. Behaviorally, both age groups benefited from target pairs presented in a visual format that was congruent with how the pair was learned. While no age difference was observed in hits, the typical age-related increase in false alarms was found. Congruent with behavioral results, neither the relationship between target-related patterns of neural activity across memory phases (as measured by ERS) nor the discriminability of target classification as a function of condition at retrieval (as measured by MVPA). However, with regard to false memories, older adults exhibited overall lower pattern similarity for hits and FAs compared to hits and CRs (as measured by RSA). Additionally, Hit-FA RSA correlated with age-related increases in associative FAs across visual, frontal, and parietal cortices. Results suggest that while neural processes supporting associative memory retrieval are dependent on configural congruency between encoding and retrieval, there is no difference as to how congruency affects these processes in aging. Additionally, similarity of target and lure processing may reflect reduced diagnosticity of information processing in aging.

Introduction

Associative memory is essential to daily life. It requires the ability to not only remember items and events of the past, but to remember the specific relationship between details of a given event. For example, it is important to remember both the faces and the names of new people you meet, as well as remembering which name is associated to each face. Misremembering one or more of these associative details, such as calling someone by the wrong name, can feel like a relatively minor memory error, but even these minor errors can cause embarrassment and frustration. Associative memory success is more critical in cases where the consequences of errors are more serious, such as remembering medications and their accompanying dosages, a task that many older adults regularly encounter in their daily routines. Unfortunately, while associative memory errors occur throughout the lifespan, they have been shown to be more frequent in older individuals (Chen & Naveh-Benjamin, 2012; Kilb & Naveh-Benjamin, 2007; Naveh-Benjamin, 2000; Naveh-Benjamin et al., 2004). Given that successfully navigating the world depends on making and retrieving accurate associations, it is critical to understand how such associative false memories arise and what leads to this increased error rate in older adults.

Age-deficits in associative memory have been observed using a wide array of stimuli and experimental paradigms (e.g., Chalfonte & Johnson, 1996; Chen & Naveh-Benjamin, 2012; Kausler & Puckett, 1981a, 1981b; Kilb & Naveh-Benjamin, 2007; Naveh-Benjamin, 2000; Naveh-Benjamin et al., 2004; Naveh-Benjamin & Craik, 1995; Park et al., 1982; Park & Puglisi, 1985; Spaniol et al., 2006). The focus of this prior work has largely been on associative encoding and has examined how age-related deficits in binding contribute to memory errors (Earles et al., 2016; Nashiro & Mather, 2010; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). Associative memory requires binding features of co-occurring stimuli such as words or pictures

(Castel & Craik, 2003). Behavioral and hippocampal evidence suggests that older adults exhibit a reduced ability to encode the relationship amongst discrete pieces of information, leading to associative information not being as well remembered as individual items (e.g., Bastin & Van der Linden, 2006; Chalfonte & Johnson, 1996; Dennis, Hayes, et al., 2008; Giovanello, Kensinger, Wong, & Schacter, 2009; Mitchell, Raye, Johnson, & Greene, 2006; Naveh-Benjamin, 2000; Sperling et al., 2003). This deficit is largely reported as a reduction in d' and often conceptualized as a reduction in associative hits in older adults compared to younger adults. However, a closer look at the results of prior studies, our own included (Dennis, Hayes, et al., 2008; Overman, McCormick-Huhn, Dennis, Salerno, & Giglio, 2018), suggests that older adults' associative memory deficit also arises from the endorsement of recombined lures during retrieval, resulting in higher false alarm (FA) rates in older compared to younger adults (e.g., Castel & Craik, 2003; Healy, Light, & Chung, 2005; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003; Old & Naveh-Benjamin, 2008b; Overman & Stephens, 2013; Rhodes, Castel, & Jacoby, 2008). The ability to correctly reject a lure is especially challenging in associative memory studies, as the lure is often composed of items that have been previously presented during encoding, but in a different arrangement. As such, the *items* in recombined lures are highly familiar to the participant, yet an individual must decide not simply that they have seen each item previously, but whether that specific *pair* was previously presented. For older adults who exhibit deficits in hippocampal-based binding processes and an overreliance on familiarity during memory retrieval (Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Dennis, Hayes, et al., 2008; Duarte, Henson, & Graham, 2008; Giovanello et al., 2009; Rugg et al., 2012), overcoming the item familiarity in order to retrieve of the specific associative link across items in the pair may be especially challenging.

Erroneously endorsing a recombined lure is a type of false memory. False memories occur when we remember an event, or details, that did not occur previously, or we remember information in a way that is different from how it actually occurred. Age-related increases in false memories have been found across a wide range of memory paradigms (for reviews see Dennis, Bowman, & Turney, 2015; Devitt & Schacter, 2016). False memories become increasingly pronounced when there is a high degree of perceptual overlap between studied targets and lures presented at retrieval (Koutstaal & Schacter, 1997; Norman & Schacter, 1997). This overlap leads to a reclassification of related lures as "remembered" at a similar rate as targets (Glanzer & Adams, 1985; Hockley, 2008). Therefore, the higher rate of false memories may be attributed to the fact that older adults fail to make use of successfully encoded perceptual details when confronted with lures at retrieval, particularly when those lures are novel pairs comprised of previously-seen items that are now recombined (Bulevich & Thomas, 2012; Koutstaal, 2003; Mitchell, Ankudowich, Durbin, Greene, & Johnson, 2013).

The transfer of information from encoding to retrieval is a key component to associative memory success. Specifically, in associative memory, not only does memory for the individual items not only do the individual items need to be encoded well and recapitulated at retrieval, but critically the relationship between them needs to be recapitulated in order to endorse the *target* pair and reject a *lure* pair (a recombination of target items). The reactivation of this encoded representation can be examined by assessing the similarity of neural patterns between individual trials across memory phases (i.e., encoding/retrieval) using encoding–retrieval similarity (ERS) analysis (e.g., Jonker, Dimsdale-Zucker, Ritchey, Clarke, & Ranganath, 2018; Kuhl, Rissman, Chun, & Wagner, 2011; Ritchey, Wing, LaBar, & Cabeza, 2013; Wing, Ritchey, & Cabeza, 2015). This previous work using ERS analysis within the domain of episodic memory has

suggested that overlapping patterns of activation between encoding and retrieval correlates with item memory success. For example, research shows that ERS is capable of detecting the reinstatement of individual episodic memories in the hippocampus and the perirhinal cortex, regions critical to associative memory processing (Tompary, Duncan, & Davachi, 2016), as well as in other temporal cortex regions, the occipital lobe, and the frontoparietal cortex (Wing et al., 2015; Xiao et al., 2017).

Additionally, work from our group suggests that one's ability to generate similar neural patterns across memory phases differs with respect to the similarity of stimulus configuration across memory phases (Gerver, Overman, Babu, Hultman, & Dennis, 2020). Specifically, we found that, with respect to associative memory in younger adults, regions within visual cortices exhibit higher correlations between patterns of activity at encoding and retrieval when the relative configuration of paired stimuli remained consistent across memory phases, opposed to when the contextual configuration of stimuli was disrupted. We interpreted this finding as reflecting the fact that changes in configural context can lead to reductions in memory transfer across memory phases. Examining age differences in ERS of targets will help us understand whether there are age differences in how the encoded representations of associative information are recapitulated at retrieval, and whether reductions in pattern similarity across memory phases contributes to age-related decreases in associative memory. If older adults experience difficulty binding associative information during encoding and/or recapitulating associative information during the retrieval process, we would expect to see age-related reductions in ERS within regions critical to perception and binding processes, including regions in the ventral visual cortex and hippocampus. This may be especially problematic for targets that are configurally incongruent with how they were presented at encoding, as older adults are unable to draw upon the

familiarity of the configural context when making memory decisions. Additionally, if target representations are degraded in aging and the benefits of configural congruency on target identification at retrieval is affected, we predict that older adults would also exhibit a deficit in the discriminability between congruent and incongruent targets compared to that shown in younger adults (Gerver et al., 2020).

In addition to the need to maintain associative links between items across phases of memory, the recombined associative lure must be perceived and processed in a manner that distinguishes it from the intact target pair. When this process is successful, one is able to correctly reject the lure, whereas a failure of this process results in a false alarm. Noted above, behavioral work in the domain of false memories finds that older adults suffer in their ability to distinguish between target and lure representations during retrieval because of the influence of the item familiarity in the novel pair combination. That is, they have particular difficulty when the lure is similar to the target which was presented at encoding (e.g., Old & Naveh-Benjamin, 2008b; Rhodes et al., 2008). This difficulty may arise because targets and related lures that ultimately lead to a behavioral response of "old" (hits and FAs, respectively), are represented more similarly than hits and lures that lead to a behavioral response of "new" (correct rejections). In fact, neural pattern similarity analysis in younger adults has shown that false memories are more prevalent when there is higher overlap in similarity between representations of targets and related lures in cortical regions and the hippocampus/temporal pole (Chadwick et al., 2016; Wing et al., 2020).

Being able to recognize the item-related familiarity inherent within an associative lure, yet identify the novel associative information is a critical factor in avoiding false associative memories. Again, age-related increases in related and associative false alarms rates (Naveh-

Benjamin, 2000; Naveh-Benjamin et al., 2003; Old & Naveh-Benjamin, 2008) would suggest that older adults have difficulty overcoming the similarities between lures and targets (because of the items that comprise the pair are familiar) in order to process the recombined pair as a novel stimulus. Reflective of this difficulty, we posit that older adults will show greater overlap in similarity between the neural patterns underlying hits and false alarms, compared to patterns underlying hits and correct rejections. That is, we predict that representational similarity will be greater for pairs that are behaviorally labeled as "old" compared to when targets and lures are correctly differentiated (i.e., less representational similarity between hits and correct rejections than between hits and false alarms). We also posit that this representational overlap between hits and false alarms will be related to false alarm rates in older adults.

Methods

Participants. Thirty-one right-handed young adults (the same sample as reported in Gerver et al. 2020) and thirty right-handed older adults were recruited from the Pennsylvania State University community and greater State College area, respectively. All participants provided written consent and received compensation for their participation. Participants were screened for history of psychiatric and neurological illness, head injury, stroke, learning disability, medication that affects cognitive and physiological function, and substance abuse. On the day of the study, all participants provided written informed consent for a protocol approved by the Pennsylvania State University institutional review board. All participants were native English speakers with normal or corrected-to-normal vision. One older adult was excluded due to an inability of the analysis program to process their data and one older adult because they received the wrong version of the memory task. Three younger adults were removed from the study due to necessary removal from

the scanner, one because of excess movement in the scanner, and one because of misunderstanding the paradigm. Thus, the reported results are based on data from 26 young adult participants (19 Female; age: M = 20.5 years, SD = 1.98 years) and 28 older adult participants (21 Female; age: M= 71.04 years, SD = 6.02 years).

Cognitive Assessments. All participants provided demographic information. In addition, older participants completed a battery of cognitive assessments on the day of the study prior to being scanned to assess general cognitive function. The cognitive assessment battery included MMSE (*M*=29.52, *SD*=0.98), Digit Symbol Coding (*M*=12.43, *SD*=2.29), Symbol Copy (*M*=102.5, *SD*=23.76), Digit Span (*M*=12.48, *SD*=2.64), Letter-Number Sequencing (*M*=12.09, *SD*=3.11), WAIS-III Vocabulary (*M*=11.39, *SD*=1.68), and the Geriatric Depression Scale (*M*=0.86, *SD*=1.14) (Kurlowicz & Wallace, 1999; Wechsler, 1981; Yesavage et al., 1982).

The stimuli and procedure were the same as that reported in Gerver et al. 2020, and are replicated here for completeness.

Stimuli. Stimuli consisted of 170 color photographs of faces and 170 color photographs of scenes paired together. Face stimuli consisted of both male and females faces, each exhibiting a neutral expression, taken from the following online databases: the Color FERET Database (Phillips, Moon, Rizvi, & Rauss, 2000), adult face database from Dr. Denise Park's laboratory (Minear & Park, 2004), the AR Face Database (Martinez & Benavente, 1998), and the FRI CVL face database (Solina, Peer, Batageli, Juvan, & Kovac, 2003). Scene stimuli consisted of outdoor and indoor scenes collected from an Internet image search. Using Adobe Photoshop CS2 Version

9.0.2 and Irfanview 4.0 (www.irfanview.com/), we edited face stimuli to a uniform size (320 × 240 pixels) and background (black), and scene stimuli were standardized to 576 × 432 pixels.

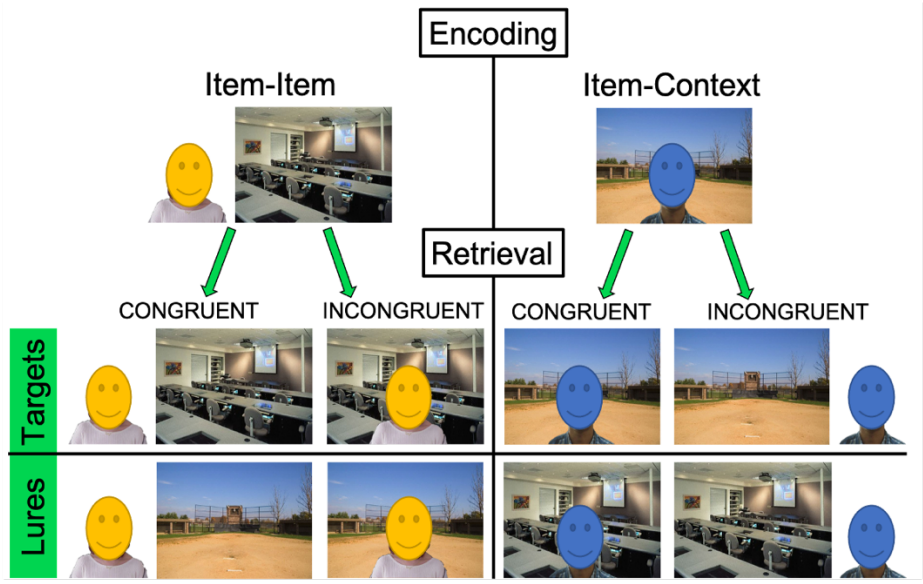

Figure 1. Task Design. Example of encoding and retrieval conditions for both congruent and incongruent targets and lures.

During encoding, half of the face–scene pairs were presented side by side; and the other half, with the face superimposed on top of the scene (see Figure 1). At retrieval, half of the pairs were present in a manner congruent with their original contextual configuration; and the other half, in the opposite configuration (i.e., incongruent contextual configuration). Each encoding and retrieval block consisted of 36 total pairs. Within the 36 pairs per retrieval block, 10 were lures (five of which were side-by-side configured and five of which were superimposed configured) in which the face was rearranged with a different scene than was originally presented at encoding. During encoding, pairs were presented for 4 sec and for 4 sec at retrieval. A jittered ISI (2–8 sec) separated the presentation of each image. Each encoding and retrieval block lasted 4 min 18 sec. A second version of this task was created to counterbalance the design such that

the same stimuli were presented in the opposite configuration across versions (e.g., a face–scene pair presented side by side in Version A was presented as superimposed in Version B).

Procedure. Before scanning, all participants practiced several trials of encoding and retrieval. Participants were encouraged to ask questions during this time. The scanning session began with a structural scan (magnetization prepared rapid gradient echo) that took approximately 7 min. During this time, the participants were asked to remain as still as possible. After the structural scan, participants completed five encoding and five retrieval blocks presented in an alternating order. Instruction screens were presented before each block reiterating the verbal instructions participants received before entering the scanner.

Presentation of all instruction screens was self-paced, meaning that the participants pressed "1" on the handheld button box to advance to the next screen when they read the instructions and were ready to begin the task. When the instruction slides appeared on the screen, the participant was asked to explain the instructions verbally before proceeding with the experiment to verify an accurate understanding of the task.

After advancing past the instruction slides in encoding, the participant was presented with a series of face and scene pairings displayed on the screen in either an item–item or an item–context configuration. Each pair was presented for 4 sec, during which time the participant responded to the question "How welcoming are the scene and face?" presented in text below each pair by utilizing a rating scale from 1 to 4 (1= not at all, 4=very) and making a key-press on their handheld button box (See Figure 1a). The instructions emphasized that the participants should choose the rating based on how welcoming the face and scene pairing was together to facilitate encoding of both the face and the scene, rather than only one or the other. This question also helped ensure that participants paid attention to the scene, even when it was configured

behind the face in the item–context condition because we did not want the scene to be incidentally encoded while the face was intentionally encoded. Across versions, faces and scenes were counterbalanced for their inclusions in either an item–item or an item–context pair. No differences across versions were noted, and all analyses were collapsed across versions.

Each encoding block was followed by a retrieval block. Similar to encoding, each face–scene pair at retrieval was presented for 4 sec. During this time, participants were asked to respond to the question: "Please identify the pairings that have been presented previously." Displayed below the question were the following choices: 1 = remember, 2 = know, and 3 = new. A remember–know–new design was chosen to isolate recollection-related activity, associated with "remember" responses, from that of familiarity, associated with "know" responses. This distinction has shown to be critical when assessing memory-related activity particularly within the MTL (Yonelinas, 2002; Yonelinas et al., 2005, 2007). Participants were instructed to make their memory judgments based on the co-occurrence of the face and scene and not to base their judgments on the configuration of the display. Specifically, participants were instructed to select "Remember" if they were able to retrieve details of the face and scene appearing together at study, select "Know" if they thought the face and scene appeared together previously but they could not remember specific details about the original appearance, and select "New" if they believe that the face–scene pair appeared together previously. Thus, whether a retrieval configuration was congruent or incongruent, the Remember/Know/New labels applied equally to both types of configurations, with a participant's response simply dependent on the vividness of their memory. Similar to encoding, all responses were made using the button box (only retrieval data are analyzed in the current analysis). With respect to retrieval configurations, half of the trials were congruent with their encoding configuration and half were incongruent

(such that a side-by-side trial at encoding was presented as a superimposed trial at retrieval) (See Figure 1b).

Image Acquisition. Structural and functional images were acquired using a Siemens 3-T scanner equipped with a 12-channel head coil, parallel to the AC–PC plane. Structural images were acquired with a 1650-msec repetition time, a 2.03-msec echo time, a 256-mm field of view, a 2562 matrix, 160 axial slices, and a 1.0-mm slice thickness for each participant. Echo-planar functional images were acquired using a descending acquisition, a 2500-msec repetition time, a 25-msec echo time, a 240-mm field of view, a 802 matrix, a 90° flip angle, and 42 axial slices with a 3.0-mm slice thickness resulting in 3.0-mm isotropic voxels.

Image Processing. Raw anatomical and functional brain images were first skull stripped using the Brain Extraction Tool (Smith, 2002) in the FMRIB Software Library (FSL) Version 5.0.10 (www.fmrib.ox.ac.uk/fsl). FSL's MCFLIRT function (Jenkinson et al., 2002, 2012) was then applied for realignment and motion correction within each functional run. All volumes were aligned to the middle volume of the middle run of encoding. The realigned functional images were then processed by FSL's fMRI Expert Analysis Tool (Woolrich et al., 2001), where they were high-passed filtered and spatially smoothed at 6-mm FWHM. These data were then pre-whitened to account for temporal autocorrelations within voxels. Finally, the structural data underwent nonlinear transformation into the standardized Montreal Neurological Institute (MNI) space by using the warping function in FSL's FNIRT (Andersson et al., 2007). For multivariate analyses, the raw data underwent the exact same steps as above, absent smoothing.

Behavioral Analyses. All behavioral analyses were conducted in Rstudio using base R functions and rstatix (www.rstudio.com; Kassabara, 2020). Because this study aimed to examine false associative memory, behavioral and neuroimaging analyses were focused on accurately and inaccurately recollected memory decisions, in the form of d' (calculated in Excel as norm.s.inv(hits) – norm.s.inv(FAs)). To test for congruency with encoding configuration-related differences in memory, false memory rates, hit rates and calculated d' rates were tested via a series of two-way mixed model ANOVAs, with age being a between factor and congruency with encoding configuration conditions (side-by-side congruent, side-by-side incongruent, superimposed congruent, and superimposed incongruent) being a within factor. To examine significant main effects further, paired-sample t-tests were run.

Multivariate Pattern Classification and Pattern Similarity Analyses. To estimate neural activity associated with individual trials, separate GLMs were estimated in SPM12 defining one regressor for each trial at encoding and retrieval (170 in total for each respective memory phase). An additional six nuisance regressors were included in each run corresponding to motion. Whole-brain beta parameter maps were generated for each trial at retrieval for each participant. In any given parameter map, the value in each voxel represents the regression coefficient for that trial's regressor in a multiple regression containing all other trials in the run and the motion parameters. These beta parameter maps were next concatenated across runs and submitted to the CoSMoMVPA toolbox (Oosterhof et al., 2016) for pattern classification and similarity analyses.

ROIs. All analyses were computed in ROIs previously identified as critical to associative memory retrieval. These include regions across the MTL including bilateral hippocampus, PHC, PrC, and temporal pole. We also included regions from the PFC, fusiform, posterior parietal cortex, early visual cortex, and late visual cortex. Regions that comprised PFC were identified

from meta-analyses of memory, including dorsolateral and medial frontal gyri (Kim, 2011; Maillet & Rajah, 2014). These regions were then identified in AAL PickAtlas using anatomically defined boundaries identified by the anatomical labeling. Because of our previous work indicating that encoding configuration significantly influences patterns of neural activity in the inferior occipital cortex (IOC; Brodmann's area [BA] 17/18) and middle occipital cortex (MOC; BA 19) (Dennis et al., 2019), these regions were also selected using the AAL PickAtlas. Finally, parts of the posterior parietal cortex, including the angular gyrus and precuneus, were chosen based on previous work that showed consistent involvement of these regions in memory retrieval (Spaniol et al., 2009; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Along with this, recent MVPA studies suggest that regions within the posterior parietal cortex, which includes the angular gyrus and precuneus (Brodt et al., 2018; Sestieri, Shulman, & Corbetta, 2017) can represent content-specific episodic information during retrieval.

ERS analysis. Given our interest in whether changes in the configural context had an effect on the similarity of target representations between encoding and retrieval, we directly compared neural patterns of activation between encoding and retrieval across configurally congruent and incongruent conditions. On the basis of our previous work indicating that encoding configuration (i.e., side-by-side, superimposed) significantly influences patterns of neural activity during encoding (Dennis et al., 2019), we separated all targets into four conditions of interest: side-by-side (II) congruent targets, superimposed (IC) congruent targets, side-by-side (II) incongruent targets, and superimposed (IC) incongruent targets. To compute pattern similarity, we used the beta estimates extracted from the single trial models for encoding and retrieval described above. Activation for each individual trial for a given condition at encoding was correlated with every trial of the same type at retrieval (e.g., targets at encoding that were presented as a side-by-side

configuration that were congruently re-presented as side-by-side at retrieval). This resulted in similarity scores, as operationalized by Pearson's *r* correlation values, for each trial. The correlations were then averaged within condition for each participant. Group-level results were generated from averaging within condition across all participants. To correct for multiple comparisons, we conducted permutation testing for each significant finding within the ERS ROI ANOVA. We shuffled the data for every subject and re-ran the ANOVA . This procedure was repeated 10,000 times per ANOVA within each ROI. We found no differences in significance following this permutation testing.

MVPA analysis. Given our interest in determining which regions in the associative retrieval network discriminated between congruent and incongruent targets, separate classification accuracies were computed in each ROI. Classification analyses were computed for retrieval runs using a support vector machine classifier with a linear kernel using all voxels within an ROI (Mumford et al., 2012). Training and testing followed an n − 1 cross-validation procedure with four runs used as training data and one run used as testing data. Group-level results were generated from averaging across validation folds from all possible train-data/test-data permutations from the individual participant level. We tested whether a classifier was significantly able to discriminate above theoretical chance between targets presented across the four configural trial types (side-by-side congruent, side-by-side incongruent, superimposed congruent, and superimposed incongruent; 25% chance) using a one-tailed one-sample t-test for classification accuracy within each ROI. Last, to assess whether classifier accuracy was related to behavioral performance, separate repeated-measures ANOVAs were computed for each ROI that contained significant classification with overall recollection rates as the dependent measure. All significant findings were confirmed using permutation testing to correct for the occurrence of

false positives (Etzel & Braver, 2013; Gaonkar & Davatzikos, 2012; Kriegeskorte et al., 2006; Stelzer et al., 2013). Specifically, we ran a follow-up test that repeatedly randomized the retrieval labels and reran the classification analysis on the permuted data. This was done 1,000 times for each significant region to produce a null distribution that simulates the potential accuracy scores that could be obtained if the retrieval manipulation had no effect.

Pattern similarity analysis. Pattern similarity analysis (Kriegeskorte et al., 2008) was conducted to examine the representation of stimuli associated with targets and lures associated with different behavioral conditions. Specifically, given our interest in understanding what underscores older adults' false memories, we examined similarities in the neural patterns underlying Hits and FAs as well as Hits and Correct Rejections (CRs) at retrieval within each ROI described above. Given trial counts across each condition and the fact that false memories were not affected by contextual congruency, we collapsed across this factor in the current analysis. To compute pattern similarity, we used the beta estimates extracted from the retrieval single trial model described above to run two separate Pearson correlations between Hits and FAs and Hits and CRs. The resulting correlation matrices were Fisher's z transformed then averaged to get a single correlation value per trial pair (Hits and FAs and Hits and CRs; see Trelle et al., 2019 for a similar methodological approach) for each older adult participant. We then compared the resulting correlations between trial pairs for each participant within each ROI using a paired-samples t-test. To correct for multiple comparisons, we conducted permutation testing for each significant finding within the pattern similarity analysis correlated with behavior. We shuffled the data for every subject and re-ran the regressions (Kherad-Pajouh & Renaud, 2010, 2015; Winkler et al., 2014). This procedure was repeated 10,000 times per regression within each ROI. We found no differences in significance following this permutation testing.

Results

Behavioral results

Three 2 (Between Age Group: Old, Young) x 4 (Within Retrieval Condition: Item-item congruent, item-context congruent, item-item incongruent, item-context incongruent) mixed model ANOVAs were performed to examine the relationships between age group and condition with respect to memory behavior.

For the d' measures, the ANOVA revealed a significant main effect of age group, $F(1,37)=13.74$, $p<.001$, $\eta^2 = 0.27$, such that young adults (M=1.36) had better target vs. lure discrimination than older adults (M= 0.67). The main effect of condition and the two-way interaction between age group and condition were not significant, Condition: $F(3,111)=2.17$, p=ns, η^2 =0.06; Age Group x Condition: $F(3,111)=0.50$, p=ns, η^2 =0.01.

Breaking the d' measure down by hit and FA rates we found that the hit ANOVA revealed a significant main effect of condition, $F(3,156)$ =24.52, $p<.001$, η^2 =0.32, such that item-item congruent presentations (M= 0.86) resulted in higher hit rates than item-item incongruent (M=0.77), $t(53) = 5.32$, $p<.001$, 95% CI [0.05, 0.12], and item-context incongruent (M=0.80), $t(53) = 4.42$, $p<.001$, 95% CI [0.03, 0.09], as well as higher hit rates for item-context congruent (M=0.88) than item-item incongruent (M=0.77), $t(53) = 7.17$, $p<.001$, 95% CI [0.08, 0.14], and item-context incongruent (M=0.80), $t(53) = 6.05$, $p<.001$, 95% CI [0.05, 0.11]. However, the item-item congruent t-tested with the item-context congruent and the item-item incongruent t-tested with the item-context incongruent were both not significant. The main effect of age group and the two-way interaction between age group and condition were not significant, Age Group: $F(1,52)$ =.19 , p=ns, η^2 =0.004; Age Group x Condition: $F(3,156)$=.41, p=ns, η^2 =0.01.

With regard to FA rates, the ANOVA revealed a significant main effect of age group, $F(1,52)=19.27$, $p<.001$, $\eta^2=0.27$, and a significant main effect of condition, $F(3, 156)=7.84$, $p<.001$, $\eta^2=0.13$, such that older adults (M=0.63) made more FAs compared to younger adults (M=0.39) and both groups had higher FA rates for item-item congruent (M=0.58) than item-context congruent (M= 0.52), $t(53)= 2.27$, p=.028, 95% CI [0.01, 0.11], item-context incongruent (M=0.48), $t(53)=4.13$, $p<.001$, 95% CI [0.05, 0.14], and item-item incongruent (M=0.46), $t(53)= 4.84$, $p<.001$, 95% CI [0.06, 0.16], and additionally had higher FA rates for item-context congruent (M= 0.52) compared to item-item incongruent (M=0.46), $t(53)=2.16$, p=.036, 95% CI [0.00, 0.10]. However, item-context congruent t-tested with item-context incongruent and item-item incongruent t-tested with item-context incongruent were not significantly different. The two-way interaction between age group and condition was not significant, $F(3,156)=0.13$, p=ns, $\eta^2= 0.003$. See Table 1 for means in each measure, across both age groups. Taken together the results support prior work replicating age deficits in associative memory, with the results finding that such deficits are driven by age-related increases in FAs to associative lures. The results also show that stimuli that is presented as congruent at retrieval with encoding contexts leads to both increases in hits and FA rates.

Multivariate results. While Gerver et al., 2020 examined ERS and MVPA metrics with respect to targets in younger adults in a handful of brain regions known to play a role in associative memory, the purpose of the following analyses was to examine whether there were any age differences in these metrics and whether such differences were related to age deficits in associative memory performance. In doing so we also expanded the set of brain regions we originally interrogated and included age as a factor in all ERS and MVPA analyses.

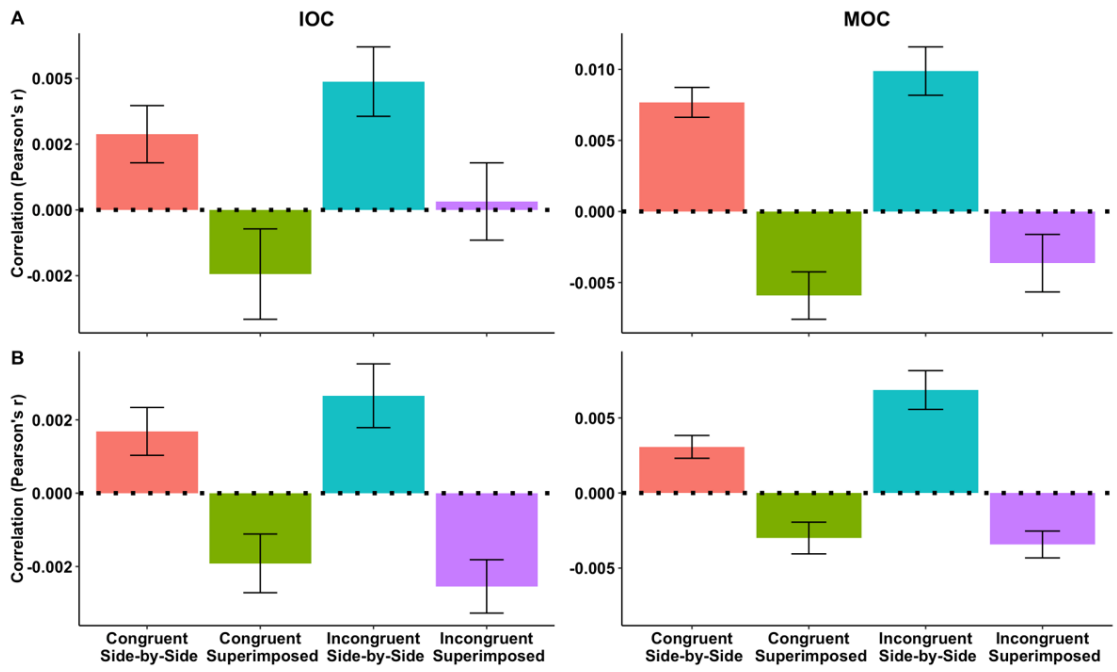

Figure 2. ERS in A) younger and B) older adults broken down by the four target conditions in the Inferior Occipital Cortex (IOC) and the Middle Occipital Cortex (MOC). Error bars represent standard error of the mean.

ERS. To examine the effect of condition and age on ERS for targets we conducted a 4 (condition: II congruent, IC congruent, II incongruent, IC incongruent) x 2 (age: young, old) repeated measures ANOVA within each ROI. There was a significant effect of condition within the IOC, $F(3,156)=17.75$, $p<.001$ and MOC, $F(3,156)=43.06$, $p<.001$ To further examine the effect within each condition, paired sample t-tests were conducted comparing ERS metrics between conditions in each region. Within the IOC ERS significantly differed for the II congruent ($M=0.002$) and II incongruent targets ($M=-0.002$), $t(52)= 4.59$, $p<.001$, 95% CI [0.00,0.01] as well as IC incongruent targets ($M=-0.002$), $t(52)= 4.07$, $p<.001$, 95% CI [0.00, 0.01]. Additionally, ERS differed significantly within the IOC for the IC congruent targets and II incongruent targets ($M=-0.002$), $t(52)= 5.33$, $p<.001$, 95% CI [0.00, 0.01] as well as the IC incongruent targets ($M=-0.002$), $t(52)= 5.08$, $p<.001$, 95% CI[0.00, 0.01]. The same pattern was found in the MOC where ERS significantly differed for II congruent targets ($M=0.005$) and IC congruent targets

(*M*=0.008), *t*(52)= -3.01, *p*<.001, 95% CI [-0.01, -0.00], II incongruent targets (*M*=-0.004), *t*(52)= 7.43, *p*<.001, 95% CI [0.01, 0.01] and IC incongruent targets (*M*=-0.004), *t*(52)= 6.58, *p*<.001, 95% CI [0.01, 0.01]. Additionally, ERS significantly differed in the MOC for IC congruent targets (*M*=0.008), and II incongruent targets (*M*=-0.004), *t*(52)= 7.78, *p*<.001, 95% CI [0.01, 0.02] as well as IC incongruent targets (*M*=-0.004), *t*(52)= 6.73, *p*<.001, 95% CI [0.01, 0.02].). There was no effect of age in any ROI, suggesting that neural pattern similarity of all four contextual and configural conditions across encoding and retrieval yielded comparable ERS between young and older adults across all *a priori* regions of interest (all *p*'s > .05)[1]. [See Figure 2 for ERS values broken down by age group and condition within each ROI. See Supplemental Table A for ERS values reported for each age group for each ROI.]

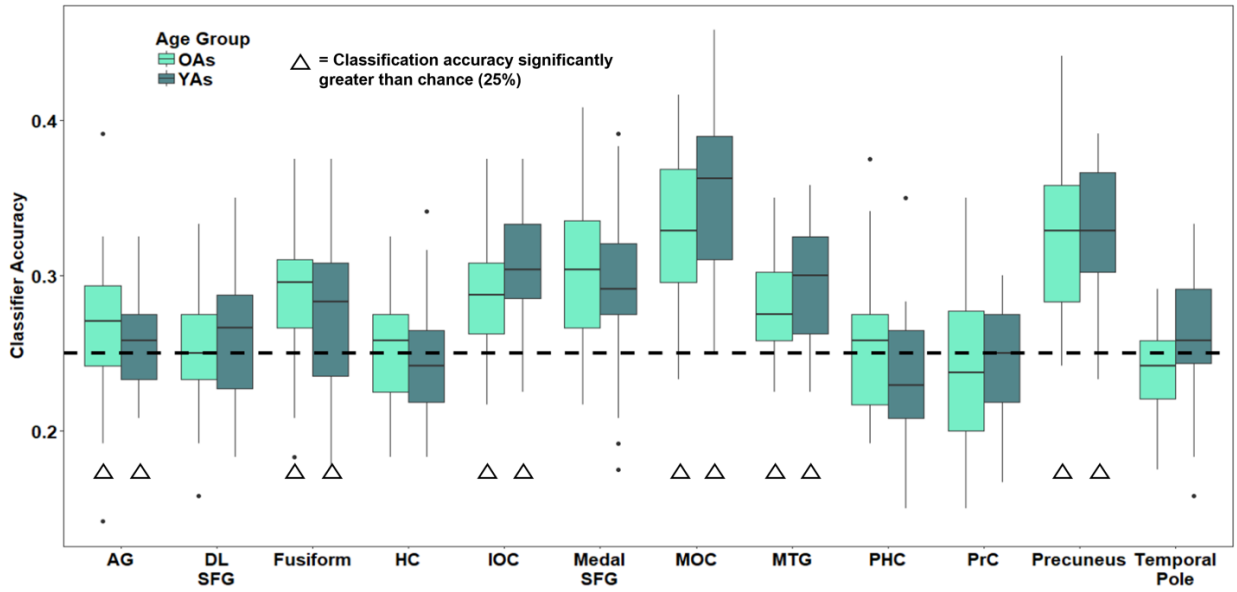

Figure 3. MVPA classifier discriminability across the 4 target conditions within each ROI. Chance classification (25%) is noted by the dashed line. No age differences were detected in any ROI. Inferior Occipital Cortex (IOC); Middle Occipital Cortex (MOC); Middle Temporal Gyrus (MTG); Hippocampus (HC); Parahippocampal Cortex (PHC); Perirhinal Cortex (PrC); Angular Gyrus (AG); Dorsolateral Superior Frontal Gyrus (DLSFG); Medial Superior Frontal Gyrus (SFG); Older Adults (OAs); Younger Adults (YAs).

[11] In order to verify that ERS results were not driven by YAs, we also performed ERS analyses in OAs only. Results were consistent with the findings reported in the reported ANOVA. Specifically, in OAs alone we saw a main effect of condition in the IOC and MOC. See Supplemental Table A for full results

MPVA. On the basis of our previous work showing that the configural context at encoding is a critical factor in classifying neural patterns of activation (Dennis et al., 2019), we next examined the effect of configural congruency on target classification, considering the configural context at encoding (i.e., II congruent, IC congruent, II incongruent, IC incongruent). One sample t-tests were performed within each ROI, collapsed across age groups to determine if the classifier accuracy was above chance (>25%). Results found that the classifier was reliably able to discriminate across the four categories of targets in IOC, (M=0.30), $t(53)=8.52$, $p<.001$, MOC, (M= 0.34), $t(53)=12.87$, $p<.001$, Fusiform, (M=0.29), $t(53)=5.04$, $p<.001$, MTG, (M= 0.29), $t(53)=7.70$, $p<.001$, Precuneus, (M= 0.33), $t(53)=11.56$, $p<.001$, and AG (M=0.26), $t(53)=2.28$, $p=.026$. Follow-up t-tests showed no age difference in any of the foregoing regions, suggesting that the distinctiveness between target conditions yielded comparable discriminability metrics between young and older adults[2].[See Figure 3 for MVPA accuracies reported per region, broken down by age group and Supplemental Table B for MVPA accuracies reported for each age group for each ROI, alongside significance level].

RSA. Because the d' difference between age groups was driven by higher false alarms in older adults, we investigated whether older adults' increased production of false memories was due to underlying neural pattern similarity between targets and related lures and behavior. Specifically, we correlated neural pattern similarity between two pairs of trial types at retrieval: Hits and CRs (representing pattern similarity between different types of veridical memories) and Hits and FAs (representing pattern similarity between different types of "old" responses; i.e., veridical and false memories). We then compared the correlations between trial pairs. In older adults, Hits and

[2] In order to verify that MVPA results were not driven by YAs, we also performed MVPA analyses in OAs only. Results mirror the reported results with OAs showing significant classification in fusiform, IOC, MOC, MTG, precuneus, and medial SFG. See Supplemental Table B for full results.

CRs demonstrated significantly higher pattern similarity than Hits and FAs in all of our ROIs. See Table 2 for relevant statistics.

Next, we correlated the pattern similarity between Hits and FAs with FA rates, and did the same with Hits and CRs and CR rates, in our older sample. We found that while CRs were not correlated with pattern similarity across the Hit and CR trials, pattern similarity across Hits and FAs were significantly correlated with FA rates in the MOC (r= 0.47, p=.013), MTG (r= 0.42, p=.031), fusiform (r= 0.45, p=.017), AG (r= 0.43, p=.024), precuneus (r= 0.47, p=.013), and medial SFG (r= 0.46, p=.016). [See Table A in supplemental materials for complete correlation results]. All results were confirmed with permutation testing.

Discussion

The current study aimed to shed light on the neural processes underlying age-related associative memory deficit. Behaviorally, our results revealed the associative memory deficit was driven by greater false alarm rates in older adults, rather than by a reduction in the hit rate. In alignment with the absence of age deficits in hit rates, we also found no age-related differences in either the relationship between target-related patterns of neural activity across memory phase (as measured by ERS) nor the discriminability of target classification as a function of condition at retrieval (as measured by MVPA). Within both sets of results, we also saw an advantage for representing and processing targets as a function of intact configural congruency across memory phases. Specifically, older adults, like young, exhibited greater correspondence of neural activity between encoding and retrieval for targets that maintained the same configural context across memory phases than targets that did not. This differentiation as a function of configural

congruency was also present at retrieval, whereby both age groups were able to successfully distinguish between target conditions across much of the associative retrieval network. At the same time, as measured by RSA, older adults exhibited overall lower pattern similarity for hits and FAs when compared to hit and CRs. However, age-related increases in associative false memories were associated with the extent of pattern similarity identified between Hits and FAs across visual, frontal, and parietal cortices. Behavioral and multivariate findings will be discussed in turn.

Behavioral Results. Consistent with a wealth of past research (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000; Naveh-Benjamin, Guez, Kilb, & Reedy, 2004; Old & Naveh-Benjamin, 2008a; Overman & Becker, 2009; Overman et al., 2018; Rhodes et al., 2008), older adults exhibited deficits in associative memory compared to younger adults. Specifically, older adults showed overall lower behavioral discriminability, measured by d', between targets and lures in both the congruent and incongruent retrieval conditions (see Figure 3). When breaking down d' and examining hit and false alarm rates, results showed that the foregoing age reductions in d-prime were driven not by age differences in hit rates, by age-related increases in associative false alarms across both congruent and incongruent retrieval conditions. While age-related associative memory deficits are often conceptualized with respect to errors in target detection, the current finding is consistent with past research that also finds errors in lure rejection (i.e., false memories) to underlie age-related associative memory deficits (e.g., Castel & Craik, 2003; Healy et al., 2005; Naveh-Benjamin et al., 2003; Old & Naveh-Benjamin, 2008b; Overman & Stephens, 2013; Rhodes et al., 2008). Moreover, this pattern of results is consistent with the fact that older adults tend to make memory responses based on a feeling of familiarity opposed to

utilizing item-specific details during memory retrieval (e.g., Bastin & Van der Linden, 2006; Davidson & Glisky, 2002). In the present memory study, lure familiarity arises due to the fact that the lures were composed of recombined item-item pairs from encoding, such that all *items* within a lure pair are 'old'. In order to identify a recombined lure as new, one must overcome the item familiarity and respond based on the novel combination of items (Cohn & Moscovitch, 2007; Lepage, Brodeur, & Bourgouin, 2003; Rotello & Heit, 2000). This is generally considered a more difficult evaluation and monitoring process than endorsing a target pair as old.

The current pattern of results suggests that while older adults exhibit little difficulty in recognizing the item-item pairs as 'old', there is an age-related decline in their ability to undertake this more difficult task of identifying the novel association as new, with older adults making more false alarms than younger adults. This is consistent with a reduction in strategic processing at retrieval (Cohn, Emrich, & Moscovitch, 2008). The current set of findings also suggest that this age-related deficit in correctly classifying associative lures is not dependent upon the contextual congruency of the association at retrieval. That is, whether the configural context of the lure is consistent or inconsistent with the way in which the individual items were presented at encoding (II or IC) had no effect on the false alarm rates in older adults. Given that older adults demonstrated similar hit rates to younger adults but higher false alarm rates, it appears that older adults' hits are mainly an outcome of reliance on familiarity. As such, the results are consistent with previous work showing that older adults have difficulty employing strategic processing at retrieval to reject similar but novel information (i.e., lack of recall-to-reject processing) (Bowman & Dennis, 2015; Pierce, Waring, Schacter, & Budson, 2008).

ERS analyses. To understand why older adults endorse associative lures as 'old' pairs at higher rates than younger adults, we first examined whether there were age differences in how encoded information related to targets was recapitulated during retrieval. Specifically, following earlier work with younger adults (Gerver et al., 2020) we examined the similarity of neural patterns of target pairs as a function of both the encoding configuration and configural congruency across memory phases. We hypothesized that, consistent with prior research in item memory (Chamberlain, Bowman, & Dennis, under review; Folville et al., 2020; Hill, King, & Rugg, 2021; Trelle, Henson, & Simons, 2019), older adults would exhibit reduced ERS of target pairs, particularly for contextual incongruent targets, compared to younger adults. We theorized that such a reduction in the transfer of associative information from encoding to retrieval would contribute to the reduced distinctiveness of targets and lures within retrieval itself. While our results showed that in older, like younger adults (Gerver et al., 2020), both configural context and configural congruency were critical factors in examining ERS within visual regions, we observed no age-related decline in ERS with any examined ROI. Specifically, breaking down the effect of condition within IOC and MOC, ERS was higher for the congruent conditions compared to both incongruent conditions. As noted in Gerver et al 2020, these findings suggest that when an associative target is presented in the same configural context across both memory phases, it evokes greater recapitulation of visual processes associated with the encoding episode than if the configural context is altered amongst the item-item pair. The current findings extend this work to aging by showing the same pattern of configural congruency effects is present for target stimuli in older adults. The absence of age differences in this pattern of ERS across target conditions suggests that, like younger adults, older adults take advantage of stability in the configural context across memory phases when reinstating memory representations associated

with associative pairs across memory phases. While we didn't find that that ERS correlated with behavioral metrics of associative memory success, it is likely that this consistency for congruent pairs supports identification of targets using both item-item details and general familiarity of the associative configurations.

The lack of age differences in ERS within visual regions (or in any other ROI), suggests that aging does not affect how information from encoding is being recapitulated during retrieval in the older adults within our sample. While this finding stands in contrast to past research that has observed age-related decline in the reinstatement of target processing, (Chamberlain et al., under review; Folville et al., 2020; Hill et al., 2021; Trelle et al., 2019), our current behavioral results also did not replicate age-related deficits in recollection observed in these previous studies. That is, our ERS finding parallels our behavioral results wherein we found no age-related decline in hit rates. Taken together, the results show consistent support for an absence of an age deficit in how targets are processed across memory phases when contextual congruency is present to support target identification, highlighting the beneficial role of encoding-retrieval contextual configuration congruency. One caveat to this conclusion is that ERS analyses do not account for the specificity of the information that is carried over from encoding to retrieval or whether the same type of processing is occurring within the same ROIs across age groups. They merely account for similarity in neural patterns within an individual. Thus, it cannot be concluded that both age groups encode and maintain the same information from encoding to retrieval, simply that there is no age difference in the relative similarity in patterns of encoding and retrieval activity across age groups. It may be that younger adults encode and maintain more nuanced or detailed associative representations compared to older adults, whereas older adults process information in a more generic or gist-based manner (e.g., Pierce, Sullivan, Schacter, &

Budson, 2005; Schacter, Koutstaal, & Norman, 1997; Stephens & Overman, 2018; Tun, Wingfield, Rosen, & Blanchard, 1998). With more advanced analyses, we will hopefully be able to assess the specificity of the memory representations across age groups.

MVPA analyses. A similar result with respect to associative configuration and aging was found when examining target discriminability at retrieval. That is, using MVPA we found that a classifier was able to distinguish between targets with respect to both the configural context in which they were originally encoded and whether that context was reinstated at retrieval in regions in the occipital cortex including IOC, MOC, and fusiform cortex, as well as MTG, AG and precuneus. Critically, this discrimination amongst target conditions was observed irrespective of behavior such that significant classification was based on all target trials, and not simply accurate trials. This suggests that there is an inherent difference in the cognitive and neural processing of the four target trial types, based on their current and past configural history, that is upheld within the both the occipital and parietal cortices. The pattern of results across trial types also suggests that the diagnosticity of the information that is encoded (Stephens & Overman, 2018) is increased when the configural congruency matches between encoding and retrieval (i.e., II and IC congruent configurations). This difference may reflect reduced demands on strategic processing, which may be particularly beneficial to older adults.

This finding may be rooted in the perceptual differences across configural contexts within the current set of target trials. That is, we previously noted (Gerver et al., 2020) that the current pattern of discriminability within occipital and parietal cortex is consistent with work highlighting the role of the occipital cortex in processing the physical and categorical properties of visual stimuli (Dennis et al., 2019; Harrison & Tong, 2009; Kanwisher, McDermott, & Chun, 1997; Kapadia, Westheimer, & Gilbert, 2000) as well as role of the parietal cortex in processing

spatial information stimuli (Crowe, Averbeck, & Chafee, 2010; Johnson, McDuff, Rugg, & Norman, 2009; Kuhl & Chun, 2014; Vilberg & Rugg, 2008). The current results extend this finding to aging, showing that classification accuracy across target trials is maintained and did not differ as a function of age. Overall, the results suggest that the specificity of the target representations is preserved in aging in regions that support associative memory retrieval.

On one hand, the absence of age differences in the overall distinctiveness of target-related information during information was surprising. Given age deficits in recollection of item-specific information (Bastin & Van der Linden, 2003; Davidson & Glisky, 2002) and univariate analyses of retrieval success activity (Dennis, Bowman, & Peterson, 2014; Dennis, Kim, & Cabeza, 2008; Dulas & Duarte, 2014; Gutchess et al., 2005; St Jacques, Rubin, & Cabeza, 2012) we might have expected that both the correspondence between encoded and retrieved representations and the specificity of target representations would also exhibit age-related deficits. Such a result would fit with accounts of memory in aging that posit older adults do not utilize detailed mnemonic representations during retrieval tasks to endorse targets (Koutstaal, 2003) as well as work showing age-related dedifferentiation of category-level information at retrieval (Horne, Koen, Hauck, & Rugg, 2020; Koen, Srokova, & Rugg, 2020; St-Laurent, Abdi, Bondad, & Buchsbaum, 2014; Zheng et al., 2018). In contrast, the current results suggest no age-related decline in the specificity of activation patterns across target categories, perhaps due to a relatively strong contribution of visual configuration to the activation patterns in both age groups that dampened the ability to detect subtle age-related differences in the patterns.

On the other hand, the absence of age differences in the distinctiveness of target-related information during retrieval is consistent with some prior work in aging (Thakral, Wang, & Rugg, 2017; Wang, Yue, & Huang, 2016), suggesting that the specificity of such information is

stable as people advance in age. Additionally, the current results support and extend our previous findings examining associative encoding, highlighting the importance of configural context to associative encoding in both younger and older adults (Dennis et al., 2019). Specifically, previous multi-voxel pattern analyses focusing solely on associative encoding configurations (II vs. IC during encoding) of the current data found that the distinctiveness underlying encoding processing was shown to not diminish in aging. The current results further suggest that this distinctiveness is maintained at retrieval as well. The results are also consistent with recent work by Trelle and colleagues (2019) who found little age differences in neural processes underlying associative hits compared to correct rejections. They suggest that, when retrieval demands are low and retrieval support is high, such is the case of intact pair recognition, age-related differences in neural mechanisms supporting associative retrieval are minimized. Rather, demands invoked by low retrieval support and the need for increased monitoring and evaluation, such is the case with recombined lures, will lead to greater difficulties in aging and differentiation in processing compared to younger adults. The preserved discriminability of targets within the visual cortex across age in our study may reflect the robustness of the role configural congruency plays in information processing across the lifespan. Furthermore, the fact that there were no age differences in classification accuracies amongst targets within IOC and MOC supports the idea that the quality of representations is similar across age groups. That is, if older adults maintained overall lower fidelity representations of targets at retrieval, then one would expect classification accuracies to be reduced in aging. Alternatively, older adults could be maintaining lower fidelity representations, yet ones that are equally as effective at discriminating between target trials. Again, advances in our ability to understand what is being

represented at the neural level is needed to truly understand how processing differs between age groups.

RSA analyses. While the investigation of target-related patterns of activity indicates stability across age, the possibility of age differences in the representation of lures remains unexamined, as does the relationship of lure representation to false alarm rates. To investigate the neural processes underlying older adults' reduced ability to distinguish between targets and lures, we used pattern similarity analyses to determine how the relationship between hits and false memory processing differs from that of hits and correctly rejected lures. We also directly investigated whether this relationship was related to false memory rates within our older adult sample. Our results showed that ROIs throughout occipital, prefrontal, and parietal cortex exhibited significantly greater similarity when comparing patterns of neural activity underlying hits and correct rejections than neural patterns underlying hits and erroneous false alarms (see Figure 3). These results suggests that, in aging, neural patterns underlying veridical memories, in any form, are more similar than those corresponding to the same behavioral response of 'old'. This may be reflective of overlap that exists between target identification and recall-to-reject strategies in recognition memory (Brainerd, Reyna, Wright, & Mojardin, 2003; Gallo, Bell, Beier, & Schacter, 2006; Rotello & Heit, 2000). That is, in order to overcome the familiarity inherent in targets and recombined lures in associative memory retrieval, one needs to recall the specific correspondence between the items within the association and not merely the past occurrence of the individual items. The current results suggest that when this process of lure rejection is successful older adults exhibit higher similarity between hits and the lures being correctly rejected than between hits and lure trials where the novel lure pair is erroneously identified as old.

However, this similarity in veridical processing did not predict behavior, specifically correct rejections, in our aging group. Rather, high rates of false memories in the older adults were related to the similarity in neural patterns of activity underlying Hits and FAs. This relationship was observed throughout the occipital, prefrontal, and parietal ROIs that were identified as showing overall reduced Hit and FA- compared to Hits and CR- similarity in the previous analysis. While the forgoing differences across trial types were not predicted, this correlation is precisely in line with our predictions that greater similarity in the processing of target and lures would lead to memory errors for the associative lures. Specifically, we theorized that older adults would have difficulty in maintaining detailed representations of encoded information to be used at the time of retrieval and that similarity of target and lure processing would underlie associative false memories.

In line with well documented age-related deficits in recollection, yet intact familiarity (e.g., Bastin & Van der Linden, 2003; Davidson & Glisky, 2002), associative memory tests necessitate retrieval of specific item-item associations in order to correctly reject recombined lures during retrieval. When the strength of these contextual links is weak or unavailable at retrieval, older adults are likely to make use of more general, and less detail specific, representations when monitoring and evaluating the associative pair. Regarding episodic representations, the MTG has been shown to be involved in processing the gist associated with episodes (Simons et al., 2005; Wise & Price, 2006) and MOC in processing more general properties of stimuli (Slotnick & Schacter, 2004, 2006; Vaidya, Zhao, Desmond, & Gabrieli, 2002). Given the correspondence in the relationship between Hit and FA representations and false memory rates in these regions, results suggest that the extent to which related lured invoke

the general feeling of oldness associated with past veridical item-item associations, the more likely they will evoke an erroneous response of "old" at retrieval.

Yet the similarity of representations within these lower-level processing regions is not alone in creating this memory error. The current results also suggest that similarities in the manner in which a Hit and FA are processed within higher level monitoring and evaluation regions, including both the medial SFG and parietal cortex, is also related to increased false alarm rates in older adults. The correlation between Hit and FA RSA in the both the medial SFG and parietal cortex and false memories is particularly interesting given that these regions have consistently been identified in false memory studies across a wide variety of paradigms (for a metanalysis see Kurkela & Dennis, 2016), including studies involving older adults (Dennis, Bowman, et al., 2014; Dennis & Turney, 2018; Webb & Dennis, 2019). Noted above, the role of the medial SFG during false memory retrieval has been linked to part of a frontal-parietal cognitive control network responsible for the evaluation and monitoring of critical lures (Atkins & Reuter-Lorenz, 2011; Dennis, Bowman, & Vandekar, 2012; Dennis, Johnson, & Peterson, 2014; Garoff-Eaton, Kensinger, & Schacter, 2007; Hofer et al., 2007; Iidaka, Harada, Kawaguchi, & Sadato, 2012; Kensinger & Schacter, 2006; Slotnick & Schacter, 2004; von Zerssen, Mecklinger, Opitz, & von Cramon, 2001). Included in this work researchers have linked processing within the medial prefrontal cortex with top-down retrieval monitoring in the absence of a strong sensory signal (Dennis, Bowman, et al., 2014), in the face of competing representations (Iidaka et al., 2012), and when there is a strong conceptual similarity between targets and lures (Garoff-Eaton et al., 2007). Both the medial SFG and parietal cortex (BA 40) have also been found active in a previous study of associative false memories from our lab (Dennis, Johnson, et al., 2014). The current results extend this univariate work from younger

adults to show not only that activity within these regions support false associative memories in aging, but that the extent to which lure processing within the medial SFG and parietal cortex corresponds to that underlying a veridical memory response, the greater the likelihood of a false memory. Given the current finding, and the strong relationship between the medial SFG and parietal cortex and false memories in younger adults (e.g., Kurkela & Dennis, 2016), the role of this fronto-parietal network should continue to be explored as a significant contributor to memory errors across the lifespan.

Interestingly, the MTL ROIs were among the very few regions within the associative memory network we interrogated that did not exhibit differences in pattern similarity across trial types, or show a correlation with memory errors in aging. While common MTL activity has been found in previously false memory studies (Dennis et al., 2012; Gutchess & Schacter, 2012; Schacter et al., 1996; Stark, Okado, & Loftus, 2010; von Zerssen et al., 2001), there is often also greater activation in MTL regions when directly comparing Hits and FAs (Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Dennis et al., 2012; Dennis, Kim, et al., 2008; Kahn, Davachi, & Wagner, 2004), suggesting that commonalities within MTL ROIs are also accompanied by differential processing between veridical and false memories. However, we find no evidence in our current sample using any analysis methods for condition or veracity differences within the MTL. While this distinction may be reduced in aging, the work noted above, as well as prior work investigating such processes as recall to reject (Bowman & Dennis, 2016; Trelle et al., 2019) and pattern completion and separation (Yassa et al., 2011; Yassa & Stark, 2011) suggests that patterns of activation and connectivity within subregions of the MTL are sensitive to this distinction. High-resolution imaging, as well as a specific focus on what experimental factors lead to these differences, is likely needed to elucidate how regions within the MTL respond to

related lures and contribute to memory errors in aging. An additional point to consider regarding the absence of MTL findings is that the size of the RSA metrics (both Hit and CR overlap as well as Hit and FA overlap) within MTL regions was qualitatively smaller than that observed in all other ROIs. While we cannot make any definitive conclusions about this difference, we do note that it may be an area worth exploring in future work.

General Conclusions

The current results shed light on the neural processes underlying age-related associative memory deficit. Behaviorally, our results highlight the role of false memories of recombined pairs at retrieval as a significant, contributing factor to age deficits in associative memory performance. That is, the associative memory deficit was driven by greater false alarm rates in older adults, rather than by a reduction in the hit rate. Paralleling the absence of age deficits in hit rates, we also found no age-related differences in either the relationship between patterns of neural activity underlying targets across memory phase (as measured by ERS) nor the discriminability of target classification as a function of condition at retrieval (as measured by MVPA). Within both sets of results we also saw an advantage for representing and processing targets as a function of intact configural congruency across memory phases. Specifically, older adults, like young, exhibited greater correspondence of neural activity between encoding and retrieval for targets that maintained the same configural context across memory phases than targets that did not. This differentiation as a function of configural congruency was also present at retrieval, whereby both age groups were able to successfully distinguish between target conditions across much of the associative retrieval network. The results highlight the strength of configural arrangements as part of the associative memory trace and the importance of maintaining configural congruency

across memory phases as a means to bolster the transfer of associative information across phases in older adults. This finding is consistent with earlier behavioral work from our collaborative group (Overman, Dennis, McCormick-Huhn, Steinsiek, & Cesar, 2019; Overman et al., 2018) where we found that both the manner of encoding presentation as well as congruency of configural display was critical to memory success. Importantly, the current results suggest that the strength of this representation is preserved across the adult lifespan.

At the same time, age-related increases in associative false memories were accompanied by overall lower pattern similarity for hits and FAs when compared to hit and CRs. This difference between a consistent behavioral response (a.k.a. “old”) and a correct memory decision suggests that there is more neural uniformity associated with veridical memory decisions across the associative memory network than for trials that share a similar behavioral response but differ with regard to memory veracity. Interestingly, in these same regions, it was the overlap in neural pattern similarity across hits and FAs that correlated with false memory rates in older adults. This latter finding speaks directly to the idea that, when older adults experience a high correspondence in neural processing between targets and related lures, they are more apt to erroneously identify the lure as previously studied. Thus, the current results continue to underscore the importance of understanding errors of commission in aging in order to account for age-related memory decline.

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