Effects of aging on true and false memory formation: An fMRI study

Nancy A. Dennis [a,*], Hongkeun Kim [b], Roberto Cabeza [a]

[a] *Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, United States*
[b] *Department of Rehabilitation Psychology, Daegu University, Daegu 705-714, South Korea*

Abstract

Compared to young, older adults are more likely to forget events that occurred in the past as well as remember events that never happened. Previous studies examining false memories and aging have shown that these memories are more likely to occur when new items share perceptual or semantic similarities with those presented during encoding. It is theorized that decreased item-specific encoding and increased gist encoding contribute to these age differences in memory performance. The current study used a modified version of the Deese–Roediger–McDermott (DRM) paradigm to investigate the neural correlates of true and false memory encoding. Results indicated that, compared to young, older adults showed reduced activity in medial temporal lobes (MTL), left ventrolateral prefrontal cortex (VLPFC), and visual cortices associated with subsequent true memories. Despite these decreases older adults showed increased activity in right VLPFC and left superior temporal gyrus (STG) for subsequent true memories. Age-related increases in STG were also associated with subsequent false memories. Results support the theory that older adults engage in less item-specific encoding and greater gist encoding, and that these increases in gist encoding support both subsequent true and false memories. Furthermore, results extend findings of reduced frontal asymmetry in aging, often found in block designs, to the subsequent memory paradigm. Results suggest that greater bilateral frontal activity during encoding in aging are not just task-related, but may be associated with subsequent successful memory performance.
© 2007 Published by Elsevier Ltd.

Keywords: Aging; False memory; Encoding; fMRI

1. Introduction

Compared to young adults, older adults are not only more likely to forget events that happened in the past but also to remember events that never happened (Koutstaal & Schacter, 1997; Norman & Schacter, 1997; Tun, Wingfield, Rosen, & Blanchard, 1998). Research has shown that this age-related increase in false memories is especially salient when new items presented during retrieval are closely related to those encountered during encoding (e.g., Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997). For example, in the Deese–Roediger–McDermott (DRM) paradigm, participants who study lists of words that are all semantically related to a word that is not presented (related lure), show a strong tendency to falsely recall or recognize the related lure at test (Roediger & McDermott, 1995). In this paradigm, older compared to younger adults show both a reduction in accurate retrieval of the words presented in the list and an increase in erroneous retrieval of the related lure (Balota et al., 1999).

Theoretical accounts of the age-related increase in false memories have postulated deficits in memory for item-specific information (Koutstaal & Schacter, 1997; LaVoie & Faulkner, 2000; Norman & Schacter, 1997; Spencer & Raz, 1995; Tun et al., 1998) as well as reliance on semantic gist (Balota et al., 1999; Tun et al., 1998). One theory that incorporates both mechanisms is the fuzzy trace theory. According to this theory, two types of memory traces are created during encoding: item-specific (verbatim) traces and gist traces (Brainerd & Reyna, 1990; Schacter, Verfaellie, & Pradere, 1996). Item-specific traces retain the distinctive features of the individual items, whereas gist traces retain the general meaning of the event, but lack perceptual details or information about specific instances of the encoding

* Corresponding author at: Center for Cognitive Neuroscience, Duke University Box 90999, LSRC Bldg. Durham, NC 27708, United States.
Tel.: +1 919 668 5262; fax: +1 919 681 0815.
E-mail address: ndennis@duke.edu (N.A. Dennis).

event. Both types of memory traces can be employed during retrieval to endorse an item as 'old'. Fuzzy trace theory can account for age-related increases in false memories by assuming that older adults have a deficit in memory for item-specific traces but not for gist traces (Tun et al., 1998). A positive outcome is that memory for gist traces may partly offset item-specific memory deficits in older adults. In the DRM paradigm, for example, older adults may successfully endorse a studied item as old because it matches the gist trace for the studied list, even if they cannot remember item-specific information for that item. Unfortunately, relying on gist traces in the absence of item-specific traces has the negative side effect of increasing false memories. For instance, in older adults the tendency to endorse the gist-matching related lure is not opposed by item-specific memories indicating that the particular item was not in the study list. The differential effects of aging on memory for item-specific and gist information may occur during encoding and/or during retrieval. In the present study, we used functional neuroimaging to investigate the effects of aging on the neural correlates of encoding gist and item-specific information.

Previous functional neuroimaging studies of encoding and aging have found significant age effects in prefrontal cortex (PFC) and medial temporal lobe (MTL) activity (for a review see Daselaar, Browndyke, & Cabeza, 2006a). The most typical finding within PFC has been an age-related decrease in left PFC activity coupled with an age-related increase in right PFC activity (e.g., Anderson et al., 2000; Cabeza et al., 1997; Grady et al., 1995). As a result, the pattern of PFC activity tends to be more bilateral in older than in young adults. This finding is consistent with many functional neuroimaging studies that have shown a hemispheric asymmetry reduction in older adults (HAROLD) in other cognitive domains, including episodic retrieval, working memory, attention, and perception (Cabeza, 2002). While the exact role of increased bilaterality in older adults is still under investigation, one theory posits that it may counteract age-related neurocognitive deficits (Cabeza et al., 1997). To investigate this compensation account it is useful to isolate activity associated with successful cognitive processes.

Only a few functional neuroimaging studies of encoding and aging have used a technique that allows for the isolation of brain activity specifically associated with successful encoding processes: the subsequent memory paradigm (see Paller & Wagner, 2002). This method associates successful encoding processes with brain regions that show greater study-phase activity for items that are remembered rather than forgotten in a subsequent memory test. The difference in activity between subsequently remembered versus forgotten items is known as 'difference in memory' or Dm (hereafter referred to as true Dm). In young adults, true Dm activity is typically found in ventrolateral PFC and MTL regions (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Davachi, Maril, & Wagner, 2001; Otten & Rugg, 2001; Prince, Daselaar, & Cabeza, 2005; Wagner et al., 1998). To date, only three studies have used the subsequent memory paradigm to investigate the effects of aging on successful encoding activity (Dennis, Daselaar, & Cabeza, 2006; Morcom, Good, Frackowiak, & Rugg, 2003). These studies have yielded two consistent findings. First, compared to young adults, older adults
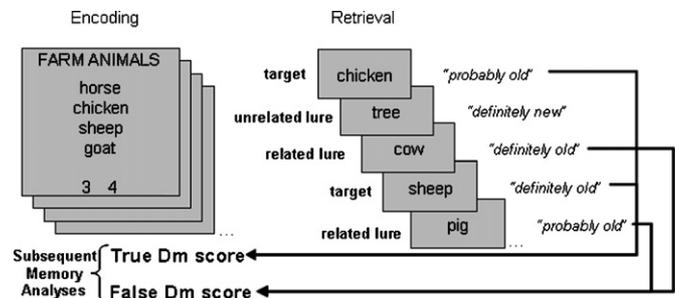

Fig. 1. During encoding participants were presented with short DRM lists. At retrieval they viewed words from the list (targets), new words from different, unpresented categories (unrelated lures), and new words from presented categories (related lures). Participants' memory scores to each word from the list composed the subsequent true recognition (true Dm) score whereas memory scores to the related distractors composed the subsequent false recognition (false Dm) score.

showed reduced true Dm activity in MTL regions (Dennis et al., 2006; Gutchess et al., 2005), possibly reflecting a deficit in the formation of new memory traces. Second, compared to young adults, older adults showed greater true Dm activity in dorsolateral and anterior PFC regions (Dennis et al., 2006; Gutchess et al., 2005; Morcom et al., 2003), possibly reflecting a compensatory mechanism. In these studies, the finding of bilateral recruitment in older adults (HAROLD) has been less consistent (see however, Morcom et al., 2003), which raises the question of whether this effect can be directly linked to successful encoding operations.

In the present fMRI study we combined the subsequent memory paradigm with a variation of the DRM paradigm in order to investigate the effects of aging on encoding activity leading to subsequent true memories (i.e., true Dm) and on encoding activity leading to subsequent false memories (a "false Dm"). As illustrated by Fig. 1, in each encoding trial, participants studied a "mini word-list" comprising four instances (e.g., horse, chicken, sheep, goat) of a semantic category (e.g., farm animal). To promote gist encoding we instructed participants to check if all instances belonged to the category, and included several 'catch trials' in which one instance did not match. At test, participants performed an old/new recognition test with confidence ratings that included studied words (e.g., targets: horse, chicken) as well as non-studied words from studied categories (related lures: e.g., cow, pig). Using the subsequent memory procedure we calculated two different measures for each encoding trial: (i) how many (and how confidently) studied words were later remembered (subsequent hit rate); (ii) how many (and how confidently) non-studied semantic associates were later falsely remembered (subsequent false alarm rate). Using these two measures, we conducted parametric analyses of fMRI activity during encoding that identified regions where activity increased as a function of subsequent true memory (true Dm) or as a function of subsequent false memory (false Dm).

Our study had two goals. The first goal was to investigate age-related differences in item-specific encoding in a task that promotes gist processing. In accord with previous subsequent memory studies involving older adults, we predicted that older adults would show age-related decreases in item-specific encoding activity in the MTL coupled with age-related compensatory

increases in both lateral and rostral medial PFC activity. The second goal was to examine regions associated with subsequent false alarms in older adults and determine whether increased gist processing during encoding contributes to both true and false Dm. Regarding age differences in false Dm our investigation is more exploratory in nature. In accord with previous work in the DRM literature and evidence suggesting an age-related deficit in distinctive processing, we predicted that older adults would show an increased number of false alarms to related distractors compared to younger adults. Furthermore, we predicted that activity associated with gist processing of categories and category memberships would contribute to both true and false Dm in older adults. Given the semantic nature of the encoding task, we expected that this activity would occur in semantic processing regions, such as left temporal cortex.

2. Methods

2.1. Participants

Sixteen young adults (nine female; age range 18–31) and 17 older adults (six female; age range 61–86) participated in the experiment. Young were recruited from Duke's undergraduate and graduate populations; older adults were recruited from community advertisements. [Data from the young adults were previously reported in (Kim & Cabeza, 2006)]. All participants were healthy, right-handed, native English speakers, with no history of neurological or psychiatric episodes. All gave informed consent to a protocol approved by the Duke University Institutional Review Board. Due to scanner error resulting in missing data, one older adult was excluded from analyses. In a separate session from the scanning session described below all older adults completed a battery of neuropsychology tests derived from the Cambridge Neuropsychological Test Automated Battery (CANTAB). Results and group characteristics are reported in Table 1. As noted, older participants scored, on average, above that which would be expected for their age group on all neuropsychological measures. Data indicates that they were a high performing group of participants and free of dementia or other cognitive impairments.

Table 1
Mean and standard deviation for age, years of education, Shipley vocabulary score, and several standard ('*z*') scores from the Cambridge Neuropsychological Test Automated Battery (CANTAB)

	Mean	S.D.
Age	69.26	6.61
Education(years)	16.94	2.05
Shipley vocabulary	37.38	1.82
CANTAB		
Spatial working memory: a self-ordered task, which also assesses heuristic strategy	0.62	1.16
Pattern recognition memory: a test of visual pattern recognition memory	0.75	0.7
Reaction time: a latency task w/a comparative history	0.49	1.07
Rapid information processing: a test of sustained attention	0.16	0.91
Spatial span: a computerized version of the Corsi Blocks task	0.88	0.81
Intra-extra dimensional set shifting: a computerized analogue of the Wisconsin Card Sorting test	0.41	0.41
Paired associates learning: assesses visual memory and new learning	0.27	0.76

2.2. Behavioral methods

The present encoding task was an adaptation of the DRM paradigm (Roediger & McDermott, 1995). Materials consisted of 72 categorical six-word lists selected from category norms (Battig & Montague, 1969; Yoon et al., 2004). Each list consisted of the six most typical instances (e.g., cow, pig, horse, chicken, sheep, goat) of a category (e.g., farm animal), with minor exceptions. In each list, the third to sixth most typical instances were used as encoding stimuli (targets); the first and the second most typical instances were used as critical lures (related lures) in the test phase. Additionally, semantically unrelated words, matched in letter number, frequency, and concreteness to the category words, were used as control words (unrelated lures) in the test phase. The categories were carefully chosen so that their instances did not overlap. Thus, both 'farm animal' and 'wild animal' categories were included in the stimulus set, but 'four-legged animal' was not included. To make sure minimal associative overlap between the categories, the probability that the related lures would be generated as an associative response to the other categories (e.g., the probability that 'cow' would be generated as an associative response to 'wild animal') was examined. The associative response probability was less than 1% in 10,211 out of 10,224 ($72 \times 2 \times 71$) examined and less than 5% in the remaining 13.

The study phase consisted of a single scan of 82 trials/lists: 72 encoding trials and 10 'catch' trials. Each encoding trial simultaneously showed a category name followed by four category members (see Fig. 1). For each 'catch' trial, only three of the four examples belonged to the category. Each encoding trial was presented for 4 s, followed by a fixation cross for 2 s. The participants' task was to decide whether all four or only three examples belonged to the category. Responses were made by pressing one of two keys on a response box using the first two fingers of the right hand. Trials were separated using an inter-trial fixation period which varied randomly between 1.5 and 4.5 s, allowing for event-related fMRI analyses. The words were displayed in colors to promote the encoding of sensory/perceptual information (Cabeza et al., 2001). Each trial consisted of all words presented in one of five randomly assigned colors.

The test phase, which began approximately 10 min after completion of the study phase, consisted of six scans. fMRI data from these scans are not reported or discussed here, and will be the focus of a separate publication. There were a total of 288 targets, 144 related lures, and 144 unrelated lures across all 6 scans. Trials were presented in a predetermined, pseudo-random order. On each trial, a word was shown for 2 s, followed by a fixation cross for 1 s. All words in the test phase were displayed in white color against black background. Participants responded by pressing one of four keys according to whether the word was judged to be 'definitely old', 'probably old', 'probably new', or 'definitely new'. Participants practiced both encoding and retrieval before entering the scanner.

Using the subsequent memory procedure, we calculated two different measures for each encoding trial: (i) how many (and how confidently) studied words were later remembered (subsequent hit rate: a measure of subsequent true memories); (ii) how many (and how confidently) non-studied semantic associates were later falsely remembered (subsequent false alarm rate: a measure of subsequent false memories). Each high-confidence hit response was assigned 1 point, and each low-confidence hit was assigned 0.5 point, yielding a 0–4 range for the subsequent hit measure. Each high-confidence false alarm to a related lure was assigned 2 points, and each low-confidence false alarm was assigned 1 point, also yielding a 0–4 range for the subsequent false alarm measure. This scoring scheme reflected our reasoning that strength of subsequent true memory (or false memory) for the encoding lists is reflected in the number of hits (or false alarms) as well as in degree of confidence associated with hits (or false alarms). Based on subsequent hit and subsequent false-alarm measures, we conducted a parametric study of fMRI signals at the encoding phase (see below). It should be noted that parametric analyses as implemented in SPM2 are scale-invariant in so far as the scales are linearly related. Thus, assignment of [1, 2] to low versus high confidence false alarms yields numerically identical results to assignment of [0.5, 1] to low versus high confidence hits. We further assured that there were sufficient trials scored above zero (e.g., predicting modulation of neural activity) for both true and false Dm in both age groups. A look at the Dm vectors for each parametric modulator indicated that, on average, 46 trials received a score above zero in young and 50 trials in older adults for the false Dm analysis. For the true Dm analysis, on average, 66 trials were scored above zero in both young and older adults. These numbers indicate that there were a substantial number

of trials contributing to each Dm vector and this was sufficient for investigating both true and false Dm effects in each age group.

2.3. fMRI methods

Images were collected using a 4T GE scanner. Stimuli were presented using liquid crystal display goggles (Resonance Technology, Northridge, CA) and behavioral responses were recorded using a four button fiber optic response box (Resonance Technology). Scanner noise was reduced with earplugs and head motion was minimized using foam pads and a headband. Anatomical scanning started with a T2-weighted sagittal localizer series. The anterior (AC) and posterior commissures (PC) were identified in the midsagittal slice, and 34 contiguous oblique slices were prescribed parallel to the AC–PC plane. High-resolution T1-weighted structural images were collected with a 500-ms repetition time (TR), a 14-ms echo time (TE), a 24-cm field of view (FOV), a 256^2 matrix, 68 slices, and a slice thickness of 1.9 mm. Functional images were acquired using an inverse spiral sequence with a 1500-ms TR, a 31-ms TE, a 24-cm FOV, a 64^2 matrix, and a $60°$ flip angle. Thirty-four contiguous slices were acquired with the same slice prescription as the anatomical images. Slice thickness was 3.75 mm, resulting in cubic 3.75 mm^3 isotropic voxels.

fMRI analyses focused on data collected from the encoding phase. Preprocessing and data analyses were performed using SPM2 software implemented in Matlab (www.fil.ion.ucl.ac.uk/spm/). After discarding the first six volumes, the functional images were slice-timing corrected and motion-corrected, and then spatially normalized to the Montreal Neurological Institute (MNI) template and spatially smoothed using an 8 mm isotropic Gaussian kernel, and resliced to a resolution of 3.75 mm^3 isotropic voxels.

In accord with the previous analysis of this data (Kim & Cabeza, 2006), trial-related fMRI activity was first modeled by convolving a vector of the onset times of each trial with a canonical hemodynamic response function (HRF) within the context of the general linear model (GLM), as implemented in SPM2. Confounding factors (head motion, magnetic field drift) were also included in the model. No participant moved more than 3 mm in any direction either within or across runs. Thus, no data was eliminated in either age group due to motion artifacts. While the typical subsequent memory study would model activity separately for subsequent hit and subsequent miss trials, that cannot be done in the current design as each encoding trial contained four words which were tested separately at retrieval. Thus hits and misses are confounded within a given encoding trial. In place of the standard subsequent memory analysis we parametrically modeled the activity associated with each encoding trial as a function of both the subsequent hits and subsequent false alarms associate with each encoding trial (see also Dennis et al., 2006). This allowed us to look for regions which increased in activation as either subsequent hit rate or subsequent false alarm rate increased.

Specifically, the height of the modeled HRF was parametrically modulated separately by (i) the subsequent hit measure (i.e., the HRF was multiplied by a linear increase function of subsequent hit measure) and by (ii) the subsequent false alarm measure. Thus, by varying the parametric modulator associated with each encoding trials, we were able to use the same encoding trials to assess both subsequent true and subsequent false memories. Catch trials and trials on which encoding responses were incorrect were modeled by a separate regressor, but not considered in the analyses. For each participant, statistical parametric maps pertaining to the parametric regressors were identified and subsequently integrated across participants using a random-effects model for each age group. These analyses informed us which brain regions show true Dm activity (i.e., positive covariation between encoding trial activations and later hit rate for words from those trials) and which brain regions show false Dm activity (i.e., positive covariation between encoding trial activations and later false alarm rate for semantic associates of words from those trials).

For assessing age independent activations associated with true Dm, a conjunction map was created thresholding each age group's random effects of the true Dm parametric regressor at $p = 0.05$ with a minimum of 10 contiguous voxels (joint probability = $0.05 * 0.05 = 0.0025$). This procedure yielded an activation map containing only those voxels that showed true Dm in both age groups. A similar analysis was conducted for false Dm. These results are reported in Table 3.

In order to identify regions that showed significant group differences we used a multiple contrast approach. We first identified those regions that show significant between group effects at $p < 0.05$ with a minimum of five contiguous voxels by directly contrasting the statistical maps of older and younger adults. We then also required that those regions show a significant within-group effect at $p < 0.005$ with minimum cluster size of 10 voxels. This was done by inclusively masking the between group contrast (e.g., true Dm activity for Young greater than Old) with the main effects of the group contrast (e.g., true Dm activity in Young). This approach was taken such that resulting regions would (a) be significantly active in one group ($p < 0.005$) and (b) demonstrate a moderate, yet significant, group difference ($p < 0.05$). While probabilities are not completely independent this results in an approximate joint probability of $p = 0.00025$ (Lazar, Luna, Sweeney, & Eddy, 2002). Results of age effects are reported in Table 4.

2.4. Behavioral results

Table 2a breaks down the hit rate by confidence (e.g., dividing all low confidence hits by all old items and doing the same for high confidence hits). Adding the two confidence-based hit rates provides the total hit rate for each age group (i.e., 0.74 for young and 0.72 for older adults). The same analysis was done for related lures and unrelated lures. In order to better understand age differences in classifying an item as 'old' we conducted the analyses shown in Table 2b. Here we broke down all the trials to which participants responded 'old' by trial type (targets, related lures, unrelated lures) and confidence (e.g., proportion of high confidence targets were calculated by dividing all high confidence 'old' response to a target by the total number of high confidence 'old' responses). The same logic was used to compute low confidence responses. From this latter analysis we found that older adults made more high confidence 'old' responses to related lures than did younger adults (0.20 and 0.14, respectively) whereas younger adults made more high confidence 'old' responses to target than older adults (0.83 and 0.76, respectively). Unpaired *t*-

Table 2

(a) Portion of high and low confidence "old" responses by trial type (targets, related lures and unrelated lures); (b) Portion of trial types responded to as "old" broken down by confidence (high or low confidence "old" responses); (c) Reaction Time (RT) in seconds; significant age differences ($p < 0.05$) are highlighted in bold

	Hit rate				(c) RT	
	(a) Based on 'old' items		(b) Based on response type			
	Y	O	Y	O	Y	O
LC						
Targets	0.26(0.10)	0.24(0.09)	0.53(0.08)	0.54(0.09)	**1.48(0.14)**	**1.80(0.18)**
Related lures	0.32(0.14)	0.27(0.12)	0.32(0.05)	0.30(0.06)	**1.53(0.17)**	**1.81(0.18)**
Unrelated lures	0.15(0.11)	0.13(0.08)	0.15(0.10)	0.16(0.09)	**1.54(0.23)**	**1.88(0.25)**
HC						
Targets	0.48(0.16)	0.48(0.12)	**0.83(0.09)**	**0.76(0.08)**	**1.21(0.14)**	**1.43(0.19)**
Related lures	0.18(0.14)	0.28(0.16)	**0.14(0.07)**	**0.20(0.06)**	**1.29(0.16)**	**1.56(0.23)**
Unrelated lures	0.04(0.05)	0.04(0.04)	0.03(0.03)	0.03(0.02)	1.23(0.70)	1.55(0.49)

Table 3

The table reports common areas of activation for both young and old groups associated with subsequent true recognition (true Dm) and subsequent false recognition (false Dm)—conjunction analysis at $p = 0.05$ with a minimum cluster size ≥ 10 in each age group

	H	BA	Voxels	Coordinates (T&T)							
				Young				Old			
				x	y	z	T	x	y	z	T
true Dm-common areas											
Frontal											
VLPFC/DLPFC	L	44/9/45/47	126	−38	9	24	4.33	−41	5	28	4.02
	R	44/45/46	44	45	26	13	4.92	45	23	16	5.85
Oribitofrontal cortex	M	6/8	10	−4	14	55	2.3	−4	17	48	2.97
Globus pallidus	L		13	−11	4	3	3.37	−15	1	10	2.76
PHG	L	27/30	50	−4	−44	−1	3.92	−8	−52	−4	6.97
Occipital											
Occipitotemporal cortex	L	37/19	15	−49	−52	−13	4.48	−60	−41	−8	3.22
	R	18/17	20	15	−85	8	3.49	11	−84	11	3.05
Occipital pole	L	18	10	−4	−77	11	2.74	−8	−77	11	3.27
Occipitoparietal cortex	R	18/19	139	23	−96	8	5.68	34	−80	18	4.58
Occipital pole	L	17/18/19	152	−19	−100	2	4.58	−38	−88	4	4.69
false Dm-common areas											
Middle temporal gyrus	L	37	13	−56	−52	−7	4.13	−60	−45	−7	2.53
Occipitotemporal cortex	R	18/19	10	26	−74	−9	3.12	23	−71	−12	3.45
	L/R	18/19	46	−8	−89	−2	2.7	8	−85	1	3.15
Occipitoparietal cortex	L	19	10	−26	−83	36	2.69	−26	−83	36	3.32

Notes: VLPFC = ventrolateral prefrontal cortex; DLPFC = dorsolateral prefrontal cortex; PHG = parahippocampal gyrus; BA = Brodmann area; T = statistical t value; H = hemisphere; Talairach & Tournoux (T&T) coordinates reported.

tests on each measure revealed a significant age difference for high confidence targets [$t(30) = 2.23$, $p < 0.05$] and high confidence related lures [$t(30) = 2.57$, $p < 0.05$]. No other age difference was found to be significant. These results are consistent with previous studies investigating age differences using the DRM paradigm.

Accuracy during the encoding task was quite high and did not differ between young and older adults [mean accuracy = 0.95 for both groups]. However, younger adults did responded slightly faster than their older counterparts [mean reaction time (RT): 2.59 s for young and 2.84 s for older adults, $t(30) = 2.17$, $p < 0.05$]. Regarding retrieval responses, there was no significant difference in response rate. Both older and younger adults responded to 98% of retrieval trials, resulting in an average "no response" rate of 10.5 and 10.94 trials for young and older adults, respectively. Again younger adults responded slightly faster than older adults [mean RT: 1.44 s for young and 1.69 s for older adults, $t(30) = 4.10$, $p < 0.05$]. Based upon these results we conclude that both age groups were able to adequately execute both the encoding and the memory tasks in the allotted time.

There was a modest, but significant correlation between true and false Dm scores in both young [mean = 0.20, $t(15) = 3.76$ $p < 0.01$] and older adults [mean = 0.34, $t(15) = 8.5$ $p < 0.001$]. The correlation provides behavioral evidence that a common factor does contribute to subsequent true and subsequent false memory formation within each age group. Previously reported data from this study (Kim & Cabeza, 2006) suggested this to be controlled elaborative processing in young, while the current analyses suggest that semantic gist is the common factor in older adults (see below).

2.5. fMRI results

The average correlation between the true Dm and false Dm regressors was −0.0081 in the young group and −0.0058 in the older group. Because there was no significant positive overlap between regressors they are assumed to be modeling separate and non-overlapping activations. In turn, because the two regressors do not share a significant amount of common variance, there should be no violations of collinearity within the GLM.

Table 3 reports true Dm activity common to both age groups, as well as false Dm activity common to both age groups. As previously noted, true Dm was identified as parametric increases in encoding activity as a function of the hit score for each trial and false Dm was identified as parametric increases in encoding activity as a function of the related FA score for each trial. Results show true Dm activity in bilateral prefrontal, left MTL and visual cortex. Common areas associated with false Dm in both young and older adults included occipitotemporal and occipitoparietal cortices and left middle temporal gyrus.

Table 4 reports age-related differences in brain activity for each encoding measure. Consistent with our predictions, older adults exhibited reduced true Dm activation in left ventrolateral PFC, left parahippocampal gyrus (PHG) extending into hippocampus, and bilateral occipitotemporal cortex compared to young adults. These results suggest that older adults do not activate or modulate these regions to same degree as young adults when encoding subsequent true memories. Given that theses regions have previous been associated with item-specific processing, the data are consistent with the notion that older adults have a deficit in encoding item-specific information. At the same time, older adults showed increased true Dm activation in right ventrolateral PFC, medial rostral PFC, and bilateral superior temporal gyrus (STG) compared to younger adults. Furthermore, age-related decreases in left ventrolateral PFC coupled with increased activity in right PFC resulted in a more bilateral pattern of frontal activation in older adults (i.e., HAROLD). These age-related true Dm increases, and the bilateral pattern of frontal recruitment in particular, support the idea of compensatory mechanisms in the aging brain.

Finally, in regards to false Dm, younger showed greater activity in left VLPFC, left parietal cortex, and bilateral occipitotemporal cortex, whereas older adults showed greater activity in bilateral middle temporal gyrus and left STG. Again, results suggest age-related decreases in engaging the former regions (and processing they sub-serve) associated with subsequent false memories, but age-related increases in the engagement of middle and superior temporal gyrus. Age-related increases in left STG for both true Dm and false Dm are consistent with our predictions of age-related increases in gist processing, supporting subsequent true and false memories.

Table 4
The table reports age differences in regions significant at $p < 0.05$ uncorrected, with a minimum cluster size ≥ 5; inclusively masked with the primary analysis of interest (e.g., Young true Dm, Old true Dm, Young false Dm, or Old false Dm) at $p > 0.005$ with a minimum cluster size ≥ 10

	H	BA	Voxels	coordinates (T&T)			
				x	y	z	T
true Dm-group differences							
Y > O							
VLPFC	L	44/45	39	−53	12	24	3.4
PHG/hippocampus	L		47	−11	−37	−1	3.71
SMA	L	6	10	−41	−5	53	3.05
Thalamus	L		71	−8	−7	11	3.8
Precuneus	L	7	30	−26	−68	35	3.55
Occipital cortex	R	19	31	26	−52	−10	5.97
Occipito-temporal Cortex	R	18	215	19	−96	8	3.8
	L	19/37	50	−49	−56	−13	3.73
O > Y							
Frontal							
Rostral PFC	L	9/10	7	−15	56	22	2.93
VLPFC	R	44/45	9	45	16	17	2.88
Superior temporal gyrus	R	21	8	49	−11	−6	4.3
	L	24/42	9	−49	−36	16	2.34
false Dm-group differences							
Y > O							
VLPFC	L	46	17	−34	52	4	6.83
	L	45/44	112	−38	1	24	4.52
Parietal cortex	L	19	72	−26	−71	49	4.53
Brainstem			30	19	−11	−3	5.7
Parietal cortex	L	40	14	−45	−42	44	3.85
Occipito temporal cortex	R	19/37	29	41	−60	−10	4.06
	R	19/39	19	34	−76	21	3.07
	L	19/37	13	−60	−43	27	3.5
	L	19/37	18	−38	−59	−7	3.2
O > Y							
Superior temporal gyrus	L	BA 22	6	−60	−14	8	3.08
Middle temporal gyrus	R	BA 21	6	56	−11	−6	2.99
	L	BA 21	6	−56	0	−10	2.38

Notes: VLPFC = ventrolateral prefrontal cortex; PHG = parahippocampal gyrus; BA = Brodmann area; T = statistical *t* value; H = hemisphere; Talairach & Tournoux (T&T) coordinates reported.

3. Discussion

In order to test age differences in item-specific encoding and false memory formation we used a paradigm sensitive to both types of encoding processes. The study yielded three main findings. First, regarding true Dm activity and consistent with previous blocked and event-related designs, older adults exhibited reduced modulation of activity associated with subsequent true memories in left PFC and MTL compared to younger adults. Second, older adults exhibited greater modulation of activity associated with true Dm in right PFC and medial rostral PFC. The increase in right PFC activity resulted in a less lateralized pattern of PFC activation in older compared to younger adults, also a finding consistent with previous studies examining memory functioning in aging. Finally, older compared to younger adults exhibited greater increases in true and false Dm activity in left middle and superior temporal gyri, regions previously associated with semantic processing.

Parametric modulation analysis is based on the premise that regional cerebral blood flow (rCBF) varies with the amount of processing engaged in by a given experimental task or condition (Buchel, Wise, Mummery, Poline, & Friston, 1996). That is, analyses underscore the relationship between a study parameter (e.g., subsequent memory in our study) and brain activity. We consider this an advantage in the current experiment because we are interested in activity associated with particular cognitive processes (e.g., episodic encoding) rather than in absolute differences in neural activity. For example, if a brain region shows greater Dm activity in young than older adults, this indicates that the region had greater contributions to subsequent memory in young adults; it does not indicate that the absolute level of activity of the region was greater in young adults. Thus, when we describe age effects as reflecting deficits or compensation it is important to keep in mind that these changes reflect the recruitment of regions to support encoding processes rather than general statements about functional integrity of these regions in older adults.
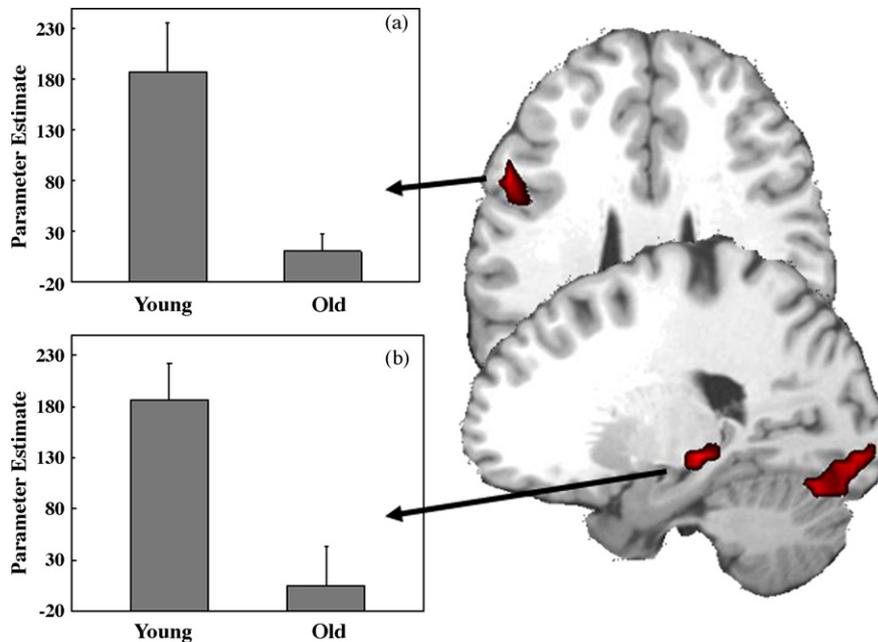
Fig. 2. Age related decreases in item-specific encoding regions. Areas showing greater activity in younger compared to older adults for (a) left ventrolateral prefrontal cortex and (b) parahippocampal gyrus/hippocampus. Bar graphs represent functional activation (and standard error) associated with true Dm (e.g., beta weights of the true Dm parametric regressor) for both age groups. See Table 4 for coordinates.

3.1. Age-related true Dm decreases in LPFC and MTL

In the current study both younger and older adults showed true Dm activity in regions including bilateral PFC, left posterior PHG/hippocampus, and visual cortex. However, older adults exhibited decreased modulation of this activity in all aforementioned regions (but right PFC) (see Fig. 2). These results support previous studies of subsequent memory in aging which also showed age-related reductions in MTL and visual cortex (Dennis et al., 2006; Gutchess et al., 2005). While increased hippocampal activity has been shown to reduce reality monitoring errors (e.g., Kensinger & Schacter, 2005) and code for source information (e.g., Davachi, Mitchell, & Wagner, 2003), reductions in MTL activity have been associated with deficits in item-specific processing (e.g., Davachi & Wagner, 2002; Staresina & Davachi, 2006). Age-related reduction in PHG and hippocampal activity in the current study support previous evidence indicating that older adults show reduced item-specific encoding (e.g., LaVoie & Faulkner, 2000; Spencer & Raz, 1995). Deficits in the engagement of item-specific encoding processes may lead to less detailed encoding traces available for subsequent retrieval. In the absence of a strong individual encoding trace, older adults may need to rely on other encoding processes to support subsequent retrieval (else exhibit a deficit in subsequent true retrieval). Despite these reductions in item-specific encoding, older adults do not exhibit deficits in true memory performance, suggesting that these MTL processing deficits must be compensated for by other types of encoding processing (see below).

The current study also extend the finding of age-related decreases in left PFC during encoding often found in blocked designs (Logan, Sanders, Snyder, Morris, & Buckner, 2002; Stebbins et al., 2002) to the subsequent memory paradigm.

Results indicate that these decreases are not related to task-related activity alone, but may be associated with memory performance. While left PFC activity in subsequent memory tasks has been thought to involve semantic processing and organization of encoding trials for input into MTL (e.g., Wagner et al., 1998), decreased activation in this region could reflect reductions in item-specific information processing and subsequent transfer of that information to the MTL.

3.2. Age-related true Dm increases in PFC

Despite the observed decrease in left VLPFC activity, older adults exhibited increased true Dm activity in right VLPFC compared to young adults (Fig. 3). Age-related decreases in lateralization stemming from increased contralateral recruitment in frontal regions is frequently observed in aging studies (for a review see Cabeza, 2002). This increase in frontal bilaterality in aging, or HAROLD pattern, is most often regarded as compensatory, offsetting age-related neurocognitive decline (e.g., reductions in left PFC) (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002). Unlike previous blocked designs (e.g., Cabeza et al., 1997; Logan et al., 2002) the current study was able to link this activity with successful encoding performance. Thus, we are able to expand the finding of HAROLD from one of task-related activity during encoding to activation supporting successful subsequent memory performance in aging. Although a previous subsequent memory study also found reduced frontal asymmetric in older adults (Morcom et al., 2003), the analysis was based on voxels-of-interest from a different study. The current study expands upon this work by demonstrating HAROLD within regions significantly activated in the study at hand.
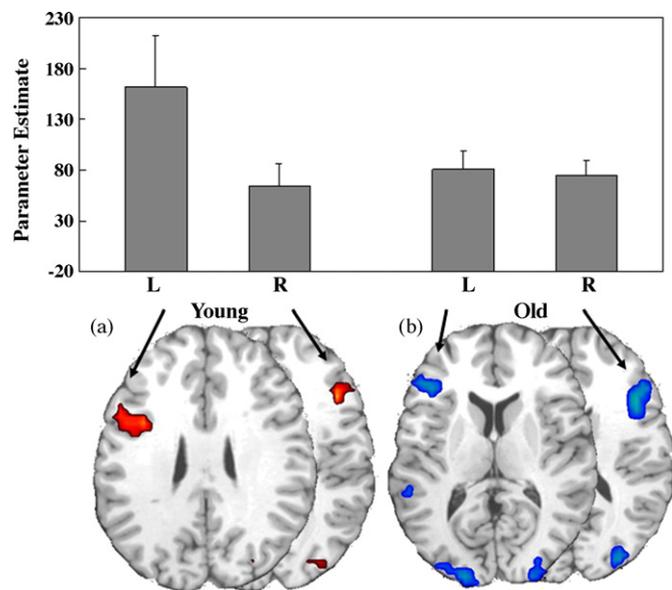
Fig. 3. Ventrolateral PFC activity for both (a) young and (b) older adults. Bar graphs represent functional activation (and standard error) associated with true Dm (e.g., beta weights of the true Dm parametric regressor) for each age group for both left and right prefrontal regions. See Table 3 for coordinates.
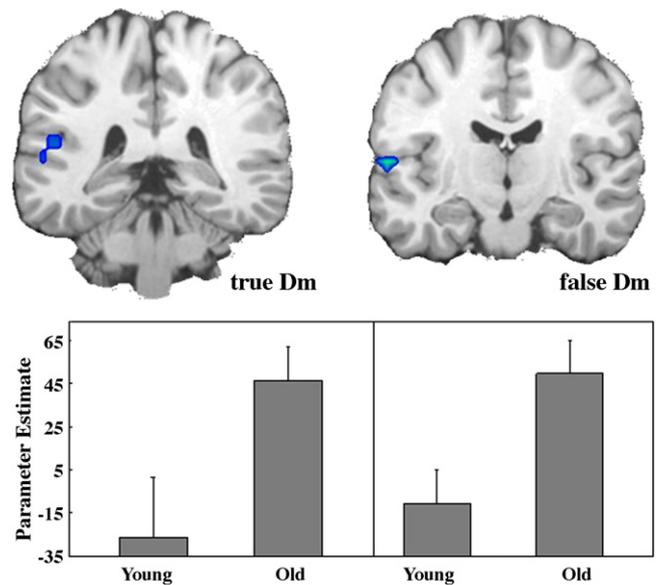

Fig. 4. Age-related increases in superior temporal gyrus activity associated with (a) subsequent true recognition (true Dm) and (b) subsequent false recognition (false Dm). Bar graphs represent functional activation (and standard error) associated with true or false Dm (e.g., beta weights of the true and false Dm parametric regressors) for each age group. See Table 4 for coordinates.

Additional age-related frontal increases associated with true Dm activity were observed in medial rostral PFC. This finding is consistent with all three previous subsequent memory and aging studies (Dennis et al., 2006; Gutchess et al., 2005; Morcom et al., 2003). Activation in this region has been associated with recollection of context (e.g., Rugg, Fletcher, Chua, & Dolan, 1999; Simons, Owen, Fletcher, & Burgess, 2005a), promoting attention towards the external environment (Gilbert, Spengler, Simons, Frith, & Burgess, 2006), and directing one's attention between current sensory input and internally generated thought processes (e.g., Christoff, Ream, Geddes, & Gabrieli, 2003; Gilbert, Frith, & Burgess, 2005; Gilbert et al., 2006; Simons et al., 2005a). In accord with this last interpretation of rostral PFC function, older adults in the current and other subsequent memory studies could be recruiting this area by internally generating associations with the encoding items. Since this activity is associated with successful memory performance, recruitment of rostral PFC may function in a compensatory fashion, offsetting age-related deficits in item-specific processing regions (i.e., MTL, left VLPFC).

3.3. Age-related Dm increases in STG: gist encoding

As noted, younger adults exhibited false Dm activity within a subset of those regions activated for true Dm (see Kim & Cabeza, 2006). Older adults did not activate this same network, but showed modulation of activity associated with false Dm in bilateral middle temporal gyrus and left superior temporal gyrus. Furthermore, older compared to younger adults showed greater modulation of activity within left superior temporal gyrus associated with true Dm activity as well (see Fig. 4). Given the role of these regions in language and semantic processing (Kable, Lease-Spellmeyer, & Chatterjee, 2002; Wise

& Price, 2006), we suggest that older adults are engaging in greater or deeper semantic processing during encoding. Additionally, because this activity is associated with subsequent true as well as subsequent false retrieval we further suggest that semantic processing associated with the category or integration of the category and exemplars supports subsequent retrieval by providing individuals with a strong representation of semantic gist. The inference that STG is involved in the representation of semantic gist stems from the fact that increased activation in this regions supports both true and false subsequent retrieval—and is not associated specifically with true Dm and item-specific processing. Furthermore, patients with semantic dementia (and damage to this region) are impaired at extracting and/or utilizing semantic gist (Simons et al., 2005b). Thus we suggest that an increased semantic gist associated with the category leads to subsequent endorsement of a category member as having been presented previously (whether or not it actually was). Again, while this activation may help compensate for item-specific encoding deficits (i.e., decreased VLPFC and MTL activation) in older adults, increased gist representation also leads to an increased number of subsequent false memories. Regarding the novelty of this result, we recognize that further work and replication is needed to confirm this finding and the foregoing interpretation.

The question remains whether aging enhances gist processing and that in turn elicits a strategic shift in older adults to a more gist-based encoding strategy or if growing deficits in item-specific processing abilities (mediated by VLPFC and MTL) diminish, prompting older adults to default to gist encoding. While more research is needed to answer this question, there is evidence from studies examining language processing in children indicating increased age (and presumably increased semantic knowledge) is associated with increased activity in

lateral temporal cortices and more efficient semantic processing (Blumenfeld, Booth, & Burman, 2006; Chou et al., 2006). However, we cannot rule out the more likely possibility that as item-specific processes diminish in aging, older adults are simply more likely to "fall back on" what they know best—semantic processing. Behavioral reviews of cognitive aging indicate that semantic abilities are preserved, if not enhanced with age (e.g., Light, 1991; Park, 2000). Thus, it is most likely that older adults use these abilities to compensate for 'traditional' memory processes once those processes diminish. Results should be interpreted with caution, as we only report main effects of age on subsequent true and subsequent false memories, as we lacked the power to investigate any three-way interactions.

According to Koutstaal et al. (2003), "preexistent semantic or conceptual information detracts from the processing of non-conceptual, item-specific perceptual information" (p. 499). This semantic-perceptual interference hypothesis predicts that the rate of false memories in older adults should increase more when salient conceptual information is available than when it is not. The current encoding paradigm was design to promote such conceptual-based encoding—with encoding on a given trial promoting the semantic relatedness of items within the encoding category. Retrieval of such semantic associations may have lead to the increased production of related lures during encoding (Hancock, Hicks, Marsh, & Ritschel, 2003) and to subsequent FAs by older adults.

4. Conclusions

The current findings suggest that older adults experience deficits in engaging item-specific encoding processes, coupled with greater engagement of gist encoding—with the latter supporting both subsequent true and subsequent false recognition. Despite activating a similar network for true Dm, older adults showed reduced modulation of activity in left VLPFC and left posterior PHG/hippocampus compared to young adults. Under recruitment of left VLPFC was also accompanied by age-related increases in medial rostral PFC and right PFC activity. This latter PFC increase resulted in greater frontal bilaterality in older adults, a pattern (HAROLD) previously associated with cognitive tasks such as encoding and retrieval. Here we expand upon these previous studies, showing that HAROLD supports successful subsequent memory performance in aging as well as general task-related encoding processes. Age-related increases in rostral PFC are also interpreted as compensatory, with older adults internally generating associations with encoding items and these associations leading to successful memory performance. Age deficits in modulation of left PHG/hippocampus for true Dm together with increased age-related modulation in superior and middle temporal gyrus for both true Dm and false Dm suggests that older adults engage in decreased item-specific encoding, but increased gist encoding. While greater engagement of gist encoding by older adults may lend itself to compensate for decreases in item-specific encoding, it also increases the likelihood of making subsequent false alarms to related items.

This age-related shift from item-specific processing to a greater reliance on gist processing follows a similar model in the retrieval literature in regards to recollection and familiarity. While recollection is defined as recall of specific aspects of the encoding episode, familiarity reflects a general feeling of oldness in the absence of specific encoding details. Research investigating the behavioral and neural basis of recollection and familiarity in aging suggests that older adults have more difficulty with recollection-based retrieval and may rely more on familiarity when assessing 'oldness' (Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006b). Thus, one may predict that this shift from recollection to familiarity-based retrieval strategy in aging is due, at least in part, from a similar shift at encoding from item-specific processing to more general gist-based processing. The current results support such a theory.

References

Anderson, N. D., Iidaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. (2000). The effects of divided attention on encoding- and retrieval-related brain activity: A PET study of younger and older adults. *Journal of Cognitive Neuroscience*, *12*(5), 775–792.

Balota, D. A., Cortese, M. J., Duchek, J. M., Adams, D., Roediger, H. L., McDermott, K. B., et al. (1999). Veridical and false memories in healthy older adults and in dementia of the Alzheimer's Type. *Cognitive Neuropsychology*, *16*, 361–384.

Battig, W. F., & Montague, W. E. (1969). Category norms for verbal items in 56 categories: A replication and extension of the connecticut norms. *Journal of Experimental Psychology*, *80*, 1–46.

Blumenfeld, H. K., Booth, J. R., & Burman, D. D. (2006). Differential prefrontal-temporal neural correlates of semantic processing in children. *Brain and Language*, *99*(3), 226–235.

Brainerd, C. J., & Reyna, V. F. (1990). Gist is the gist: The fuzzy-trace theory and new intuitionism. *Developmental Review*, *10*, 3–47.

Brewer, J. B., Zhao, Z., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1998). Making memories: Brain activity that predicts how well visual experience will be remembered. *Science*, *281*(5380), 1185–1187.

Buchel, C., Wise, R. J., Mummery, C. J., Poline, J. B., & Friston, K. J. (1996). Nonlinear regression in parametric activation studies. *NeuroImage*, *4*(1), 60–66.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, *17*(1), 85–100.

Cabeza, R., Grady, C. L., Nyberg, L., McIntosh, A. R., Tulving, E., Kapur, S., et al. (1997). Age-related differences in neural activity during memory encoding and retrieval: A positron emission tomography study. *Journal of Neuroscience*, *17*(1), 391–400.

Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, *17*(3), 1394–1402.

Cabeza, R., Daselaar, S. M., Dolcos, F., Prince, S. E., Budde, M., & Nyberg, L. (2004). Task-independent and task-specific age effects on brain activity during working memory, visual attention and episodic retrieval. *Cerebral Cortex*, *14*(4), 364–375.

Chou, T. L., Booth, J. R., Burman, D. D., Bitan, T., Bigio, J. D., Lu, D., et al. (2006). Developmental changes in the neural correlates of semantic processing. *NeuroImage*, *29*(4), 1141–1149.

Christoff, K., Ream, J. M., Geddes, L. P., & Gabrieli, J. D. (2003). Evaluating self-generated information: Anterior prefrontal contributions to human cognition. *Behavioral Neuroscience*, *117*(6), 1161–1168.

Daselaar, S., Browndyke, J., & Cabeza, R. (2006). Functional neuroimaging of cognitive aging. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging and cognition*. Cambridge, MA: MIT Press.

Daselaar, S. M., Fleck, M. S., Dobbins, I. G., Madden, D. J., & Cabeza, R. (2006). Effects of Healthy Aging on Hippocampal and Rhinal Memory Functions: An Event-Related fMRI Study. Cerebral Cortex.

Davachi, L., & Wagner, A. D. (2002). Hippocampal contributions to episodic encoding: Insights from relational and item-based learning. *Journal of Neurophysiology*, *88*(2), 982–990.

Davachi, L., Maril, A., & Wagner, A. D. (2001). When keeping in mind supports later bringing to mind: Neural markers of phonological rehearsal predict subsequent remembering. *Journal of Cognitive Neuroscience*, *13*(8), 1059–1070.

Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *PNAS*, *100*(4), 2157–2162.

Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology*, *58*(1), 17–22.

Dennis, N. A., Daselaar, S., & Cabeza, R. (2006). Effects of aging on transient and sustained successful memory encoding activity. Neurobiology of Aging.

Fisher, R. A. (1950). *Statistical methods for research workers*. London: Oliver and Boyd.

Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2005). Involvement of rostral prefrontal cortex in selection between stimulus-oriented and stimulus-independent thought. *European Journal of Neuroscience*, *21*(5), 1423–1431.

Gilbert, S. J., Spengler, S., Simons, J. S., Frith, C. D., & Burgess, P. W. (2006). Differential functions of lateral and medial rostral prefrontal cortex (area 10) revealed by brain-behavior associations. Cerebral Cortex.

Gonsalves, B., Reber, P. J., Gitelman, D. R., Parrish, T. B., Mesulam, M. M., & Paller, K. A. (2004). Neural evidence that vivid imagining can lead to false remembering. *Psychology and Science*, *15*(10), 655–660.

Grady, C. L., McIntosh, A. R., Horwitz, B., Maisog, J. M., Ungerleider, L. G., Mentis, M. J., et al. (1995). Age-related reductions in human recognition memory due to impaired encoding. *Science*, *269*(5221), 218–221.

Gutchess, A. H., Welsh, R. C., Hedden, T., Bangert, A., Minear, M., Liu, L. L., et al. (2005). Aging and the neural correlates of successful picture encoding: Frontal activations compensate for decreased medial-temporal activity. *Journal of Cognitive Neuroscience*, *17*(1), 84–96.

Hancock, T. W., Hicks, J. L., Marsh, R. L., & Ritschel, L. (2003). Measuring the activation level of critical lures in the deese-roediger-mcdermott paradigm. *American Journal of Psychology*, *116*(1), 1–14.

Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002). Neural substrates of action event knowledge. *Journal of Cognitive Neuroscience*, *14*(5), 795–805.

Kensinger, E. A., & Schacter, D. (1999). When true memories suppress false memories: Effects of aging. *Cognitive Neuropsychology*, *16*, 399–415.

Kensinger, E. A., & Schacter, D. L. (2005). Emotional content and reality-monitoring ability: fMRI evidence for the influences of encoding processes. *Neuropsychologia*, *43*(10), 1429–1443.

Kim, H., & Cabeza, R. (2006). Differential contributions of prefrontal, medial temporal, and sensory-perceptual regions to true and false memory formation. Cerebral Cortex.

Koutstaal, W., & Schacter, D. L. (1997). Gist-based false recognition of pictures in older and younger adults. *Journal of Memory & Language*, *37*, 555–583.

Koutstaal, W., Reddy, C., Jackson, E. M., Prince, S., Cendan, D. L., & Schacter, D. L. (2003). False recognition of abstract versus common objects in older and younger adults: Testing the semantic categorization account. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*(4), 499–510.

LaVoie, D. J., & Faulkner, K. (2000). Age differences in false recognition using a forced choice paradigm. *Experimental Aging Research*, *26*(4), 367–381.

Lazar, N. A., Luna, B., Sweeney, J. A., & Eddy, W. F. (2002). Combining brains: A survey of methods for statistical pooling of information. *NeuroImage*, *16*(2), 538–550.

Light, L. L. (1991). Memory and aging: Four hypotheses in search of data. *Annual Review of Psychology*, *42*, 333–376.

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*(5), 827–840.

Martin, A. (2001). Functional neuroimaging of semantic memory. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging*. Cambrisge, MA: The MIT Press.

Morcom, A. M., Good, C. D., Frackowiak, R. S. J., & Rugg, M. D. (2003). Age effects on the neural correlates of successful memory encoding. *Brain*, *126*(1), 213–229.

Norman, K. A., & Schacter, D. L. (1997). False recognition in younger and older adults: Exploring the characteristics of illusory memories. *Memory and Cognition*, *25*(6), 838–848.

Otten, L. J., & Rugg, M. D. (2001). Task-dependency of the neural correlates of episodic encoding as measured by fMRI. *Cerebral Cortex*, *11*(12), 1150–1160.

Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences*, *6*(2), 93–102.

Park, D. C. (2000). The basic mechanisms accounting for age-related decline in cognitive function. In D. C. Park & N. Schwarz (Eds.), *Cognitive aging: A primer*. Philadelphia, PA: Taylor & Francis.

Prince, S. E., Daselaar, S. M., & Cabeza, R. (2005). Neural correlates of relational memory: Successful encoding and retrieval of semantic and perceptual associations. *Journal of Neuroscience*, *25*(5), 1203–1210.

Roediger, H. L., & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *21*, 8033–8814.

Rugg, M. D., Fletcher, P. C., Chua, P. M., & Dolan, R. J. (1999). The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *NeuroImage*, *10*(5), 520–529.

Schacter, D., Verfaellie, M., & Pradere, D. (1996). The neuropsychology of memory illusions: False recall and recognition in amensiac patients. *Journal of Memory & Language*, *35*, 319–334.

Simons, J. S., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Anterior prefrontal cortex and the recollection of contextual information. *Neuropsychologia*, *43*(12), 1774–1783.

Simons, J. S., Verfaellie, M., Hodges, J. R., Lee, A. C., Graham, K. S., Koutstaal, W., et al. (2005). Failing to get the gist: Reduced false recognition of semantic associates in semantic dementia. *Neuropsychology*, *19*(3), 353–361.

Spencer, W. D., & Raz, N. (1995). Differential effects of aging on memory for content and context: A meta-analysis. *Psychology and Aging*, *10*(4), 527–539.

Staresina, B. P., & Davachi, L. (2006). Differential encoding mechanisms for subsequent associative recognition and free recall. *Journal of Neuroscience*, *26*(36), 9162–9172.

Stebbins, G. T., Carrillo, M. C., Dorfman, J., Dirksen, C., Desmond, J. E., Turner, D. A., et al. (2002). Aging effects on memory encoding in the frontal lobes. *Psychology and Aging*, *17*(1), 44–55.

Tun, P. A., Wingfield, A., Rosen, M. J., & Blanchard, L. (1998). Response latencies for false memories: Gist-based processes in normal aging. *Psychology and Aging*, *13*(2), 230–241.

Tyler, L. K., Stamatakis, E. A., Dick, E., Bright, P., Fletcher, P., & Moss, H. (2003). Objects and their actions: Evidence for a neurally distributed semantic system. *NeuroImage*, *18*(2), 542–557.

Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., et al. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*(5380), 1188–1191.

Wise, R. J. S., & Price, C. J. (2006). Functional imaging of language. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging of cognition*. Cambridge, MA: MIT Press.

Yoon, C., Feinberg, F., Hu, P., Gutchess, A. H., Hedden, T., Chen, H. Y., et al. (2004). Category norms as a function of culture and age: Comparisons of item responses to 105 categories by american and chinese adults. *Psychology of Aging*, *19*(3), 379–393.