Aging Affects the Interaction between Attentional Control and Source Memory: An fMRI Study

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Abstract

■ Age-related source memory impairments may be due, at least in part, to deficits in executive processes mediated by the PFC at both study and test. Behavioral work suggests that providing environmental support at encoding, such as directing attention toward item–source associations, may improve source memory and reduce age-related deficits in the recruitment of these executive processes. The present fMRI study investigated the effects of directed attention and aging on source memory encoding and retrieval. At study, participants were shown pictures of objects. They were either asked to attend to the objects and their color (source) or to their size. At test, participants determined if objects were seen before, and if so, whether they were the same color as previously. Behavioral results showed that direction of attention improved source memory for both groups; however, age-related deficits persisted. fMRI results revealed that, across groups, direction of attention facilitated medial temporal lobe-mediated contextual binding processes during study and attenuated right PFC postretrieval monitoring effects at test. However, persistent age-related source memory deficits may be related to increased recruitment of medial anterior PFC during encoding, indicative of self-referential processing, as well as underrecruitment of lateral anterior PFC-mediated relational processes. Taken together, this study suggests that, even when supported, older adults may fail to selectively encode goal-relevant contextual details supporting source memory performance. ■

INTRODUCTION

Neuroimaging research has demonstrated that, although both source memory (memory for an item and its associated details) and item memory may rely on medial temporal lobe mediated memory processes, source memory may rely on executive processes mediated by the PFC to a much greater extent than item memory (see Mitchell & Johnson, 2009; Blumenfeld & Ranganath, 2007, for reviews). These executive processes may support source memory performance by facilitating organization and binding of information at encoding (Ranganath, 2010), as well as strategic retrieval processes at test, such as monitoring the products of retrieval (Dulas & Duarte, 2012; Badre & Wagner, 2007; Henson, Shallice, & Dolan, 1999). This imaging evidence has been further substantiated by lesion studies, which have also shown that the PFC may be critical for source memory performance (Duarte, Ranganath, & Knight, 2005; Janowsky, Shimamura, Kritchevsky, & Squire, 1989; Janowsky, Shimamura, & Squire, 1989; see Mitchell & Johnson, 2009, for a review; Swick, Senkfor, & Van Petten, 2006). Furthermore, a common finding in the field of memory and aging is that older adults show disproportionate impairments to source memory compared with item memory (see Mitchell & Johnson, 2009; Spencer & Raz, 1995, for reviews). Thus, it has been suggested that these source memory deficits may be due, at least in part, to deficits in the recruitment of PFC-mediated executive control processes supporting source memory (Johnson, Hashtroudi, & Lindsay, 1993; Hasher & Zacks, 1979); that is in line with the Frontal Aging Hypothesis (see Raz, 2000; West, 1996, for reviews). In correspondence with these results, fMRI studies of memory and aging have shown age-related alterations in PFC recruitment at both study (Dulas & Duarte, 2011; Duverne, Motamedinia, & Rugg, 2009b; Dennis et al., 2008) and test (Dulas & Duarte, 2012; McDonough, Wong, & Gallo, 2013; Rajah, Languay, & Valiquette, 2010). Taken together, these results suggest that memory tasks placing higher demands on PFC-mediated processes (such as source memory tasks) will show larger age-related performance deficits.

However, it is unclear if these age-related alterations are because of irreparable changes in PFC functioning or because of a failure to spontaneously engage these processes in older adults. Thus, the question remains: Can source memory deficits in older adults be reduced with sufficient environmental support (see Luo & Craik, 2008, for a review)? One possibility is that older adults may not sufficiently attend to relevant source information during encoding. Previous evidence suggests that attention can impact both memory strength and content (Chun & Turk-Browne, 2007). Furthermore, fMRI evidence suggests that older adults may not sufficiently maintain attention across an encoding period (Dennis, Daselaar, & Cabeza, 2007).

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Interestingly, behavioral work has shown that directing participants to attend to specific associations during study, such as asking "How well does a chair (item) fit with a room (source)," improves source memory accuracy for these associations in both young and older adults (Glisky & Kong, 2008; Naveh-Benjamin, Brav, & Levy, 2007; Glisky, Rubin, & Davidson, 2001; Hashtroudi, Johnson, Vnek, & Ferguson, 1994). Furthermore, fMRI evidence suggests that orienting instructions that support semantic encoding relative to intentional encoding instructions may reduce age-related underrecruitment of PFC-mediated processes and age-related memory deficits (Logan, Sanders, Snyder, Morris, & Buckner, 2002). Thus, instructions that direct one's attention at encoding toward task-relevant associations may reduce age-related source memory deficits, in part, by supporting encoding processes such as dorsolateral PFC (DLPFC) and/or anterior PFC (aPFC)-mediated relational processes (Ranganath, 2010; Badre, 2008; Blumenfeld & Ranganath, 2007; Koechlin, Ody, & Kouneiher, 2003; Koechlin, Corrado, Pietrini, & Grafman, 2000). These relational processes may serve to build relationships between objects and source (e.g., color) that are held in working memory or to allow for comparison between multiple relationships during encoding (Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Ramnani & Owen, 2004).

Although attention likely affects encoding mechanisms, it is equally possible that directed attention during encoding may affect strategic retrieval processes that are also believed to be impaired in older adults (Naveh-Benjamin et al., 2009; Cohn, Emrich, & Moscovitch, 2008). Evidence from ERP literature has suggested that direction of attention at encoding may reduce the need for these PFC-mediated strategic retrieval processes at test in young adults (Kuo & Van Petten, 2006) and similarly in older adults (Dulas & Duarte, 2013). In these studies, directing attention to the color of an object improved subsequent object–color memory and reduced late-right frontal ERP effects, thought to represent postretrieval monitoring processes, which may involve evaluating the products of retrieval, resolving interference, as well as initiating additional retrieval searches. Postretrieval monitoring is thought to be engaged to a greater extent when participants are closer to their memory decision criterion (Henson, Rugg, Shallice, & Dolan, 2000). Similar work using fMRI suggests that postretrieval monitoring effects may be mediated, at least in part by the right lateral PFC (Rugg, Henson, & Robb, 2003; Henson et al., 1999). The neural correlates of postretrieval monitoring have been shown in multiple largely right PFC regions, including both DLPFC and ventrolateral PFC (VLPFC), across myriad tasks such as exclusion tasks, proactive interference, and source memory (Dulas & Duarte, 2012; Shimamura, 2011; Badre & D'Esposito, 2009; Bunge, Burrows, & Wagner, 2004; Rugg et al., 2003; Henson et al., 1999, 2000). The exact locus of postretrieval monitoring or specific aspects thereof may depend upon the task demands and/or stimulus modalities. Regardless, direction of atten-

tion during encoding may attenuate the need to engage in the postretrieval operations by creating a strong item–source association.

In addition to alterations in the recruitment of PFC-mediated processes, direction of attention may also facilitate additional processes supporting source encoding and retrieval. Direction of attention may support medial temporal lobe (MTL)-mediated contextual binding processes, which associate item and context (e.g., object and color, object and source) information in memory (Ranganath et al., 2004; Davachi, Mitchell, & Wagner, 2003). It is also possible that direction of attention may facilitate contextual binding by enhancing perceptual processing for relevant features (Gazzaley & D'Esposito, 2007; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Gazzaley, Cooney, Rissman, & D'Esposito, 2005). For example, some evidence has suggested that attention modulates subsequent source memory activity in extrastriate cortical regions involved in online processing of the relevant source details (i.e., color, location; Uncapher, Otten, & Rugg, 2006). Furthermore, direction of attention may subsequently enhance MTL-mediated contextual memory retrieval processes (Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Kensinger & Schacter, 2006) as well as bottom–up attention to memory effects in the ventral parietal cortex (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008). One possibility is that this enhancement of source memory encoding and retrieval effects may underlie the attenuation of PFC-mediated postretrieval monitoring processes. Taken together, the benefit of directed attention at encoding may be twofold: (1) facilitating item–source binding at encoding and (2) reducing the demands on strategic retrieval processes, both of which may be impaired with age.

Although behavioral evidence suggests encoding support may enhance source memory in young and older adults, little is known about the neural mechanisms supporting this effect during both encoding and retrieval. Thus, we sought to investigate the effect of directed attention toward item–feature conjunctions on age-related source memory accuracy deficits, as well as its effect on age-related changes in functioning of memory processes via fMRI. At study, participants were shown images of colorized objects. Each object was presented in either an encoding condition, which directed the participant's attention toward the conjunction of the object and its color (Association-directed), or in a condition that directed attention toward the object's size, but with no explicit instruction to attend to the color (Item-directed). At test, participants were shown old and new objects. Half of the old objects were presented in the same color as study, and half were presented in a different color. Participants were first asked to determine if they had seen each object previously, regardless of its color. Then, if the object was judged to be "old," they decided if the object was presented in the same color as it was during study, or if it was presented in a different color. Critically, we also

included a "Don't Know" response option for both questions to reduce dilution of source memory accuracy estimates and fMRI effects via guessing, as has been implemented in prior studies (Dulas & Duarte, 2011, 2012; Dulas, Newsome, & Duarte, 2011; Gottlieb, Uncapher, & Rugg, 2010; Duarte, Henson, Knight, Emery, & Graham, 2009; Duarte, Henson, & Graham, 2008; Morcom, Li, & Rugg, 2007; Smith, Dolan, & Rugg, 2004). In addition, we attempted to match performance between age groups by halving the memory load for older adults, as we have successfully done in a previous study (Dulas & Duarte, 2013). Previous evidence suggests large performance differences between young and older adults may confound age-related neural effects with performance-related neural effects and compromise the interpretation of age-related differences in neural activity (reviewed in Rugg & Morcom, 2005).

We predicted the following:

1. Source memory accuracy should be greater following directed attention toward object–color associations (Association-directed trials) than for Item-directed trials for both young and older adults. However, we predicted that age-related differences in source memory accuracy may persist, as evidence suggests supporting encoding may be insufficient to completely ameliorate age-related source memory deficits (Dulas & Duarte, 2013; Naveh-Benjamin et al., 2007).

2. In conjunction with this source memory benefit, we predicted the direction of attention would increase subsequent source accuracy effects at study in the PFC and the MTL. This would reflect a facilitation of relational processes in PFC (Ranganath, 2010; Badre, 2008) as well as contextual binding in the MTL (Ranganath et al., 2004; Davachi et al., 2003).

3. Directing attention toward object–color associations may enhance perceptual processing of the attended-to information (Uncapher et al., 2006; Gazzaley, Cooney, McEvoy, et al., 2005). Previous evidence has suggested that the fusiform gyrus may be particularly involved in object–color perceptual representations (Beauchamp & Martin, 2007; Martin, 2007; Zeki & Marini, 1998). Thus, directing attention toward object–color associations may enhance subsequent source memory effects in the fusiform gyrus, representing increased attention toward these goal-relevant perceptual features.

4. At test, consistent with ERP findings in young (Kuo & Van Petten, 2006) and older adults (Dulas & Duarte, 2013), we predicted our direction of attention manipulation would reduce recruitment of postretrieval monitoring processes thought to be mediated by right lateral DLPFC and VLPFC (Dulas & Duarte, 2012; Donaldson, Wheeler, & Petersen, 2010; Rugg et al., 2003; Henson et al., 1999). This would reflect a reduced need for strategic retrieval processes, likely because of the stronger object–color associations bound in memory via attention. In turn, these strengthened source associations may be reflected in increased activity in hippocampus

(contextual recollection) and ventral parietal cortex (bottom–up attention to memory) for the Association-directed condition.

METHODS

Participants

Twenty-one young adults, ages 18–29 years, were recruited from the Georgia Institute of Technology, as well as community solicitation, and 21 older adults, ages 60–73 years, were recruited via community solicitation. Group characteristics can be seen in Table 1. All participants were right-handed, native English speakers, with normal or corrected-to-normal vision, and with no reports of psychiatric/neurological disorders, vascular disease, or psychoactive drug use. None of the participants were taking CNS-active medications or antihypertensive medications. All participants were paid $10 an hour for their time and signed consent forms approved by the Georgia Institute of Technology Institutional Review Board. Young adults and older adults did not significantly differ in sex proportion or level of education.

Neuropsychological Assessment

All participants were administered a battery of standardized neuropsychological tests after a short rest break after

Table 1. Group Characteristics

Measure	Young (n = 21)	Old (n = 21)
Age	22.62 (3.02)	64.81 (3.61)
Sex	10/21 female	9/21 female
Education	16.05 (1.92)	16.00 (2.39)
Letter fluency	49.86 (9.69)	53.29 (13.41)
List recall (immediate)	11.14 (0.96)	10.00 (1.41)*
List recall (immediate, cued)	11.04 (1.02)	10.38 (1.60)
List recall (delayed)	11.76 (0.44)	10.71 (1.52)*
List recall (delayed, cued)	11.67 (0.66)	10.86 (1.53)*
List recognition	11.95 (0.22)	11.81 (0.40)
MAS digit span forward	7.62 (1.20)	6.67 (1.06)*
MAS digit span backward	5.71 (1.52)	4.85 (1.11)*
Trails A (in sec)	23.58 (7.71)	33.81 (10.60)*
Trails B (in sec)	46.77 (13.64)	72.87 (19.99)*
Visual recognition	19.00 (1.55)	16.48 (2.27)*
Delayed visual recognition	19.57 (0.60)	17.42 (2.27)*
Visual reproduction	8.90 (1.67)	5.57 (1.78)*

Standard deviations in parentheses. All neuropsychological test scores are reported as raw scores.

*Significantly different from Young ($p < .05$).

completing the fMRI portion of the experiment. Tests were specifically chosen to assess memory ability and executive functioning, so as to ensure no gross differences in performance because of cognitive impairment such as dementia in the older adult group. The battery included subtests from the Memory Assessment Scale battery (Williams, 1991): digit span forward and backward, list learning, recognition, recall and delayed recall, object recognition, recall, reproduction, and delayed recognition. Additionally, Trail Making Tests A and B (Reitan & Wolfson, 1985) as well as the Controlled Oral Word Association Test ("FAS"; Benton, Hamsher, & Sivan, 1983) were included.

Materials

Three hundred fifteen colored images were used as stimuli. All images depicted a single, nameable object on a white background. Images were taken from the Hemera Technologies Photo-Objects DVDs and also from Google. Adobe Photoshop was used to color the objects in one of four possible colors: red, green, blue, or brown. The same shade of each color was used to colorize the objects (e.g., identical shade of brown for a box and a ball). Each stimulus was centrally presented and subtended a maximum vertical and horizontal visual angle of up to 5.9°.

Design

Before entering the scanner, participants completed a short practice of both study and test trials, until they demonstrated that they understood the tasks. This assured that both groups were able to perform the task sufficiently before entering the scanner. All participants were therefore aware their memory would be tested, although they were instructed to attend to the orienting tasks during encoding. The experimental practice and all study and test blocks lasted approximately 2 hr total. There were four blocks of study and four blocks of test. Young adults performed all four blocks of study, followed by all four blocks of test. For older adults, the memory load was split in half, so that they performed two blocks of study, followed by the corresponding two blocks of test, and then completed the remaining two blocks of study and their corresponding blocks of test. Delays were imposed between study and test phases for both groups, during which participants performed a short vocabulary test (5 min for the old and 10 min for the young) to reduce item recognition from ceiling. Participants remained in the scanner during this task although no scans were acquired.

At study, 210 trials were divided across four blocks. Participants were presented with objects in one of four colors and were asked one of two possible yes/no questions for 3000 msec, followed by a fixation cross that was presented for 500 msec. For the Association-directed condition, participants were shown the question "Likely?" for each object. Participants were instructed that they had to determine if the color of the object was probable (likely) for that object. For the Item-directed condition, participants were shown the question "Shoebox?" for which they had to determine if the object was bigger than a shoebox. Half of the objects were presented in a color that was deemed by the investigators to be likely for that object (e.g., a red fire hydrant), whereas half were deemed to be unlikely for that object (e.g., a green gorilla). Similarly, half of the objects were deemed by the investigators to be bigger than a shoebox (e.g., a horse), whereas half were deemed to be smaller than a shoebox (e.g., a pack of gum). To minimize task-switching costs, which might be especially problematic for older adults, each study block was further divided into four miniblocks of 13–14 trials each. During each miniblock, one question was asked for a series of objects (e.g., 13 objects in a row would be presented with the question "Likely?"). Furthermore, each miniblock was introduced by a 6-sec cue indicating which question would now be answered. All responses were made with the index and middle finger of the right hand using buttons 1 ("yes") and 2 ("no"), respectively, on an MRI-compatible keypad.

At test, 315 trials were divided across four blocks, with all studied and 105 new items. Furthermore, half of all studied objects at test were presented in the same color as study, whereas half were presented in a different color. For each trial, participants were first asked if the object was old (Button 1) or new (Button 2) and then answered whether the color of the object was the same (Button 1) or different (Button 2) from encoding. For both questions at test, the third option, "Don't Know" (Button 3), was offered to decrease the potential for guessing. This option has been used in previous studies (Dulas & Duarte, 2011, 2012; Duarte, Graham, & Henson, 2010; Gottlieb et al., 2010; Duarte et al., 2009). Participants responded with the first, second, and third fingers of the right hand for Buttons 1, 2 and 3, respectively. Each question was presented for 3000 msec, with a 500-msec fixation cross presented between questions and a 500-msec fixation cross presented between the second question and the next object. Participants were instructed to respond that an object was old regardless of whether its color was the same/different from study. For items deemed "New," participants were still presented the "Same/Different" question and were told to simply press any key. This was done to ensure the same duration and number of responses across trial types. Across participants, objects were counterbalanced so that they appeared in each of the three possible conditions (Association-directed, Item-directed, New). The order of blocks was also counterbalanced across participants. 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. Where appropriate, reported p values were corrected using Huynh–Feldt corrections.

fMRI Acquisition

Scanning was performed on a 3T Siemens TIM Trio system. 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 of 2 sec, echo time of 30 msec, $3 \times 3 \times 3.5$ mm voxels, 0.8 mm interslice gap). There were four study blocks in total, two with 113 volumes and two with 111 volumes. Four test blocks were also acquired, with three blocks consisting of 275 volumes and one block consisting of 270 volumes. These differences across blocks were due to some blocks having one extra trial compared with others. The first five volumes of each block were discarded to allow for equilibration effects. A high-resolution T1-weighted magnetization-prepared rapid acquisition gradient-echo (MP-RAGE) image was collected for normalization (see below).

fMRI Analysis

Data were analyzed with SPM8 (SPM8, www.fil.ion.ucl.ac.uk/spm/software/spm8/). 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 MP-RAGE 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) SPM 8 toolbox (Ashburner, 2007).[1] 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 participant were used to normalize each participant's realigned and resliced EPIs to Montreal Neurological Institute (MNI) space. Normalized EPI images were written to $3 \times 3 \times 3$ mm and smoothed with an 8-mm FWHM isotropic Gaussian kernel. The EPI data were then high-pass filtered to a maximum of 1/128 Hz and grand mean scaled to 100.

Statistical analysis was performed in two stages. First, neural activity was modeled as a series of 0-sec epochs at study and 4-sec epochs at test of the various event types and convolved with a canonical hemodynamic response function. For test, which included two response prompts, activity was only modeled to the onset of the first prompt, as participants were aware of the second prompt and may have been anticipating their responses (making it difficult to accurately model activity separately). The time courses were down-sampled to the middle slice to form the covariates for the general linear model. For each participant and block, six covariates representing residual movement-related artifacts, determined by the spatial realignment step, were included in the first-level model to capture residual (linear) movement artifacts. Voxel-wise parameter estimates for these covariates were obtained by restricted maximum-likelihood estimation, using a temporal high-pass filter (cutoff 128 sec) to remove low-frequency drifts and modeling temporal autocorrelation across scans with an AR(1) process.

Contrasts of the parameter estimates for each participant were submitted to the second stage of analysis (treating participants as a random-effect). A mixed ANOVA model was created for the test period that allowed us to examine both within group effects and group interactions. At study, the $2 \times 2 \times 2$ model included factors of Response (source correct [SC], source incorrect/don't know source [SINCDK]), Condition (Association-directed, Item-directed), and Age Group (young, old). At test, the $3 \times 2 \times 2$ model included factors of Response (SC, SINCDK, correctly rejected unstudied item [Correct Rejections, CR]), Condition (Association-directed, Item-directed), and Age Group (young, old). Incorrect source and don't know source trial types were combined to form a category representing instances where the item was recognized but correct source information was unavailable, as has been done previously (Dulas & Duarte, 2012; Gottlieb et al., 2010; Duarte et al., 2008, 2009; Duverne, Habibi, & Rugg, 2008).

There were insufficient numbers of incorrect "new" responses to studied items ("misses") and incorrect "old" responses to unstudied items ("false alarms") for all participants to examine separately, and so they were not included in the ANOVA. Covariates modeling the mean across conditions for each participant were also added to each model for all contrasts in the second-level model to remove between-subject variance of no interest, as per the optimal event-related fMRI suggestions in chapter 10 of the SPM manual (SMP8; www.fil.ion.ucl.ac.uk/spm/doc/manual.pdf). A weighted least squares estimation procedure was used to correct for inhomogeneity of covariance across within-group conditions and inhomogeneity of variance across groups.

The SPM for the main effects of Condition (across groups) and Age Group (across conditions) were masked exclusively with the SPMs for the Group × Condition interactions using a liberal uncorrected threshold of $p < .05$ for the masks to restrict memory effects to those "common" (i.e., similar size) across groups/conditions.[2] All masked, as well as unmasked, contrasts were evaluated using t contrasts under an uncorrected alpha level of 0.001 (i.e., each direction of the t test at 0.0005) and a minimum cluster size of five contiguous voxels as we and others have done previously (Dulas & Duarte, 2012; Uncapher & Rugg, 2005; Tsivilis, Otten, & Rugg, 2003; Otten, Henson, & Rugg, 2002).[3]

In addition to these whole-brain analyses, we conducted ROI analyses using regions from prior studies that had clear anatomical delineation and about which we had a priori hypotheses, specifically the hippocampus and parahippocampal cortex. ROI analyses were examined using a family-wise error-corrected threshold of $p < .05$, using bilateral

masks from the Automatic Anatomical Labeling of the MNI brain and the Small-Volume Correction (SVC), as we (Dulas & Duarte, 2011, 2012) and others have done previously (e.g., van Kesteren et al., 2013; Barense, Henson, Lee, & Graham, 2009). The SVC approach corrects for multiple comparisons based on the number of voxels within the apriori ROI (rather than across the whole brain; Worsley et al., 1996). This analysis reveals peak voxels within the ROI masks that are reliable for the effect of interest; thus, peak voxels that survived the corrected threshold are reported.[4] These ROI analyses were subjected to the same inclusive and exclusive masking procedures as described above for the whole-brain analyses.

For both whole-brain and ROI analyses, simple effect SPMs were performed to elucidate the source of interactions (e.g., Young > Old: SC > SINCDK) and to ensure that main effects were reliable for each group and were conducted using the same whole-brain or SVC procedure (for ROI regions). Importantly, as these simple effect comparisons for a particular region were made independently to the initial contrast, they were not statistically biased (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009).

Maxima of significant clusters were localized on individual normalized structural images. Neural activity from these maxima was plotted for SC and SINCDK at study and for SC, SINCDK, and CR conditions at test. Neural activity reflected the parameter estimates for the convolved regressors and had arbitrary units.

RESULTS

Neuropsychological Assessment Results

Group characteristics and results for neuropsychological tests are shown in Table 1. All participants scored within 1 standard deviation of age-adjusted normative averages for all neuropsychological tests. Older adults exhibited significantly poorer performance than young adults on several tests including Immediate List Recall, Delayed List Recall, Cued/Delayed List Recall, Verbal Span Forward and Backward, Trails A and B, Visual Recognition, Delayed Visual Recognition, and Visual Reproduction, $t(40) > 2.09$, $p < .04$. There were no other significant group differences, $t(40) < 1.6$, $p > .12$.

Behavioral Results

The mean proportions of correct, incorrect, and don't know source judgments, as well as "new" responses made to studied items (misses), are presented in Table 2, along with the proportions of CR new items. Item recognition

Table 2. Response Proportions and Performance Indices Times to Studied and Unstudied Objects at Test

	Young Adults		Older Adults	
	Association-directed	*Item-directed*	*Association-directed*	*Item-directed*
Response Proportions				
Studied objects				
Correct Source	0.70 (0.11)	0.53 (0.09)	0.56 (0.11)	0.44 (0.11)
Incorrect Source	0.13 (0.06)	0.25 (0.08)	0.19 (0.06)	0.26 (0.06)
Don't Know Source	0.05 (0.07)	0.08 (0.11)	0.05 (0.07)	0.07 (0.12)
Miss	0.12 (0.08)	0.14 (0.09)	0.20 (0.12)	0.23 (0.13)
Unstudied objects				
CR	0.87 (0.07)		0.84 (0.09)	
Source Proportions of Hits				
p(correct source)	0.84 (0.08)	0.68 (0.07)	0.75 (0.07)	0.62 (0.07)
p(incorrect source)	0.15 (0.08)	0.32 (0.07)	0.24 (0.07)	0.37 (0.07)
Performance Indices				
Item recognition (Pr-Item)	0.74 (0.11)	0.72 (0.11)	0.64 (0.14)*	0.61 (0.14)*
Corrected source (Pr-Source)	0.69 (0.16)	0.36 (0.15)	0.51 (0.15)*	0.25 (0.14)*

Standard deviations in parentheses. For Performance Indices, Chance = 0. Source proportions represent the values used for the Pr calculation of source memory, which consider only correct and incorrect source judgments of all hits, excluding miss and don't know source judgments.

*Denotes performance indices for which there were age-related differences, $p < .05$.

Table 3. Regions Showing Subsequent Source Memory Accuracy Effects and Object-processing Effects at Study

Contrast	Region	L/R	MNI Coordinates (x, y, z)	BA	t Score	Voxel Extent
SC > SINCDK						
Across conditions						
Old > Young	Medial orbitofrontal cortex[a]	R	9, 69, −6	10/11	3.78	5
A-D > I-D	Inferior parietal cortex	R	42, −60, 57	40	3.80	13
	Superior parietal cortex	*R*	*45, −48, 60*	*40*	*3.74*	
	Parahippocampal cortex (ROI)[a]	L	−30, −42, −8	37	3.16	3
Young > Old	Precentral gyrus	L	−39, −3, 36	6	4.31	11
	Middle orbitofrontal cortex[a]	R	39, 57, −15	11/47	4.08	6
Object Processing Effects—SC Only						
A-D > I-D	Fusiform gyrus[a]	R	33, −69, −9	19	3.89	10
I-D > A-D	Inferior parietal cortex	L	−57, −33, 42	40	4.97	58
	Middle occipital cortex[a]	R	42, −75, 33	39	4.47	32
		L	−36, −81, 36	19	3.83	13
	Precuneus	B	−3, 66, 51	7	3.84	18

L = left; R = right; BA = Broadmann's area; A-D = Association-directed condition; I-D = Item-directed condition. Voxel extent for ROIs reported at 0.001. Italicized regions indicate subclusters.

[a]Indicates regions shown in Figures 1–3.

accuracy was estimated by the Pr measure of discriminability (Snodgrass & Corwin, 1988), that is, p(hits) − p(false alarms) for Association-directed and Item-directed encoding conditions. Source accuracy was also estimated by Pr, excluding "don't knows," that is, Pr = p(correct) − p(incorrect).[5] These item and source accuracy estimates for young and older adults are shown in Table 2.

We conducted a Memory (Item, Source) × Condition (Association-directed, Item-directed) × Age (Young, Old) ANOVA on the Pr measures of item and source memory to evaluate the effects of explicit direction of attention at encoding. The ANOVA revealed significant main effects of Memory, $F(1, 40) = 109.07$, $p < .001$, and Condition, $F(1, 40) = 144.29$, $p < .001$, the latter of which was modified by a Memory × Condition interaction, $F(1, 40) = 106.86$, $p < .001$. Furthermore, there was a main effect of Age, $F(1, 40) = 1210.13$, $p < .001$. However, there were no interactions between Age and any other factors, $F(1, 40) < 2.51$, $p > .12$. Follow-up analyses for each memory type revealed that both item and source memory showed reliable main effects of Condition, $F(1, 40) > 7.11$, $p < .01$, and Age, $F(1, 40) > 13.81$, $p < .002$. As can be seen in Table 2, older adults showed impairments across memory type and condition and attention benefitted both item and source memory accuracy. However, the Memory × Condition interaction reflected the fact that directed attention improved source memory to a much greater extent than item memory across age groups.

We also conducted an ANOVA to determine whether older adults' source memory improved from the first study test session to the second. This Condition × Session ANOVA revealed no significant effects involving Session, $F(1, 20) < 0.09$, $p > .77$, suggesting our halved-memory load did not affect performance across blocks in older adults.

Analyses for RTs showed no significant effects involving the factor of Condition. Thus, these analyses are not reported.

fMRI Results—Encoding

To identify brain regions involved in predicting source memory accuracy, we examined effects via contrasts of subsequent SC and subsequent SINCDK responses, as we and others have done previously (Dulas & Duarte, 2011; Gottlieb et al., 2010; Duarte et al., 2008; Duverne et al., 2008). These results can be seen in Table 3. Furthermore, as there were insufficient subsequent miss responses (old objects participants incorrectly labeled as new), subsequent item-memory effects could not be assessed.

Source Accuracy Effects Common to Conditions

Between-group contrasts revealed no regions showing young > old effects. However, older adults showed greater source accuracy activity than the young in the right medial
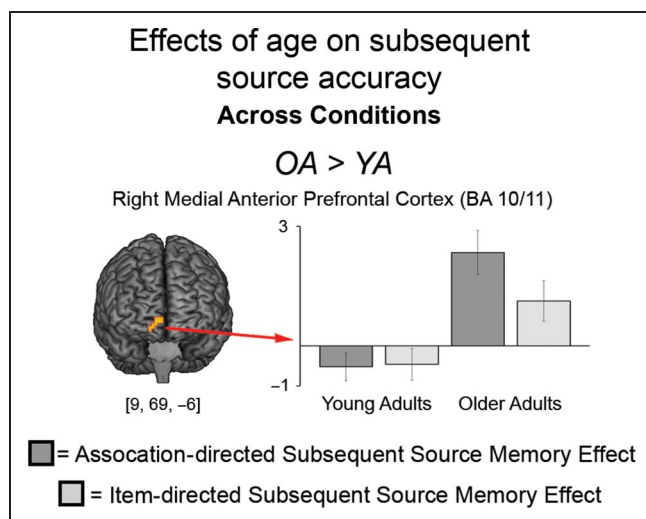
Figure 1. Subsequent source memory effects (encoding) for selected region displayed for Old > Young contrasts across conditions. Selected region is displayed on MNI reference brain. Plots show difference score of parameter estimates of SC–SINCDK for both conditions and groups. Error bars depict *SEM* across participants for each group ($p < .0005$, uncorrected, with a 5 voxel extent; exclusive masking conducted as described in fMRI Analysis).

orbitofrontal cortex (medial aPFC; Figure 1). We were interested in whether this activity impacted the source memory benefit inferred by directed attention, particularly as this was one of the few regions showing greater activity in the old than young. Interestingly, in young adults, a correlation between the medial aPFC subsequent source memory effect and the source memory benefit of directed attention revealed a significant negative correlation ($r = -.52, p = .02$). In older adults, this correlation was also negative, albeit non-significant ($r = -.16, p = .48$).

Source Accuracy Effects Differing between Conditions

Association-directed encoding elicited greater subsequent source memory effects than Item-directed encoding in right inferior parietal cortex and left posterior parahippocampal cortex (Figure 2).

Between-group, between-condition contrasts revealed that young adults showed greater Association-directed > Item-directed subsequent source memory effects than older adults, most notably in right middle orbitofrontal cortex (lateral aPFC; Figure 2).

Object–Feature Processing Effects

We were also interested in whether Association-directed attention enhanced object–feature processing. However, the subsequent source memory contrasts did not reveal any effects in visual processing regions. One possibility is that these processing effects are engaged independent of subsequent source accuracy. Thus, we performed

between-condition contrasts considering only subsequent SC responses to determine if Association-directed attention enhanced object–color processing. Although this contrast encompasses source-encoding processes that differ as a function of the attention manipulation, it does not distinguish encoding attempt from encoding accuracy. The results of these contrasts are shown in Table 3.

For both young and old, Association-directed trials showed greater activity than Item-directed trials in the right fusiform gyrus (Figure 3).

Meanwhile, the Item-directed condition showed greater activity than the Association-directed condition in left inferior parietal cortex, bilateral portions of the middle occipital cortex (Figure 3), and the precuneus for both age groups.

There were no regions identified that showed group by condition interactions for this contrast.
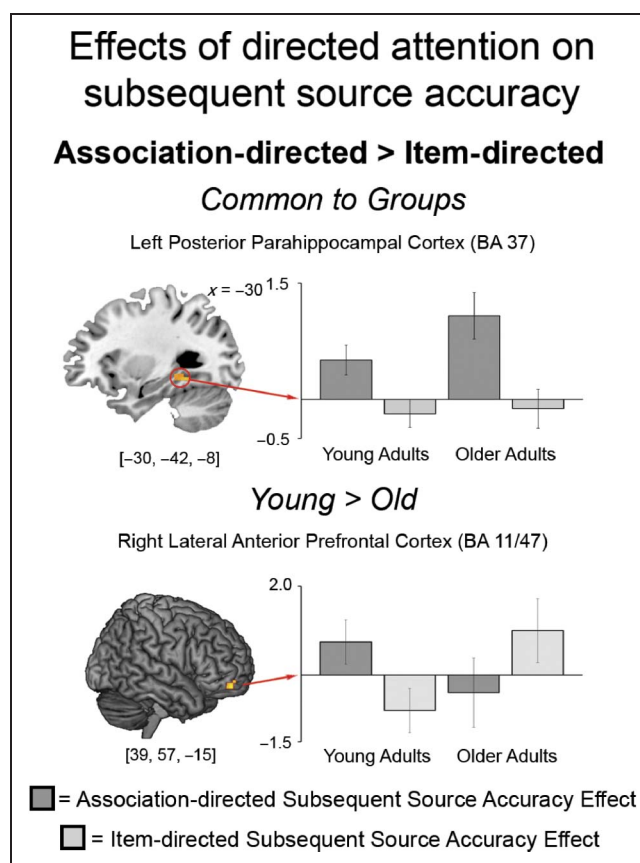

Figure 2. Subsequent source memory effects for selected regions displayed for Association-directed > Item-directed contrasts. Selected regions are displayed on MNI reference brain. Plots show difference score of parameter estimates of SC–SINCDK for both conditions and groups. There was no true baseline for this study (i.e., fixation trials); thus, the zero line of the x axis cannot be interpreted as a baseline. Therefore, any "activations" or "deactivations" relative to the zero line are more apparent than real. Only the contrasts between conditions are interpretable. Error bars depict *SEM* across participants for each group ($p < .0005$, uncorrected, with a 5 voxel extent; exclusive masking conducted as described in fMRI Analysis).
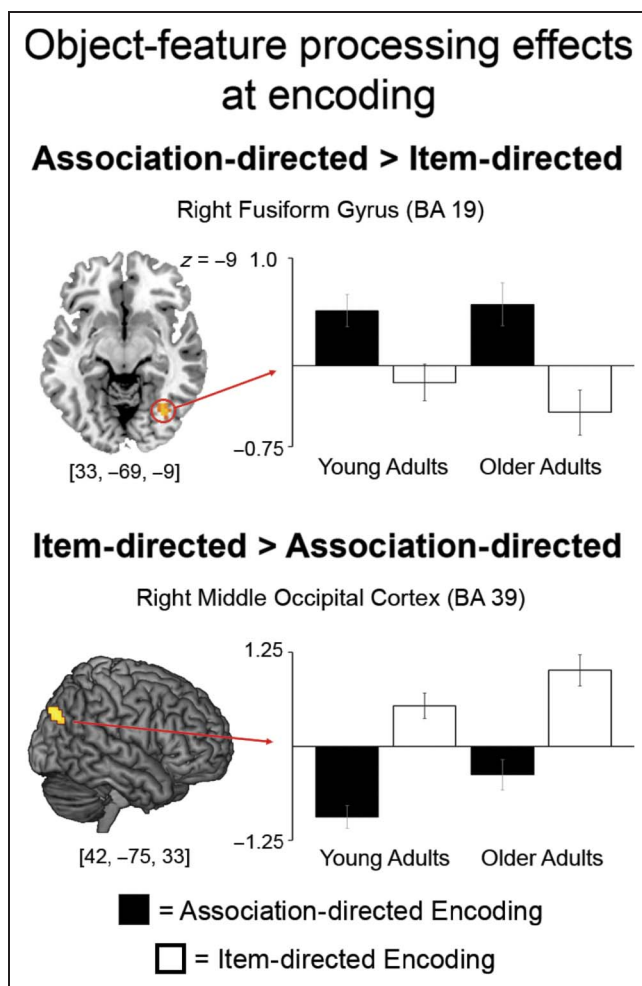
Figure 3. Object–feature processing effects at encoding for selected regions are displayed on MNI reference brain. Plots show parameter estimates of SCs for both conditions and groups. There was no true baseline for this study (i.e., fixation trials); thus, the zero line of the *x* axis cannot be interpreted as a baseline. Therefore, any "activations" or "deactivations" relative to the zero line are more apparent than real. Only the contrasts between conditions are interpretable. Error bars depict *SEM* across participants for each group (*p* < .0005, uncorrected, with a 5 voxel extent; exclusive masking conducted as described in fMRI Analysis).

fMRI Results—Retrieval

To identify brain regions involved in source memory retrieval, we first examined effects via a contrast between SC responses and CR, that is, old–new effects, consistent with other previous studies (Dulas & Duarte, 2012; Duverne et al., 2008; Morcom et al., 2007). The results of these analyses are shown in Table 4. Additionally, although contrasts comparing SC with CR responses may be robust, they likely reflect source memory effects in addition to item memory effects (i.e., brain regions supporting memory for old–new judgments). Thus, we also examined source memory accuracy specific effects (SC > SINCDK) as we have done previously (Dulas & Duarte, 2012). These results are shown in Table 5.

Old–New Effects Differing between Conditions

Association-directed trials showed greater activity than Item-directed trials in left middle temporal cortex, left parahippocampal cortex, and left angular gyrus (Figure 4). By contrast, Item-directed trials were associated with greater activity than Association-directed trials in several regions, including left insula, left middle occipital cortex, and right inferior frontal gyrus (Figure 4). No group differences in old–new effects that differed as a function of condition were observed.

Source Accuracy Effects Common to Conditions

The left anterior hippocampus showed greater activity for SC than SINCDK trials across groups. No group differences in source accuracy were observed across conditions.

Source Accuracy Effects Differing between Conditions

Young adults showed greater Association-directed than Item-directed source accuracy effects than older adults in left hippocampus, somewhat anterior to the region common to groups (Figure 5). No other condition or group differences in source accuracy were observed.

DISCUSSION

In this study, we examined the effect of directing attention toward object–feature associations on age-related alterations to the processes supporting source memory encoding and retrieval. As predicted, source memory performance was improved for both young and older adults via directed attention at encoding, though age-related deficits persisted. fMRI results showed that, across groups, directed attention facilitated object–feature processing effects and MTL-mediated contextual binding processes at encoding. Directed attention also enhanced lateral aPFC-mediated relational processes in young, but not older, adults. However, across conditions, older adults showed increased recruitment of medial aPFC, possibly reflecting self-referential processing. Direction of attention at study resulted in stronger source accuracy effects (MTL and angular gyrus) during test, as well as an attenuation of right PFC-mediated postretrieval monitoring activity across groups. Lastly, direction of attention also resulted in stronger hippocampal source accuracy effects for young, but not older, adults. These results and their implications are discussed further below.

Behavioral Results

As we have shown previously (Dulas & Duarte, 2013), directing attention at encoding toward task-relevant associations can improve source memory accuracy for young and older adults. This is in line with previous work

Table 4. Regions Showing Old – New Effects at Retrieval

Contrast	Region	L/R	MNI Coordinates (x, y, z)	BA	t Score	Voxel Extent
SC > CR						
A-D > I-D	Middle temporal cortex	L	−51, −30, −6	21	3.80	9
	Angular gyrus[a]	L	−54, −66, 39	39	3.67	9
	Parahippocampal cortex (ROI)	L	−27, −27, 12	20	3.16	2
I-D > A-D	Insula	L	−33, −24, 21	48	4.42	33
	Middle occipital cortex	L	−27, −88, 0	18	4.31	68
	Fusiform gyrus	*L*	*−21, −87, −9*	*18*	*3.74*	
	Fusiform gyrus	R	27, −81, −6	19	3.49	7
	Inferior frontal gyrus[a]	R	45, 9, 30	44	4.24	23
	Supplemental motor area	B	−3, 18, 45	32	3.88	19
	Middle temporal cortex	R	51, −75, 24	39	3.84	9
	Inferior parietal cortex	L	−45, −39, 48	40	3.88	14
	Superior parietal cortex	L	−15, −63, 45	7	3.69	5
	Cerebellum	L	−9, −72, −42		3.96	14

L = left; R = right; BA = Broadmann's area; A-D = Association-directed condition; I-D = Item-directed condition. Voxel extent for ROIs reported at 0.001. Italicized regions indicate subclusters.

[a]Indicates regions shown in Figure 4.

showing that encoding support may effectively improve performance in young (Kuo & Van Petten, 2006) and older adults (Glisky & Kong, 2008; Naveh-Benjamin et al., 2007; Glisky et al., 2001; Hashtroudi et al., 1994). As predicted, there was a significantly larger benefit to source memory accuracy across groups compared with item memory. Thus, the present results are in line with the hypothesis that directing attention at encoding to object–source associations may reduce demands on strategic retrieval processing and/or facilitate contextual binding processes at encoding. Both of these processes may be especially critical for source, rather than item, memory (Troyer, Winocur, Craik, & Moscovitch, 1999; Hasher & Zacks, 1979). Interestingly, although older adults did display a source memory accuracy benefit from the attention manipulation, age-related deficits in both item and source memory persisted, despite our attempt to match performance.[6]

It should be noted that previous studies have suggested that encoding support may attenuate memory deficits in older adults (Glisky & Kong, 2008; Glisky et al., 2001). However, these studies were conducted with much smaller memory loads (<20) compared with this study (~157 for a halved load). Thus, it is possible that directed attention may be less beneficial at higher memory loads, particularly for older adults. These results, however, are in line with evidence that age-related memory deficits may be due to multiple underlying causes (Cohn et al., 2008; Glisky et al., 2001; Dunlosky & Hertzog, 1998; Craik & Byrd, 1982; Hasher & Zacks, 1979). Previous work has also shown that supporting only encoding is insufficient to rescue older adult performance to the level of the young, but giving support at both encoding and retrieval does attenuate age-related associative memory deficits (Naveh-Benjamin et al., 2007). Future research is

Table 5. Regions Showing Source Accuracy Effects at Retrieval

Contrast	Region	L/R	MNI Coordinates (x, y, z)	BA	t Score	Voxel Extent
SC > SINCDK						
Across conditions	Hippocampus	L	−27, −7, −12	20	3.89	7
A-D > I-D						
Young > Old	Hippocampus[a]	L	−15, 0, −15	34	3.55	6

L = left; BA = Broadmann's area; A-D = Association-directed condition; I-D = Item-directed condition.
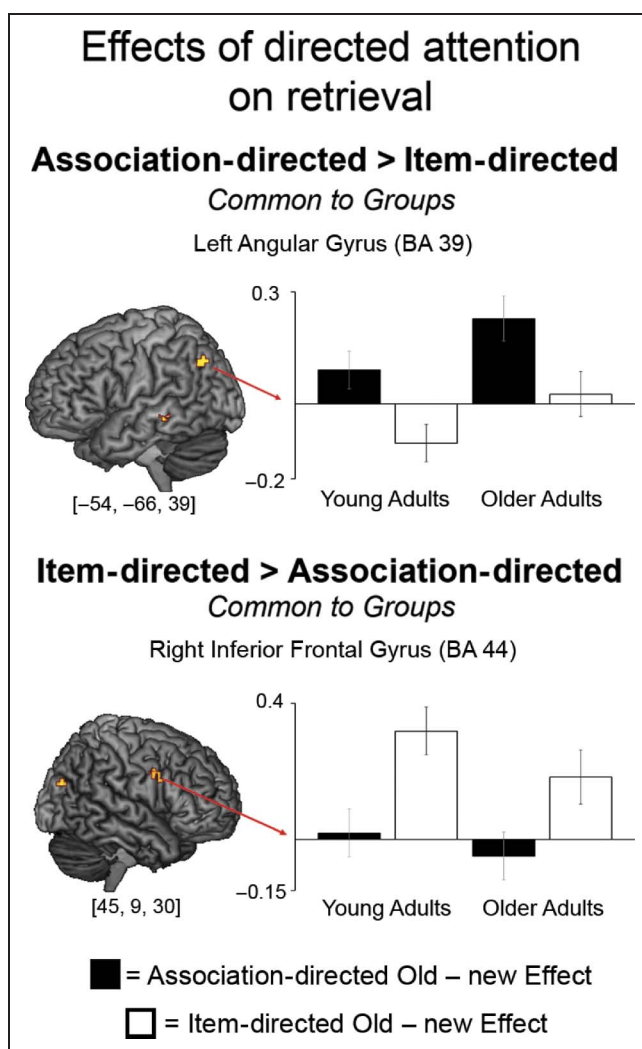
[a]Indicates region shown in Figure 5.

Effects of directed attention on retrieval

Association-directed > Item-directed
Common to Groups
Left Angular Gyrus (BA 39)

[−54, −66, 39]

Item-directed > Association-directed
Common to Groups
Right Inferior Frontal Gyrus (BA 44)

[45, 9, 30]

■ = Association-directed Old − new Effect
□ = Item-directed Old − new Effect

Figure 4. Old − new effects at test for selected regions are displayed on MNI reference brains. Plots show parameter estimates of SC–CR for both conditions and groups. There was no true baseline for this study (i.e., fixation trials); thus, the zero line of the *x* axis cannot be interpreted as a baseline. Therefore, any "activations" or "deactivations" relative to the zero line are more apparent than real. Only the contrasts between conditions are interpretable. Error bars depict *SEM* across participants for each group (*p* < .0005, uncorrected, with a 5 voxel extent; exclusive masking conducted as described in fMRI Analysis).

needed to fully understand the connection between encoding and retrieval support, as well as to determine if other forms of encoding support are sufficient to ameliorate age-related source memory deficits.

An alternative interpretation of our attention manipulation is that, rather than affecting attention per se, it encouraged intentional encoding of object and color in the Association-directed condition. Previous evidence has suggested that older adults' memory may be particularly impaired under intentional, as opposed to incidental, encoding conditions (Chalfonte & Johnson, 1996; Spencer & Raz, 1995). Thus, it is possible that age-related deficits persist even after directed attention, as

older adults do not benefit as much from intentional encoding instructions. Arguing against this possibility is the fact that both age groups received a similar source memory benefit from directed attention in this study. However, future research wherein participants are unaware of the subsequent memory task in combination with attention manipulations may be able to disentangle these interpretations.

fMRI Results

Directed Attention Facilitates MTL-mediated Binding across Groups

At study, fMRI results revealed that directing attention toward object–color associations resulted in greater activity supportive of subsequent source memory accuracy in the parahippocampal cortex for both young and older adults. Previous evidence has indicated that activity during encoding in the parahippocampal cortex may be related to contextual binding processes supportive of subsequent associative memory accuracy (Hales & Brewer, 2011; Aminoff, Gronau, & Bar, 2007; Jackson & Schacter, 2004). Thus, one effect of directing attention toward object–feature associations during study is to facilitate contextual binding processes during encoding.
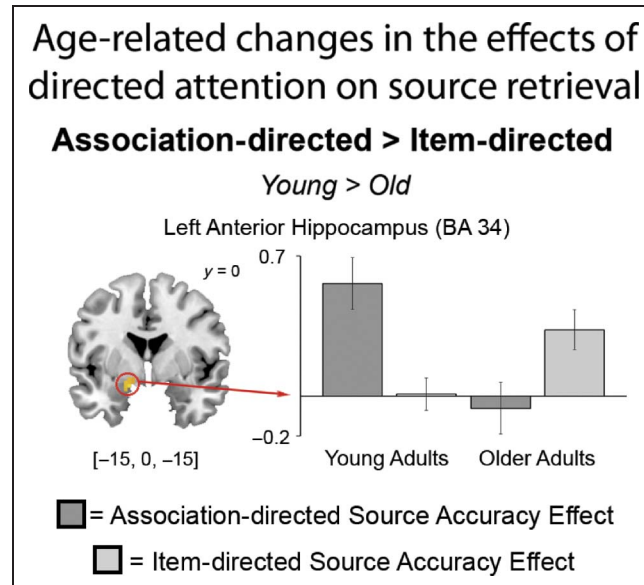

Age-related changes in the effects of directed attention on source retrieval

Association-directed > Item-directed
Young > Old
Left Anterior Hippocampus (BA 34)

y = 0

[−15, 0, −15]

■ = Association-directed Source Accuracy Effect
□ = Item-directed Source Accuracy Effect

Figure 5. Source memory accuracy effects at test for a selected region is displayed on MNI reference brains. Plots show difference score of parameter estimates of SC–SINCDK for both conditions and groups. There was no true baseline for this study (i.e., fixation trials); thus, the zero line of the *x* axis cannot be interpreted as a baseline. Therefore, any "activations" or "deactivations" relative to the zero line are more apparent than real. Only the contrasts between conditions are interpretable. Error bars depict *SEM* across participants for each group (*p* < .0005, uncorrected, with a 5 voxel extent; exclusive masking conducted as described in fMRI Analysis).

Directed Attention Facilitates Goal-relevant Perceptual Processing across Groups

Directing attention toward object–color associations increased activity in the right fusiform gyrus (BA 19) and reduced activity in the lateral occipital cortex and precuneus, irrespective of source memory success. Previous imaging evidence has suggested that the fusiform gyrus (namely BA 19/37) may be involved in object–color knowledge and representations (Wang et al., 2013; Zeki & Marini, 1998) and that right lateralized fusiform may be particularly involved in maintaining specific perceptual object–feature representations, such as color (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Koutstaal et al., 2001). In contrast, previous evidence has shown that the precuneus (Oliver & Thompson-Schill, 2003) and lateral occipital cortex (Grill-Spector, Kourtzi, & Kanwisher, 2001; Malach et al., 1995) may be involved in processing of object size or identity. Furthermore, work has suggested the lateral occipital cortex may be involved in object source memory, albeit for location, not color (Sommer, Rose, Glascher, Wolbers, & Buchel, 2005; Cansino, Maquet, Dolan, & Rugg, 2002). Thus, our attention manipulation during encoding resulted in stronger object–color representations, while possibly mitigating attention to noncriterial object features (i.e., contextual details other than source, such as size). It should be noted that, counter to our predictions, these regions did not show subsequent source accuracy effects. One possibility is that perceptual processing supports source memory only for object–color associations that were the same at study and test, for example, study–test overlap (Rugg, Johnson, Park, & Uncapher, 2008; Johnson & Rugg, 2007). However, there were insufficient numbers of trials for both same- and different-colored objects to compare across conditions. It is possible that future work employing more sensitive multivariate techniques would be better able to determine whether enhanced perceptual processing directly impacts source memory accuracy.

Age-related Alterations in PFC-mediated Encoding Processes

Results from encoding also revealed age-related differences in activity that might underlie the performance deficits seen in older adults. Across both conditions, older adults showed greater subsequent source memory effects in the medial aPFC compared with young adults. The medial PFC has been implicated in self-referential processing (D'Argembeau et al., 2005, 2007; Northoff et al., 2006; Gusnard, Akbudak, Shulman, & Raichle, 2001). Furthermore, we have shown that medial PFC activity also contributes to self-relevant source encoding in both young (Leshikar & Duarte, 2012) and older adults (Leshikar & Duarte, 2014). This region has also been implicated in mediating attention toward internal (i.e., self-generated) versus external (environmentally generated) information (Simons, Scholvinck, Gilbert, Frith, & Burgess, 2006;

Simons & Spiers, 2003). Behavioral evidence suggests that, whereas young adults may attend to and encode external contextual details, such as perceptual and semantic information, older adults may attend more to internal contextual details, such as thoughts and feelings, possibly at the cost of contextual memory for the external details (Comblain, D'Argembeau, Van der Linden, & Aldenhoff, 2004; Hashtroudi et al., 1994; Hashtroudi, Johnson, & Chrosniak, 1990). Given that this medial aPFC effect was seen across conditions, results suggest that older adults, even when directed to attend to external contextual information, may attend to self-referential information to a greater extent than young adults.

Interestingly, medial aPFC subsequent source memory effects correlated negatively with the source memory benefit inferred by directed attention in young adults. This correlation was also negative for older adults, though nonsignificant. Taken together, these results suggest this effect does not necessarily support performance for object–color memory. That said, this region showed subsequent source accuracy effects in older adults, in line with previous evidence that has shown that self-referential processing may support source memory for young and older adults (Leshikar & Duarte, 2014; Dulas et al., 2011). In the present case, it is possible that some object–color associations may be successfully encoded via self-referential processing, such as associating a brown dog with the participant's own dog. However, such a strategy may be less effective overall, given the residual age difference in source accuracy. It should be noted that this study did not directly assess self-referential processing. Thus, it is unclear if this is the process being subserved by the medial aPFC. Regardless, this result suggests older adults are at least partially encoding object–color associations in a qualitatively different, less effective manner compared with the young.

We also observed age-related alterations in right lateral aPFC during study. Specifically, directed attention during study led to enhanced subsequent source accuracy effects in this region in young, but not older, adults. The lateral aPFC has been implicated in relational processing, such as comparing multiple associations simultaneously (Wendelken, Chung, & Bunge, 2012; Badre, 2008; Ramnani & Owen, 2004; Christoff et al., 2001; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999). Thus, one possibility is that directing attention toward object–color associations encourages relational processing, such as associations between objects, colors, and the plausibility of those associations. Alternatively, other imaging work suggests the lateral aPFC may be involved in organization and maintenance of goals and subgoals during task performance (Badre, 2008; Schneider & Logan, 2006; Koechlin et al., 2000). In the present task, this may include determining whether the color of an object is likely, while also attempting to encode the object–color association for the memory task. Regardless, the processes subserved by the lateral aPFC may in turn support subsequent memory of these object–color relationships.

The finding that directed attention facilitates relational processing and/or goal maintenance in young but not older adults may fall in line with the Frontal Aging Hypothesis (see Raz, 2000; West, 1996, for reviews), which suggests that the PFC shows disproportionate alterations underlying age-related cognitive deficits. It should be noted, however, that it is unclear if this underrecruitment of the lateral aPFC represents an irreparable deficit in PFC processing or simply a failure to spontaneously engage in this relational processing. Thus, it is possible that direction of attention alone is insufficient to encourage older adults to engage in these executive processes at encoding. Future work is needed to understand whether other forms of encoding support can facilitate the engagement of PFC-mediated relational processes at encoding.

Directed Attention Enhances Source Memory Retrieval Effects

Imaging results at test showed that source-directed attention during encoding enhanced source accuracy effects in the angular gyrus and posterior parahippocampal cortex during retrieval for both young and older adults. The parahippocampal cortex has been shown to be involved in source memory retrieval (Diana, Yonelinas, & Ranganath, 2010; Eichenbaum et al., 2007). Furthermore, evidence suggests that activity in ventral portions of the parietal cortex, such as the angular gyrus, during memory retrieval may represent bottom–up attention to memory (Cabeza, 2008; Ciaramelli et al., 2008) or maintenance of retrieved memory representations (Vilberg & Rugg, 2007, 2008). The increased activity seen in both the MTL and parietal cortex supports the prediction that directing attention toward object–color associations at study leads to a stronger memory representation at test.

Across conditions, both young and older adults showed source accuracy effects in the anterior hippocampus. However, directing attention toward object–color associations enhanced source accuracy retrieval effects in another more anterior hippocampal cluster in the young, but not the old. We previously suggested that one benefit inferred by direction of attention at encoding was to facilitate relational processes at encoding, an effect seen in young but not older adults. Furthermore, we speculated that older adults may show increased self-referential processing across conditions, possibly resulting in the encoding of noncriterial details at the cost of object–color (source) memory. Taken together, we suggest that the combination of these two factors resulted in less robust object–color associations and reduced recollection of relevant source details during retrieval as indicated by the hippocampal underrecruitment in the old.

Directed Attention Reduces Recruitment of Strategic Retrieval Processes

In line with ERP evidence that directed attention at study may attenuate the need for postretrieval processing at test in young (Kuo & Van Petten, 2006) and older adults (Dulas & Duarte, 2013), our fMRI results showed that object–color directed attention reduced activity in right VLPFC for both groups at test. Previous fMRI work has suggested that the right PFC, including the posterior VLPFC region shown here, may be involved in a strategic retrieval processes such as postretrieval monitoring (Henson et al., 1999; see Mitchell & Johnson, 2009, for a review; Rugg et al., 2003; Simons & Spiers, 2003). Postretrieval monitoring may involve the maintenance of retrieved information, evaluation of the products of retrieval, as well as initiation additional retrieval searches (Dobbins & Wagner, 2005; Rugg et al., 2003; Simons & Spiers, 2003; Henson et al., 2000). Previous evidence has suggested that postretrieval monitoring is engaged to a greater extent when participants are closer to their decision criterion (Henson et al., 2000). As discussed previously, one way in which direction of attention may improve source memory is by strengthening the associations between item and source in memory. Thus, in this study, a stronger memory representation of object and color may reduce the need to engage in these monitoring processes at test.

These results stand in contrast to previous evidence suggesting that older adults may show dysfunction in recruitment of PFC-mediated processes at test (Dulas & Duarte, 2012; McDonough et al., 2013; Rajah et al., 2010), even when performance was matched across groups (Dulas & Duarte, 2012). However, these results replicate the findings from our ERP study of directed attention and source memory, where young and older adults showed similar modulations of late right frontal old–new effects, indicative of postretrieval monitoring (Dulas & Duarte, 2013). Furthermore, given that we have previously shown evidence of age-related underrecruitment of right PFC (Dulas & Duarte, 2012), these results are in line with the evidence that environmental support can attenuate age-related differences in PFC recruitment (Logan et al., 2002). One possibility is that the demands of the present source memory task encouraged older adults to engage in strategic retrieval processes similarly to the young (Duverne, Motamedinia, & Rugg, 2009a). These results lend support to the notion that age-related deficits in postretrieval processing are not intractable and that at least some PFC-mediated strategic retrieval processes may be spared with age.

Conclusion

The results of this study have shown that directing attention toward object–feature associations improves source memory for both young and older adults but does not ameliorate age-related source memory deficits. The fMRI results suggest that direction of attention enhances contextual binding (MTL) and object–color perceptual processing (fusiform) across groups during study. However, age-related increases in medial aPFC-mediated

self-referential processing, combined with age-related decreases in the engagement of lateral aPFC-mediated relational processing, may result in encoding of non-criterial contextual details, possibly at the cost of object–color source memory. Direction of attention resulted in a similar reduction in the recruitment of lateral PFC-mediated postretrieval monitoring across groups, suggesting older adults can engage in these processes to a similar extent as the young. Taken together, this study demonstrates that direction of attention alone is insufficient to attenuate age-related source memory deficits, possibly because of encoding and retrieval of noncriterial contextual details. Further research exploring the role of different types of environmental support at both encoding and retrieval, as well as further work into understanding whether the observed age-related alterations in PFC functioning are intractable, may provide future avenues to further attenuate age-related source memory deficits.

Notes

1. DARTEL is a suite of tools fully integrated with SPM8, which the SPM8 manual recommends over optimized normalization, to achieve sharper nonlinear registration, for intersubject alignment. This method also achieves better localization of fMRI activations in MNI space. This method has been used successfully in several previous studies with various healthy and neurological populations (Spreng & Grady, 2010; Glisky & Marquine, 2009). Comparison of the current results produced by DARTEL with the standard unified segmentation normalization procedure revealed largely similar patterns of activity for the contrasts assessed in this study, although DARTEL provided noticeably better overall coverage.

2. Note that a liberal threshold for an exclusive mask is more conservative in excluding regions from the masked SPM.

3. Data were also analyzed at a slightly reduced threshold of 0.001 to see if any regions of note were being excluded via our threshold. However, no new clusters of particular interest were significant at this threshold.

4. Cluster size is not easily reported for the MTL ROIs given that the SVC cluster size (k) equals the SVC search volume in voxels associated with the MTL masks. However, to give an idea of the extent of activation, the number of voxels within these ROIs is reported at an uncorrected alpha of $p < .001$.

5. Analyses were also conducted when source accuracy was estimated by Psr, derived from a single high threshold model (Snodgrass & Corwin, 1988), as used in previous source memory studies (e.g., Dulas & Duarte, 2012; Duverne et al., 2008). Psr = (p(correct) − 0.5(1 − p(don't know)))/(1 − (0.5(1 − p(don't know)))). Analyses using Psr showed the exact same pattern of results as Pr. Psr provides an index of a participant's accuracy for choosing the source when the contribution of lucky guessing is removed, whereas Pr provides an estimate of accuracy for source out of all source attempts.

6. We tested a second group of young adults who also performed the experiment with the halved memory load, like the old. Results showed that age-related differences in source memory were much greater when young and older adults performed the task with the same memory load. Thus, our memory load manipulation more closely matched performance, although age-related deficits persisted.

REFERENCES

Aminoff, E., Gronau, N., & Bar, M. (2007). The parahippocampal cortex mediates spatial and nonspatial associations. *Cerebral Cortex, 17,* 1493–1503.

Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage, 38,* 95–113.

Badre, D. (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends in Cognitive Sciences, 12,* 193–200.

Badre, D., & D'Esposito, M. (2009). Is the rostro-caudal axis of the frontal lobe hierarchical? *Nature Reviews Neuroscience, 10,* 659–669.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45,* 2883–2901.

Barense, M. D., Henson, R. N., Lee, A. C., & Graham, K. S. (2009). Medial temporal lobe activity during complex discrimination of faces, objects, and scenes: Effects of viewpoint. *Hippocampus, 20,* 389–401.

Beauchamp, M. S., & Martin, A. (2007). Grounding object concepts in perception and action: Evidence from fMRI studies of tools. *Cortex, 43,* 461–468.

Benton, A. L., Hamsher, S. K. D., & Sivan, A. B. (1983). *Multilingual aplasia examination* (2nd ed.). Iowa City, IA: AJA Associates.

Blumenfeld, R. S., Parks, C. M., Yonelinas, A. P., & Ranganath, C. (2011). Putting the pieces together: The role of dorsolateral prefrontal cortex in relational memory encoding. *Journal of Cognitive Neuroscience, 23,* 257–265.

Blumenfeld, R. S., & Ranganath, C. (2007). Prefrontal cortex and long-term memory encoding: An integrative review of findings from neuropsychology and neuroimaging. *Neuroscientist, 13,* 280–291.

Bunge, S. A., Burrows, B., & Wagner, A. D. (2004). Prefrontal and hippocampal contributions to visual associative recognition: Interactions between cognitive control and episodic retrieval. *Brain and Cognition, 56,* 141–152.

Cabeza, R. (2008). Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis. *Neuropsychologia, 46,* 1813–1827.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex, 12,* 1048–1056.

Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory & Cognition, 24,* 403–416.

Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J. K., Holyoak, K. J., et al. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage, 14,* 1136–1149.

Chun, M. M., & Turk-Browne, N. B. (2007). Interactions between attention and memory. *Current Opinion in Neurobiology, 17,* 177–184.

Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top–down and bottom–up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia, 46,* 1828–1851.

Cohn, M., Emrich, S. M., & Moscovitch, M. (2008). Age-related deficits in associative memory: The influence of impaired strategic retrieval. *Psychology and Aging, 23,* 93–103.

Comblain, C., D'Argembeau, A., Van der Linden, M., & Aldenhoff, L. (2004). The effect of ageing on the recollection of emotional and neutral pictures. *Memory, 12,* 673–684.

Craik, F. I. M., & Byrd, M. (1982). Aging and cognitive deficits: The role of attentional resources. In F. I. M. Craik & S. E. Trehub (Eds.), *Aging and cognitive processes* (pp. 191–211). New York: Plenum Press.

D'Argembeau, A., Collette, F., Van der Linden, M., Laureys, S., Del Fiore, G., Degueldre, C., et al. (2005). Self-referential reflective activity and its relationship with rest: A PET study. *Neuroimage, 25,* 616–624.

D'Argembeau, A., Ruby, P., Collette, F., Degueldre, C., Balteau, E., Luxen, A., et al. (2007). Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *Journal of Cognitive Neuroscience, 19,* 935–944.

Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences, U.S.A., 100,* 2157–2162.

Dennis, N. A., Daselaar, S., & Cabeza, R. (2007). Effects of aging on transient and sustained successful memory encoding activity. *Neurobiology of Aging, 28,* 1749–1758.

Dennis, N. A., Hayes, S. M., Prince, S. E., Madden, D. J., Huettel, S. A., & Cabeza, R. (2008). Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 791–808.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences, 11,* 379–386.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2010). Medial temporal lobe activity during source retrieval reflects information type, not memory strength. *Journal of Cognitive Neuroscience, 22,* 1808–1818.

Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex, 15,* 1768–1778.

Donaldson, D. I., Wheeler, M. E., & Petersen, S. E. (2010). Remember the source: Dissociating frontal and parietal contributions to episodic memory. *Journal of Cognitive Neuroscience, 22,* 377–391.

Duarte, A., Graham, K. S., & Henson, R. N. (2010). Age-related changes in neural activity associated with familiarity, recollection and false recognition. *Neurobiology of Aging, 31,* 1814–1830.

Duarte, A., Henson, R. N., & Graham, K. S. (2008). The effects of aging on the neural correlates of subjective and objective recollection. *Cerebral Cortex, 18,* 2169–2180.

Duarte, A., Henson, R. N., Knight, R. T., Emery, T., & Graham, K. S. (2009). Orbito-frontal cortex is necessary for temporal context memory. *Journal of Cognitive Neuroscience, 22,* 1819–1831.

Duarte, A., Ranganath, C., & Knight, R. T. (2005). Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *Journal of Neuroscience, 25,* 8333–8337.

Dulas, M. R., & Duarte, A. (2011). The effects of aging on material-independent and material-dependent neural correlates of contextual binding. *Neuroimage, 57,* 1192–1204.

Dulas, M. R., & Duarte, A. (2012). The effects of aging on material-independent and material-dependent neural correlates of source memory retrieval. *Cerebral Cortex, 22,* 37–50.

Dulas, M. R., & Duarte, A. (2013). The influence of directed attention at encoding on source memory retrieval in the young and old: An ERP study. *Brain Research, 1500,* 55–71.

Dulas, M. R., Newsome, R. N., & Duarte, A. (2011). The effects of aging on ERP correlates of source memory retrieval for self-referential information. *Brain Research, 1377,* 84–100.

Dunlosky, J., & Hertzog, C. (1998). Aging and deficits in associative memory: What is the role of strategy production? *Psychology and Aging, 13,* 597–607.

Duverne, S., Habibi, A., & Rugg, M. D. (2008). Regional specificity of age effects on the neural correlates of episodic retrieval. *Neurobiology of Aging, 29,* 1902–1916.

Duverne, S., Motamedinia, S., & Rugg, M. D. (2009a). Effects of age on the neural correlates of retrieval cue processing are modulated by task demands. *Journal of Cognitive Neuroscience, 21,* 1–17.

Duverne, S., Motamedinia, S., & Rugg, M. D. (2009b). The relationship between aging, performance, and the neural correlates of successful memory encoding. *Cerebral Cortex, 19,* 733–744.

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience, 30,* 123–152.

Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top–down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience, 17,* 507–517.

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top–down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience, 8,* 1298–1300.

Gazzaley, A., & D'Esposito, M. (2007). Top–down modulation and normal aging. *Annals of the New York Academy of Sciences, 1097,* 67–83.

Glisky, E. L., & Kong, L. L. (2008). Do young and older adults rely on different processes in source memory tasks? A neuropsychological study. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 809–822.

Glisky, E. L., & Marquine, M. J. (2009). Semantic and self-referential processing of positive and negative trait adjectives in older adults. *Memory, 17,* 144–157.

Glisky, E. L., Rubin, S. R., & Davidson, P. S. (2001). Source memory in older adults: An encoding or retrieval problem? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27,* 1131–1146.

Gottlieb, L. J., Uncapher, M. R., & Rugg, M. D. (2010). Dissociation of the neural correlates of visual and auditory contextual encoding. *Neuropsychologia, 48,* 137–144.

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research, 41,* 1409–1422.

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences, U.S.A., 98,* 4259–4264.

Hales, J. B., & Brewer, J. B. (2011). The timing of associative memory formation: Frontal lobe and anterior medial temporal lobe activity at associative binding predicts memory. *Journal of Neurophysiology, 105,* 1454–1463.

Hasher, L., & Zacks, R. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General, 108,* 356–388.

Hashtroudi, S., Johnson, M. K., & Chrosniak, L. D. (1990). Aging and qualitative characteristics of memories for perceived and imagined complex events. *Psychology and Aging, 5,* 119–126.

Hashtroudi, S., Johnson, M. K., Vnek, N., & Ferguson, S. A. (1994). Aging and the effects of affective and factual focus on source monitoring and recall. *Psychology and Aging, 9,* 160–170.

Henson, R., Shallice, T., & Dolan, R. J. (1999). Right prefrontal cortex and episodic memory retrieval: A functional MRI test of the monitoring hypothesis. *Brain, 122,* 1367–1381.

Henson, R. N., Rugg, M. D., Shallice, T., & Dolan, R. J. (2000). Confidence in recognition memory for words: Dissociating right prefrontal roles in episodic retrieval. *Journal of Cognitive Neuroscience, 12,* 913–923.

Jackson, O., III, & Schacter, D. L. (2004). Encoding activity in anterior medial temporal lobe supports subsequent associative recognition. *Neuroimage, 21,* 456–462.

Janowsky, J. S., Shimamura, A. P., Kritchevsky, M., & Squire, L. R. (1989). Cognitive impairment following frontal lobe damage and its relevance to human amnesia. *Behavioral Neuroscience, 103,* 548–560.

Janowsky, J. S., Shimamura, A. P., & Squire, L. R. (1989). Source memory impairment in patients with frontal lobe lesions. *Neuropsychologia, 27,* 1043–1056.

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex, 17,* 2507–2515.

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Review, 114,* 3–28.

Kensinger, E. A., & Schacter, D. L. (2006). Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *Journal of Neuroscience, 26,* 2564–2570.

Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of the anterior prefrontal cortex in human cognition. *Nature, 399,* 148–151.

Koechlin, E., Corrado, G., Pietrini, P., & Grafman, J. (2000). Dissociating the role of the medial and lateral anterior prefrontal cortex in human planning. *Proceedings of the National Academy of Sciences, U.S.A., 97,* 7651–7656.

Koechlin, E., Ody, C., & Kouneiher, F. (2003). The architecture of cognitive control in the human prefrontal cortex. *Science, 302,* 1181–1185.

Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia, 39,* 184–199.

Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S., & Baker, C. I. (2009). Circular analysis in systems neuroscience: The dangers of double dipping. *Nature Neuroscience, 12,* 535–540.

Kuo, T. Y., & Van Petten, C. (2006). Prefrontal engagement during source memory retrieval depends on the prior encoding task. *Journal of Cognitive Neuroscience, 18,* 1133–1146.

Leshikar, E. D., & Duarte, A. (2012). Medial prefrontal cortex supports source memory accuracy for self-referenced items. *Society for Neuroscience, 7,* 126–145.

Leshikar, E. D., & Duarte, A. (2014). Medial prefrontal cortex supports source memory for self-referenced materials in young and older adults. *Cognitive, Affective & Behavioral Neuroscience, 14,* 236–252.

Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-recruitment and nonselective recruitment: Dissociable neural mechanisms associated with aging. *Neuron, 33,* 827–840.

Luo, L., & Craik, F. I. (2008). Aging and memory: A cognitive approach. *The Canadian Journal of Psychiatry, 53,* 346–353.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A., 92,* 8135–8139.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology, 58,* 25–45.

McDonough, I. M., Wong, J. T., & Gallo, D. A. (2013). Age-related differences in prefrontal cortex activity during retrieval monitoring: Testing the compensation and dysfunction accounts. *Cerebral Cortex, 23,* 1049–1060.

Mitchell, K. J., & Johnson, M. K. (2009). Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? *Psychological Bulletin, 135,* 638–677.

Morcom, A. M., Li, J., & Rugg, M. D. (2007). Age effects on the neural correlates of episodic retrieval: Increased cortical recruitment with matched performance. *Cerebral Cortex, 17,* 2491–2506.

Naveh-Benjamin, M., Brav, T. K., & Levy, O. (2007). The associative memory deficit of older adults: The role of strategy utilization. *Psychology and Aging, 22,* 202–208.

Naveh-Benjamin, M., Shing, Y. L., Kilb, A., Werkle-Bergner, M., Lindenberger, U., & Li, S. C. (2009). Adult age differences in memory for name-face associations: The effects of intentional and incidental learning. *Memory, 17,* 220–232.

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain—A meta-analysis of imaging studies on the self. *Neuroimage, 31,* 440–457.

Oliver, R. T., & Thompson-Schill, S. L. (2003). Dorsal stream activation during retrieval of object size and shape. *Cognitive, Affective & Behavioral Neuroscience, 3,* 309–322.

Otten, L. J., Henson, R. N., & Rugg, M. D. (2002). State-related and item-related neural correlates of successful memory encoding. *Nature Neuroscience, 5,* 1339–1344.

Rajah, M. N., Languay, R., & Valiquette, L. (2010). Age-related changes in prefrontal cortex activity are associated with behavioural deficits in both temporal and spatial context memory retrieval in older adults. *Cortex, 46,* 535–549.

Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience, 5,* 184–194.

Ranganath, C. (2010). Binding items and contexts: The cognitive neuroscience of episodic memory. *Current Directions in Psychological Science, 19,* 131–137.

Ranganath, C., Yonelinas, A. P., Cohen, M. X., Dy, C. J., Tom, S. M., & D'Esposito, M. (2004). Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia, 42,* 2–13.

Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Intergration of structural and functional findings. In F. I. M. Craik & T. A. Salthouse (Eds.), *Handbook of aging and cognition* (2nd ed., pp. 1–90). Mahweh, NJ: Lawrence Erlbaum Associates.

Reitan, R., & Wolfson, D. (1985). *The Halstead-Reitan Neuropsychological Test Battery: Therapy and clinical assessment*. Tucson, AZ: Neuropsychological Press.

Rugg, M. D., Henson, R. N., & Robb, W. G. (2003). Neural correlates of retrieval processing in the prefrontal cortex during recognition and exclusion tasks. *Neuropsychologia, 41,* 40–52.

Rugg, M. D., Johnson, J. D., Park, H., & Uncapher, M. R. (2008). Encoding-retrieval overlap in human episodic memory: A functional neuroimaging perspective. *Progress in Brain Research, 169,* 339–352.

Rugg, M. D., & Morcom, A. M. (2005). The relationship between brain activity, cognitive performance and aging: The case of memory. In R. Cabeza, L. Nyberg, & D. C. Park (Eds.), *Cognitive neuroscience of aging* (pp. 132–154). Oxford, UK: Oxford University Press.

Schneider, D. W., & Logan, G. D. (2006). Hierarchical control of cognitive processes: Switching tasks in sequences. *Journal of Experimental Psychology: General, 135,* 623–640.

Shimamura, A. P. (2011). Episodic retrieval and the cortical binding of relational activity. *Cognitive, Affective & Behavioral Neuroscience, 11,* 277–291.

Simons, J. S., Koutstaal, W., Prince, S., Wagner, A. D., & Schacter, D. L. (2003). Neural mechanisms of visual object priming: Evidence for perceptual and semantic distinctions in fusiform cortex. *Neuroimage, 19,* 613–626.

Simons, J. S., Scholvinck, M. L., Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2006). Differential components of prospective memory? Evidence from fMRI. *Neuropsychologia, 44,* 1388–1397.

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience, 4,* 637–648.

Smith, A. P., Dolan, R. J., & Rugg, M. D. (2004). Event-related potential correlates of the retrieval of emotional and nonemotional context. *Journal of Cognitive Neuroscience, 16,* 760–775.

Snodgrass, J., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology, 116,* 34–50.

Sommer, T., Rose, M., Glascher, J., Wolbers, T., & Buchel, C. (2005). Dissociable contributions within the medial temporal lobe to encoding of object-location associations. *Learning and Memory, 12,* 343–351.

Spencer, W. D., & Raz, N. (1995). Differential effects of aging on memory for content and context: A meta-analysis. *Psychology and Aging, 10,* 527–539.

Spreng, R. N., & Grady, C. L. (2010). Patterns of brain activity supporting autobiographical memory, prospection, and theory-of-mind and their relationship to the default mode network. *Journal of Cognitive Neuroscience, 22,* 1112–1123.

Swick, D., Senkfor, A. J., & Van Petten, C. (2006). Source memory retrieval is affected by aging and prefrontal lesions: Behavioral and ERP evidence. *Brain Research, 1107,* 161–176.

Troyer, A. K., Winocur, G., Craik, F. I., & Moscovitch, M. (1999). Source memory and divided attention: Reciprocal costs to primary and secondary tasks. *Neuropsychology, 13,* 467–474.

Tsivilis, D., Otten, L. J., & Rugg, M. D. (2003). Repitition effects elicited by objects and their contexts: An fMRI study. *Human Brain Mapping, 19,* 145–154.

Uncapher, M. R., Otten, L. J., & Rugg, M. D. (2006). Episodic encoding is more than the sum of its parts: An fMRI investigation of multifeatural contextual encoding. *Neuron, 52,* 547–556.

Uncapher, M. R., & Rugg, M. D. (2005). Effects of divided attention on fMRI correlates of memory encoding. *Journal of Cognitive Neuroscience, 17,* 1923–1935.

van Kesteren, M. T., Beul, S. F., Takashima, A., Henson, R. N., Ruiter, D. J., & Fernandez, G. (2013). Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. *Neuropsychologia, 51,* 2352–2359.

Vilberg, K. L., & Rugg, M. D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia, 45,* 2216–2225.

Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia, 46,* 1787–1799.

Wang, X., Han, Z., He, Y., Caramazza, A., Song, L., & Bi, Y. (2013). Where color rests: Spontaneous brain activity of bilateral fusiform and lingual regions predicts object color knowledge performance. *Neuroimage, 76,* 252–263.

Wendelken, C., Chung, D., & Bunge, S. A. (2012). Rostrolateral prefrontal cortex: Domain-general or domain-sensitive? *Human Brain Mapping, 33,* 1952–1963.

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin, 120,* 272–292.

Williams, J. (1991). *Memory assessment scales professional manual.* Odessa: Psychological Assessment Resources.

Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified approach for determining significant signals in images of cerebral activation. *Human Brain Mapping, 4,* 58–73.

Zeki, S., & Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain, 121,* 1669–1685.