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Age Differences in Hippocampal Activation during Gist-based False Recognition

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Abstract

Age-related increases in reliance on gist-based processes can cause increased false recognition. Understanding the neural basis for this increase helps to elucidate a mechanism underlying this vulnerability in memory. We assessed age differences in gist-based false memory by increasing image set size at encoding, thereby increasing the rate of false alarms. False alarms during a recognition test elicited increased hippocampal activity for older adults as compared to younger adults for the small set sizes, whereas the age groups had similar hippocampal activation for items associated with larger set sizes. Interestingly, younger adults had stronger connectivity between the hippocampus and posterior temporal regions relative to older adults during false alarms for items associated with large versus small set sizes. With increased gist, younger adults might rely more on additional processes (e.g., semantic associations) during recognition than older adults. Parametric modulation revealed that younger adults had increased anterior cingulate activity versus older adults with decreasing set size, perhaps indicating difficulty utilizing monitoring processes in error-prone situations.

Keywords

gist; false memory; aging; memory; fMRI; hippocampus

Prior research has shown that older adults have difficulty remembering previous events as well as younger adults (Light, 1991). This age-related difference is likely the result of deficits in recollection for specific contextual details, whereas familiarity-based recognition remains intact with age (e.g., Spencer & Raz, 1995; Yonelinas, 2002). Extant work suggests that encoding engenders two types of memory traces: verbatim and gist traces (Brainerd & Reyna, 1990). Verbatim traces contain the distinctive details of an event, whereas gist traces retain the general meaning of the event without specific perceptual details (Brainerd &

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Reyna, 1990). False memories typically occur when the gist trace is retrieved and no verbatim trace is accessible. Consistent with this notion, age-related increases in false memories are most robust when old and new information share common semantic or perceptual characteristics (Balota et al., 1999; Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997; Norman & Schacter, 1997).

Although reliance on gist processing has been shown to vary by task demands among younger adults (Loftus, Feldman, & Dashiell, 1995; Roediger & McDermott, 1995; Schacter, 1999, 2008), aging increases the use of gist, resulting in poor memory in older adults when recollection requires remembering specific details (Brainerd & Reyna, 2002; Tun, Wingfield, Rosen, & Blanchard, 1998). Identifying mechanisms underlying age differences in false recognition that result from gist-based processing is important for understanding how to reduce vulnerability to such errors, especially given a shift toward greater reliance on gist-based memory processes with age (Koutstaal & Schacter, 1997). The present study employed neuroimaging to elucidate a neural mechanism for age differences in false memory at retrieval that results from gist-based processing.

Extant neuroimaging research has revealed age differences in activation relative to verbatim versus gist retrieval. Regions including the hippocampus, early visual cortex, lateral parietal cortex, occipitoparietal cortex, and rhinal cortex are involved at retrieval, although their roles depend on the processes required, namely recollection versus familiarity. At retrieval, these regions associated with recollection (e.g., the hippocampus, early visual cortex, and lateral parietal cortex) show age-related deficits in activation (Ally et al., 2008; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Duarte, Henson, & Graham, 2008). However, regions implicated in familiarity (e.g., rhinal cortex, occipitoparietal cortex) show intact or often enhanced functioning with age (Daselaar et al., 2006; Dennis, Kim, & Cabeza, 2008; Duarte, Graham, & Henson, 2010). This work evidences that older adults typically show significant reductions in true recollection (Bastin & Van der Linden, 2003; Davidson & Glisky, 2002), while familiarity processes remain preserved throughout the lifespan (Bastin & Van der Linden, 2003; Naveh-Benjamin, 2000).

In memory, hippocampal activation contributes to binding details during encoding and reconstructing them during retrieval (Yassa, Mattfeld, Stark, & Stark, 2011). In younger adults, the hippocampus can be differentially activated on a within-subject basis by varying the amount of to-be-remembered information. For example, set size of information at encoding (i.e., manipulating the number of object exemplars at encoding to evoke more gist-based processing) is positively associated with both false alarm rates and increased hippocampal activity at retrieval in younger adults (Gutchess & Schacter, 2012). Increased hippocampal activity for larger set sizes suggests that features shared by target and lure items elicit similar reconstructive processes that ultimately lead to false memories.

Among older adults, the role of the hippocampus in gist processing at retrieval may be responsible for eliciting errors in several ways. First, older adults may have difficulty monitoring retrieval attempts (e.g., Fandakova, Shing, & Lindenberger, 2013a, 2013b). In this case, the hippocampus may fail to access the correct information, possibly due to a failure in binding the details together (Naveh-Benjamin, 2000). Here, *decreased*

hippocampal activity would reflect deficient processing in which original encoding information is not properly reactivated. However, *increased* hippocampal engagement may lead to reactivation failure if this engagement corresponds with the number of reactivated features. In this case, older adults may retrieve more information by activating irrelevant features, ultimately eliciting more incorrect bindings.

Second, hippocampal activation may also play a role in false recognition with regard to gist processing through pattern separation. Aging diminishes the capacity to separate new information from similar inputs that could cause interference (pattern separation), leading to an increase in the retrieval of previous information from a partial cue (pattern completion) (Yassa & Stark, 2011). True recollection requires memories to be unique enough from other interfering information, relying on pattern separation (Norman, 2010). The more interference from overlapping events that needs to be overcome, the more separation becomes critical for recollection to occur (Yassa & Stark, 2011). Prior work in both rodents (e.g., Wilson, Gallagher, Eichenbaum, & Tanila, 2006) and humans (e.g., Stark, Yassa, & Stark, 2010; Yassa, Muftuler, & Stark, 2010) suggests that false memories elicited through deficient pattern separation occurs specifically in the dentate gyrus, and is coupled with pattern completion in older adults. In this case, the hippocampus responds to the novelty of information, with *decreased* activation suggesting impaired pattern separation abilities (Duncan, Ketz, Inati, & Davachi, 2012; Fandakova et al., 2013a; Kumaran & Maguire, 2006). With regard to the present work, we hypothesized that decreased hippocampal activation would occur concomitantly with increased false alarms, due to age-related differences in the ability to differentiate target from novel stimuli. This may potentially result from deficits in pattern separation ability.

In the present study, we analyzed younger and older adults' neural activity when recognizing novel exemplars taken from small, medium, or large set sizes of objects drawn from the same category (e.g., bicycles). This manipulation varied the level of gist associated with each category. Younger adults employ reconstructive processes as shown with increases in hippocampal activation during gist-related false recognition (Gutchess & Schacter, 2012). Given declines in hippocampal activation with age (Fandakova et al., 2013a; Naveh-Benjamin, 2000), we anticipated reduced hippocampal activity in younger versus older adults, suggestive of a shift toward gist-based processing, and induced through the use of large versus small set sizes. However, although we expected hippocampal engagement to change with age due to gist, this could be reflected through several patterns of neural activity. Whether hippocampal activation tracks the level of gist to a lesser degree for older versus younger adults, or does not respond to manipulation of gist at all in older adults, is an open question addressed through this work.

Due to age-related differences in the ability to differentiate target from novel stimuli, older adults may instead draw on other processes to help memory performance. One possibility is that given age-related deficits in pattern separation (Duncan et al., 2012; Fandakova et al., 2013a; Kumaran & Maguire, 2006), older adults may recruit regions implicated in semantic processes during retrieval (Dennis, Hayes, et al., 2008; Dennis, Kim, & Cabeza, 2007). We thereby predicted that older versus younger adults would activate *more* lateral temporal regions associated with semantic processing for large versus small set sizes. These

predictions coalesce with patterns found in prior aging research at retrieval using both verbal (Dennis, Kim, et al., 2008) and visual (Koutstaal & Schacter, 1997) stimuli. The present study extends this work by further manipulating gist in a graded fashion for visual stimuli sharing perceptual as well as semantic properties to investigate how gist reliance influences age differences in the neural correlates of false memory at retrieval.

Beyond assessing age differences in activity related to gist-based processing and consequent false memory in isolated regions, we tested how hippocampal connectivity changes with age given different levels of gist contributing to false memories. Age-related decreases in connectivity between the hippocampus and posterior temporal regions underlie memory deficits in aging, and specifically, increases in false memories (Dennis, Kim, et al., 2008). Despite reduced connectivity between the hippocampus with posterior regions, however, enhanced hippocampal connectivity with frontal regions at encoding predicts better memory performance for older adults (Daselaar et al., 2006; Dennis, Hayes, et al., 2008). Hippocampal-frontal cortex connectivity suggests that older adults compensate for deficits in posterior connectivity by relying on frontal top-down modulation (Daselaar et al., 2006; Dennis, Hayes, et al., 2008; Grady, McIntosh, & Craik, 2003). However, little research has considered age-related functional connectivity changes between the hippocampus and these regions during *false recognition* for items that vary in gist. For large versus small set sizes, we predicted that younger adults would have greater connectivity relative to older adults from the hippocampus to regions involved in perceptual processes. Although older adults may exhibit increased activation in inferior temporal regions during false recognition (Daselaar et al., 2006), the *connectivity* between these regions and the hippocampus may be weakened with age (Dennis, Kim, et al., 2008). Concomitant with age-related reductions in posterior connectivity, we predicted that older adults would have greater connectivity with frontal regions, a pattern suggested to reflect strategic shifts to support task performance (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). Further we predicted that connectivity would be greater for large relative to small set sizes due to the heavy reliance on gist-based processing.

Finally, we conducted a parametric modulation analysis to capitalize on our graded levels of gist, allowing us to assess age-related changes in neural activity corresponding to increasing or decreasing levels of gist that are associated with varying levels of false memory. Beyond the hippocampus, we identified lateral temporal cortex as a candidate region whose activity may be modulated by the extent of gist-based processing, given its involvement in semantic processing. Extant work has shown age differences in reliance on semantic processes with increased activation in the lateral temporal cortex for older adults at retrieval (Davis et al., 2008; Dennis, Hayes, et al., 2008). We predicted that with *increasing* set size (i.e., small-medium-large), older adults would show increased reliance on semantic processes, reflected in increased lateral temporal cortex activation. These analyses can help distinguish the potential roles of the hippocampus and lateral temporal cortex in gist-based memory errors.

2. Method

2.1 Participants

Sixteen younger (*M age* = 24.13 years, *SD* = 4.57; 8 male; age range = 19–33 years) and 16 older (*M age* = 71.81 years, *SD* = 5.58; 7 male; age range = 61–80 years) adults participated. An additional seven younger adults and 3 older adults were excluded due to failure to respond to large numbers of trials (> 40% no responses; 1 younger adult, 1 older adult), failure to follow instructions (1 younger adult), too few false alarms in at least one condition (< 6 items; 5 younger adults), or excessive movement in the scanner (2 older adults). Participants were right-handed, native English speakers with no usage of medications known to affect the central nervous system, and no neurological, psychological, or physical conditions that were problematic for MRI scanning. Education levels were similar for younger (*M* = 16.41 years, *SD* = 2.85) and older (*M* = 15.00 years, *SD* = 2.03) adults, $t(30) = 1.61$, $p = 0.12$. Younger adults (*M* = 79.44, *SD* = 13.29) had increased processing speed than older adults (*M* = 54.56, *SD* = 10.45), $t(30) = 5.89$, $p < 0.001$, as measured by digit comparison (Hedden et al., 2002). Participants provided written informed consent. The Harvard University and Partners Institutional Review Boards approved this study.

2.2 Materials and Procedure

468 pictures of single objects were incidentally encoded by participants, who were unaware there would be a future recognition test. Participants made yes/no decisions via a button box about whether each object was something they would use or interact with during an average day. Pictures were selected from photo CDs (Hemera Technologies, Gatineau, Quebec) to include 54 sets of categorized objects (e.g., umbrellas, chairs, cats). Eighteen categories were assigned to each condition (small, medium, or large set size). The number of object exemplars in each category determined set size. Small study sets contained four studied exemplars (e.g., four umbrellas). Medium sets contained eight studied exemplars (e.g., eight chairs). Large sets contained fourteen exemplars (e.g., fourteen cats). Exemplars were distributed across three encoding runs (e.g., the eight chairs would be distributed as evenly as possible across the three runs), with each run lasting approximately 7 minutes. Across the three encoding runs, participants viewed 72 pictures from small sets, 144 pictures from medium sets, and 252 pictures from large sets (see Figure 1). Each picture was presented for one second followed by a one second blank interval. All stimuli were presented via E-Prime (Psychology Software Tools, Pittsburgh, PA). Trials were randomly ordered through a jittered event-related design (Dale, 1999) with a fixation cross appearing for times varying from 2000 to 10000 ms throughout the scans (for results at encoding, see Gutchess & Schacter, 2012).

After an approximately ten minute delay, during which structural images were acquired, participants received a surprise recognition test over four functional scans. The recognition test included a total of 456 pictures (216 studied and 240 lures). Each studied small, medium, and large object category (e.g., chairs) was tested with four studied exemplars and four novel lure exemplars, both randomly selected from the studied and unstudied items for each category (see Figure 1). Therefore, there were a total of 72 items in each of the conditions (small, medium, large set size) evenly distributed across four runs, with each run

approximately 10 minutes long. To determine a baseline false alarm rate, an additional 24 novel unrelated pictures were included from distinct object classes not previously studied. Eight different recognition orders across participants counterbalanced assignment of object classes to each of the four set sizes (i.e., unrelated, small, medium, and large) and assignment of tested items as either lures or studied targets. Participants had a four second interval to respond "yes" (i.e., had seen the exemplar before) or "no" (i.e., had not seen the exemplar before).

2.3 Functional MRI data acquisition

Images were acquired using a Siemens Avanta 1.5 Tesla whole-body scanner. Thirty-two slices 3.2 mm thick with a .3 mm skip were acquired with an echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 30, FOV = 200 mm, and a flip angle of 90°). In each of the three encoding runs, 212 volumes were collected; in each of the four recognition runs, 304 volumes were collected. Besides the number of volumes collected, all other parameters were the same for both encoding and recognition.

2.4 Functional MRI analyses

2.4.1 General linear model—Preprocessing and analyses were conducted in SPM8 (Wellcome Department of Cognition Neurology, London, UK). Images were slice-time corrected, realigned to correct for motion, normalized to the MNI (Montreal Neurological Institute) template, and smoothed using an 8-mm FWHM isotropic Gaussian kernel. Estimates of canonical hemodynamic responses were included for each participant in a whole-brain random effect analysis, used to assess age differences in brain activation. We included eight regressors in a first-level model: False alarms (FA)-large, FA-medium, FA-small, Hits-large, Hits-medium, Hits-small, Zero-Correct Rejections (novel lures), and Miscellaneous (i.e., all misses and remaining correct rejections, false alarms to the Zero category, and non-response trials). We separated correct rejections into two different regressors, as items that have not been seen previously may rely on gist processing (e.g., I did not see any bicycles), whereas items from categories previously presented (novel lures) may rely on detail-specific recollection. Behavioral false alarm estimates for each participant were included in a group level analysis, treating participants as a random effect. A 2 (Age Group: Younger, Older) × 2 (Set Size: Small, Large) ANOVA model was created to explore any effects of set size during false recognition differing by age group. FMRI results were thresholded at $p < 0.001$ with an extent threshold of $k = 5$ voxels, parameters widely used in aging-related neuroimaging work (Duarte et al., 2008; Dulas & Duarte, 2011; Kensinger & Schacter, 2008). Peak activations on the cortical surface were determined using SPM8 and Brodmann areas labeled with MRIcron (Rorden & Brett, 2000). Based on the whole-brain analysis, we characterized activity in a priori regions of interest (e.g., hippocampus) by extracting parameter estimates from significant clusters and plotting them, where relevant. To specifically address our hypothesis regarding age differences in brain activity during false recognition of objects in large versus small set sizes, we created the following interaction contrasts: [Young > Old for (Large > Small)], [Old > Young for (Large > Small)]. We compared small and large set sizes given that it would be the most robust analysis to detect age-related differences in hippocampal activation to gist-based false recognition based on our predictions.

2.4.2 Functional connectivity—Psychophysiological interactions (PPI) assess task dependent functional connectivity analyses for a seed region. Functional connectivity evaluates how activity in a given region covaries with activity in other areas of the brain when comparing across conditions (e.g., in the present study, hippocampal activity during false alarms to large set size versus false alarms to small set size) (Friston et al., 1997). For our analysis, we used the gPPI toolbox, which accommodates more than two task conditions in the same PPI and has been argued to be more sensitive than standard PPI implementation through SPM (McLaren, Ries, Xu, & Johnson, 2012). In this follow-up analysis, we used the left hippocampus region identified by our whole brain GLM (see results below) as a seed region to examine age differences in connectivity with the hippocampus when making false alarms to items from large versus small set sizes, as this constitutes the most extreme comparison across levels of gist. We extracted the deconvolved time series from a 6mm radius sphere around the group peak by testing the connectivity for false alarms to large versus small set size items. We entered the contrast files from participant-level PPI analyses into a two-sample t-test, comparing connectivity from the hippocampal seed between younger and older adults in the comparison of large vs. small set size false alarms.

2.4.3 Parametric modulation—Parametric modulation analyses allowed for identification of regions whose activity increases or decreases as a function of gist-based false memories. That is, this analysis revealed neural activity varying with increasing or decreasing set size. Unlike the previous first level model (see section 2.4.1), the parametric modulation model used FA-set size (i.e., small, medium, and large) as a covariate of interest to identify neural regions whose activation tracks across the three levels of set size during false recognition responses. Like the previous analysis (see section 2.4.1), we included Hits, Zero-Correct Rejections (novel lures), and Miscellaneous (i.e., all misses and remaining correct rejections, false alarms to the Zero category, and non-response trials) in this model. These analyses identified regions whose activity positively or negatively correlated with increasing or decreasing set size for false recognition responses. To identify any age differences in how brain regions track set size during false recognition, we submitted best-fit first-level components to second-level two-sample t-tests comparing younger to older adults, and older to younger adults.

3. Results

3.1 Behavioral Data

We assessed age differences in false recognition by entering false alarm rates into a 2 (Age: Young, Old) × 3 (Set Size: Small, Medium, Large) mixed ANOVA (See Table 1). Older adults had higher false recognition rates (M = 0.32, SD = 0.10) than younger adults (M = 0.24, SD = 0.10), $F(1,30) = 4.70$, $p = 0.04$, partial $\eta^2 = 0.14$. A main effect of Set Size emerged, $F(2, 60) = 42.66$, $p < 0.001$, partial $\eta^2 = 0.59$. Across age, false alarm rate was greater for the large set size (M = 0.34, SD = 0.12) versus medium (M = 0.28, SD = 0.12), $t(31) = 4.31$, $p < 0.001$, and for the medium set size versus the small (M = 0.22, SD = 0.10), $t(31) = 5.67$, $p < 0.001$. No interaction emerged, $p = 0.20$. Because several younger adults (N = 5) were excluded for having too few false alarm trials, the behavioral data from the participants included in the fMRI analyses may underestimate potential age differences (see

Bastin & Van der Linden, 2003; Davidson & Glisky, 2002; Naveh-Benjamin, 2000 for more thorough consideration of the effects of aging) in false alarm rates across the set sizes. When the ANOVA is conducted with all participants who completed the study, an age by set size interaction emerged, $F(2,78) = 4.951$, $p = 0.01$, partial $\eta^2 = 0.11$, consistent with prior behavioral literature.

Although not our primary interest, behavioral hit rate was also analyzed in a 2 (Age: Young, Old) × 3 (Set Size: Small, Medium, Large) mixed ANOVA to determine age-related differences in correct responses to old items (See Table 1). Older adults did not differ from younger adults on hit rate, $F(1,30) = 0.005$, $p = 0.94$, partial $\eta^2 < 0.01$. A main effect of Set Size emerged, $F(2,60) = 4.27$, $p = 0.018$, partial $\eta^2 = 0.13$. Hit rate was not greater at the large set size ($M = 0.64$, $SD = 0.13$) versus medium ($M = 0.62$, $SD = 0.14$), $t(31) = 0.98$, $p = 0.33$, but was greater for the large set size versus the small ($M = 0.59$, $SD = 0.14$), $t(31) = 2.95$ $p = 0.006$. Hit rate at the medium set size was marginally greater than the small, $t(31) = 1.84$, $p = 0.08$. No interaction emerged, $p = 0.70$.

3.2 Functional MRI Data

3.2.1 Age by Set Size Interaction: [(Young > Old) for (Large > Small)]—

Comparing age differences in brain activity for false alarm responses for large versus small set sizes revealed a singular activation in the left hippocampus (Figure 2A; $k = 9$; MNI coordinates: −30, −18, −18). To characterize the pattern of the age differences in this interaction, we entered and compared parameter estimates from this hippocampal region in a 2 (Age Group: Young, Old) × 2 (Set Size: Small, Large) mixed ANOVA. This revealed a significant Set Size × Age Group interaction, $F(1, 30) = 10.46$, $p = 0.003$, partial $\eta^2 = 0.26$. Older adults recruited left hippocampus more than young when set size was small, $t(30) = 3.26$, $p = 0.003$, $d = 1.15$. No age differences emerged when set size was large, $t(30) = 0.38$, $p = 0.71$, $d = 0.13$. No other regions emerged from this interaction contrast or from comparing [(Old > Young) for (Large > Small)].

3.2.2 Functional connectivity—

Consistent with our predictions, at the large versus small set size, younger adults showed greater functional connectivity between the hippocampus and temporal regions than older adults. Specifically, relative to older adults, younger adults had greater functional connectivity between the left hippocampus (MNI coordinates: −30, −18, −18) and right inferior temporal cortex (k = 21; BA 37, MNI coordinates: 60, −50, −16), as well as with left superior temporal cortex (k = 21; BA 22, MNI coordinates: −54, −26, 6) (Figure 2B). No regions emerged as greater for older adults than younger adults for the large versus small set size.

3.2.3 Parametric modulation—

For false recognition, decreasing set size (i.e., large-medium-small exemplars studied) was associated with increased activation in a singular region of left anterior cingulate gyrus (BA 24; $k = 5$; MNI coordinates: −14, 42, 0) for younger relative to older adults (Figure 2C). No other age differences emerged for decreasing set size, and no age differences emerged for increasing set size.

4. Discussion

The present study investigated the neural underpinnings of how increased use of gist-based processing affects false memory for visual stimuli in aging. We had predicted involvement of the hippocampus, as previous work has suggested that the more closely items are related (e.g., items that share the same verbal label), the more processes involved in false recognition are activated (Koutstaal & Schacter, 1997). This yields a greater need for hippocampal-based reconstruction as the degree of gist increases for false memories in younger adults (Gutchess & Schacter, 2012). However, the pattern is far less clear for older adults who have been shown to consistently rely on gist-memory (Tun et al., 1998). In the present study, older adults exhibited increased hippocampal activation for false memories for items at the small set size relative to younger adults. Initially, we had predicted that older adults would show less hippocampal activation relative to younger adults and given that reliance on gist should increase with set size, this difference would be more prominent at the large set size. However, we observed an unexpected pattern such that older adults tend to activate the hippocampus more for the small set size, which leads to age differences in this condition. In contrast, hippocampal activity was equivalent at the large set size between younger and older adults, reflecting a tendency for older adults to activate the region less for large than small set sizes. No other age differences emerged from the random effects analyses.

Age-related differences in hippocampal activation between the small and large set size may potentially reflect deficits in pattern separation ability. Increased age corresponds with a reduced capacity to separate new information from related inputs causing interference (pattern separation) and an increased tendency to retrieve related information from a partial cue (pattern completion) (Yassa & Stark, 2011). For true recollection to occur, memory traces for information must be unique enough compared to other interfering information, thus requiring pattern separation (Norman, 2010). The more information overlaps causing interference, the more separation becomes critical (Yassa & Stark, 2011). In the present task, participants had to retrieve information that was tightly connected with other information (e.g., exemplars in an object category). For older adults at the small set size, increased activation in the hippocampus relative to younger adults may suggest effortful retrieval. However, at the large set size, equivalent hippocampal activation between younger and older adults suggests deficient pattern separation (i.e., too much interference to resolve) and a shift toward pattern completion (i.e., retrieving the gist of the information) (e.g., Stark et al., 2010; Yassa et al., 2010). In this case, the hippocampus works to detect novelty of information at the small set size, but at the large set size there is too much information to separate (Duncan et al., 2012; Fandakova et al., 2013a; Kumaran & Maguire, 2006).

These findings may also be interpreted using the scaffolding theory of aging and cognition (STAC). STAC posits that the brain adapts with age to engage in compensatory “scaffolding” in response to challenges as a result of declining neural structure and function (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014). STAC suggests that despite neural changes, behavior can be maintained with age due to the engagement of compensatory scaffolding. Scaffolding processes may operate on a lesser scale in youth, only engaged in novel situations, new learning, or neural challenges (Park & Reuter-Lorenz, 2009). With

increased age, in contrast, scaffolding processes may be engaged even for familiar tasks or basic cognitive operations as these become more difficult with degradation of previous neural circuitry (Park & Reuter-Lorenz, 2009). For older adults to have increased hippocampal activation at the small set size relative to younger adults, this suggests that compensatory recollection responses (by way of pattern separation, for example) are engaged for older adults. However, large set sizes might exceed older adults' capacity to counteract gist-based false memories, and they are unable to harness additional resources to support performance, making younger and older adults comparable in hippocampal activation. The equivalent hippocampal response for younger and older adults at large set sizes may reflect both extrinsic challenge (e.g., higher task demand in younger adults at the large set size) and intrinsic challenge (e.g., aging brain) at the large set size.

Because greater hippocampal activation for older adults relative to young adults at the small set size does not clearly delineate the processes engaged differently across the age groups as gist *increases*, we assessed how functional connectivity differs across set size with age. With regard to STAC, it is possible that beyond the small set size, older adults are relying on activation in secondary scaffolded areas (Park & Reuter-Lorenz, 2009). We thus sought to identify connections potentially involved as a function of greater gist processing. Connections between the hippocampus and both the right inferior and left superior temporal cortex were greater for younger adults relative to older adults for the large versus small set size. Consistent with these findings, previous memory work has revealed an age-related decrease in connectivity between the hippocampus and posterior regions, such as the parietotemporal network, at encoding (Daselaar et al., 2006; Dennis, Hayes, et al., 2008). Prior work manipulating gist information in younger adults has shown that semantic processing is involved in this type of graded visual task using gist-processing (Gutchess & Schacter, 2012), potentially suggesting that these age-related changes in functional connectivity reflect the contribution of semantic processes. As the amount of gist increases (such as in the large set size), younger adults may compensate via greater functional connectivity with regions associated with semantic processes (Daselaar et al., 2006).

Extant work has also suggested an age-related decrease in inferior temporal activity (Davis et al., 2008) and connectivity suggesting older adults are less efficient at these processes (Dennis, Hayes, et al., 2008). However, we did not find support for our hypothesis that older adults may compensate for weaker posterior connectivity with increased connectivity between the hippocampus and frontal cortex. This prediction based on prior work suggesting that this pattern predicts better subsequent memory performance (Daselaar et al., 2006; Dennis, Hayes, et al., 2008; Grady et al., 2003). This could suggest that prior findings from work on correct recognition may not extend to false recognition.

Interestingly, anterior cingulate cortex increased in activity with decreasing set size for younger adults more than older adults. Prior work has shown that true recognition is associated with increased engagement of visual, posterior parietal, and temporal cortex, suggesting reactivation of sensory information, whereas false recognition is associated with engagement of the frontal cortex, specifically the anterior cingulate, representative of monitoring of retrieved memories (Cabeza, Rao, Wagner, Mayer, & Schacter, 2001). Anterior cingulate is engaged during both correct and incorrect responses, suggesting its

involvement in situations where errors are *likely* to occur rather than solely during specific errors (Carter et al., 1998). In contrast to younger adults, older adults do not differentially recruit anterior cingulate to assess salient categorical differences in unrelated items, suggesting age-related deficits in using specific details to assess novelty (Bowman & Dennis, 2015). In the present data, anterior cingulate activity increased as set size decreased. A possible explanation is that older adults did not differentially recruit the anterior cingulate to distinguish salient differences in novel items, whereas younger adults were able to utilize this monitoring when there was less gist information.

4.1 Conclusions

This research extends prior gist and false memory research by investigating neural age differences in false memories for graded gist information. Our results suggest that hippocampal involvement extends to visual stimuli in regards to false memory and gist. That younger adults exhibited enhanced connectivity with inferior and superior temporal regions relative to older adults at the large versus small set size suggests that younger versus older adults use additional resources (e.g., semantic processes) to distinguish between old and new information when the level of gist is greater. Age-related increases in gist-based processes may result from deficits in hippocampal activation, affecting capabilities such as pattern separation, and impaired connectivity with semantic regions.

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Highlights

- We assessed age differences in retrieving false memories using fMRI.
- The number of encoded categorically-related pictures varied (small to large sets).
- At retrieval, older adults activated the hippocampus more than young for small sets.
- For large sets, hippocampal and posterior temporal connectivity decreased with age.
- Younger and older adults differ in the processes that contribute to false memory.

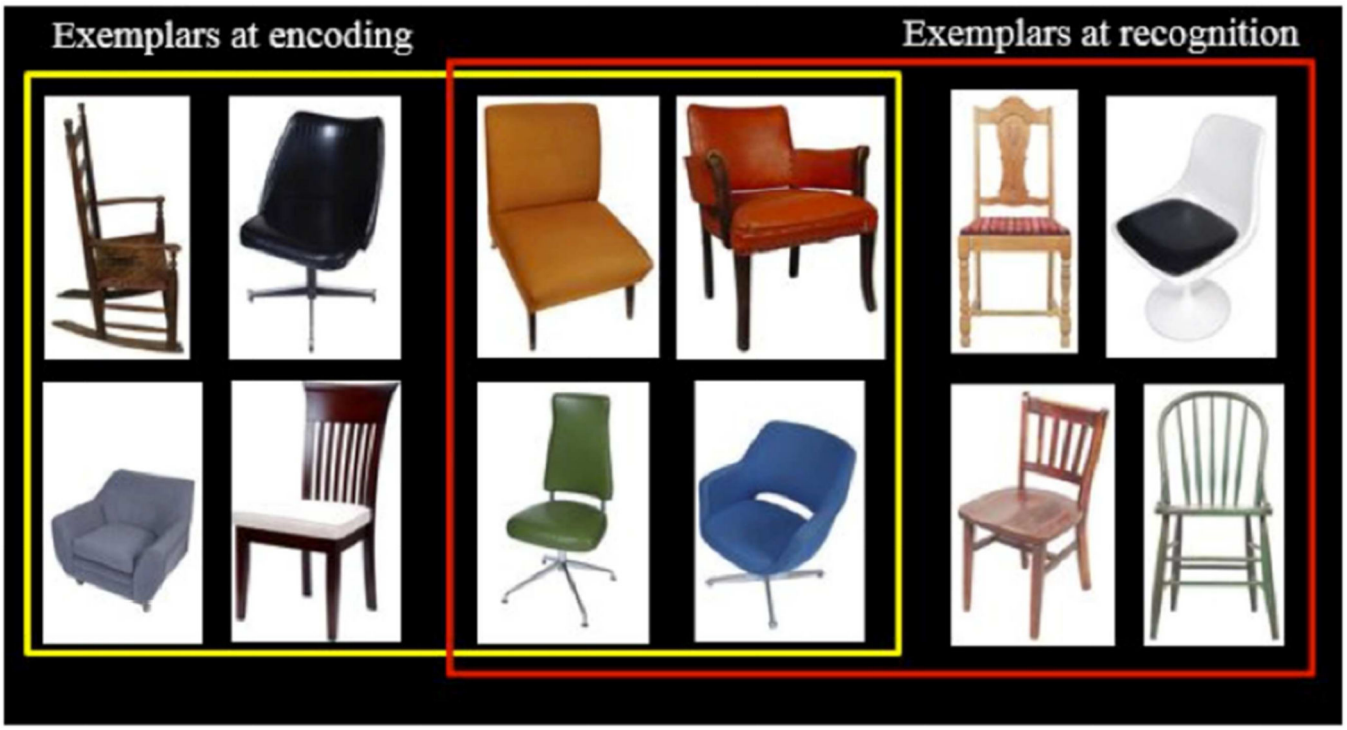

Figure 1.

In the task, participants incidentally encoded 468 pictures of single objects (as shown on the left). The number of object exemplars in each category determined its set size. After a delay participants completed a recognition test that included a total of 456 pictures (216 studied and 240 lures). Each studied small, medium, and large object category (e.g., chairs) was tested with four studied exemplars and four novel lure exemplars (as shown on the right), both randomly selected from the studied and unstudied items for each category. An additional 24 novel unrelated pictures were included from distinct object classes not previously studied.

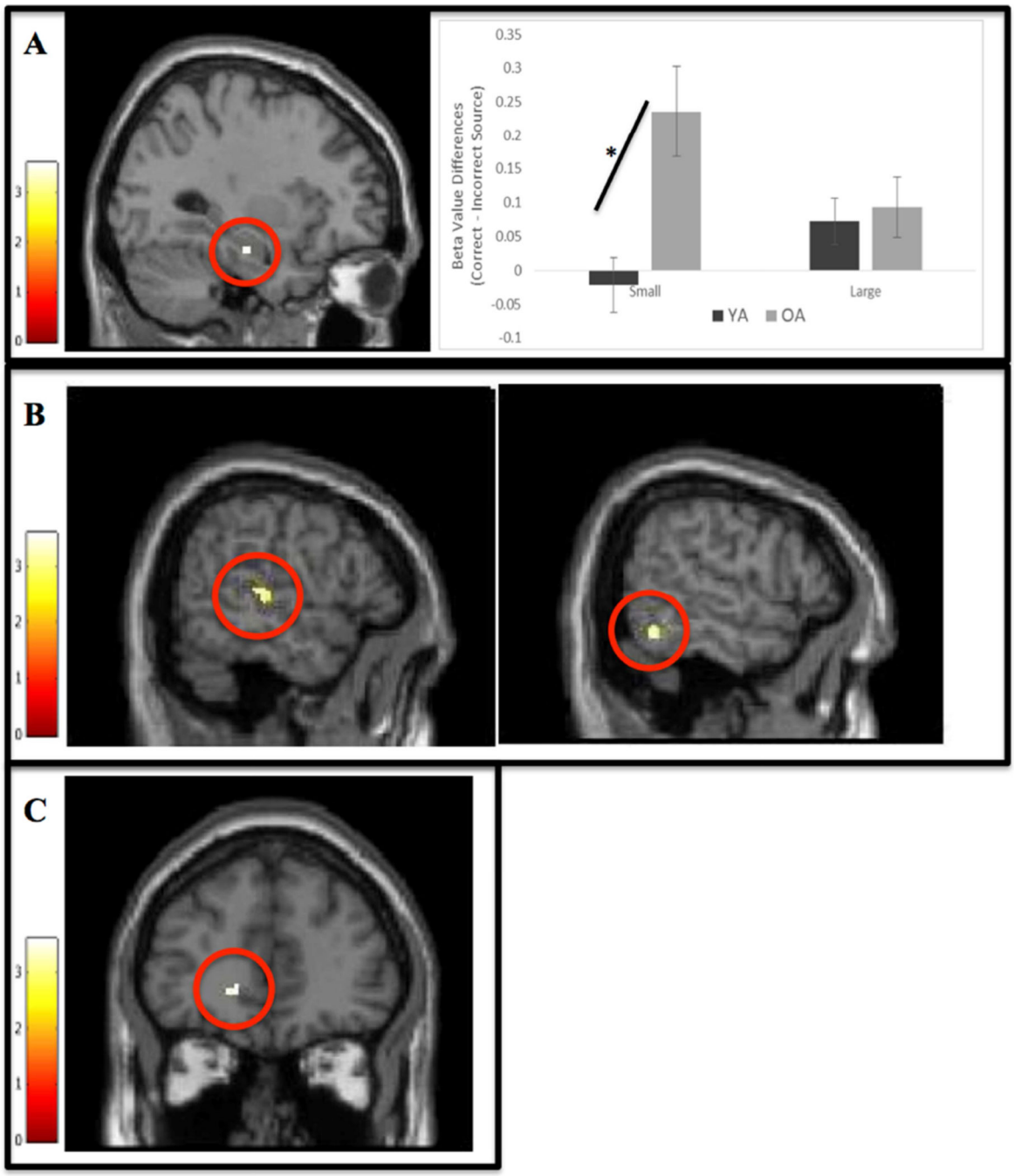

Figure 2.

A) A region in left hippocampus emerged when comparing age differences in activity for false recognition at the large versus small set size (left). Plotting parameter estimates to characterize this activation revealed the interaction to be driven by more activity among older adults versus young at the small set size, with no age difference at the large set size (right).

B) At the large versus small set size, younger adults exhibited increased functional connectivity between the left hippocampus and the left superior temporal cortex (left) and the right inferior temporal cortex (right) relative to older adults.

C) When examining decreasing set size (i.e., large to medium to small exemplars) in a parametric modulation analysis, younger adults showed increased left anterior cingulate cortex activity relative to older adults.

Table 1

Behavioral data for false alarms and hits.

		Old	Young
False Alarms	Small	0.24 (0.11)	0.19 (0.09)
	Medium	0.33 (0.10)	0.24 (0.13)
	Large	0.39 (0.12)	0.30 (0.10)
Hits	Small	0.59 (0.14)	0.60 (0.14)
	Medium	0.62 (0.14)	0.63 (0.15)
	Large	0.65 (0.14)	0.63 (0.12)