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## Multielement Episodic Encoding in Young and Older Adults

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### Abstract

Previous research on age-related associative memory deficits has generally focused on memory for single associations. However, our real-world experiences contain a multitude of details that must be effectively integrated and encoded into coherent representations to facilitate subsequent retrieval of the event as a whole. How aging interferes with the processes necessary for multielement encoding is still unknown. We investigated this issue in the current fMRI study. While undergoing scanning, young and older adults were presented with an occupation and an object and were asked to judge how likely the two were to interact, either in general or within the context of a given scene. After scanning, participants completed recognition tasks for the occupation–object pairs and the sources/contexts with which the pairs were studied. Using multivariate behavioral partial least squares analyses, we identified a set of regions including anterior pFC and medial-temporal lobes whose activity was beneficial to subsequent memory for the pairs and sources in young adults but detrimental in older adults. An additional behavioral partial least squares analysis found that, although both groups recruited anterior pFC areas to support context memory performance, only in the young did this activity appear to reflect integration of the occupation, object, and scene features. This was also consistent with behavioral results, which found that young adults showed greater conditional dependence between pair and context memory compared with older adults. Together, these findings suggest that binding and/or retrieving multiple details as an integrated whole becomes increasingly difficult with age.

### INTRODUCTION

Considerable evidence suggests that in healthy aging, older adults' episodic memory deficits stem from a diminished ability to bind and/or retrieve associations that enable us to distinguish one event from another (Mitchell & Johnson, 2009; Old & Naveh-Benjamin, 2008a; Swick, Senkfor, & Van Petten, 2006; Glisky, Rubin, & Davidson, 2001; Spencer & Raz, 1995). It should be noted, however, that a majority of this research has focused on memory for single associations, for example, between individual items (Dulas & Duarte, 2016; Fandakova, Lindenberger, & Shing, 2014; Patterson & Hertzog, 2010; Cohn, Emrich, & Moscovitch, 2008) and between an item and its source or context (Ankudowich, Pasvanis,

& Rajah, 2016, 2017; Leshikar & Duarte, 2014; Dulas & Duarte, 2011; Dennis et al., 2008). In real-world situations, our experiences include several elements that require us to process multiple associations between people and objects within the context of the current setting. The literature on such multielement binding is scarce, and no studies, to our knowledge, have investigated this question as it relates to healthy aging. The aim of the current study is to address this question by exploring the neural processes recruited by young and older adults during associative encoding of multielement events.

Episodic memory in everyday life includes numerous elements as well as the contextual details that, together, create a vivid record of experienced events. It may, therefore, be necessary for laboratory tasks to assess associative encoding of distinct elements within a larger context to more closely align with real-world experiences. Horner and Burgess (2013) sought to better understand how multielement associations are represented in memory by testing two alternative hypotheses. That is, whether associations between three separate elements (a person, object, and location) are represented as distinct pairwise relations, where retrieval of one is independent of the others, or whether these elements are encoded to form a single representation, such that retrieval exhibits some degree of dependency. Young adult participants were asked to imagine themselves within a constructed scene containing all three elements. Retrieval trials cued participants with one of the three elements and asked them to recall the remaining two. Results pointed toward a model of dependence, where retrieval of one element was contingent on retrieval of the other, thus supporting the hypothesis that episodic details are bound together into a single representation or engram.

Horner and Burgess (2013, 2014) and others (Backus, Bosch, Ekman, Grabovetsky, & Doeller, 2016; Shohamy & Turk-Browne, 2013; Eichenbaum, Yonelinas, & Ranganath, 2007) implicate the medial-temporal lobes (MTLs), specifically, the hippocampus, as a “convergence zone” critical for multielement binding. A number of studies have linked age-related binding deficits to reduced MTL activity (Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Morcom, Good, Frackowiak, & Rugg, 2003; Mitchell, Johnson, Raye, & D’Esposito, 2000). Many studies also report differential recruitment of pFC areas between young and older adults. Age-related reductions in pFC activity have been reported during both associative encoding (Dulas & Duarte, 2011; Dennis et al., 2008) and retrieval (McDonough & Gallo, 2013; Dulas & Duarte, 2012; Rajah, Languay, & Valiquette, 2010; Duarte, Henson, & Graham, 2008; Rajah & McIntosh, 2008). More rostral pFC regions (e.g., dorsolateral pFC [DLPFC], anterior pFC [aPFC]) have been implicated in interitem evaluations and relational integration (Badre, 2008; Badre & D’Esposito, 2007) and therefore may be particularly important for multielement binding. Furthermore, prior work has shown older adults underrecruit rostral pFC areas during associative encoding (Dulas & Duarte, 2014; Fandakova et al., 2014).

The current study aimed to assess not only age-related behavioral differences in multielement associative encoding but also to investigate neural regions recruited by young and older adults to support subsequent retrieval of the event elements. During fMRI scanning, participants completed an incidental encoding task where they assessed the likeliness that a person with a given occupation would interact with a given object, either in general (our “nonintegrative” condition in which two elements were associated) or with a

specific scene context feature (our “integrative” condition in which three elements were associated). Trials were designed to present half as likely interactions and half as unlikely interactions. At retrieval, participants’ memory was assessed for three event elements: pairs, sources, and contexts. Although source and context memory have been used somewhat interchangeably in the literature, we distinguish the two by defining source as the condition in which the pair was studied (Leshikar & Duarte, 2012; Vilberg & Rugg, 2009) and context as the specific scene with which the pair was studied (James, Strunk, Arndt, & Duarte, 2016; Staresina, Cooper, & Henson, 2013; see Spencer & Raz, 1994, for a similar distinction between source and context). First, participants were asked whether occupation–object pairs were intact or rearranged (i.e., paired associate retrieval). Next, they made a source judgment, deciding whether the pair was studied in the integrative or nonintegrative condition. Finally, if they determined the pair was studied in the integrative condition, participants were then asked to select the correct scene context. This design, therefore, allowed us to assess individual and group differences in success of binding and retrieving the various elements of the encoding event. We conducted multivariate behavioral partial least squares (B-PLS) analyses to identify whole-brain patterns of encoding activity that maximally related to (1) pair memory discriminability, (2) source memory discriminability and response bias, and (3) context memory accuracy in the two age groups.

Based on previous findings (e.g., Horner & Burgess, 2013, 2014), we predicted that accurate retrieval of the event would depend to some extent on one’s ability to successfully bind all relevant elements (i.e., pair, source, and context) into one, integrated memory trace. Therefore, we expected participants, particularly young adults, to show conditional dependence in retrieval of the event elements, such that accurate retrieval of the source/context is dependent on accurate retrieval of the occupation–object pair. Older adults’ memory trace may be impoverished if they are unable or less able than the young to recruit the necessary processes for integrating the stimuli into a coherent representation that facilitates subsequent retrieval of the event as a whole. This may be reflected in young adults to a greater extent than older adults showing recruitment of feature-binding processes mediated by the MTL and executive/organizational processes mediated by the pFC to support subsequent retrieval of the pair, source, and context. Furthermore, if older adults have difficulty suppressing prior knowledge about the stimuli as a result of impaired inhibitory processes (i.e., noncritical recollection; Dulas & Duarte, 2016; Healey, Hasher, & Campbell, 2013; Campbell, Hasher, & Thomas, 2010), their attention will not be constrained to relevant associations, and superfluous details may be bound in addition to or, perhaps, instead of the critical information. In such a scenario, older adults may show similar recruitment of integration regions as the young; however, activity will be differentially associated with retrieval performance across groups.

## METHODS

### Participants

Thirty-two young adults, ages 18–33 years, and 30 older adults, ages 61–77 years, were recruited from Georgia Institute of Technology and the Atlanta community. Six of these participants were excluded: one young adult due to claustrophobia, one young and one older

adult due to computer malfunction (i.e., responses did not record properly), and one young and two older adults due to excessive movement (i.e., head movement exceeded 4 mm). The remaining 29 young and 27 older adults were included in all behavioral and fMRI analyses. Groups did not significantly differ in terms of sex,  $\chi^2(1, n = 56) = .28, p = .599$ , or education,  $t(37.71) = 1.96, p = .058, d = 0.53$ . Group characteristics are presented in Table 1. All included participants were right-handed, native English speakers, with normal or corrected-to-normal vision, and with no reports of psychiatric or neurological disorders, vascular disease, psychoactive drug use, or use of CNS-active or antihypertensive medications. Participation was compensated with class credit or \$15 per hour, plus an additional \$5 for travel expenses. All participants signed consent forms approved by the Georgia Institute of Technology institutional review board.

### Neuropsychological Assessment—WAIS Subtests

After completing the fMRI and behavioral components of the study, participants were administered the Similarities and Visual Puzzles subtests from the Wechsler Adult Intelligence Scale—Fourth Edition (WAIS; Wechsler, 2008) to provide additional measures of semantic and visuospatial reasoning. All participants were within the normal range for their age group. Mean raw scores can be seen in Table 1.

### Materials

Two hundred sixty unique images were used as stimuli (8 in practice trials, 252 in task trials). All images depicted a single, namable object presented in color on a white background. Images were acquired from the Hemera Technologies Photo-Objects DVDs and from Google. An equal number of unique occupations were generated to be paired with the objects. Half of the occupation–object pairs appeared in integrative trials, and half appeared in nonintegrative trials (described in detail below). Additionally, we generated a list of 42 different scenes to be used as context cues for the integrative trials.<sup>1</sup> Each scene was used between two and four times across the encoding trials or three times on average. The context cues and occupations were presented in white text, 48-point Arial font on a black background. Each stimulus subtended a maximum vertical and horizontal visual angle of 4.0° at encoding and 6.2° at retrieval.

### Design and Procedure

The study was divided into encoding and retrieval stages (Figure 1A and B, respectively); retrieval was further divided into two stages for pair and source/context memory. fMRI data were collected only during encoding. Before beginning each stage of the experiment, participants were guided through instructions and practice trials. Practice was repeated as necessary until clear understanding was demonstrated.

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<sup>1</sup>The scene contexts and occupations were presented as words instead of images because for a number of occupations, a context is necessary for the occupation to be identified. For example, while a firefighter or police officer may be easily identified in a picture, an image of an anchorperson may simply show an individual wearing a suit. The person would need to be shown sitting behind a desk in a newsroom to be correctly identified. If this same person was shown in a courtroom, they may be misidentified as a lawyer. In order to create a balanced design (i.e., equal numbers of integrative and nonintegrative trials, as well as equal numbers of trials presenting likely and unlikely interactions), we felt it was necessary to present these elements as words rather than images. This also allowed us to create the 260 unique occupation–object pairings. Objects were presented as images because all 260 stimuli could be easily identified independent of additional context.

**Encoding**—The encoding stage was divided into four blocks, each consisting of 63 trials. Half of the encoding trials presented the occupation–object pair following a scene cue (“integrative trials” hereafter), and the other half presented the pair following a placeholder (i.e., “- - - -”) cue (“nonintegrative trials” hereafter). Participants were asked to make a judgment about the likelihood of an interaction between the presented stimuli. For nonintegrative trials, participants simply had to determine whether a person with the given occupation would interact with the associated object. For integrative trials, participants made a similar decision regarding the occupation–object pair—only this time, the decision had to be made within the context of the given scene. Therefore, integrative trials required that participants jointly consider the scene– occupation, scene–object, and occupation–object relations, which was emphasized in the task instructions. Participants indicated likely interactions by pressing “1” and unlikely interactions by pressing “2” on an MRI-compatible response box.

To minimize task switching, integrative and nonintegrative trials were presented in miniblocks, where seven to eight trials of each type were presented consecutively. At the beginning of each miniblock, a prompt was shown to inform participants that they should judge the likelihood of the occupation–object interaction either in isolation or within the context of the given scene. Participants performed a brief “arrows task” between trials, which maximizes design efficiency by pseudorandomly interspersing event trials with “active” baseline trials lasting between 2000 and 6000 msec, jittered in increments of 2000 msec (Dale, 1999). Every 2000 msec, an arrow appeared on the screen, and participants were asked to indicate its direction using the response box: “1” for a left-pointing arrow and “2” for a right-pointing arrow. The arrow task ensured participants remained engaged in the task and minimized default mode network activity (Stark & Squire, 2001).

Integrative and nonintegrative trials were equally represented across the four encoding blocks. Both conditions were designed to present half of their respective trials as likely interactions and half as unlikely interactions. Integrative unlikely trials were additionally designed to present equal numbers of unlikely scene– occupation, scene–object, and occupation–object relations. Initial behavioral piloting ensured that the design produced high (>80%) agreement with the intended responses.

After participants exited the scanner, they were asked to complete a short questionnaire before beginning retrieval. This questionnaire was administered to obtain information about participants’ experience in the scanner and their approach to the task. The latter was assessed with three main questions of interest: (1) Did you have or form any strategies during the task? If so, briefly elaborate. (2) Did you find yourself visualizing the scenes/ occupations/objects to make your decisions?(3) Did you find yourself coming up with your own scenes when given the nonintegrative source cue?

**Paired Associate Retrieval**—Similar to encoding, this task (Figure 1B, left) was divided into four blocks with 63 trials in each. All stimuli had been encountered at encoding; no new occupations or objects were used. Participants were presented with an occupation–object pair and were instructed to determine whether the pair was intact (i.e., the occupation is presented with the same object with which it was paired during encoding) or rearranged (i.e.,

the occupation is presented with a different object) by pressing “1” or “2,” respectively, on the keyboard. Intact/rearranged status was counterbalanced, such that each pair appeared as an intact pair twice and a rearranged pair once across participants.

Because of low miss rates in piloting, the orientation of the occupation and object was rotated 90° from the encoding presentation so that, at retrieval, the occupation appeared to the right or left of the object, counter-balanced across participants. When the pair is learned during encoding, it is possible for the two elements to become unitized and later remembered as a function of familiarity-based item recognition (Diana, Yonelinas, & Ranganath, 2008). By changing the orientation, the pair cannot be recognized purely on the basis of visuospatial unitization.

**Source and Context Retrieval**—Following paired associate retrieval, participants completed an additional memory test to assess success of encoding the source and scene context for each intact object–occupation pair (Figure 1B, right). Source and context were tested only for trials where the pair appeared as intact during the paired associate retrieval task, as rearranged pairs were associated with two different encoding trials and thus two different sources/contexts. Furthermore, source and context were tested for all intact trials, regardless of pair memory accuracy. This task was divided into four blocks with 42 trials in each. Participants were first asked to make a source memory judgment by determining whether the pair had been studied with a scene (i.e., in the integrative condition) or placeholder (i.e., “- - - -”; in the nonintegrative condition) by pressing “1” or “2,” respectively. If participants selected “scene,” they were then asked to choose the correct scene context from two options, again by pressing “1” or “2” on the keyboard. Two scene options were presented even when participants incorrectly selected “scene” for the source memory probe so as to avoid providing memory-related feedback, which may have had negative subsequent effects on performance.

### Behavioral Analysis

Pair and source memory performance were assessed using measures of signal detection theory:  $d'$  as an estimate of sensitivity/discriminability and  $c$  as an estimate of response bias (Stanislaw & Todorov, 1999). For pair memory, hits were defined as correctly identified intact pairs, and false alarms were defined as trials where rearranged pairs were incorrectly identified as intact. Calculations were performed separately for integrative and nonintegrative trials. Negative values of  $c$  indicate a more liberal bias toward selecting “intact,” and positive values indicate a more conservative bias toward selecting “rearranged.” For source memory, a hit was defined as selecting “scene” when the pair was studied as an integrative trial, and a false alarm was defined as selecting “scene” when the pair was studied as a nonintegrative trial. Response bias ( $c$ ) reflects a participant’s tendency to select the scene or placeholder option, where negative values indicate a more liberal bias toward selecting “scene” and positive values indicate a more conservative bias toward selecting the placeholder option.

Additionally, an estimate of context memory accuracy was calculated for integrative trials to assess participants’ more specific memory for the exact scene associated with the studied

pair. This was calculated as the proportion of integrative pair and context hits, relative to all pair hits for that condition.<sup>2</sup> For the context to be considered correct, the participant needed to select “scene” for the first question, then select the correct scene from the two options in the second question. Thus, chance was 25%. For all behavioral analyses, significant interactions at an alpha level of .05 were followed up with subsidiary ANOVAs and *t* tests to determine the source of the effects.

### fMRI Acquisition

Scanning was performed on a 3T Siemens TIM Trio system at the Center for Advanced Brain Imaging on the Georgia Institute of Technology campus. Functional data were acquired using a gradient-echo pulse sequence (37 transverse slices oriented along the anterior–posterior commissural axis with a 30° upward tilt to avoid the eyes, repetition time = 2000 msec, echo time = 30 msec,  $3 \times 3 \times 3.5$  mm voxels, 0.8 mm interslice gap). Four encoding blocks of 345 volumes each were acquired. The first 2 volumes of each block were discarded to allow for equilibration effects. A high-resolution T1-weighted magnetization-prepared rapid acquisition gradient-echo image was collected for normalization.

### fMRI Analysis

**Preprocessing**—Data were preprocessed with SPM12 (SPM12, [www.fil.ion.ucl.ac.uk/spm/software/spm12/](http://www.fil.ion.ucl.ac.uk/spm/software/spm12/)). Functional images were corrected for differences in slice timing acquisition using the middle slice of each volume as the reference, spatially realigned and resliced with respect to the first volume of the first block. Each participant’s magnetization-prepared rapid acquisition gradient-echo scan was coregistered to the mean EPI image, produced from spatial realignment. Each coregistered structural scan was then segmented using the Diffeomorphic Anatomical Registration Through Exponentiated Lie algebra (DARTEL) SPM12 toolbox (Ashburner, 2007). DARTEL is a suite of tools fully integrated with SPM12, which the SPM12 manual recommends over optimized normalization, to achieve sharper nonlinear registration, for intersubject alignment. This method also achieves better localization of fMRI activations in Montreal Neurological Institute (MNI) space and has been used successfully in several studies with healthy and neurological populations (Pereira et al., 2010; Yassa & Stark, 2009). Briefly, the gray and white matter segmented images were used to create a study-specific template using the DARTEL toolbox and the flow fields containing the deformation parameters to this template for each subject were used to normalize each participant’s realigned and resliced EPIs to MNI space. Normalized EPI images were written to  $3 \times 3 \times 3$  mm and smoothed with an 8-mm FWHM isotropic Gaussian kernel.

**Multivariate Partial Least Squares Analysis**—We conducted two multivariate B-PLS analyses to identify whole-brain patterns of encoding-related activity that correlated with pair memory discriminability, source memory discriminability and response bias, and context memory accuracy in the two age groups. The first analysis (pair and source memory B-PLS) examined subsequent memory discriminability for integrative and nonintegrative

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<sup>2</sup>Note that context accuracy was calculated as a proportion of pair hits rather than all integrative intact trials to minimize the possibility that context hits were a result of guessing, which would likely be the case for pair misses.

pair memory, and source memory and response bias for pair hit trials. The second analysis (integrative pair and context memory B-PLS) examined subsequent pair memory discriminability and context memory accuracy for integrative pair hit trials (McIntosh & Lobaugh, 2004). We ran these analyses separately because the first included trials from both the integrative and nonintegrative conditions whereas the second included trials only from the integrative condition, as nonintegrative trials did not have contexts. Analyses were conducted using PLSGUI software (<https://www.rotman-baycrest.on.ca/index.php?section=84>). This approach was chosen because partial least squares (PLS) is a powerful, data-driven method that identifies spatially and temporally distributed patterns of activated voxels that differ across experimental conditions and relate to specific behavioral measures. PLS does not require that the assumptions of normality, independence of observations, or linearity for general linear models be met (Van Roon, Zakizadeh, & Chartier, 2014).

For both B-PLS models, only subsequent pair hits were included, as there were not enough pair misses in each condition. fMRI data for subsequently remembered pairs were stored in a data matrix, organized by condition, and stacked across participants within age group (detailed below). Behavioral vectors (specific for each model; see below) were created and stacked in the same order as the fMRI data matrix. fMRI data for each event onset (time lag = 0), as well as the subsequent seven volumes ( $2 \text{ sec} \times 7 = 14 \text{ sec}$ ) following each onset were included in the data matrix. The behavioral vectors were cross-correlated with the fMRI data, and the singular value decomposition of the resulting cross-correlation matrix was conducted to yield a set of orthogonal latent variables (LVs). Each LV consists of (1) a singular value reflecting the amount of covariance accounted for by the LV and (2) a singular image representing a pattern of whole-brain activity that is symmetrically related to (3) a correlation profile depicting how participants' behavioral measures related to the pattern observed in the singular image. The singular image includes brain saliences, which are numerical weights assigned to each voxel at each repetition time/time lag included in the data matrix. Brain saliences can be positive or negative: Regions with positive voxel saliences are positively related to the correlation profile, whereas those with negative voxel saliences are negatively related to the correlation profile. Thus, the pattern of whole-brain activity identified by the singular image is symmetrically related to the correlation profile (Ankudowich et al., 2016, 2017; Rajah et al., 2017).

Significance of the LVs was assessed via permutation tests on the singular values ( $p < .05$ ; 1000 permutations). This involved sampling each participant's behavioral measure and event-related activity without replacement, thus randomly reassigning the brain-behavior associations. For each permuted iteration, a PLS model was recalculated, and the probability of the permuted singular value exceeding the observed value for a given LV was the basis of the significance test at  $p < .05$  (McIntosh, Chau, & Protzner, 2004). This permutation method met the exchangeability criterion described in McIntosh and Lobaugh (2004). Bootstrapping (500 iterations) was used to calculate the standard error for each singular image by sampling participants with replacement while maintaining the experimental condition and group order. The bootstrap ratio (BSR; i.e., the ratio of the original brain salience to the bootstrap standard error) was used to identify maximally reliable patterns of positive and negative brain saliences represented in the singular image. Significance of the BSR was set to  $\pm 3.28$  (equivalent to  $p < .001$ ), with a minimum cluster size of 15. To

determine the subset of time lags that maximally represented the correlation profiles of LVs, we computed temporal brain scores for each condition in each significant LV (see McIntosh & Lobaugh, 2004). These temporal brain scores were used to identify the peak time lags as 2–6 (i.e., 4–12 sec after event onset). All reported activations are within these lags.

**Pair and source memory B-PLS.:** The first objective was to identify regions recruited during encoding that support subsequent pair and source memory and determine how this recruitment differs with age. The model specified two conditions (integrative and nonintegrative hit trials) and two groups (young and older adults). Age groups were stacked as follows: young integrative hit, young nonintegrative hit, old integrative hit, and old nonintegrative hit. Three behavioral vectors, containing participants'  $d'$  estimates for integrative and nonintegrative pair memory discriminability,  $d'$  estimates for source memory discriminability, and  $c$  estimates for source memory response bias, were created and stacked in the same order as the fMRI data matrix. Response bias was included as a behavioral regressor to provide supporting evidence for the source  $d'$  estimate. For example, a low  $d'$  could indicate low hit rate or high false alarm rate;  $c$  can disambiguate this—a conservative (i.e., positive)  $c$  suggests a participant's tendency to select the nonintegrative source resulted in few hits (i.e., correctly selecting “scene”) whereas a liberal (i.e., negative)  $c$  suggests a tendency to select “scene” that resulted in a high false alarm rate (i.e., selecting “scene” when the pair was studied as a nonintegrative trial).

**Integrative pair and context memory B-PLS.:** The objective of this model was to identify regions with encoding activity that correlated with memory for the integrative pairs and their specific scene contexts and determine how this activity differed across age groups. Because non-integrative trials had no scene contexts, they were not included in this model. Integrative pair hits were split by subsequent context accuracy to create two conditions: pair + context hits (i.e., both pair and context subsequently remembered) and pair – context hits (i.e., pair but not context subsequently remembered). This model specified these two conditions and two groups, stacked in an fMRI data matrix as follows: young pair + context hit, young pair – context hit, old pair + context hit, old pair – context hit. Two behavioral vectors, containing participants'  $d'$  estimates for integrative pair memory discriminability and context memory accuracy estimates, were created and stacked in the same order as the fMRI data matrix.

## RESULTS

### Behavioral Results

**Pair Memory Sensitivity and Response Bias—**Mean proportions of hits, misses, correct rejections, and false alarms for integrative and nonintegrative trials are presented in Table 2, and mean  $d'$  estimates are displayed in Figure 2. An ANOVA with factors of Condition (integrative, nonintegrative) and Group (young, old) comparing  $d'$  estimates revealed only a main effect of Group,  $F(1, 54) = 11.11, p = .002, \eta_p^2$ , indicating young adults outperformed older adults. No other effects were reliable ( $F_s < 1$ ).

We also assessed pair memory response bias ( $c$ ) for each condition. Mean estimates for young adults were 0.31 ( $SD = 0.24$ ) for integrative pairs and 0.33 (0.30) for nonintegrative pairs. For older adults, mean estimates were 0.24 (0.37) for integrative pairs and 0.22 (0.48) for nonintegrative pairs. An ANOVA with factors of Condition (integrative, nonintegrative) and Group (young, old) did not reveal any reliable effects ( $F_s < 1$ ), suggesting response bias did not differ across conditions or groups.

**Source Memory Sensitivity and Response Bias**—To calculate source memory estimates, a hit is defined as correctly selecting the integrative source (i.e., the scene option), whereas a false alarm is defined as incorrectly selecting the integrative source when the pair was studied as a nonintegrative trial. This was calculated across all trials, regardless of pair memory accuracy. Mean hit rate was 0.58 ( $SEM = 0.03$ ) for young adults and 0.57 ( $SEM = 0.05$ ) for older adults. Mean false alarm rate was 0.15 ( $SEM = 0.02$ ) for young adults and 0.47 ( $SEM = 0.06$ ) for older adults. Mean  $d'$  and  $c$  estimates are presented in Figure 3. Although young adults only showed conservative bias, older adults were more heterogeneous, with 41% showing liberal bias and the remaining 59% showing conservative bias. To compare response bias between groups, the absolute value of  $c$  was used in an independent groups  $t$  test, which found that older adults exhibited greater overall bias,  $t(32.34) = 2.19$ ,  $p = .036$ ,  $d = 0.77$ . Discriminability estimates were significantly greater for young than older adults,  $F(1, 54) = 31.44$ ,  $p < .001$ ,  $\eta^2 = .37$ . Notably, similar results were found when source  $d'$  was calculated using only pair hits,  $F(1, 54) = 33.37$ ,  $p < .001$ ,  $\eta^2 = .38$ . Additionally, ANCOVA results showed the Group difference in source discriminability remained after controlling for pair memory performance (i.e., integrative and nonintegrative pair  $d'$ ),  $F(1, 52) = 19.35$ ,  $p < .001$ ,  $\eta^2 = .27$ . Together, these last two points suggest source memory impairments were not due simply to low paired associate memory performance in older adults.

**Integrative Context Memory Accuracy**—Context memory accuracy is presented in Figure 4. Performance in both young adults,  $t(28) = 10.23$ ,  $p < .001$ ,  $d = 1.90$ , and older adults,  $t(26) = 5.22$ ,  $p < .001$ ,  $d = 1.00$ , was significantly above chance. Young adults' performance was more accurate than that of the older adults,  $F(1, 54) = 6.70$ ,  $p = .012$ ,  $\eta^2 = .11$ ; however, the significance of this group difference was reduced when controlling for integrative pair memory performance,  $F(1, 53) = 2.40$ ,  $p = .127$ ,  $\eta^2 = .04$ .

**Conditional Dependency**—Finally, to explore whether the probability of correctly remembering the context was affected by the success of retrieving the pair, we conditionalized accuracy for context according to the accuracy of the pair judgment. These conditional probabilities were calculated as follows: (1) the probability of correctly endorsing the context, given the pair was also correct,  $p(\text{Context}_{\text{correct}} | \text{Pair}_{\text{correct}}) = p(\text{pair} + \text{context hit})/p(\text{pair hit})$ , and (2) the probability of correctly endorsing the context, given the pair was incorrect,  $p(\text{Context}_{\text{correct}} | \text{Pair}_{\text{incorrect}}) = p(\text{pair miss context hit})/p(\text{pair miss})$ . Note that the same analysis could not be performed for source, as source accuracy must be considered across integrative and non-integrative conditions.

Means, presented in Table 3, were entered into an Accuracy of Pair (correct, incorrect)  $\times$  Group (young, old) ANOVA. Only effects involving accuracy of pair, suggestive of

conditional dependence, are reported. The analysis revealed a significant main effect of Accuracy of Pair,  $F(1, 54) = 109.32, p < .001, \eta^2 = .67$ , which was modified by an interaction with Group,  $F(1, 54) = 6.15, p = .016, \eta^2 = .10$ . Follow-up  $t$  tests revealed that the probability of remembering the context was dependent on whether memory for the pair was also successful, young:  $t(28) = 8.42, p < .001, d = 1.56$ ; old:  $t(26) = 6.36, p < .001, d = 1.22$ . This suggests that both groups were more likely to get the context correct when the pair was also correct and that this conditional dependence was more robust in the young than older adults.

## fMRI Results

**Pair and Source Memory B-PLS**—The data-driven B-PLS identified one significant LV (LV1), which accounted for 28.08% of the total cross-block covariance ( $p < .001$ ). The singular image and correlation profile are presented in Figure 5A and B, respectively, and the local maxima are presented in Table 4. Only negative salience regions (colored in blue, Figure 5A) surpassed the spatial threshold cutoff of 15 contiguous voxels and the BSR threshold of  $\pm 3.28$ . Young adults who showed more activity in these regions exhibited better pair and source memory discriminability, across conditions, and a greater tendency to endorse the non-integrative source for these trials. By contrast, older adults who showed more activity in these same regions exhibited worse nonintegrative pair memory and source memory discriminability (across conditions), as well as a greater tendency to endorse the integrative source (i.e., more liberal bias). These regions included large areas of bilateral medial and lateral posterior parietal cortices, medial and lateral pFC (including aPFC, DLPFC, dorsomedial pFC [DMPFC], and right ventrolateral pFC [VLPFC]), and medial-temporal lobes (including hippocampi).

**Integrative Pair and Context Memory B-PLS**—This B-PLS identified one significant LV, which accounted for 23.39% of the total cross-block covariance ( $p < .016$ ). The singular image and correlation profile are presented in Figure 6A and B, respectively, and the local maxima are presented in Table 5. A majority of the peaks identified were negative brain saliences (colored in blue, Figure 6A), which included bilateral medial and lateral posterior parietal cortices and medial and lateral pFC (including aPFC, VLPFC, left DLPFC, and right DMPFC). The correlation profile indicated that young adults who showed more activity in these regions exhibited better pair and context memory performance across the two conditions (i.e., pair + context and pair – context trials). By contrast, older adults who showed more activity in these same regions for pair + context trials exhibited better context memory. For pair – context trials, greater recruitment of these regions was associated with better pair memory. Positive saliences (colored in red/orange, Figure 6A), which included bilateral anterior cingulate, and left inferior and right superior parietal cortices showed the opposite pattern. That is, greater recruitment of these regions was associated with worse memory performance. Findings from this B-PLS suggest that only in young adults do regions such as aPFC support binding of the pair and context elements into an integrated whole.

## DISCUSSION

The current study explored age-related differences in the neural correlates of multielement binding during associative encoding. We were particularly interested in investigating how aging affects recruitment of pFC and MTL regions, which are believed to be critically involved in the binding of various event details into an integrated memory trace. As predicted, young adults outperformed older adults on memory for the pairs and associated sources, as well as for the specific scene context features. Furthermore, young adults showed greater conditional dependence between pair and context memory, suggesting a superior ability to bind multiple elements into a coherent whole. Consistent with behavioral results, our B-PLS analyses of the fMRI data identified a set of regions including MTL and aPFC whose activity differentially supported subsequent memory across groups: Young adults who engaged these regions showed better memory for the pairs and their sources, whereas older adults who engaged these regions demonstrated worse memory performance. Additionally, only young adults engaged regions such as aPFC to support memory for both the pairs and their associated contexts. These results and their implications are discussed below.

### Behavioral Results

In line with previous findings from our lab (James et al., 2016; Dulas & Duarte, 2012, 2014; Duarte et al., 2008) and others (Mitchell & Johnson, 2009; Glisky et al., 2001; Naveh-Benjamin, 2000), older adults exhibited impaired paired associate memory and memory for source and context features with which the pairs were studied. We designed this study to present naturalistic stimuli that would be encountered in everyday life, reasoning that participants should be able to leverage existing knowledge about the occupations, objects, and locations to optimally perform the task. Previous work has shown memory benefits when material is related to or consistent with prior knowledge (e.g., Gilboa & Marlatte, 2017; Brod, Lindenberger, Werkle-Bergner, & Shing, 2015; DeWitt, Knight, Hicks, & Ball, 2012; Anderson, 1981), and notably, this schema consistency can mitigate age-related memory deficits (Castel, 2005; Shi, Tang, & Liu, 2012). Nevertheless, deficits were quite apparent in the current study. As is typical in aging studies, older adult's impairments did not arise from disproportionately low hit rates but, rather, from high false alarm rates (Old & Naveh-Benjamin, 2008b; Boutet & Faubert, 2006). In the current study, not only were the stimuli highly familiar in nature, but because all were encountered during encoding, rearranged pairs likely elicited familiarity when encountered at test. Participants may need to recollect the additional details of the encoding episode to identify the pair as rearranged—essentially a recall-to-reject strategy, which is impoverished in aging (Patterson & Hertzog, 2010; Cohn et al., 2008; Healy, Light, & Chung, 2005). Under these conditions, older adults may have lacked the source-specifying details that would otherwise inform them that the items were studied in separate trials, leading to a greater false alarm rate than that of young adults. Older adults' greatly reduced source accuracy estimates, discussed below, support this hypothesis.

Source discriminability was substantially lower in older than young adults, consistent with many previous studies (see Mitchell & Johnson, 2009). This age-related source memory impairment persisted even after controlling for paired associate memory performance,

indicating that generally poor associative memory performance cannot fully account for older adults' source memory impairments. This dissociation between associative and source memory is consistent with previous evidence showing impaired source memory despite intact subjective reports of recollection in older adults (Duarte et al., 2008; Duarte, Ranganath, Trujillo, & Knight, 2006). Furthermore, substantial age group differences in response bias, with many older adults showing either liberal or conservative choice bias and young adults showing little bias, contributed to source memory impairments. Though we did not make predictions about age differences in source response bias and, indeed, most studies have not assessed it, we believe the task procedure and similarity across source conditions may have contributed to this effect. That is, if participants selected "scene" for their source memory judgment, they were then presented with a two-alternative forced-choice decision for the scene context. Although yes/no recognition tasks often place greater demands on recollection, forced-choice tasks are believed to rely more heavily on familiarity-based processes, which are relatively preserved in aging (Patterson & Hertzog, 2010; Migo, Montaldi, Norman, Quamme, & Mayes, 2009; Prull, Dawes, Martin, Rosenberg, & Light, 2006; Westerberg et al., 2006). It is plausible that some older participants may have tended toward "scene" source selection, even if internal accumulated evidence for scene information was low, if they felt they could recognize the correct scene once presented with the two options. The pattern of context memory performance suggests that, although this strategy may have been generally successful, it could not ameliorate older adults' impairments. By contrast, some older adults may have adopted a conservative bias if their memories lacked sufficient scene-specifying information to support familiarity-based decisions or if they were unwilling to base their decisions on familiarity. A future study in which the contributions of recollection and familiarity to context memory decisions are measured would be helpful in directly testing this possibility. Another interesting avenue for future research is to investigate whether presenting the scene contexts as images rather than words would facilitate binding of the event elements and whether this facilitation could reduce response bias in older adults and improve their overall performance.

The results discussed thus far suggest that older adults showed worse memory performance than young adults for occupation-object pairs, the source condition in which they were encoded, and the specific scene contexts associated with integrative trials. Unlike prior studies in which the effects of age on these aspects of episodic memory have been assessed separately, we measured them within single events, which is arguably a closer approximation to encoding in everyday life. Previous evidence from young adults has shown that the multiple elements that comprise events are stored as "coherent representations" in which the retrieval of one element is dependent on retrieval of the others (Horner, Bisby, Bush, Lin, & Burgess, 2015; Horner & Burgess, 2014). We compared the conditional dependency of memory for pairs and their presented scene contexts between young and older adults to formally test for age-related differences in the successful integration of these multiple event elements. Although both young and older adults were more likely to correctly remember the scene context when they correctly remembered the occupation-object pair, as opposed to when they did not remember the pair, this conditional dependency was greater for the young. This suggests that older adults had difficulty binding the multiple episodic elements together and/or subsequently retrieving the elements as an integrated whole. The

imaging results, presented below, suggest age-related differences in recruitment of the “core episodic network” during encoding may contribute to this reduced dependency.

## Neuroimaging Results

The first B-PLS analysis, which examined patterns of activity that correlated with integrative and nonintegrative pair and source memory, identified a set of regions whose engagement was beneficial to subsequent memory performance in the young adults and detrimental in the older adults. These regions included MTL, pFC, and posterior parietal regions, which comprise the core episodic memory network (Addis, Roberts, & Schacter, 2011)—a network believed to be particularly important for both reconstruction of past experiences and construction or simulation of hypothetical events (Hassabis & Maguire, 2007; Schacter, Addis, & Buckner, 2007). Specifically, parahippocampal cortex and hippocampus in the MTL are believed to play critical roles in spatial representation (Kravitz, Peng, & Baker, 2011; Mullally & Maguire, 2011) and associative encoding (Davachi, Mitchell, & Wagner, 2003). Medial pFC areas such as DMPFC are believed to be important for self-referential and evaluative processes (Leshikar & Duarte, 2014; Whitfield-Gabrieli et al., 2011; Cabeza & St Jacques, 2007; Gusnard, Akbudak, Shulman, & Raichle, 2001). Posterior cingulate and retrosplenial cortices in medial parietal regions are believed to function as a multimodal association area that integrates new information with prior knowledge (Vann, Aggleton, & Maguire, 2009; Zysset, Huber, Ferstl, & von Cramon, 2002), whereas lateral parietal regions like precuneus are important for imagery and encoding of multifeature perceptual representations.

Our finding that young adults who showed more activity in this core episodic memory network at encoding exhibited better subsequent memory for the pairs and their associated sources is consistent with the constructive episodic simulation hypothesis (Schacter & Addis, 2007). This hypothesis proposes that (1) past and simulated events draw on similar information and rely on related underlying processes and (2) episodic memory supports the construction of events by extracting and recombining stored information into a simulation of a novel event. Our encoding task required that participants draw from their own experiences with the scenes, occupations, and objects and integrate these details to simulate a scenario to determine the likelihood that such an event would occur in reality. Thus, we predicted that success of this demanding task would rely heavily on recruitment of integration processes mediated by the most anterior aspects of the pFC. Consistent with this prediction, we observed that young adults who exhibited greater activity in aPFC and DLPFC (regions involved in higher order cognitive control operations such as multi-feature processing and relational integration; Christoff, Keramatian, Gordon, Smith, & Mädler, 2009; Mitchell & Johnson, 2009; Badre, 2008; Christoff & Gabrieli, 2000), also performed better on subsequently paired associate and source memory measures, which required the successful integration of mnemonic elements. Interestingly a meta-analysis (Benoit & Schacter, 2015) that set out to determine whether any brain areas were more activated during simulation of events than recollection identified a number of frontal regions that were also observed in our PLS results, including DLPFC, aPFC, and DMPFC. This suggests that greater activity in these regions may have played a role in the successful integration of encoding stimuli to support subsequent retrieval of multi-element episodic events.

Our finding that older adults who engaged these same regions at encoding tended to show worse subsequent memory performance is consistent with the associative deficit hypothesis (Naveh-Benjamin, 2000), which proposes that age-related memory impairments stem from older adults' difficulties in forming and retrieving associations that link disparate pieces of information. These difficulties could arise as a result of impaired executive functions mediated by the pFC (Moscovitch & Winocur, 1995) or binding deficits mediated by the hippocampus and other MTL structures (Ryan, Leung, Turk-Browne, & Hasher, 2007). A number of studies have reported that, relative to the young, older adults show reduced recruitment of both MTL (Daselaar et al., 2003; Morcom et al., 2003; Mitchell et al., 2000) and pFC regions (McDonough & Gallo, 2013; Dulas & Duarte, 2011, 2012; Dennis et al., 2008; Duarte et al., 2008). Interestingly, our current findings suggest that older adults are not necessarily under-recruiting pFC and MTL regions but rather recruiting them in a manner that hinders subsequent memory performance. This is in contrast to the young adult group, in which greater pFC and MTL activation was associated with better performance. This suggests that these regions differentially supported episodic encoding across age groups. This is consistent with our findings from the second PLS analysis, discussed below.

Associative memory deficits in older adults have been linked to failures to spontaneously initiate semantic elaborative processes that support rich episodic encoding ( Craik & Simon, 1980). That said, previous research has shown that older adults can engage such processes when environmental support is provided (Leshikar, Dulas, & Duarte, 2015; Logan, Sanders, Snyder, Morris, & Buckner, 2002). Results from our first B-PLS analysis suggest that activating the traditional network used by the young does not support older adults' memory performance. We suspect that the familiar experimental stimuli and demands on one's personal experiences with them may have spurred these elaborative processes as participants tapped into their rich and detailed schemas during encoding. Older adults may have been less able to suppress or prune the contents of these retrieved autobiographical details (Andrews-Hanna, Smallwood, & Spreng, 2014; Campbell et al., 2010; Anderson et al., 2004), interfering with their ability to form a concise representation of the event. It is therefore possible that the unconstrained nature of the elaboration may have resulted in superfluous details becoming bound in the memory trace that hindered subsequent retrieval of the relevant information. Though we did not assess noncriterial details generated by participants as they performed the encoding task, this could be an informative measure to include in future studies (see Parks, 2007).

Another possible source of interference is the repetition of scene contexts. Although we would argue that this is more similar to real-world scenarios where different events can occur in overlapping contexts, this repetition may have affected performance and could have contributed to the age effect (Dulas & Duarte, 2016; Ikier, Yang, & Hasher, 2008). However, our paradigm was designed this way to accommodate the necessary number of trials for imaging analyses while at the same time balancing congruency across the different kinds of associations (e.g., scene–occupation; see Method). Future studies could investigate whether age differences in memory performance are reduced by using unique scenes for the integrative trials.

The large swath of posterior parietal regions, such as precuneus and posterior cingulate, identified in our first PLS analysis supports the idea that participants constructed a mental image of the occupations, objects, and scenes to make their encoding decisions. Further support for this possibility comes from our postscan questionnaire, in which a large majority (93%) of young adults and a slightly lower majority (64%) of older adults indicated they were visualizing the scenes to make their judgments about the occupations and objects. Although engagement of mental imagery regions appeared to benefit memory performance in the young, it hindered subsequent retrieval in the old. Age-related reality monitoring deficits may explain this discrepancy. Schacter, Gaesser, and Addis (2013) note that the flexibility of memory-based construction that allows alternative novel scenarios to be simulated also increases vulnerability to memory distortions. About half of both young (52%) and older adults (44%) indicated in the postscan questionnaire that they were consciously coming up with their own scenes at least some of the time for nonintegrative trials. The source monitoring framework predicts that greater similarity between potential sources of memories generally leads to increased source errors (Johnson, Hashtroudi, & Lindsay, 1993; Hashtroudi, Johnson, & Chrosniak, 1989). In the absence of a specific given scene, participants may have pieced together various details from their own experiences, creating mental images that were rich in content but lacking in informative detail. Although this imagery strategy appears to have benefitted young adults, many of whom seemed able to effectively discriminate between perceived and imagined scenes, older adults may have been less able to make this distinction. For older adults, during both integrative and nonintegrative trial encoding, those who showed greater recruitment of imagery regions had a greater tendency to select the integrative scene source during retrieval (i.e., more liberal bias). Thus, it may be that both young and older adults were able to paint vivid mental images to facilitate their encoding decisions, but older adults who did this later misattributed these retrieved scene-specifying details as evidence for a perceived scene rather than an imagined scene as a result of impaired monitoring processes (Lyle & Johnson, 2007; Gonsalves et al., 2004).

Our second B-PLS analysis was used to test the hypothesis that young adults, but not older adults, were engaging a set of regions to support integration of the pair with the specific scene context. This analysis identified a set of regions that supported both pair and context memory performance in young adults only, suggesting this group was able to recruit regions such as aPFC to successfully bind the pair and context features into an integrated memory trace. Interestingly, this pattern was observed for pair + context trials as well as pair – context trials, suggesting context misses may have arisen from retrieval-related errors in this age group. Engagement of these same regions by older adults for pair + context trials was associated with higher context but not pair memory performance. This may seem at odds with the previous analysis, in which engagement of aPFC was associated with worse source memory performance for older adults. However, it should be noted that source and context memory, though related, are different in an important way: Context memory accuracy was calculated as a function of integrative pair hits, and for the context to be considered correct, it required that participants correctly endorse the scene source as well as the specific scene context. Source confusions in older adults often prevented them from getting to the stage where context memory was assessed. However, when they did reach this stage, the two-

alternative forced-choice task may have allowed them to rely more heavily on familiarity-based processes, which, as discussed above, are relatively preserved in aging (Patterson & Hertzog, 2010; Migo et al., 2009; Westerberg et al., 2006). Our second PLS analysis allowed us to more precisely assess such a scenario by partitioning the integrative pair hits into trials where the context was correctly remembered and those where it was not. When narrowing the focus to those trials where the event as a whole (i.e., pair and context) was subsequently remembered, we see that older adults were able to engage the same regions as the young to support their context memory performance. Unlike the young, however, this activity in older adults did not appear to reflect integration of the occupation, object, and scene elements into a coherent representation. Notably, this is consistent with our behavioral findings showing greater conditional dependency between pair and context memory in young adults relative to older adults.

Finally, as we only scanned the encoding portion of the study, we cannot rule out the possibility that older adults' memory deficits additionally arose from retrieval difficulties. For example, the "indiscriminate binding" at encoding paves the way for additional interference that must be resolved at retrieval (Healey et al., 2013). Resolving this interference becomes increasingly difficult with age (Dulas & Duarte, 2016; Ikier et al., 2008). Another possibility to be explored in a future study is that group differences in performance are attributable to reduced pattern completion triggered by the partial cueing with the intact pair. That is, episodic recollection is believed to occur when a "partial input" cue prompts the retrieval of the additional elements associated with the original event to produce a complete representation or pattern of that event (Horner et al., 2015). If older adults are less able than the young to recruit these hippocampal-mediated processes when cued with the intact pairs, their ability to recover the contextual details associated with that pair may be reduced. Although the results of our conditional dependency analyses (i.e., young adults show a greater dependence between pair and context memory than older adults) and our second B-PLS analysis (i.e., only young adults engage the same set of regions to support memory for both the pair and context) speak to this, imaging data collected during retrieval are needed to directly test this possibility.

## Conclusions

The current study provides novel evidence of multi-element binding deficits in older adults. Contrary to predictions based on prior work that aging is associated with reduced recruitment of regions believed to be important for relational integration and binding, namely, MTL and aPFC, our PLS analyses revealed that, although both groups engaged these regions as a part of the larger "core episodic network," this recruitment differentially supported memory performance across groups. We attribute this pattern to older adults who have more difficulty suppressing noncritical details, increasing the likelihood of these details being integrated and bound alongside the relevant information, thus creating a cluttered memory trace that must be resolved at retrieval. These poorly organized connections may lead to a heightened sense of familiarity, which results in increased false alarms on recognition tests. Although older adults were able to recruit some of the most aPFC areas to support context memory performance, this activity did not appear to reflect integration of the occupation, object, and scene features as it did in the young adults.

Though future work is needed to clarify the role that dysfunctional retrieval processes, such as differences in pattern completion, played in older adults' memory impairments, the findings presented here illustrate that binding and/or retrieving multiple event elements as an integrated whole becomes increasingly challenging as we age.

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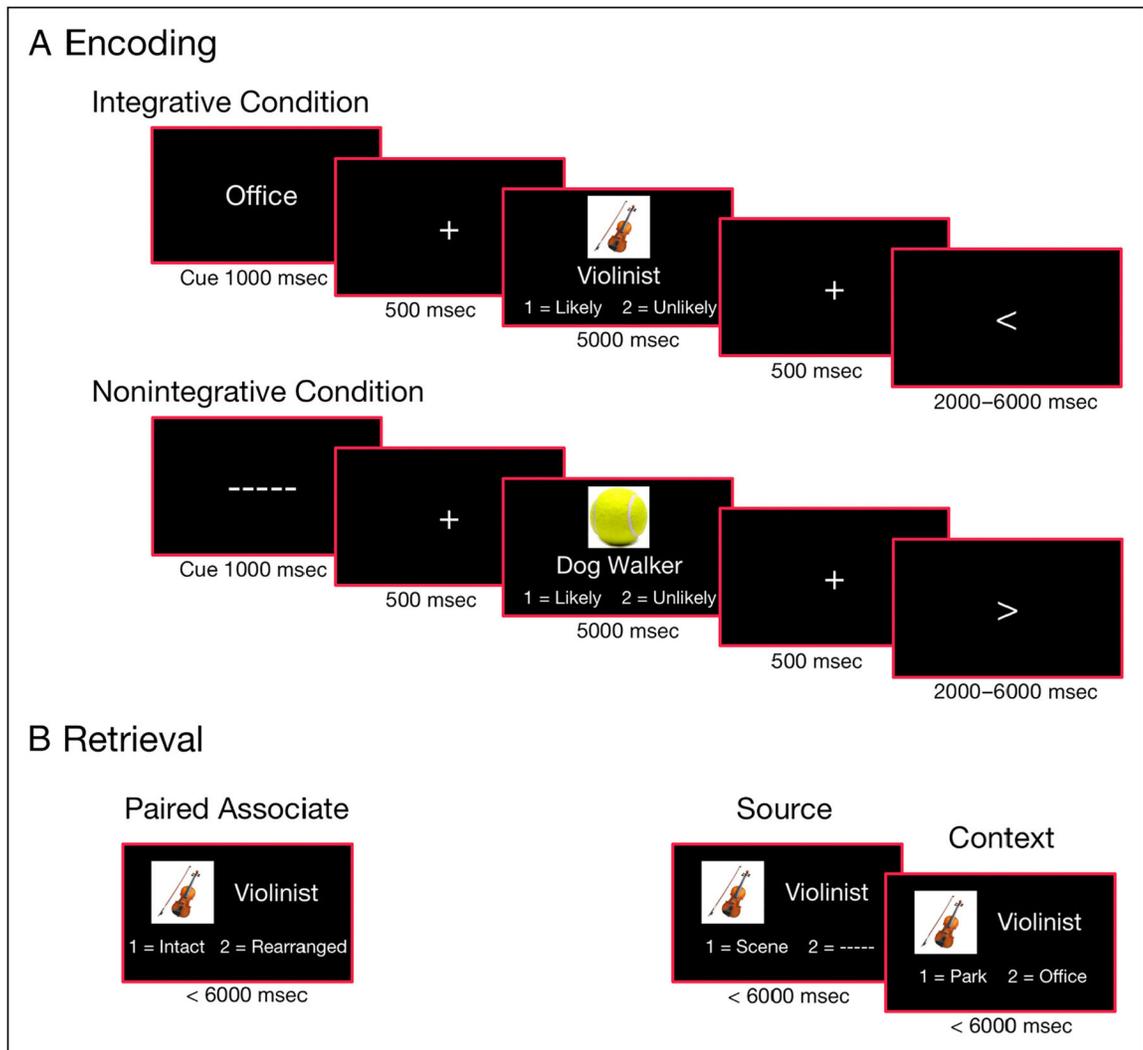
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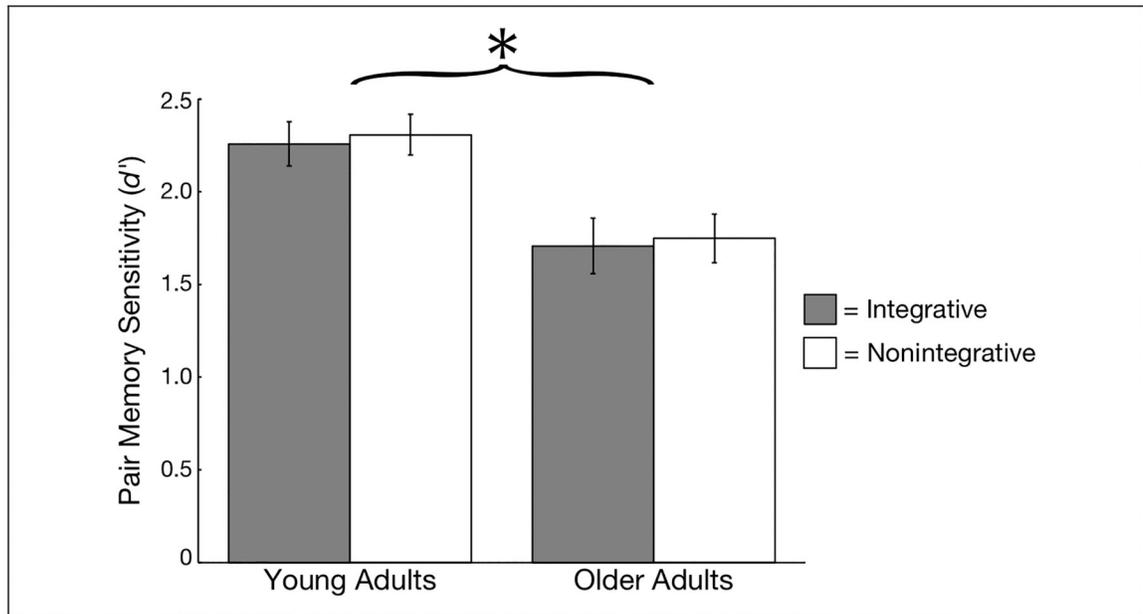
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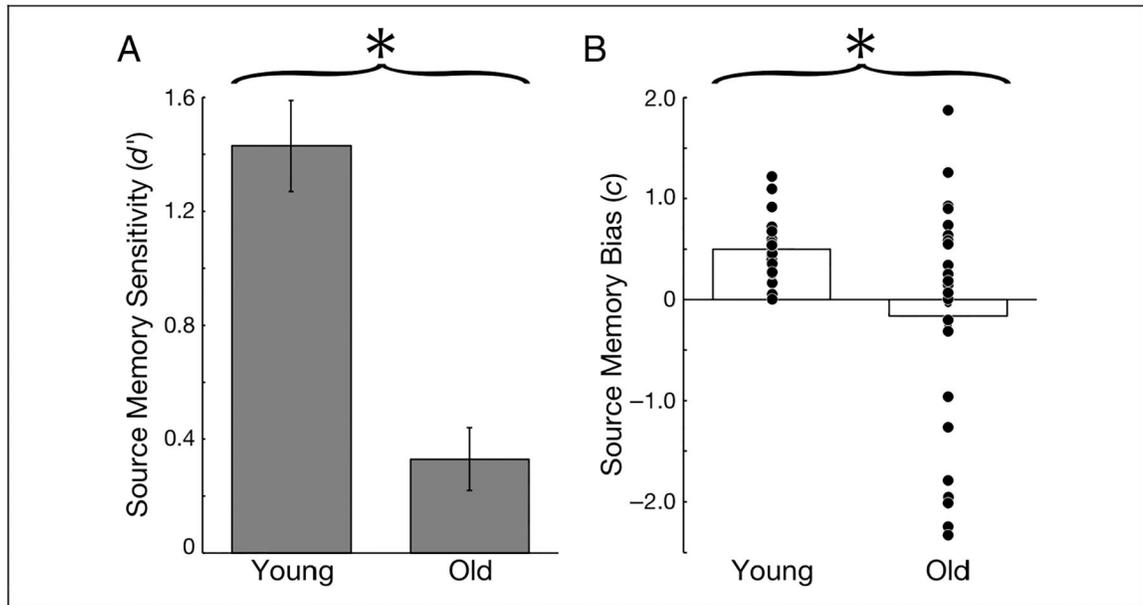
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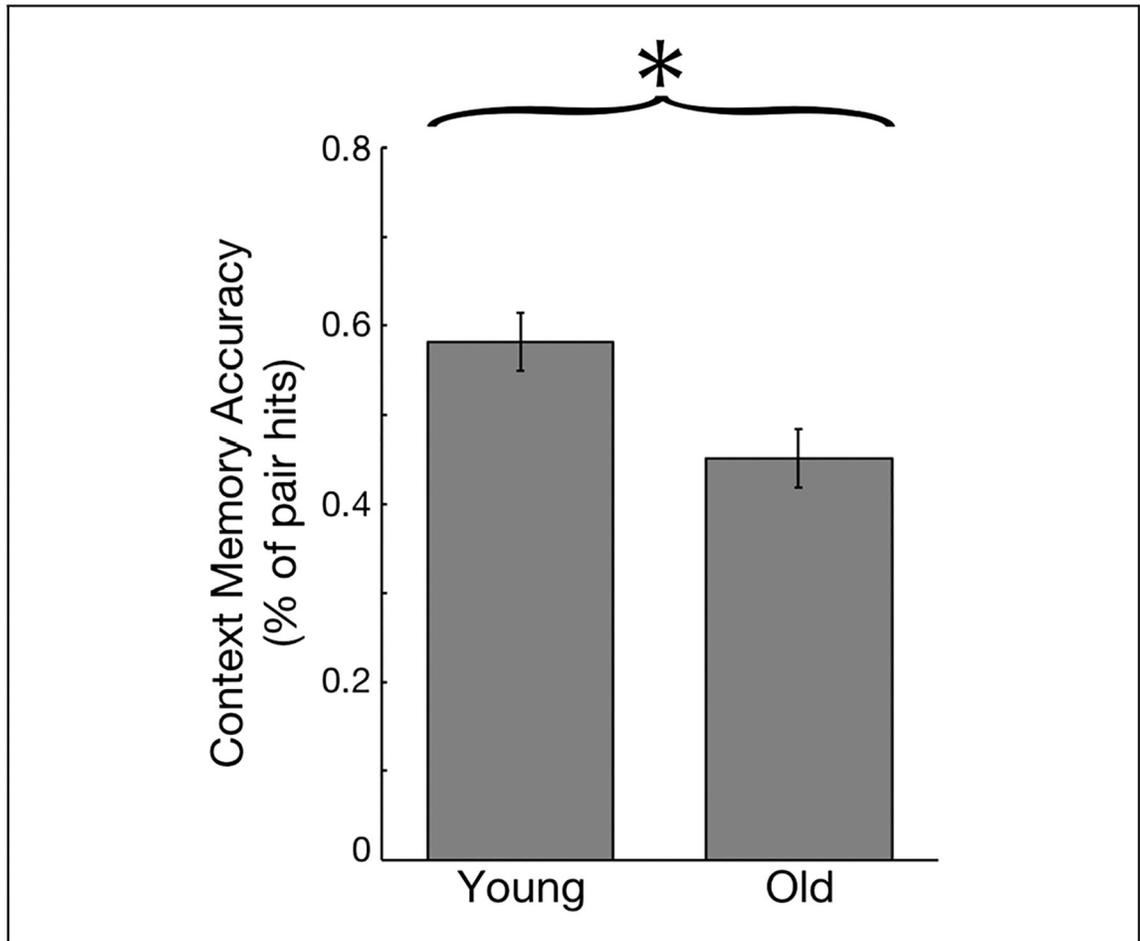
**Figure 1.**  
Experimental design.



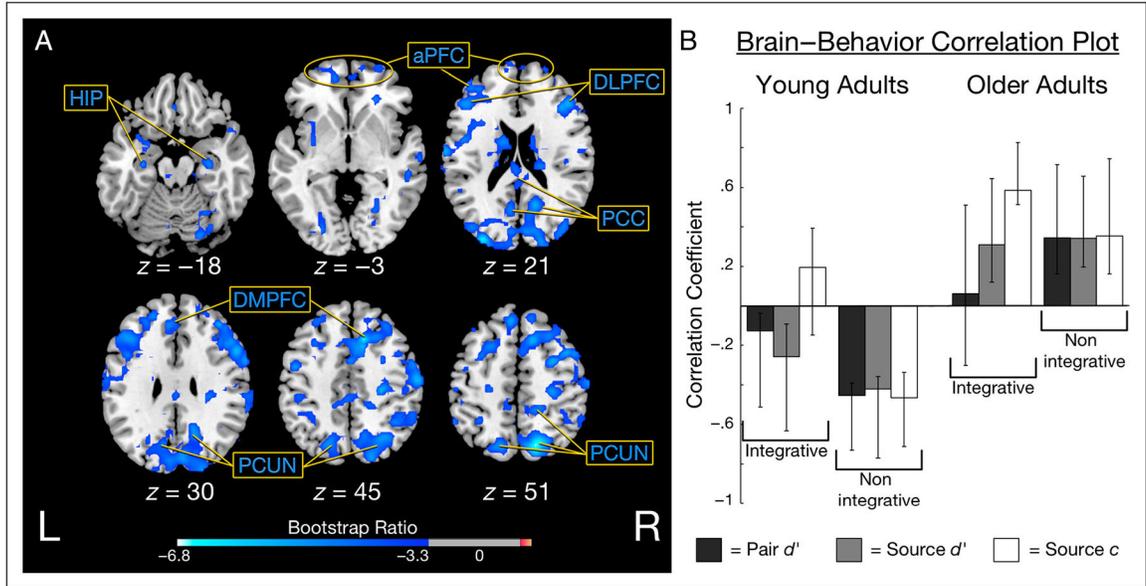
**Figure 2.** Mean  $d'$  estimates for integrative and nonintegrative pair memory for young and older adults. Error bars depict *SEM*.



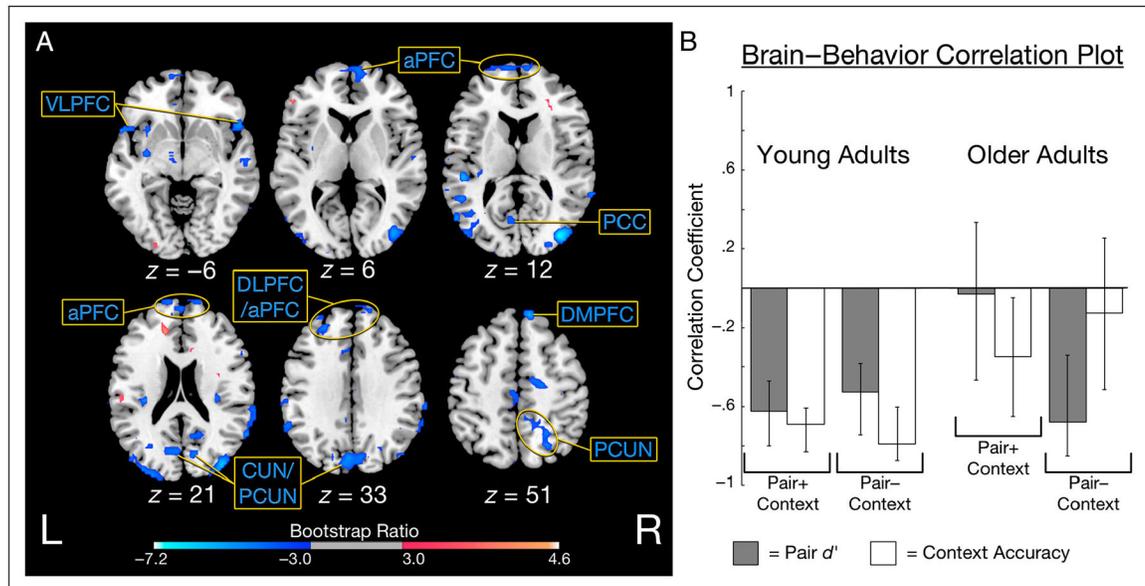
**Figure 3.** (A) Mean source memory sensitivity ( $d'$ ) for each age group. (B) Mean response bias ( $c$ ) for each age group. Error bars in A depict *SEM*. Circles in B represent each participant's bias estimate.



**Figure 4.** Mean integrative context memory accuracy for each age group. Error bars depict *SEM*.



**Figure 5.** Singular image and corresponding correlation profile for pair and source memory B-PLS LV1. (A) Singular image. Blue regions reflect negative brain saliences, threshold BSR of  $\pm 3.28$ ,  $p < .001$ . HIP = hippocampus; PCC = posterior cingulate cortex; PCUN = precuneus. (B) Brain-behavior correlation profile for each condition/age group. Error bars represent 95% confidence interval. Integrative source  $c$  for young adults and integrative pair  $d'$  for older adults do not contribute to this LV as error bars cross zero.



**Figure 6.**

Singular image and corresponding correlation profile for integrative pair and context memory B-PLS LV1. (A) Singular image. Blue regions reflect negative brain saliences, red/orange regions reflect positive saliences, threshold BSR of  $\pm 3.00$  (BSR lowered from  $\pm 3.28$  to improve visibility in the figure),  $p < .001$ . PCC = posterior cingulate cortex; CUN = cuneus; PCUN = precuneus. (B) Brain–behavior correlation profile for each condition/age group. Error bars represent 95% confidence interval. Pair + Context Pair  $d'$  and Pair – Context Context Accuracy for older adults do not contribute to this LV as error bars cross zero.

**Table 1.**

## Group Characteristics

Measure	Young (n = 29)	Old (n = 27)
Age	22.55 (3.75)	66.56 (4.18)
Sex (female/male)	16/13	13/14
Education	15.10 (1.52)	16.37 (3.03)
Similarities	31.31 (4.05)	28.89 (6.90)
Visual puzzles *	19.72 (4.79)	14.89 (4.96)

Standard deviations in parentheses. WAIS subtest scores reported as raw scores.

\*  $p < .05$ .

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Mean Proportions of Integrative and Nonintegrative Hits and Misses for Intact Pairs, and Correct Rejections and False Alarms for Rearranged Pairs

**Table 2.**

	Young		Old	
	Integrative	Nonintegrative	Integrative	Nonintegrative
<i>Intact</i>				
Hit	0.78 (0.02)	0.77 (0.03)	0.72 (0.02)	0.71 (0.03)
Miss	0.22 (0.02)	0.23 (0.03)	0.28 (0.02)	0.29 (0.03)
<i>Rearranged</i>				
CR	0.91 (0.01)	0.91 (0.01)	0.84 (0.03)	0.84 (0.03)
FA	0.09 (0.01)	0.09 (0.01)	0.16 (0.03)	0.16 (0.03)

*SEM* in parentheses. CR = correct rejection; FA = false alarm.

**Table 3.**

Conditional Probabilities between Pair and Context Memory Accuracy

	Young	Old
$(\text{Context}_{\text{correct}}   \text{Pair}_{\text{correct}})$	0.58 (0.03)	0.45 (0.04)
$(\text{Context}_{\text{correct}}   \text{Pair}_{\text{incorrect}})$	0.25 (0.02)	0.24 (0.04)

*SEM* in parentheses.

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Table 4.

## LV1 Brain Regions for Pair and Source Memory B-PLS

Lag	BSR	Spatial Extent	MNI Coordinates			Gyral Location	Brodmann's Area
			x	y	z		
<i>Negative Salience Regions</i>							
Left Hemisphere							
2, 5, 6	-6.07	602	-51	3	39	Precentral	6
2	-5.60	92	-15	-3	24	Caudate	
3, 4	-5.20	22	-45	51	18	Middle frontal (l. aPFC)	10/46
3, 4, 5, 6	-5.19	152	-33	45	24	Middle frontal (DLPFC)	9/46
2, 3, 4	-5.15	103	-30	-90	18	Middle occipital	19
2, 3, 5	-5.11	139	-30	6	57	Middle frontal	6
3, 5, 6	-4.85	27	-9	-18	39	Cingulate (dPCC)	31
5, 6	-4.78	18	-33	0	-27	Parahippocampal/hippocampus	34
2, 6	-4.68	109	-6	-63	24	Precuneus	31
3	-4.67	41	-6	39	30	Superior frontal (DMPFC)	9
2, 5	-4.66	62	-45	-30	39	Inferior parietal lobule	40
6	-4.58	40	-12	54	-3	Medial frontal (aPFC)	10
2	-4.46	33	-24	-81	-3	Lingual	18/19
5	-4.29	19	-9	-21	18	Thalamus	
5	-4.02	26	-6	30	27	Anterior cingulate	32
Right Hemisphere							
4, 5, 6	-6.83	1847	15	-69	51	Precuneus <sup>a</sup>	7
2	-6.82	797	12	21	45	Superior frontal (DMPFC)	6/8
2, 4, 5	-5.87	198	63	6	30	Precentral	6
3, 4, 5	-5.63	127	12	15	45	Cingulate (dACC)	24/32
5	-5.60	267	54	15	30	Inferior frontal	9/44
2, 5	-5.57	475	27	-24	48	Cingulate (dPCC)	31
2, 3	-5.48	244	45	33	21	Middle frontal (DLPFC)	9/46
6	-5.15	29	39	12	-33	Temporal pole	38
2	-5.14	283	12	-30	18	Posterior cingulate	23

Lag	BSR	Spatial Extent	MNI Coordinates			Gyrus Location	Brodmann's Area
			x	y	z		
5, 6	-4.89	73	48	-54	6	Middle temporal	37
6	-4.80	20	24	36	-3	Inferior frontal (VLPFC)	47
3, 5	-4.73	28	30	-15	-18	Hippocampus	
2, 5, 6	-4.69	140	39	-51	45	Inferior parietal lobule	40
5, 6	-4.49	29	69	-39	3	Middle temporal	21/22
4	-4.45	20	42	-78	3	Middle occipital	19
4, 6	-4.20	21	45	-21	24	Insula	13
2, 6	-4.10	22	24	63	21	Superior frontal (aPFC)	10
6	-4.10	31	6	60	-6	Medial frontal (aPFC)	10
4	-4.09	56	18	-78	30	Cuneus	18

Peaks ranked according to BSR within hemisphere. dACC = dorsal ACC; dPCC = dorsal posterior cingulate cortex.

<sup>a</sup>Cluster also included precuneus (BA 31), cuneus (BA 18/19), and posterior cingulate (BA 30).

Table 5.

## LV1 Brain Regions for Integrative Pair and Context Memory B-PLS

Lag	BSR	Spatial Extent	MNI Coordinates			Gyral Location	Brodmann's Area
			x	y	z		
<i>Negative Salience Regions</i>							
Left Hemisphere							
6	-5.76	57	-51	-30	12	Superior temporal	41/22
5, 6	-5.76	17	-57	-69	9	Middle temporal	37/39
4, 5	-5.63	259	-3	-75	27	Cuneus <sup>a</sup>	18/19
5	-5.11	49	-6	-15	42	Cingulate	24
5	-5.06	29	-57	15	-6	Temporal pole/inferior frontal (VLPFC)	38/47
5, 6	-4.92	49	-48	-81	18	Middle occipital	19/18
6	-4.87	17	-30	-66	18	Posterior cingulate	30
4	-4.68	32	0	-57	42	Precuneus	7
5	-4.54	16	-33	-6	-6	Putamen	
5	-4.54	25	-27	42	33	Middle frontal (DLPFC)	9/46
6	-4.49	64	-6	-21	57	Medial frontal/paracentral lobule	6/5
5	-4.49	25	-60	-48	33	Supramarginal	40
5	-4.47	57	-3	51	27	Medial frontal (aPFC)	10/9
6	-4.08	15	-63	-42	0	Middle temporal	21
Right Hemisphere							
5	-7.18	167	36	-84	15	Middle occipital	19
6	-5.68	116	66	-45	15	Superior temporal	22
5, 6	-5.54	59	54	21	-3	Inferior frontal (VLPFC)	47/45
5	-5.51	24	9	45	51	Superior frontal (DMPFC)	9
5	-5.50	102	24	-63	54	Precuneus	7
5	-4.51	19	69	-30	33	Supramarginal	40
6	-4.51	16	54	-63	-15	Fusiform	37
5, 6	-4.45	196	12	63	3	Medial frontal (aPFC)	10
6	-4.44	30	12	-9	51	Medial frontal	6
5, 6	-4.42	20	42	-24	63	Precentral	4

Lag	BSR	Spatial Extent	MNI Coordinates			Gyral Location	Brodmann's Area
			x	y	z		
6	-4.04	24	3	39	-21	Medial frontal (aPFC)	10/11
4, 5	-3.98	37	18	-63	27	Precuneus	31
<i>Positive Salience Regions</i>							
Left Hemisphere							
2	4.56	22	-12	39	24	Cingulate (dACC)	32
3	4.34	19	-57	-27	24	Inferior parietal lobule	40
3	4.26	19	-24	-87	0	Middle occipital	18
Right Hemisphere							
5	4.08	15	30	30	15	Anterior cingulate	32
3	4.04	16	15	-60	60	Superior parietal lobule	7

Peaks ranked according to BSR within hemisphere.

<sup>a</sup>Cluster also included precuneus (BA 31).