Age Differences in False Memory: The Importance of Retrieval Monitoring Processes and Their Modulation by Memory Quality

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Older adults are more likely than younger adults to falsely recall past episodes that occurred differently or not at all. We examined whether older adults' propensity for false associative memory is related to declines in postretrieval monitoring processes and their modulation with varying memory representations. Younger ($N = 20$) and older adults ($N = 32$) studied and relearned unrelated scene-word pairs, followed by a final cued recall that was used to distribute the pairs for an associative recognition test 24 hours later. This procedure allowed individualized formation of rearranged pairs that were made up of elements of pairs that were correctly recalled in the final cued recall ("high-quality" pairs), and of pairs that were not correctly recalled ("low-quality" pairs). Both age groups falsely recognized more low-quality than high-quality rearranged pairs, with a less pronounced reduction in false alarms to high-quality pairs in older adults. In younger adults, cingulo-opercular activity was enhanced for false alarms and for low-quality correct rejections, consistent with its role in postretrieval monitoring. Older adults did not show such modulated recruitment, suggesting deficits in their selective engagement of monitoring processes given variability in the fidelity of memory representations. There were no age differences in hippocampal activity, which was higher for high-quality than low-quality correct rejections in both age groups. These results demonstrate that the engagement of cingulo-opercular monitoring mechanisms varies with memory representation quality and contributes to age-related deficits in false associative memory.

Keywords: aging, episodic memory, hippocampus, insula, anterior cingulate

The ability to remember past episodes rich in contextual detail declines in later adulthood. Older adults remember fewer details of previously encountered events (Spencer & Raz, 1995), and are less likely to remember the associative bindings among different features of an episode (Old & Naveh-Benjamin, 2008a). At the same time, older adults show an increased propensity to remember episodes that are partially or entirely false (Devitt & Schacter, 2016; Fandakova, Shing, & Lindenberger, 2013a; Jacoby & Rhodes, 2006; Shing, Werkle-Bergner, Li, & Lindenberger, 2009). In fact, age effects on false memory may be even stronger than age effects on true memory (Bender, Naveh-Benjamin, & Raz, 2010; Fandakova et al., 2013b; McCabe, Roediger, McDaniel, & Balota,

2009; Old & Naveh-Benjamin, 2008b). While the literature has paid considerable attention to understanding age differences in true memory, the neural mechanisms of false associative memory in aging remain largely elusive. In the present study, we investigated how the involvement of monitoring processes at retrieval is modulated by the availability of bound representations of associative information, and whether age differences in selective modulation contribute to higher false memory in late adulthood.

Age-related deficits in the ability to monitor the outcomes of memory retrieval may play a key role for age-related increases in false associative memory (Fandakova, Lindenberger, & Shing, 2014; Gutchess et al., 2007; Mitchell & Johnson, 2009). Monitoring processes are recruited when uncertainty is high and errors are likely (e.g., Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Fandakova et al., 2016): for example, when only partial information is available at retrieval or when cues elicit strong feelings of familiarity (e.g., Dobbins, Foley, Schacter, & Wagner, 2002; Rugg, 2004). Accordingly, activity in frontal-parietal and cingulo-opercular regions supporting monitoring and control is enhanced for different types of false memories (Dennis, Johnson, & Peterson, 2014; Kim & Cabeza, 2007; Okado & Stark, 2003; Slotnick & Schacter, 2004) as well as for correct rejections of similar lures such as rearranged pairs, in which both parts of a pair are familiar but were not studied together (Achim & Lepage, 2003; Bowman & Dennis, 2016; Fandakova et al., 2014; Giovanello & Schacter, 2012; Lepage, Brodeur, & Bourgouin, 2003). Greater frontal engagement in the correct rejection of rearranged pairs is thought to reflect a recall-to-reject process (e.g., Gallo, 2004; Gallo, McDonough, & Scimeca, 2010), whereby the presentation of a lure that shares features with the target triggers the recall of target information that is utilized to identify the mismatch between the lure and the retrieved target, resulting in a correct rejection of the lure.

Older adults show diminished monitoring of memory outcomes, especially when presented with lure or contextual information that is highly similar to the originally studied information (e.g., Fandakova et al., 2013b; Gutchess et al., 2007; Hay & Jacoby, 1999; Kliegl & Lindenberger, 1993). Consistent with an age-related decline in recall-to-reject (e.g., Gallo, Bell, Beier, & Schacter, 2006), older adults show reduced fronto-parietal activity when correctly rejecting highly familiar associative information, which places increased demands on retrieval monitoring (e.g., Duarte, Graham, & Henson, 2010; Duarte, Henson, & Graham, 2008; Dulas & Duarte, 2016; Fandakova et al., 2014; McDonough, Wong, & Gallo, 2013).

Detecting novel configurations, as in the case of rearranged pairs, also involves the medial temporal lobe (MTL), and the hippocampus, in particular, which may reinstate stored patterns and detect mismatches between current input and stored mnemonic representations (e.g., Kumaran & Maguire, 2007; Rotello, Macmillan, & Van Tassel, 2000; Turk-Browne, Simon, & Sederberg, 2012). While hippocampal operations may facilitate recall-to-reject when a bound representation between two items was successfully formed, they may impede recall-to-reject when binding of items in a coherent memory representation failed, resulting in high item familiarity and increased demands on monitoring processes. Thus, monitoring processes supporting recall-to-reject during associative recognition may be selectively recruited depending

on the fidelity or quality of the underlying bound memory representations.

Investigating how representation quality, defined as the successful formation of a bound associative representation, modulates monitoring processes is particularly pertinent in the context of aging (Sander, Lindenberger, & Werkle-Bergner, 2012; Shing et al., 2010). It has been proposed that older adults have specific deficits in the ability to form and retrieve associations among specific contextual details (e.g., Naveh-Benjamin, 2000). Furthermore, while recollection of target details declines in old age, familiarity, or recognition without accompanying contextual information, is relatively preserved (Koen & Yonelinas, 2014; Light, Prull, Voie, & Healy, 2000). These binding deficits are accompanied by functional and structural changes in the hippocampus (e.g., Foster, Picklesimer, Mulligan, & Giovanello, 2016; Persson et al., 2012; Raz et al., 2005), and contribute to false recognition in older adults (e.g., Daselaar, Fleck, & Cabeza, 2006; Dennis, Bowman, & Peterson, 2014; Dennis, Kim, & Cabeza, 2008; Duarte, Henson, & Graham, 2008; Duverne, Habibi, & Rugg, 2008; Giovanello, Kensinger, Wong, & Schacter, 2010). However, the extent to which variability in binding successes across episodes modulates the engagement of monitoring processes differentially in younger and older adults is currently unclear.

In the present study, we developed a novel paradigm (Figure 1) to track the quality of associative memory representations within individuals and to assess age differences in false memory and in modulation of brain activity associated with monitoring processes at retrieval. We used repeated cued-recall tests with feedback to track learning of scene-word pairs in younger and older adults. Participants studied such pairs by building a common image of the pair (cf., Shing, Werkle-Bergner, Li, & Lindenberger, 2008). Thereafter, each pair was recalled with feedback once (younger adults) or twice (older adults): here, the scene served as a cue to recall the corresponding word, and the original pair was presented again for restudy irrespective of retrieval success. All participants underwent a final cued-recall phase without feedback that was used to sort the studied pairs for each individual participant into (a) successfully remembered (high-quality) pairs, or (b) unsuccessfully remembered (low-quality) pairs. Approximately 24 hour later, younger and older adults underwent an associative recognition test during functional MRI (fMRI) consisting of intact targets and rearranged lures from both high-quality and low-quality pairs.

Using this paradigm, we investigated how variability in the quality of memory representations, defined as failure versus success in forming a bound associative representation, modulates the engagement of monitoring processes, and the resulting effects on false memory in younger and older adults. As monitoring processes are particularly important when uncertainty is high and errors likely, we expected frontal regions associated with monitoring processes to show greater activity for false alarms to rearranged pairs as well as for correct rejection of low-quality pairs. This pattern should reflect greater demands on monitoring processes when item familiarity is high but a bound associative representation was not formed successfully. We hypothesized that age-related declines in monitoring processes would result in reduced modulation of frontal activity for the correct rejection of low-quality and high-quality pairs in older adults. In line with hippocampal engagement in recall-to-reject, we expected that correct rejection of high-quality rearranged pairs, for which partici-
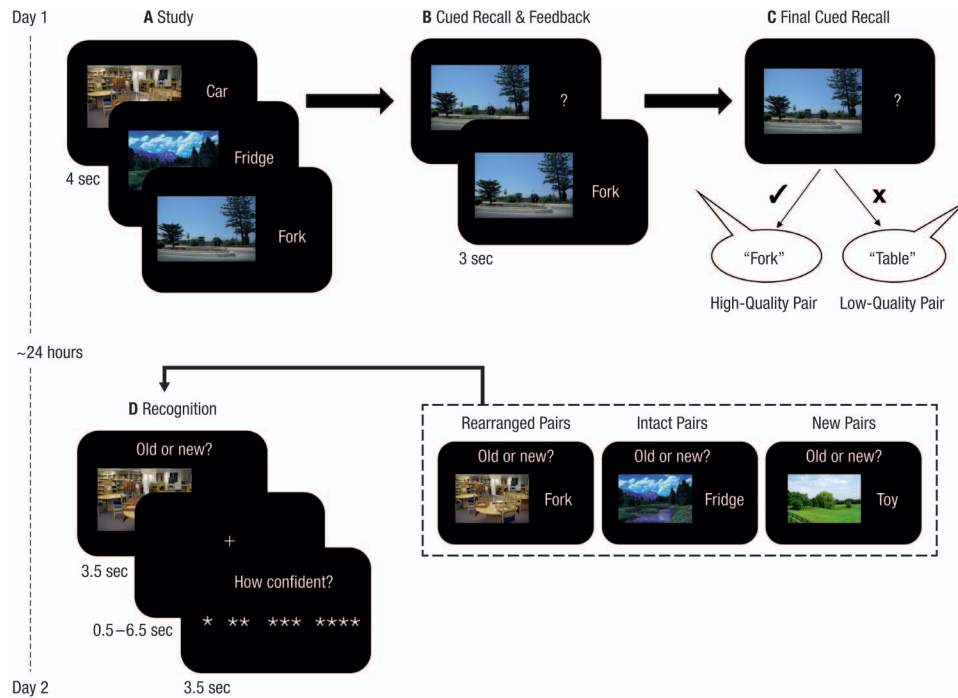
Figure 1. Experimental paradigm. (A) During study participants were instructed to remember 440 scene-word pairs (younger adults) or 280 scene-word pairs (older adults) by using an elaborative imagery strategy. (B) During the cued-recall and feedback phase each scene-word pair was recalled with feedback once (younger adults) or twice (older adults). The scene served as a cue to recall the corresponding word and the original pair was presented again for restudy irrespective of retrieval success. (C) In the final-recall phase scenes served as cues to recall the corresponding word, but no feedback was provided. Recall success in this phase was used to sort scene-word pairs into high-quality (i.e., corresponding word correctly recalled) or low-quality (i.e., corresponding word was either not recalled or inaccurate) pairs. (D) The recognition phase took place approximately 24 hour later. Participants were presented with intact, rearranged, and new pairs and were instructed to decide if the corresponding pair was old (i.e., studied on Day 1) or new (i.e., not studied on Day 1), followed by a confidence rating. See the online article for the color version of this figure.

pants had formed a bound representation of the original pair, would involve greater hippocampal activity due to the reinstatement of the bound representation to facilitate recall-to-reject. Based on their associative binding deficit, one could predict decreased hippocampal modulation in older adults. Alternatively, when binding success versus failure is defined within each individual participant, modulation effects could be similar, in spite of possible differences in absolute hippocampal engagement.

Materials and Method

Participants

The original sample consisted of 30 younger adults and 44 older adults. One younger adult and three older adults did not complete the study for technical reasons, resulting in an effective sample of 29 younger adults ($M(SD)_{age}$ = 24.7(2.12), 20–28 years) and 41 older adults ($M(SD)_{age}$ = 71.0(2.21), 66–76 years). A total of 20 younger adults (10 females) and 32 older adults (17 females) provided a minimum of 10 false alarms and 10 correct rejections to rearranged pairs for neuroimaging analyses. All participants were right-handed native German speakers, had normal or

corrected-to-normal vision, no history of psychiatric or neurological disease, and did not take psychiatric medication. Older adults were screened with the Mini-Mental State Exam (MMSE; Folstein, Folstein, & McHugh, 1975) and none had a value below the threshold of 26 points ($M(SD)_{MMSE}$ = 29.3(1.03)). The ethics committee of the Deutsche Gesellschaft für Psychologie approved the study.

Stimuli

A total of 580 picture stimuli were selected (500 × 333 pixels, controlled for luminance), such that half depicted indoor scenes and the other half depicted outdoor scenes, with no animals or humans present in the scenes. Words were concrete nouns with two phonetic syllables four to eight letters long, selected from the CELEX database of the Max Planck Institute for Psycholinguistics (http://celex.mpi.nl/). Words that were similar (e.g., castle vs. palace), abstract (e.g., date), referring to a category (e.g., animal) or with the highest frequency according to the "Mannheim frequency per million" were excluded. The final set of 580 words had a mean length of 5.51 letters and a mean frequency of 17.27.

Experimental Paradigm

The experimental paradigm involved two sessions on two consecutive days approximately 24 hour apart (see Figure 1).

Day 1

Instruction. Prior to the main task, participants were instructed to memorize random scene-word pairs using an imagery strategy. They were encouraged to generate integrated images of the pairs that were vivid and creative. Participants practiced using the imagery strategy on 10 trials that were not part of the main experiment.

(A) Study. During the initial learning phase, scene-word pairs were presented on a black background for 4 s. Participants were instructed to remember the pair and to indicate how well they could form an integrated image of the scene-word pair on a 4-point scale.

(B) Cued recall and feedback. Cued-recall blocks (one for younger adults, two for older adults) followed immediately after study. Scenes served as cues to verbally recall the associated word. Recall time was not constrained. Recall accuracy was immediately coded by the experimenter. Independent of recall accuracy, the correct scene-word pair was presented again for 3 s, fostering further learning of the pair.

Based on the results of pilot studies, task difficulty was adjusted between the age groups in two ways to achieve a recall success of approximately 50% in each group. First, younger adults studied a total of 440 pairs, whereas older adults studied a total of 280 pairs. Second, younger adults completed one cued-recall block with feedback, whereas older adults completed two cued-recall blocks with feedback.

(C) Final cued recall. Participants completed a final cued-recall phase without feedback. Scenes served as cues to recall the associated word. In contrast to the previous cued-recall blocks, no feedback was presented.

Electroencephalographic (EEG) recordings from all participants were assessed during all phases on Day 1, but EEG data are not reported here.

Day 2

Approximately 24 hour after learning on Day 1, participants completed an associative recognition task during scanning. They were presented with a total of 140 intact scene-word pairs (i.e., scenes and words were presented together just as they had been on Day 1), 140 rearranged pairs (i.e., scenes and words had been presented on Day 1, but as parts of different pairs; both parts were used in different pairs), and 120 new pairs (i.e., neither the scene nor the word had previously been seen).

The intact and rearranged pairs were constructed based on individual performance on the final cued-recall phase on Day 1 (see Figure 1). We sorted all scene-word pairs presented on Day 1 into two categories: (1) high-quality pairs, defined as pairs for which participants recalled the correct word when presented with the corresponding scene during the final cued recall on Day 1; (2) low-quality pairs, defined as pairs for which participants did not recall the correct word during the final cued recall. We aimed for 140 scene-word pairs of each category (high and low quality) to be

equally distributed across the intact and rearranged pairs such that each of the intact and rearranged pair groups contained 70 high-quality and 70 low-quality pairs. For younger adults, we randomly chose 140 high-quality pairs and 140 low-quality pairs from the larger set of studied pairs. If younger adults' learning success did not allow this, we split the available high- and low-quality pairs in half between intact and rearranged pairs. For older adults, all studied pairs were used on Day 2. All high-quality and low-quality pairs were divided equally between the intact and rearranged pair conditions for each participant. Thus, all participants were presented with a total of 280 trials. Since trials were equally distributed across intact and rearranged pairs, counts of high- and low-quality intact pairs were identical to those of rearranged pairs.

During the recognition task on Day 2, scene-word pairs were presented for 3.5 seconds, and participants were instructed to decide whether the pair was old (i.e., an intact pair) or new (i.e., a rearranged or new pair). Participants were then asked to indicate how confident they were in their decision on a 4-point scale. Jittered fixation-cross periods were presented after each memory, and each confidence trial (500–6,500 ms) to allow for separation of the blood oxygenation level dependent (BOLD) responses corresponding to the memory and confidence phase of each trial. The associative recognition task was completed in five identical blocks consisting of 80 recognition trials (28 intact, 28 rearranged, 24 new pairs). In addition, participants were presented with 20 active baseline trials in each block (for a total of 100 baseline trials across 5 runs) that were randomly interspersed among the memory trials. Here, participants pressed either the left or right button while viewing one of four possible scrambled pictures together with the letters "XXXX" or "YYYY" (randomly picked and paired), followed by a baseline confidence decision in which they pressed the button corresponding to a randomly highlighted number of stars.

MRI Data Acquisition

MRI data were collected on a Siemens 3T Trio Magnetom. Functional data were acquired using an echo-planar imaging sequence (repetition time [TR] = 2,000 ms, echo time [TE] = 30 ms, flip angle = 80°, field of view [FOV] = 216 mm, voxel size = $3 \times 3 \times 3$ mm^3, 36 slices). The first four volumes of each run were discarded to achieve a steady state of tissue magnetization. A high-resolution T1-weighted MPRAGE sequence (TR = 2,500 ms, TE = 4.77 ms, FOV = 256 mm, voxel size = $1 \times 1 \times 1$ mm^3) was collected for registration of the functional images.

Analysis

Behavioral analysis. All reported results are based on the sample of participants that could be included in the neuroimaging analyses (N = 20 younger adults, N = 32 older adults). Individual memory accuracy on the final cued-recall test of Day 1 was calculated as a percentage of correctly recalled words when presented with the corresponding scene out of all presented items (440 for younger adults and 280 for older adults). Recognition performance on Day 2 was calculated separately for high- and low-quality pairs as the proportion of hits (i.e., correct "old" response to an intact pair) minus false alarms (i.e., incorrect old response to a rearranged pair; Snodgrass & Corwin, 1988). To further charac-

terize age differences in true and false memory, we analyzed hit rates and false alarm rates separately. All reported results regarding age differences in true and false memory performance were replicated in the complete study sample ($N = 30$ younger adults, $N = 44$ older adults), indicating that the reported age differences are unlikely to be accounted for by sample selection. The alpha level for all reported statistical analyses was set to $\alpha = .05$ with a false discovery rate correction for multiple comparisons of post hoc tests (indicated by p_{corr}). The Huynh-Feldt corrected degrees of freedom and significance values are reported when the sphericity assumption was not met (Huynh & Feldt, 1976).

fMRI analyses. The fMRI data were analyzed using FSL FEAT (FMRIB's Software Library, http://www.fmrib.ox.ac.uk/fsl; Smith et al., 2004). Preprocessing included nonbrain tissue removal, slice-time correction, motion correction, and spatial smoothing using a 6-mm full-width half-maximum Gaussian filter. Prewhitening was used to account for the intrinsic temporal autocorrelation of BOLD imaging. A high-pass temporal filter (Gaussian-weighted straight-line fitting, $\sigma = 50$ s) was applied to remove low-frequency artifacts. Functional data was registered to high-resolution structural and to standard images using FLIRT (Jenkinson & Smith, 2001). Individual time series were modeled with separate regressors for correct rejections of low- and high-quality rearranged pairs, false alarms to rearranged pairs (collapsing high- and low-quality pairs due to low numbers of false alarms for high-quality pairs), and correct rejections of new pairs. These events were convolved with a canonical hemodynamic response function that modeled the duration of the event using a double-gamma hemodynamic response function. Hits for intact pairs (separately for low- and high-quality pairs), misses for intact pairs, false alarms to new trials, confidence responses, and trials with no response were modeled as regressors of no interest. Six motion parameters were included in the model to regress out effects of head motion.

Contrast images were computed for each run per participant, spatially normalized, transformed into Montreal Neurological Institute (MNI) standard space and submitted to a within-subject fixed-effects analysis across the five blocks. Higher-level analysis across subjects was carried out using a mixed-effects model in FSL (FLAME; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004).

First, we sought to identify the brain regions selectively involved in the correct rejection or the false recognition of associative information. To this end, we performed an exploratory whole-brain analysis comparing correct rejection of rearranged pairs ($CR_{rearranged}$) > false alarms to rearranged pairs ($FA_{rearranged}$) across all participants (i.e., collapsing across younger and older adults) to identify brain regions involved in the successful detection of novel combinations of familiar items. The whole-brain contrast $FA_{rearranged} > CR_{rearranged}$ was performed to identify brain regions engaged in false recognition of rearranged pairs (Table 1 displays trial counts). Analyses were performed with Z (Gaussianized T/F) statistic images thresholded at $Z > 3.1$ and a corrected cluster significance threshold of $p < .05$. Recent findings (e.g., Eklund, Nichols, & Knutsson, 2016) indicate that false positives are more likely at lower voxel-wise thresholds with cluster-based corrections and can be circumvented by using nonparametric tests to correct for multiple comparisons. Thus, we verified that the brain regions

Table 1
Number of Trials Included in Neuroimaging Analyses Across Participants

Condition	Mean	Range
$CR_{rearranged}$		
Younger adults	117	101–128
Older adults	103.7	72–128
CR_{high}		
Younger adults	67.4	58–83
Older adults	46.9	5–113
CR_{low}		
Younger adults	49.6	36–60
Older adults	56.8	12–104
$FA_{rearranged}$		
Younger adults	19.3	10–37
Older adults	27.6	10–66

Note. CR = correct rejection; FA = false alarm.

identified in these contrasts also survive nonparametric correction using FSL Randomize (Winkler, Ridgway, Webster, Smith, & Nichols, 2014).

Second, we examined how the brain regions identified in the whole-brain analyses comparing $CR_{rearranged}$ and $FA_{rearranged}$ were selectively modulated by the availability of bound representations between the corresponding scene and word on Day 1. We used the regions identified in $CR_{rearranged} > FA_{rearranged}$ and in $CR_{rearranged} < FA_{rearranged}$ as masks to compare correct rejections of high-quality pairs (CR_{high}) versus correct rejections of low-quality pairs (CR_{low}). Trial counts for these analyses are shown in Table 1. Reported effects did not change when the minimal number of trials was restricted to 10, or when the proportion of CR_{high} was included as a covariate in the model comparing CR_{high} and CR_{low} to control for variability in number of trials across participants. With these analyses, we were particularly interested in the Age Group × Representation Quality interaction, or the extent to which task-related activity in younger and older adults was differentially modulated by representation quality. These analyses were carried out to further clarify the functional role of the brain regions involved in successful and unsuccessful recall-to-reject: On the one hand, if regions involved in $FA_{rearranged} > CR_{rearranged}$ supported monitoring processes, they were expected to show selective engagement for $CR_{low} > CR_{high}$. On the other hand, if brain regions involved in $CR_{rearranged} > FA_{rearranged}$ supported the reinstatement of memory traces to support recall-to-reject, they were expected to show enhanced activity for $CR_{high} > CR_{low}$. Here, we also tested the main effect of representation quality collapsed across younger and older adults, as well as the main effect of age group. These analyses were performed with a voxel-wise threshold of $z > 3.1$ and a corrected cluster significance threshold of $p < .05$ within the corresponding corrected mask. Given our specific interest in examining the processes involved in successfully rejecting familiar lures and avoiding false memories, our analyses focused on neural activity associated with correct rejections and false alarms, allowing us to directly test the modulatory effects of representation quality on the selective modulation of monitoring processes at retrieval.

Results

Behavioral Results

Day 1 final cued recall.   Final recall accuracy differed be-tween younger and older adults $t(49.7) = 3.05$, $p < .05$, $d = 0.83$. Younger adults recalled, on average, 54% of the 440 scene-word pairs whereas older adults recalled, on average, 39% of the 280 scene-word pairs. Thus, our experimental manipulation was successful in allowing us to create sets of intact and rearranged pairs to be used on Day 2 that included both high- and low-quality scene-word pairs uniquely deter-mined for each participant.

Day 2 performance.   A mixed analysis of variance (ANOVA) with age group (younger adults vs. older adults) and representation quality (high vs. low) on corrected recognition (hit rate-false alarm rate) revealed a reliable effect of represen-tation quality, $F(1, 50) = 414.03$, $p < .05$, $\eta_p^2 = .89$, such that recognition was higher for high- than for low-quality pairs (Figure 2a). In addition, older adults showed an overall lower recognition performance than younger adults, $F(1, 50) = 13.7$, $p < .05$, $\eta_p^2 = .22$. The Age Group $\times$ Representation Quality interaction was not reliable, $p > .40$. These results suggest that even though older adults demonstrated lower overall recogni-tion performance than younger adults, the effects of memory quality were comparable across groups.

The age-related reduction in recognition performance could reflect a reduced proportion of hits (i.e., correct "old" responses to intact studied pairs) or an increased proportion of false alarms (i.e., incorrect "old" responses to rearranged and new pairs). For hits (Figure 2b), we observed a reliable effect of representation quality, $F(1, 50) = 213.6$, $p < .05$, $\eta_p^2 = .81$, such that high-quality intact pairs were more likely to be recognized a day later than low-quality intact pairs were. The effect of age group was also signif-icant, $F(1, 50) = 7.98$, $p < .05$, $\eta_p^2 = .14$, with older adults showing lower true recognition than younger adults. However, the Age Group $\times$ Representation Quality interaction was not signifi-cant, $p > .65$.

Next, we sought to further characterize age differences in false alarms. A mixed ANOVA with age group (younger adults vs. older adults) and representation quality (high vs. low vs. new) revealed a significant effect of representation quality, $F(1.7, 83.4) = 110.21$, $p < .05$, $\eta_p^2 = .69$, such that both younger and older adults were more likely to falsely recognize low- than high-quality rearranged or new pairs (Figure 2c). Not only did older adults show a reduced proportion of hits, but also a tendency to commit more false alarms than younger adults, $F(1, 50) = 3.97$, $p = .05$, $\eta_p^2 = .07$. In contrast to the hits, however, we found a reliable Age Group $\times$ Represen-tation Quality interaction for false alarms, $F(1.7, 83.4) = 3.67$, $p < .05$, $\eta_p^2 = .07$. Post hoc tests indicated that while there were no differences between younger and older adults for false alarms to new pairs, $p_{corr} > .40$, or for false alarms to low-quality rearranged pairs, $p_{corr} > .20$, older adults were more likely than younger adults to falsely endorse high-quality rearranged pairs, $t(42.6) = 3.57$, $p_{corr} < .05$, $d = 0.92$. In other words, both younger and older adults took advantage of the availability of bound representations to successfully reject rearranged high-quality pairs, but older adults failed to benefit to the same degree as younger adults, resulting in a larger proportion of false alarms to high-quality rearranged pairs.

Taken together, both younger and older adults committed fewer false alarms to high-quality pairs, indicating that forming a bound scene-word representation is an important prerequisite for avoid-ing false associative memories. However, with high-quality repre-sentations, older adults were more likely to falsely claim that a rearranged pair has been encountered before than younger adults were. These results suggest that the ability to form high-quality associative representations during initial experience of an episode is unlikely to be the sole factor contributing to older adults' false memory, and that monitoring processes at retrieval may also play an important role.

fMRI Results

Correct rejections > false alarms.   A whole-brain compari-son of $CR_{rearranged} > FA_{rearranged}$ across all participants (i.e.,
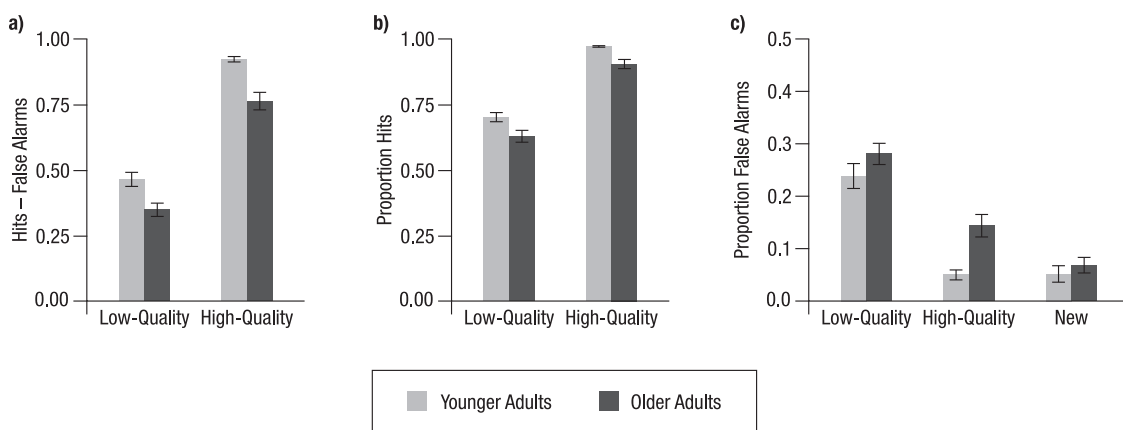

Figure 2.   Behavioral performance. (a) Overall recognition (hits-false alarms) for high-quality and low-quality pairs in younger and older adults; (b) hit rates for high-quality and low-quality pairs in younger and older adults; and (c) false alarm rates for high-quality, low-quality, and new pairs in younger and older adults. Errors bars indicate ± 1 SEM.

collapsed across younger and older adults) revealed multiple regions involved in the successful rejection of a rearranged pair, including medial and lateral anterior prefrontal cortex (PFC), middle and superior middle frontal gyrus, precuneus, and occipital cortex along with medial and lateral temporal regions, notably the left anterior hippocampus (Figure 3; Table 2). No regions demonstrated age differences for $CR_{rearranged} > FA_{rearranged}$ in a whole-brain comparison of younger and older adults.

Next, we examined the extent to which the regions preferentially engaged in $CR_{rearranged} > FA_{rearranged}$ were differentially modulated by variation in memory quality in younger and older adults. We did not find a reliable Age Group × Representation Quality interaction in any of the brain regions, indicating that task-related activity was similarly modulated by memory quality in younger and older adults. A direct comparison of younger and older adults revealed that none of the regions associated with $CR_{rearranged}$ demonstrated age differences for the comparison between CR_{high} and CR_{low}. Importantly, activity in most of the regions was higher for $CR_{high} > CR_{low}$ across younger and older adults, consistent with successful recall-to-reject (Figure 4a; Table 3). We did not observe higher activity for $CR_{low} > CR_{high}$ in any of the brain regions. To visualize these effects, Figure 4b shows patterns of activity for selected PFC regions and the hippocampus. As can be seen, the left anterior hippocampus demonstrated enhanced activity for $CR_{high} > CR_{low}$ in both younger and older adults. There were no age differences in activity modulation by representation quality in this brain region. Similar effects were observed in the left middle and superior frontal gyrus.

Together, these results suggest that activity in the regions supporting successful rejection of rearranged pairs, including lateral PFC and hippocampus, increased with higher quality of memory

representations, and this effect was comparable in younger and older adults.

False alarms > correct rejections. A whole-brain comparison of $FA_{rearranged} > CR_{rearranged}$ across all participants (i.e., collapsed across age groups) revealed that bilateral anterior insula and dorsal anterior cingulate cortex (dACC) were more strongly engaged in false than in true associative memory (Figure 3; Table 2). A whole-brain comparison of younger and older adults revealed no age differences for $FA_{rearranged} > CR_{rearranged}$. If these areas support the monitoring of uncertainty associated with ongoing retrieval, we expected them to be differentially modulated by representation quality with higher activity for CR_{low} compared with CR_{high}, since less mnemonic evidence is available for CR_{low} pairs. In the next step, we thus examined the extent to which the insular and cingulate regions identified in the $FA_{rearranged} > CR_{rearranged}$ contrast were modulated by varying memory quality in younger and older adults. The regions showing enhanced activity during false associative memory, including the bilateral anterior insula and the dACC, demonstrated a reliable Age Group × Representation Quality interaction (Figure 5a; Table 3). As is evident in Figure 5a, this interaction effect reflects enhanced activity in these areas for $CR_{low} > CR_{high}$ in younger adults, whereas no difference or even the opposite pattern was observed in older adults. None of the regions involved in $FA_{rearranged}$ demonstrated main effects of representation quality or age group.

Together, these results indicate that younger and older adults differed in the modulation of dACC and anterior insula activity by quality of memory representation. While the pattern observed in younger adults is consistent with an increased demand on retrieval monitoring for low-quality rearranged pairs, older adults showed no modulation or even greater activity for high-quality pairs. At the same time, the age groups also differed in memory performance and in Day 1 learning. To further dissociate these effects, we performed two additional analyses.

First, given that the dACC and the anterior insula were involved in false recognition of rearranged pairs, we examined whether interindividual differences in the modulation of monitoring processes in these regions were associated with interindividual differences in false memory. Since activity profiles were similar in the bilateral insula and the dACC, we averaged task-related activity across the three regions. In a hierarchical regression, false alarm rates were predicted by age group in a first step, followed by signal change for $CR_{low} > CR_{high}$ in the false memory network (i.e., averaged across dACC and anterior insula). The Activity × Age Group interaction was entered in a last step to test for age differences in the relationship between activity and false memory. The effect of age group was reliable, $\beta = .31$, $p < .05$, consistent with the age differences in false memory reported above. In addition, greater activity for $CR_{low} > CR_{high}$ was associated with fewer false alarms, $\beta = -.49$, $p < .05$, $R^2_{change} = .11$ (Figure 5b). The activity-by-age-group interaction was not significant, $p > .10$, $R^2_{change} = .04$, suggesting that the relation between activity modulation and mnemonic performance did not differ significantly between the age groups.

Second, we performed a median split of the older participants based on Day 1 final cued-recall performance. Behaviorally, the three groups (high-performing older adults, low-performing older adults, younger adults) differed in overall recognition, $F(2, 49) = 44.75$, $p < .05$, $\eta^2_p = .65$, and in false alarms to high-quality
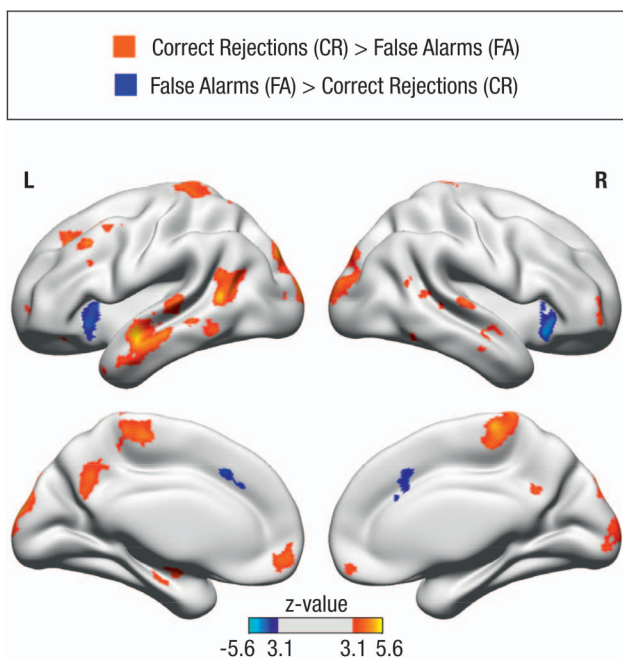

Figure 3. Whole-brain comparison of correct rejections and false alarms to rearranged pairs, $z > 3.1$, $p < .05$, corrected. L = left, R = right. See the online article for the color version of this figure.

Table 2
Peak Activations for CR$_{rearranged}$ vs. FA$_{rearranged}$ Across Younger and Older Adults

Region	Z$_{max}$	Voxels	MNI coordinates		
			X	Y	Z
CR$_{rearranged}$ > FA$_{rearranged}$					
L middle temporal gyrus	5.58	3,307	−62	−8	−14
R thalamus/caudate/posterior insula	4.92	2,750	20	−6	20
L occipital pole	5.16	2,354	−18	−98	16
L medial PFC	4.71	2,282	−18	36	−8
Precentral gyrus	5.43	2,098	0	−28	56
L precuneus	4.3	765	−2	−60	32
R superior temporal gyrus	4.63	639	66	−14	2
L middle frontal gyrus (MFG)	4.71	253	−40	22	38
L superior frontal gyrus (SFG)	4.49	232	−20	32	40
FA$_{rearranged}$ > CR$_{rearranged}$					
R anterior insula	4.69	381	34	24	−12
L anterior insula	4.53	362	−30	22	−10
L dACC	4.29	354	−4	30	34

Note. CR = correct rejection; FA = false alarm; MNI = Montreal Neurological Institute; L = left; R = right; PFC = prefrontal cortex; dACC = dorsal anterior cingulate.

rearranged pairs, $F(2, 49) = 17.996$, $p < .05$, $\eta_p^2 = .42$. Post hoc tests indicated that high-performing older adults ($N = 16$) did not differ from younger adults in overall recognition ($p_{corr} = 1$) or in high-quality false alarm rates ($p_{corr} = 1$, Figure 5c). At the same time, low-performing older adults ($N = 16$) showed lower overall recognition ($ps_{corr} < .05$) and higher high-quality false alarm rates ($ps_{corr} < .05$; Figure 5c) than both younger adults and high-

performing older adults. There were no group differences for low-quality false alarms, $p = .17$.

Next, we examined differences in selective recruitment for CR$_{low}$ > CR$_{high}$ in the dACC and bilateral insula across the three groups. This analysis revealed a main effect of group, $F(2, 49) = 40.79$, $p < .05$, $\eta_p^2 = .63$, that was similar across the regions of interest, as indicated by a nonreliable Region × Group interaction,
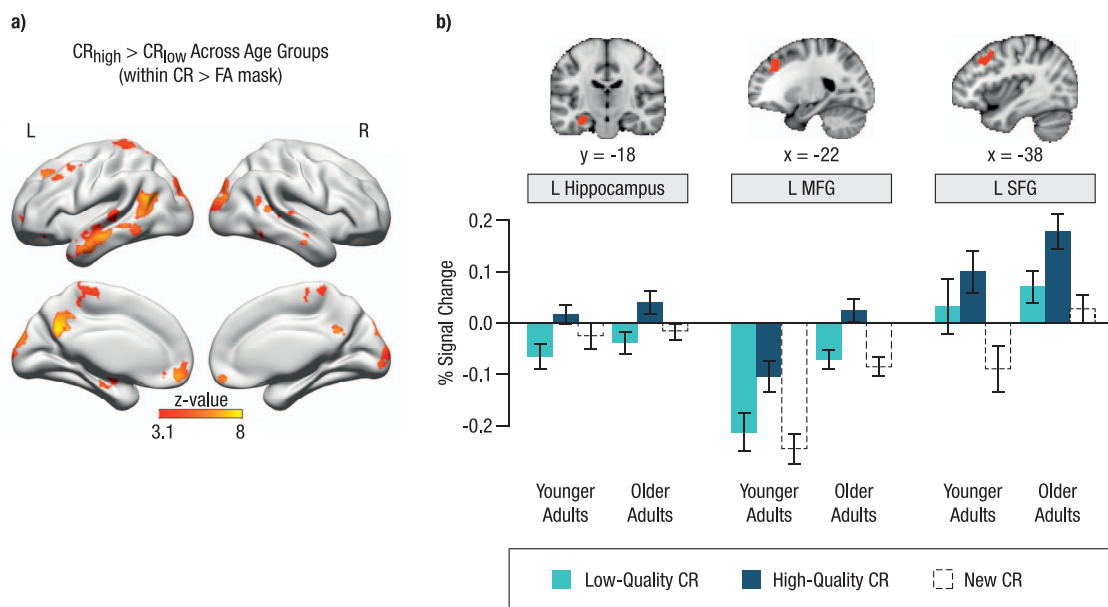

Figure 4. Correct rejections (CR) of high-quality and low-quality pairs in brain regions preferentially engaged in correct rejections of rearranged pairs. (a) Brain regions showing CR$_{high}$ > CR$_{low}$ across younger and older adults within the CR$_{rearranged}$ > FA$_{rearranged}$ mask, $z > 3.1$, $p < .05$, corrected. None of these regions displayed a main effect of age group or an interaction with representation quality. (b) Selected clusters in the left hippocampus, middle frontal gyrus (MFG), and superior frontal gyrus (SFG) depicted to demonstrate the results from (a). Activity for new pairs is plotted for reference, but is not included in the analyses. Errors bars indicate ±1 SEM. See the online article for the color version of this figure.

Table 3
Peak Activations for CR_{high} vs. CR_{low}

Region	Z_{max}	Voxels	MNI coordinates		
			X	Y	Z
$CR_{high} > CR_{low}$ (in $CR_{rearranged} > FA_{rearranged}$)					
L lateral occipital cortex/angular gyrus	7.3	2,893	−52	−66	26
L occipital pole	6.77	2,121	−12	−98	22
L postcentral gyrus	5.07	1,555	−18	−42	58
L precuneus	8.13	752	−6	−54	30
R thalamus	5.15	559	22	2	24
L hippocampus	5.55	474	−22	−8	−16
L medial PFC	6.6	464	−4	50	−14
L ventral medial PFC	7.05	393	−8	38	−8
R angular gyrus	6.53	389	58	−54	14
R ventral medial PFC	5.18	233	12	36	−8
L superior frontal gyrus	6.37	232	−18	32	38
L middle frontal gyrus	5.86	220	−38	18	38
R superior temporal gyrus	4.78	120	64	−32	4
R fusiform cortex	5.61	116	46	−52	−22
R middle temporal cortex	6.23	105	62	−12	−22
R putamen	4.73	71	−30	0	10
Representation Quality (CR_{high} vs. CR_{low}) × Age Group (younger vs. older adults) interaction (in $FA_{rearranged} > CR_{rearranged}$)					
R anterior insula	5.6	339	34	22	−2
R dACC	4.73	246	8	18	42
L anterior insula	4.24	198	−30	26	−2

Note. CR = correct rejection; MNI = Montreal Neurological Institute; FA = false alarm; L = left; R = right; PFC = prefrontal cortex; dACC = dorsal anterior cingulate.

$p = .09$. Critically, in spite of identical behavioral performance, younger adults and high-performing older adults differed in modulation of task-related activity in the insula and the dACC ($p_{corr} < .05$; Figure 5c). While the $CR_{low} − CR_{high}$ difference was positive in younger adults, suggesting increased engagement for low-quality correct rejections, high-performing older adults showed no activity differences between these trial types. These results demonstrate that even a subgroup of older adults that showed virtually no difference in memory performance to younger adults failed to selectively recruit monitoring processes for pairs for which familiarity was high, but bound information was not available. Low-performing older adults demonstrated the reversed pattern (Figure 5c), with higher activity for high-quality than low-quality correct rejections, and differed reliably from both younger and high-performing older adults ($ps_{corr} < .05$). Thus, the reversed patterns in Figure 5a seem to be driven primarily by low-performing older adults, who were also more likely to commit false alarms to high-quality rearranged pairs, in line with the correlational analyses reported above.

Discussion

This study investigated the neural mechanisms contributing to age-related increases in false memory in aging. By tracking the quality of associative memory representations at the individual level, we examined how binding success at encoding modulated the recruitment of retrieval monitoring processes, and age differences therein. Our study yielded three main findings: (1) false recognition was higher for low-quality than high-quality rearranged pairs in both younger and older adults. While no age differences were observed for low-quality pairs,

older adults were more likely to falsely endorse high-quality rearranged pairs than younger adults were. (2) False recognition was associated with enhanced activity in the cingular and anterior insular regions. These areas were more strongly engaged in the correct rejection of low-compared with high-quality pairs in younger, but not older adults. (3) Both younger and older adults showed enhanced activity in the anterior hippocampus for correct rejection of high-quality relative to low-quality rearranged pairs, with similar effects in the medial and lateral prefrontal regions. Notably, hippocampal activity modulation by representation quality was similar between age groups. These results are discussed in detail below.

Age Differences in False Associative Memory Are Modulated by Representation Quality

In the present study, we aimed to track the quality of individual memory representations within individual participants. Whereas the beneficial effect of repeated learning on true memory has been demonstrated repeatedly (e.g., Hintzman, 1976), repeated exposure to the same material frequently results in increased false recognition in older adults (e.g., Buchler, Faunce, Light, Gottfredson, & Reder, 2011; Jacoby, 1999; Light, Patterson, Chung, & Healy, 2004; but see Chung & Light, 2009; Kilb & Naveh-Benjamin, 2011; Watson, McDermott, & Balota, 2004). The procedure in the present study allowed us to extend this research and capture the nuanced ways in which within-person variation in memory quality is related to monitoring processes and the ability to avoid false memories for highly familiar associative information.
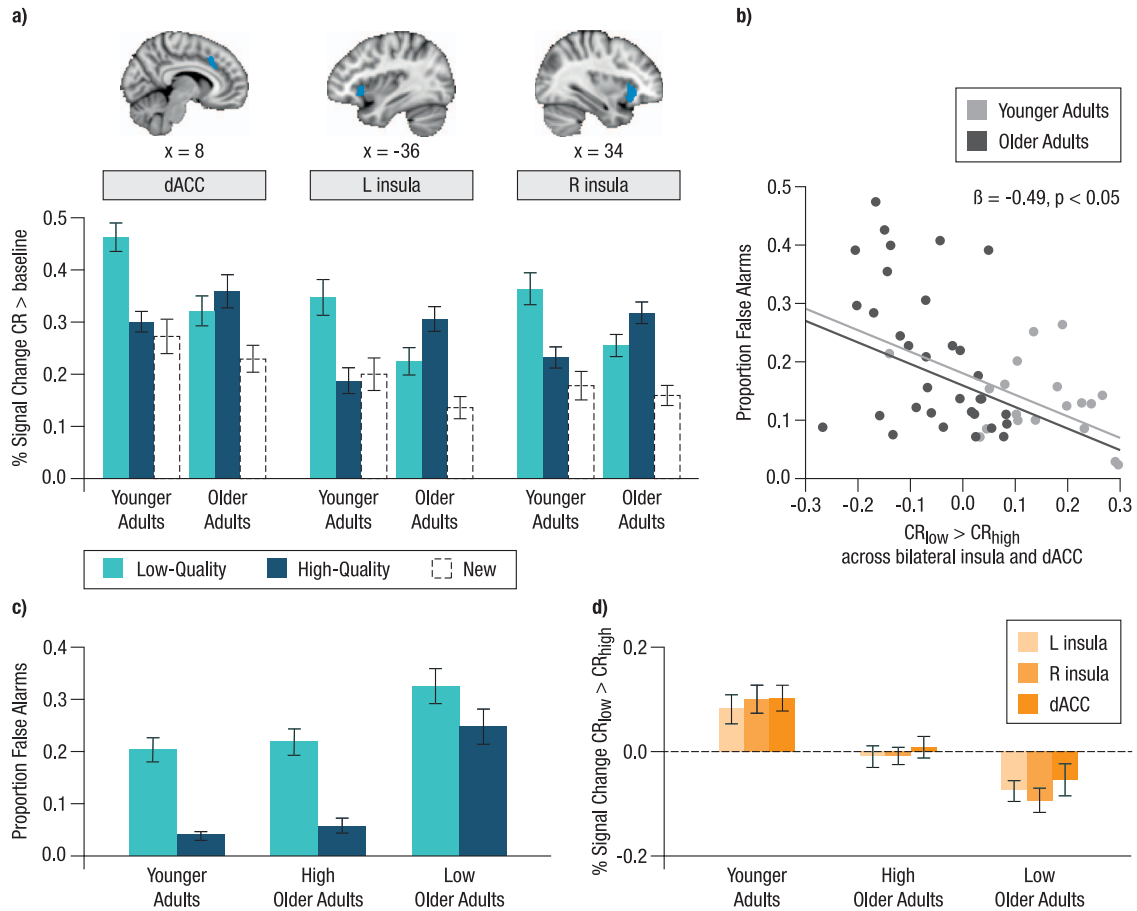
Figure 5. Correct rejections (CR) of high-quality and low-quality pairs in the brain regions preferentially engaged in false alarms (FA) of rearranged pairs. (a) All brain regions identified as part of the $FA_{rearranged} > CR_{rearranged}$ contrast demonstrated a reliable Age Group × Representation Quality interaction, $z > 3.1$, $p < .05$, corrected, depicted in the top row. Activity for new pairs is plotted for reference, but is not included in the analyses. (b) Greater activity difference for $CR_{low} > CR_{high}$ across the brain areas in (a), (i.e., dACC and bilateral anterior insula) predicted fewer false memories beyond the effect of age group. (c) False alarm rates to high-quality and low-quality rearranged pairs in younger adults, high-performing older adults, and low-performing older adults. (d) Activity difference for $CR_{low} > CR_{high}$ across the brain areas in (a), (i.e., dACC and bilateral anterior insula) in younger adults, high-performing older adults, and low-performing older adults. Errors bars indicate ±1 SEM. See the online article for the color version of this figure.

Interestingly, older adults were more likely than younger adults to wrongly endorse high-quality rearranged pairs, which consisted of features for which participants had formed, and were able to retrieve, an intact bound representation the day before. This finding clearly suggests that differences in representation quality, or binding success, alone are not sufficient to account for age-related increases in false associative memory. This does not imply that representation quality does not play an important role for false memory in aging: older adults were less likely to commit false memories for high-quality pairs, suggesting that forming bound representations of past experiences is critical for preventing false memory. The fact that accounting for the quality of individual associative representations formed during learning did not eliminate age differences in false memory, suggests that false memories can result from deficits at different stages of the memory encoding-retrieval chain (Devitt & Schacter, 2016). This behavioral pattern is further supported by our fMRI results: we found age differences in the selective recruitment of dorsal cingulate and anterior insular regions with varying memory representations, whereas hippocampal activity was modulated to a similar extent in younger and older adults.

Age Differences in dACC and Anterior Insula Involvement in Retrieval Monitoring

Our results in younger adults help uncover the type of processes supported by anterior insula and dACC during associative recognition. Increased activity in these regions as well as in lateral frontal areas has been reported in relation to both false memory (e.g., Kurkela & Dennis, 2016) and the correct rejection of similar associative foils (e.g., Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Lepage et al., 2003), presumably reflecting the increased

need to monitor uncertain decisions for which familiarity is relatively high, but less diagnostic mnemonic information is available. Here, we present novel evidence that similar neural mechanisms support monitoring processes engaged in false memory and in the correct rejection of low-quality rearranged pairs for which familiarity of the individual items is high, but hippocampal comparison processes are less likely to facilitate recall-to-reject since participants failed to form a bound representation that could help reject the rearranged foil. In fact, in younger adults, anterior insula and dACC activity for high-quality correct rejections was descriptively similar to activity for new pairs (Figure 5a), suggesting that monitoring demands were considerably reduced when participants had formed strong associations for the corresponding scene-word pairs. On the contrary, the correct rejection of rearranged pairs was associated with increased activity in the anterior and dorsal lateral PFC in younger adults ($CR_{rearranged} > FA_{rearranged}$ contrast; Figure 4a and 4b), possibly reflecting successful recall-to-reject. These findings are consistent with the broader cognitive control literature suggesting that multiple frontal regions are involved in the regulation of goal-directed behavior, with more caudal frontal regions supporting monitoring processes (e.g., Menon & Uddin, 2010; Seeley et al., 2007), and more rostral regions supporting strategic evaluation and decision-making in the context of the task at hand (e.g., Burgess & Wu, 2013; Fuster, 2003; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999).

Second, our results demonstrated age differences in the selective recruitment of anterior insular and cingulate regions: these areas were more strongly activated during low-quality than high-quality correct rejections in younger adults, but not in older adults. These findings corroborate several recent studies that demonstrated age differences between younger and older adults in monitoring processes in the ventrolateral PFC/anterior insular cortex and dorsal cingulate during item (Bowman & Dennis, 2015; Wang, Johnson, de Chastelaine, Donley, & Rugg, 2016) and associative (e.g., de Chastelaine, Mattson, Wang, Donley, & Rugg, 2016) recognition. Furthermore, a recent study (Paige, Cassidy, Schacter, & Gutchess, 2016) demonstrated that in younger, but not older adults, cingulate activity for false semantic memories was modulated by levels of gist information. The present results corroborate and extend these findings by demonstrating that older adults fail to recruit monitoring processes differentially when no bound representation was formed, resulting in higher levels of false associative memories.

Finally, interindividual differences in cingulo-opercular modulation by representation quality predicted younger and older adults' false memory, such that greater activity for low-quality relative to high-quality correct rejections was associated with fewer false memories. These results are consistent with previous studies showing that monitoring-related activity in the cingulate was positively related to memory performance in both younger and older adults (de Chastelaine et al., 2016; Wang et al., 2016), and indicate that individual differences in monitoring processes may represent a general mechanism of interindividual differences in false memory. Such a mechanism may be particularly important in aging due to overall declines in monitoring efficiency.

Following a monitoring account, activity in brain regions supporting monitoring processes should increase when uncertainty about a decision (i.e., old-new response) is high, but diagnostic mnemonic evidence is not readily available (e.g., Reas & Brewer, 2013). This is particularly the case for low-quality rearranged

pairs, for which the single items comprising a rearranged pair are familiar, but participants had not formed a bound representation of the original pair that, if recalled, could help to reject the rearranged pair. In contrast, for high-quality rearranged pairs, participants are more likely to recall details about the original pair to guide their decision, thereby resulting in lower uncertainty and lower activity in monitoring regions, along with fewer false memories. This account is consistent with our findings in younger adults as well as with the general direction of the individual difference analysis showing that enhanced activity for low-quality correct rejections is beneficial for task performance and can help avoid the incorrect decision to endorse a rearranged pair. Based on this monitoring mechanism, one explanation for the pattern observed in older adults is that high-quality pairs evoke a strong sense of familiarity, which leads to a strong conflict, resulting in increased demands on monitoring and greater cingulate and anterior insula activity. The comparable or even lower activity for low-quality than for high-quality pairs in older adults might thus reflect very weak memory for these pairs such that they do not induce the same sense of familiarity and decision uncertainty in older adults as they do in younger adults. By this account, false alarm rates for low-quality pairs should be more similar to false alarm rates for new pairs for which memory representations are absent. However, we did not observe this pattern in our data. Furthermore, older adults still committed more low-quality than high-quality false alarms.

An alternative explanation, consistent with accounts of cingulo-opercular involvement in the processing of salient information (Menon & Uddin, 2010), is that the patterns of activity modulation by memory quality might reflect different mechanisms in younger and older adults. While the activity patterns in dACC and anterior insula might reflect decision uncertainty in younger adults, they might reflect the higher salience of high-quality pairs in older adults. Such misleading activity patterns would thus be less beneficial for their memory performance. This interpretation is in line with the interindividual analyses, which demonstrated that lower false memory was associated with greater activity for correct rejections of low-quality than of high-quality pairs in both age groups. This result supports the notion of task-related activity maintenance in aging (Fandakova, Lindenberger, & Shing, 2015; Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012) such that older adults who maintain and, in the present case, modulate task-related activity in relevant regions in a manner more similar to younger adults show less age-related decline in memory performance. This interpretation is consistent with previous research (Gutchess et al., 2007) demonstrating that older adults did not recruit lateral PFC and dACC to correctly reject novel objects presented on a familiar background as compared with novel objects on a novel background. Activity patterns in these regions were even reversed for low-performing older adults, consistent with our own analysis of high- and low-performing older adults and with a salience account.

While future research should test these accounts directly, it is important to note that older adults did not show an unspecific failure to regulate monitoring processes: a closer look at Figure 5a clearly demonstrates that anterior insula and dACC activity was enhanced for rearranged relative to new pairs, suggesting that older adults' deficits were specific to variations in the quality of associative memory representations. Finally, there are different types of false memories, including semantic or perceptual-based errors,

which also increase with aging (e.g., Dennis et al., 2008; Paige et al., 2016). Examining whether monitoring processes are similarly modulated by representation quality in these types of false memories is an important task for future research.

No Age Differences in Hippocampal Modulation by Representation Quality at Retrieval

Hippocampal activity was modulated by representation quality, with greater engagement in correct rejection of high-quality pairs than low-quality pairs. These results are consistent with hippocampal involvement in the retrieval of relevant mnemonic details to reject similar foils (e.g., Kumaran & Maguire, 2007; but see Bowman & Dennis, 2016), and support the idea that differences in memory quality, as indexed by the success in forming a bound representation, result in differences in hippocampal activity at retrieval (e.g., De Zubicaray, McMahon, Dennis, & Dunn, 2011). By examining the difference between correct rejections of high-quality and low-quality pairs, the present study provides the opportunity to garner novel evidence with respect to hippocampal engagement in recall-to-reject processes. While computational models of MTL functioning (Norman & O'Reilly, 2003) predict involvement of these regions in recall-to-reject, we offer empirical evidence that the hippocampus supports recall-to-reject for associative information and is modulated by representation quality.

Importantly, we did not find age differences in hippocampal modulation. Age-related reductions in hippocampal activity have been demonstrated in cross-sectional (e.g., Daselaar et al., 2006) and longitudinal studies (e.g., Persson et al., 2012; Tisserand et al., 2004). Recent evidence suggests that different MTL regions, including the hippocampus, may become less specialized with aging (e.g., Wang, Dew, & Cabeza, 2015). Compared with younger adults, older adults do not show enhanced activity in the hippocampus during deep (i.e., semantic) versus shallow (i.e., perceptual) encoding (e.g., Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003). However, we demonstrated that, upon representation quality assessment for each individual participant and pair, hippocampal recruitment was similar in younger and older adults. This result stands in contrast to our previous observation that repetition of word pairs led to increased anterior hippocampus activity during correct rejections of rearranged word pairs in younger, but not older adults (Fandakova et al., 2014). The number of repeated exposures to the to-be-remembered material in our previous study may have been sufficient to boost processing in younger, but not in older adults. This interpretation is consistent with several recent studies of associative recognition that found no differences in hippocampal activity for successful recognition when performance was equated, or controlled for, between younger and older adults (de Chastelaine et al., 2016; Dulas & Duarte, 2016; Oedekoven, Jansen, Kircher, & Leube, 2013). When age differences in benefit from pair repetition are taken into account, beyond the effects of item familiarity, older adults do indeed benefit from repeated learning and retrieval of associative information to reduce false memory (see Kilb & Naveh-Benjamin, 2011, for differences between item and pair repetition effects). The fact that we did not observe age differences in hippocampal modulation when tracking the quality of individual memory representations indicates that a closer look at the individual learning history of an episode may provide important insights into the nature of age-related changes in hippocampal function and associative binding deficits.

Taken together, the present study provides novel insights into the neural mechanisms contributing to older adults' increased propensity to false memory. As false memories may result from failures at different memory stages, our findings highlight that older adults have particular deficits in selectively modulating monitoring processes at retrieval for memories that differ in the quality of bound representations. These results guide future interventions toward targeting older adults' memory monitoring abilities to help reduce their memory failures.

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