Age-related differences in the neural correlates mediating false recollection

Nancy A. Dennis*, Caitlin R. Bowman, Kristina M. Peterson

Department of Psychology, The Pennsylvania State University, University Park, PA, USA

ARTICLE INFO

ABSTRACT

The current study investigated the effects of aging on the neural basis underlying true and false recollection. Although older adults, compared with younger adults, exhibited equivalent rates of true recollection, age differences in true recollection showed a pattern of activity commonly found among previous memory studies (e.g., age-related decreases in occipital and increases in prefrontal cortices), suggesting reduced retrieval of perceptual details associated with encoding items and a greater reliance on top-down compensatory processing. With regard to false recollection, older adults exhibited significantly greater false recollection yet did not exhibit increased neural processing. They did exhibit decreased activity in prefrontal, parahippocampal gyrus, and occipitoparietal cortex, suggesting a reduced reliance on reconstruction processes mediating false recollection in young. An individual differences analysis in older adults found false recollection rates predicted activity in several regions. including bilateral middle/superior temporal gyrus. Taken together, these results indicate that increases in false recollection in aging may be mediated by reduced access to encoding-related details as well as reliance on semantic gist and familiarity-related neural activity.

© 2014 Elsevier Inc. All rights reserved.

1. Introduction

Age-related memory deficits are a prevailing cognitive reality for older adults. Research has found that, compared to young adults, older adults are both more apt to forget details from previous experiences as well as falsely remember erroneous details or memories of past events (Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Tun et al., 1998). Although the majority of neuroimaging research to date has focused on elucidating the neural correlates associated with age-related increases in forgetting, behavioral research has shown that age-related increases in false memories is equally disruptive to memory processing in aging (McCabe et al., 2009). Moreover, a wealth of recent work with regard to dual process theories of memory has shown that these age-related impairments in memory are not ubiquitous but are subject to both how memory is measured (e.g., recall vs. recognition; recollection vs. familiarity) (e.g., Bastin and Van der Linden, 2003; Craik and Mcdowd, 1987; Watson et al., 2004; Yonelinas, 2002) as well as person-to-person variability in behavior (Christensen et al., 1994, 1999; Lindenberger and Baltes, 1997; Nelson and Dannefer, 1992). The current study uses both a Remember/Know/New memory task and individual performance measures to investigate the neural basis of false recollection and interindividual variability associated with age-related increases in false memories.

With regard to dual process theories of memory, age-related memory deficits in retrieval have been linked to significant reductions in true recollection (Bastin and Van der Linden, 2003; Davidson and Glisky, 2002; Parkin and Walter, 1992), whereas familiarity processes appear to remain relatively intact (Bastin and Van der Linden, 2003; Naveh-Benjamin, 2000; Parkin and Walter, 1992). This behavioral dissociation has been found to correspond to a similar dissociation in neural functioning. Specifically, during memory retrieval, brain regions known to mediate recollection (i.e., the hippocampus, early visual cortex, and lateral parietal cortex) (Ally et al., 2008; Daselaar et al., 2006; Duarte et al., 2008; Duverne et al., 2008) show age-related deficits in activation, whereas those that mediate familiarity (i.e., rhinal cortex, occipitoparietal cortex) often show intact or enhanced functioning in aging (Daselaar et al., 2006; Dennis et al., 2008b; Duarte et al., 2010; Dulas and Duarte, 2012; Yonelinas et al., 2007). As such, it is posited that older adults rely to a larger extent on familiarity, as opposed to recollection, when making memory decisions.

The fuzzy trace theory of false memory encapsulates both recollection and familiarity processes in its definition of verbatim and gist traces and, in doing so, provides an appealing framework for understanding age differences in false memories. Specifically, fuzzy trace theory posits that 2 types of memory traces are created during encoding: verbatim traces and gist traces (Brainerd and

Reyna, 1990). Verbatim traces retain the distinctive features of an event, whereas gist traces retain the general meaning but lack perceptual details or information about specific instances of an encoding event. Thus, encapsulated in the theory are the concepts of recollection (memory for item-specific traces) and familiarity[1] (memory for gist traces). Although accurate memory retrieval can be based on retrieval of either memory trace, false memories typically occur when new items or events elicit retrieval of the gist trace and no verbatim trace is available (or strong enough) to oppose the familiarity elicited by retrieval of the gist trace. In the absence of a verbatim trace of the true event, the gist trace alone may form the basis of a false memory. This of course is especially problematic in aging, in which encoding and retrieval of item-specific information (i.e., verbatim traces) are impaired and gist or familiarity is left relatively intact. Consistent with the fuzzy trace theory, age-related increases in false memories are most pronounced when old and new information share common semantic, perceptual, and/or conceptual characteristics and, as such, share a common gist trace associated with one or more of these properties (Balota et al., 1999; Kensinger and Schacter, 1999; Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Schacter et al., 1997b; Tun et al., 1998). The notion that increased false memories in aging are supported by gist processing at encoding and a reliance on familiarity is consistent with a number of false memory studies (Balota et al., 1999; Benjamin, 2001; Dennis et al., 2007b, 2008b; Duarte et al., 2010; Koutstaal and Schacter, 1997; Koutstaal et al., 1999; Schacter et al., 1999; Tun et al., 1998).

However, not all false memories are reported to be associated with familiarity or gist. Some false memories are associated with high confidence and vivid details, evoking a sense of recollection associated with retrieval of the false memory. Such false memories have been noted to occur across a variety of conditions including when several targets share a similar meaning, such that gist memories for those targets are strong, in the presence of semantically related distracters, and when participants study pictures that converge on a common meaning and the distractor shares this common meaning (Brainerd et al., 2001). In a recent meta-analysis that focused on the separate contributions of recollection and familiarity to age-related memory differences, McCabe et al., 2009 found a medium-to-large effect size with regard to age-related deficits in true recollection ($d = -0.68$) and an equally large effect size associated with age-related increases in false recollection ($d = 0.61$). Although the effect size for age-related increases in false familiarity was also significant ($d = 0.36$), it was substantially smaller than that of false recollection. Hence, results indicate that aging affects both true and false recollection to a similar degree and that the impact of age on false recollection is greater than its impact on familiarity. Given this "recollection mirror effect" (McCabe et al., 2009) and abundant neural evidence showing that recollection and familiarity are mediated by distinct neural substrates that are differentially impaired in aging, this research underscores the need to examine the cognitive and neural basis of age-related increases in false recollection separate from that of false familiarity.

Atlhough examined in behavioral studies, no neuroimaging study has examined the neural correlates of false recollection separate from that of familiarity in older adults. Previous neuroimaging studies either did not use recollection and familiarity judgments at retrieval (Dennis et al., 2008b; Yassa et al., 2011) or had too few false recollection responses to analyze the data

(Duarte et al., 2010). Despite these limitations, the previous studies have concluded that age-related reductions in item specific processing in the hippocampus (Dennis et al., 2008b; Duarte et al., 2010; Yassa et al., 2011), combined with gist processing (Dennis et al., 2008b) and reduced differentiation between processing of targets and lures (Duarte et al., 2010; Yassa et al., 2011), contribute to false memories in older adults. However, given that the focus of these studies was not on recollection-related processing, it is difficult to extend these findings to the phenomenon of false recollection.

A recent study from our lab did examine the neural basis for false recollection separate from that of (false) familiarity (Dennis et al., 2012). Results showed that, in young adults, false recollection arose from erroneous reconstruction processes (Dennis et al., 2012). Specifically, both true and false recollection were found to be associated with a largely overlapping retrieval network including activity in bilateral anterior parahippocampal gyrus (PHG), fusiform gyrus, anterior cingulate cortex (ACC), and right superior parietal cortex. We concluded that this activation pattern was consistent with the theory that young adults use the retrieval of details extracted from encoding and engage in memory reconstruction to support both true and false memories. Furthermore, we concluded that although true recollection is based on reconstructing true details from the encoding episode, false recollection represents a faulty form of this reconstruction, also known as content borrowing, whereby recollection of true details are erroneously associated with related lures (Lampinen et al., 2005). This theory accounts not only for activation in recollection-related regions involved in evaluation and monitoring of difficult decisions (i.e., ACC) and confidence judgments (i.e., parietal cortex) but also for the presence of PHG and hippocampus activation (regions involved in the retrieval and reconstruction of episodic details) during false recollection.

However, given observed age deficits in recollection and general reliance on familiarity in aging, we question whether older adults rely on content borrowing and reconstruction during false recollection, especially given that they have difficulty using retrieval of details in support of true recollection. An alternative possibility is that older adults retrieve the gist trace they encoded during study and use this general detail to support recollection of related lures. For example, if studying a group of farm animals or a set of dogs, older adults might recall the semantic label or general gist of the items presented at encoding when viewing new, related items. If this gist trace is strong enough (and is unopposed by a verbatim trace), then it may be enough of an encoding "detail" to support false recollection. In accord with this idea, recent evidence has shown that, whereas an "old" item presented at retrieval serves as a retrieval cue for verbatim traces, a related lure serves as a cue for retrieval of the gist trace (Guerin et al., 2012). Although this gist is generally theorized to support familiarity-based retrieval, the fuzzy trace theory provides an explanation for how it may be used to support false recollection. Specifically, the theory posits that false recollection is based on a strong sense of familiarity, so much so that people misidentify the strong sense of familiarity for recollection (Brainerd et al., 2001). Thus, although participants may report a subjective experience of recollection, the foundation for this response may be based on familiarity elicited by the gist trace and not actual verbatim details.

In addition to considering the distinction between recollection and familiarity with regard to age-related increases in false memories, aging research also highlights the importance of considering person-to-person variability in both cognitive performance and neural activation. A wealth of behavioral research has found aging to be associated with significant increases in interindividual variability in cognitive performance (e.g., Christensen

---

[1] We do not imply that the fuzzy trace theory equates gist to familiarity but suggest that the 2 share similar theoretical constructs, and familiarity is more likely to contribute to gist than is recollection (Yonelinas, 2002).

et al., 1994; Hultsch et al., 2002; Lindenberger and Baltes, 1997; Morse, 1993; Nelson and Dannefer, 1992), with the greatest variability present in memory tasks (Christensen et al., 1994, 1999; Lindenberger and Baltes, 1997; Nelson and Dannefer, 1992). Important to neuroimaging research, cognitive variability in aging has been shown to mediate neural activity. For example, memory studies find different patterns of neural activation in older adults depending upon whether older adults are identified as "high" or "low" performers, with respect to memory performance (e.g., Cabeza et al., 2002; Daselaar et al., 2003b; Duarte et al., 2006; Fabiani et al., 1998; Rosen et al., 2002) and find cognitive performance to correlate with measures of compensatory neural activity in older adults (e.g., Davis et al., 2008; Gazzaley et al., 2005; Grady et al., 2005). Typically, this compensatory activity in high performers is found in the form of increased prefrontal cortex activity compared with low performers and younger adults. Thus, given age-related variability in memory performance and its implications for neural recruitment, the examination of individual differences in neural activity with respect to behavioral indices of true and false recollection may be critical to elucidating cognitive processes underlying age-related differences in memory performance. Specifically, to the extent that frontal cortex operates in a compensatory manner, we predict behavioral performance in older adults will be positively associated with increases in frontal activation. Additionally, to the extent that increased false recollection in aging relies on gist processing, we would expect increases in false recollection to be associated with increased neural recruitment of regions that mediate both gist and familiarity processing, including middle and superior temporal gyrus (Simons et al., 2005b; Wise and Price, 2006) and frontoparietal regions (Cansino et al., 2002; Yonelinas et al., 2005).

The current study sought to investigate the cognitive and neural processes underlying false recollection in aging as well as the effects of interindividual differences on neural activity in aging by using fMRI in conjunction with the Remember/Know/New paradigm. Whereas our previous results indicate that both true and false recollection rely on reconstruction processes in younger adults, we hypothesize that this will not be the case for older adults. Rather, in accord with the fuzzy trace theory, we predict that false recollection in aging will be supported by gist retrieval and a strong feeling of familiarity. Thus, we predict that common processes across true and false recollection in older adults will include those associated with general decision making (e.g., ACC) and gist processing (e.g., late visual cortex and lateral temporal cortices) and will not include reconstruction processing associated with the hippocampus. With regard to age differences in true recollection, we predict that older adults will exhibit age-related decreases in regions supporting true recollection and perceptual processing (e.g., medial temporal lobe [MTL], left prefrontal cortex [PFC], and early visual cortex) as well as compensatory activity in frontal cortices (e.g., Cabeza et al., 2004; Davis et al., 2008; Grady et al., 2002). We further predict that age-related increases in false recollection will be supported by familiarity and gist processing (e.g., lateral temporal cortex and occipitoparietal cortex). With regard to interindividual differences, we propose that compensatory-related PFC activity will be modulated by increased rates of true recollection, whereas gist-related activity will be modulated by behavioral indices of false recollection.

2. Methods

2.1. Participants

Twenty younger adults and 23 healthy older adults participated in the current study. Two younger participants were excluded from the analysis due to head motion >4 mm, 1 additional younger participant was also excluded for performing below chance, and 1 older adult was excluded for insufficient recollection responses, leaving data from 17 younger adults (11 women; mean age = 21.28 years; SD = 1.79) and 22 older adults [11 women; mean age = 74.18 years; SD = (5.20)] reported in all analyses. The younger adults were recruited from the Penn State University community and older adults from Centre County, Pennsylvania. All participants were right-handed, native English speakers and were screened for history of neurologic disorders and psychiatric illness, alcoholism, drug abuse, and learning disabilities. In addition, participants completed a battery of cognitive measures including the Mini-Mental State Exam (Folstein et al., 1975); subtests from the Wechsler Adult Intelligence Scale including Symbol Search, Digit Symbol Encoding, Symbol Copy, Digit Span, Arithmetic, Letter Number Sequence, and Vocabulary tasks (Wechsler, 1997); and the Beck Depression Inventory (Beck and Steer, 1993). Tests were conducted to screen for dementia and depression in the older cohort. All individuals performed well within the normal range for their age, verifying that they were cognitive healthy (see Table 1 for participant demographics). All participants provided written informed consent and received financial compensation for their participation. All experimental procedures were approved by Penn State University's Institutional Review Board for the ethical treatment of human participants.
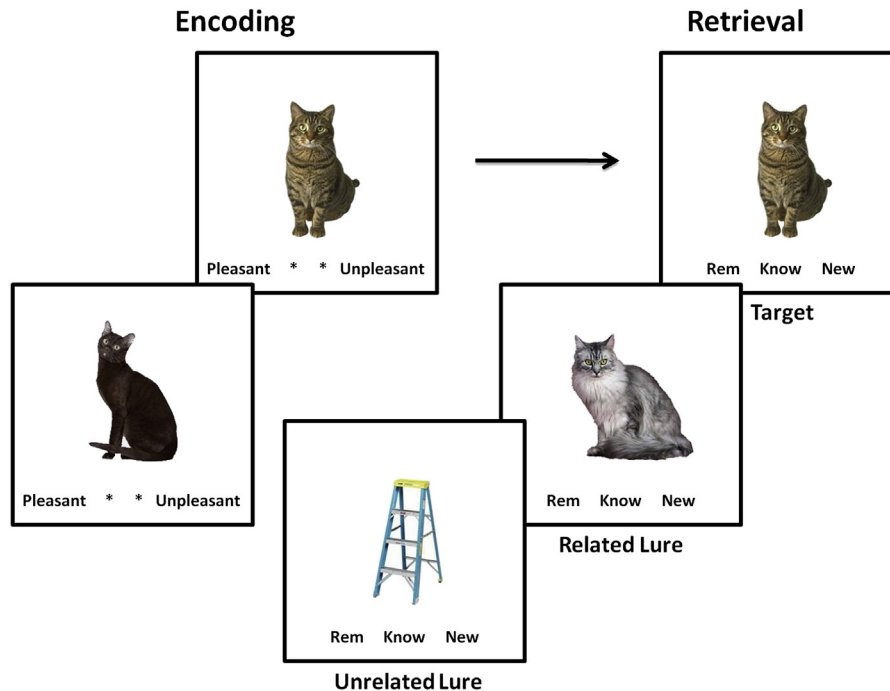
2.2. Stimuli

Stimuli consisted of 1092 color pictures of common objects. Images were obtained from an Internet image search. All backgrounds were removed, and pictures were cropped and resized to an approximate size of 480×480 pixels (Fig. 1). Images were presented focally and equated for resolution. Seven hundred twenty images were presented during encoding, including 90

Table 1
Demographics and behavioral results

	YA ($n = 17$)	OA ($n = 22$)
	M (SD)	M (SD)
Age[a]	21.28 (1.79)	74.18 (5.20)
Education (y)[a]	14.47 (1.37)	18.27 (2.71)
Cognitive assessment tasks		
MMSE	29.65 (0.61)	29.59 (0.80)
WAIS-III		
Symbol Search	13.71 (3.08)	14.24 (2.99)
Digit Symbol Encoding	12.00 (2.68)	13.41 (3.34)
Symbol Copy[a]	126.50 (13.02)	108.76 (19.24)
Digit Span	11.94 (3.05)	12.59 (2.74)
Arithmetic	11.53 (2.40)	12.76 (3.40)
Letter Number Sequencing[a]	11.12 (2.20)	12.65 (1.58)
Vocabulary	14.65 (3.02)	12.94 (2.46)
BDI	3.18 (2.74)	3.76 (3.56)
Memory task—retrieval rates		
Targets		
True recollection	0.47 (0.10)	0.49 (0.19)
True familiarity	0.31 (0.11)	0.36 (0.18)
Misses	0.19 (0.10)	0.12 (0.10)
Related lures		
False recollection[a]	0.19 (0.11)	0.34 (0.15)
False familiarity	0.30 (0.14)	0.40 (0.18)
Correct rejections	0.49 (0.12)	0.23 (0.14)
Unrelated lures		
False recollection[a]	0.04 (0.05)	0.09 (0.08)
False familiarity	0.04 (0.03)	0.20 (0.15)
Correct rejections[a]	0.90 (0.12)	0.70 (0.23)

Key: BDI, Beck Depression Inventory; M, mean; MMSE, MiniMental State Exam; OA, older adults; SD, standard deviation; YA, younger adults.
[a] Age differences: $p < 0.05$.

Encoding

Retrieval

Fig. 1. Stimuli presentation. During encoding, participants incidentally encoded 8 separate items from a given category (e.g., cats) and were asked to make pleasantness ratings for each item. At retrieval, participants were told to identify which items were presented at encoding using the Remember (Rem)/Know/New paradigm. Retrieval images included target items, related lures, and unrelated lures.

categories of stimuli with 8 exemplars per category. Six hundred and forty-two images were presented at retrieval including (1) 270 targets (3 of the 8 exemplars from each encoding category); (2) 270 related lures (3 novel images associated with each encoding category); and (3) 102 unrelated lures (including 3 novel images from each of 34 unrelated categories). More categorical items per category were presented at encoding than retrieval to build up sufficient gist for a given category and to produce sufficient rates of false recollection to examine neural activity for the trial type in isolation. Thus, the paradigm was consistent with criteria outlined by Brainerd et al. (2001) as typical of situations that produce high rates of phantom recollection. Items selected as targets were counterbalanced between participants.

2.3. Procedure

Encoding and retrieval both took place in the scanner with approximately 24 hours separating the 2 memory phases. (Only retrieval data are presented in the current analyses.) Images were displayed by COGENT in MATLAB (MathWorks) and projected onto a screen that participants viewed through a mirror attached to the head coil. Behavioral responses were recorded using a 4-button response box. Scanner noise was reduced with headphones and earplugs, and cushioning was used in the head coil to minimize head motion.

Encoding was incidental, and participants were instructed to make subjective pleasantness ratings of objects as they were presented. Encoding images were presented for 1 second, and participants were given 2 seconds to make their pleasantness rating, followed by a variable interstimulus interval. During half of the encoding runs, images from a given category were presented in a blocked design, and in the other half of the runs, categorical images from a given category were intermixed. The blocked-intermix

manipulation was presented every other run and counterbalanced between participants. There were no behavioral or neural differences between trial types of interest based on this manipulation; thus, analyses were collapsed with regard to this encoding variable.

During retrieval, participants completed 6 runs of approximately 8 minutes in length each. All stimulus categories were presented in an intermixed fashion. Each image was displayed for 2.5 seconds while participants made memory responses using the "Remember/Know/New" paradigm (see Fig. 1). In accord with typical task instructions, participants were told to respond "Remember" if they could recollect specific details about the object such as its shape, color, or their thoughts or feelings during its initial presentation. Participants were told to respond "Know" if the picture looked familiar, but they could not recollect any specific details of its previous presentation. They were told to respond "New" if they believed the picture was not presented during the encoding session. The images were pseudorandomly sorted, ensuring that no more than 3 images from any 1 category appeared in a row.

2.4. Image acquisition

Images were acquired using a Seimens 3T scanner equipped with a 12-channel head coil. A T1-weighted sagittal localizer was acquired to locate the anterior and posterior commissures. Images were then prescribed parallel to the anterior commissure-posterior commissure plane. An MPRAGE was acquired with a 2300-millisecond repetition time, 3.41-millisecond echo time, 230-mm field of view, 256^2 matrix, 160 axial slices, and 0.9-mm slice thickness for each participant. Echoplanar functional images were acquired using an interleaved acquisition, 2000-millisecond repetition time, 30-millisecond echo time, 240-mm field of view, a 64^2 matrix, 34 axial slices with 3.8 mm slice thickness resulting in 3.8 mm isotropic voxels.

2.5. Image processing

Functional data were preprocessed and analyzed with SPM8 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). Time-series data were corrected for differences in slice acquisition times and realigned. Images were checked for movement artifacts using a time series diagnostic function TSDiffAna (Freiburg Brain Imaging) in MATLAB (MathWorks). Functional images were spatially normalized to a standard stereotaxic space using the Montreal Neurological Institute templates implemented in SPM8. The coordinates were later converted to Talairach space (Talairach and Tournoux, 1988). Finally, the volumes were spatially smoothed using an 8-mm isotropic Gaussian kernel.

2.6. fMRI analyses

In accord with previous analysis of the young data in this study (Dennis et al., 2012), trial-related activity was modeled in the General Linear Model with a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function (hrf). To identify neural correlates associated with true recollection, activity associated with "Remember" responses to target items was compared with activity associated with "Know" responses to targets. A similar comparison was conducted for related lures to examine false recollection. Each regessor in the analysis contained a minimum of 15 trials, providing sufficient power for estimating the corresponding hrf function for each participant. These contrasts allowed us to control for identification of an item as "old" while simultaneously isolating recollection-related activity.

Statistical parametric maps were identified for each participant by applying linear contrasts to the beta weights for the events of interest. Regressors associated with recollection and familiarity of targets and related lures were used in defining contrasts of interest (see below). Regressors for unrelated lures and "no response" trials, as well as those for motion parameters were also included in the model and treated as regressors of no interest. All individual statistical parametric maps were subjected to a random effects analysis for group analysis.

To obtain results that were corrected for multiple comparisons we used Monte Carlo simulations (https://www2.bc.edu/~slotnics/scripts.htm) to define individual voxel and cluster extent thresholds (e.g., Forman et al., 1995; Garoff-Eaton et al., 2007; Slotnick and Schacter, 2004, 2006; Slotnick et al., 2003). Given our acquisition matrix of 64×64, 34 slices, 3.8-mm isotropic voxels, smoothness of 16.1 mm, and no reslicing of voxels, the Monte Carlo correction ($>$10,000 iterations) identified an individual voxel threshold of $p < 0.01$ and 18 resampled voxels (988 mm^3) as necessary to obtain results corrected for multiple comparisons at $p < 0.05$. In addition, we used the anatomic labeling atlas PickAtlas (Maldjian et al., 2003; Tzourio-Mazoyer et al., 2002) to restrict all analyses to cortical and subcortical regions.

To assess common recollection activity or similarities in neural processing between true and false recollection in older adults, a conjunction analysis was performed across both contrasts, using the implicit masking procedure in SPM8. Age differences analyses were conducted separately for both true and false recollection. For assessing age effects, we used a region-of-interest approach. As a first step, both true and false recollection was assessed within each age group at the aforementioned corrected threshold of $p < 0.05$. The results were then used as an inclusive mask for assessing age differences at $p < 0.05$ uncorrected. By employing a corrected threshold for the individual group data and using it as an inclusive mask for between group contrasts, we were able to focus our age difference analyses only within regions that were of primary significance to either the young or older adults. This procedure also ensures that age differences were driven by increases in activation in the primary group of interest (e.g., young adults in a young $>$ old comparison) rather than deactivations in the subsequent group (e.g., older adults). Additionally, we are able to conclude that regions identified with this analysis approach were both significantly activated in 1 group and, through a focal analysis on that region, that the region exhibited a significant group difference (see also Dennis et al., 2007a, 2007b, 2008b; Dew et al., 2012).

Finally, individual difference analyses were conducted to determine regions associated with variability in older adults' behavioral performance in true and false recollection. Using the multiple regression function at the group level, we regressed the contrast of false recollection $>$ false familiarity on false recollection rates to identify regions in which behavioral performance predicted the magnitude of activation for false recollection. A similar analysis was conducted for true recollection to identify regions in which behavioral performance predicted the magnitude of activation for true recollection.

3. Results

3.1. Behavioral

Table 1 reports means and standard deviations of recollection and familiarity rates for targets, related lures, and unrelated lures separated by age group.

To examine age differences in true and false recollection to related items, we conducted an age (young/old) × accuracy (true/false) analysis of variance (ANOVA) on related recollection rates. Results showed a significant main effect of accuracy [$F(1,37) = 136.21$, $p < 0.001$], a marginal effect of age [$F(1,37) = 3.94$, $p = 0.06$] , and a significant age × accuracy interaction [$F(1,37) = 14.56$, $p < 0.001$]. Thus, although older adults exhibited marginally higher recollection rates [0.42 (0.03)] compared with young adults [0.33 (0.03)] and both age groups showed significantly higher rates of true [0.48 (0.03)] compared with false [0.27 (0.02)] recollection, results showed that aging affected false recollection to a larger extent than true recollection. In fact, follow up t tests revealed only a significant age difference for related false recollection [$t(37) = 3.70$, $p < 0.01$], in which older adults exhibited a higher rate of false recollection [0.34 (0.15)] compared with young [0.19 (0.11)].

To examine age differences in false recollection, we conducted an age (young/old) × relatedness (related/unrelated) ANOVA on false recollection rates. Results showed a significant main effect of age [$F(1,37) = 15.22$, $p < 0.001$] and relatedness [$F(1,37) = 105.79$, $p < 0.001$], as well as a significant age × relatedness interaction [$F(1,37) = 6.37$, $p = 0.016$]. Thus, while older adults exhibited significantly higher false recollection rates [0.22 (0.02)] compared with young adults [0.11 (0.02)] and both age groups showed significantly higher rates of related [0.27 (0.02)] compared with unrelated [0.07 (0.01)] false recollection, results showed that aging affected false recollection to related lures to a larger extent than unrelated. Specifically, although follow up t tests exhibited significant age differences for related false recollection [$t(37) = 3.70$, $p < 0.01$] as well as unrelated false recollection [$t(37) = 2.57$, $p < 0.05$], the difference was numerically and proportionately greater for related [old: 0.34 (0.15); young: 0.19 (0.11) than unrelated [old: 0.09 (0.08); young 0.04 (0.05)] false recollection.

As suggested by an anonymous reviewer, we also tested whether false recollection rates were greater in the second half of testing than the first by conducting an age × block (1–4 vs. 5–8) ANOVA on false recollection rates. Results showed a significant effect of block [$F(1,37) = 24.4$, $p < 0.001$], yet inspection of the means revealed early blocks had higher false recollection rates

than later blocks (earlyM = 32.9, SD = 22.2; lateM = 21.3, SD = 19.2). No main effect of age and no interaction were found, suggesting that false recollection declined from the first half to the second half of testing similarly across age groups. Thus, results counter any concerns that false recollection rates in older adults were induced through testing manipulations such as the repetition of lures at retrieval or the number of targets preceding presentation of a lure (Dewhurst et al., 2011; Jennings and Jacoby, 1997).

3.2. Imaging

3.2.1. Common recollection in older adults

A conjunction analysis (in older adults) of true and false recollection exhibited common neural activity in the ACC., left postcentral gyrus, right fusiform gyrus, left inferior temporal gyrus, and left lingual gyrus (see Table 2). (For a similar analysis in young adults, please see Dennis et al., 2012).

3.2.2. Age related differences in true and false recollection

With regard to true recollection, younger compared with older adults exhibited increased activity in several regions including ventromedial PFC., orbitofrontal gyrus, right fusiform gyrus, bilateral superior occipital gyrus, and left occipital cortex. Older adults exhibited increased activity in dorsal ACC, bilateral superior frontal gyrus, bilateral cingulate gyrus, bilateral putamen, and posterior cingulate (see Table 3 for complete results).

With regard to false recollection, younger compared with older adults exhibited increased activity in a large network of brain regions including ventral ACC., bilateral inferior frontal gyrus, bilateral anterior PHG, right precuneus, and bilateral occipital parietal cortex (see Table 3 for complete results). No region showed increased activity for older compared with younger adults for false recollection.

3.2.3. Regression

In older adults rates of true recollection predicted increased neural activity in the right superior frontal gyrus, right inferior parietal, right insula, and left superior parietal cortex. Increased false recollection predicted increased activity in the right middle frontal gyrus, right insula, bilateral superior/middle temporal gyrus, precuneus, and right occipitoparietal cortex (see Table 4).

4. Discussion

The current study investigated the neural basis underlying age-related increases in false recollection. Although previous research has found a large degree of overlap in the neural correlates mediating true and false memory retrieval, including activation in the MTL (e.g., Cabeza et al., 2001; Dennis et al., 2012; Garoff-Eaton et al., 2006; Kahn et al., 2004; Schacter et al., 1997a, 1996; Stark et al., 2010), current results found that older adults exhibited

Table 2
Common recollection in older adults (true recollection ∩ false recollection)

| | BA | H | Coordinates[a] | | | t | mm³ |
			x	y	z		
ACC/medial frontal gyrus	32/10	L	−7	53	4	6.23	5762
Postcentral gyrus	3	L	−52	−14	52	4.03	1317
Inferior temporal gyrus	20	L	−59	−14	−22	4.19	1317
Fusiform gyrus	37	R	52	−50	−8	4.18	3292
Early visual cortex	18	L	−7	−86	−9	3.83	1975

Key: ACC, anterior cingulate cortex; BA, Brodmann's area; H, hemisphere; L, left; R, right.
[a] Coordinates from Talairach and Tournoux (1988).

Table 3
Age differences in true and false recollection

| | BA | H | Coordinates[a] (T&T) | | | t | mm³ |
			X	Y	Z		
True recollection, young > old							
Orbitofrontal cortex	10	M	−4	60	10	2.72	1536
Ventromedial PFC	11	M	0	33	−21	2.90	5816
Inferior temporal gyrus	20	L	−37	−11	−28	2.94	1591
Fusiform	19/37	R	37	−50	−8	2.46	1152
Superior/middle occipital gyrus	19	L	−30	−80	38	2.68	2689
	19	R	37	−81	34	2.96	3786
Occipital cortex	17/18/19	L	−15	−68	3	2.42	6639
True recollection, old > young							
Superior frontal gyrus	8	R	15	32	36	4.38	1372
	8/9	L	−19	43	39	2.26	1591
Cingulate gyrus	31	L	−11	7	37	3.05	1152
Cingulate gyrus/superior frontal gyrus	31/6	R	15	1	55	4.01	5103
Putamen	—	R	30	9	2	3.13	1701
	—	L	−26	−16	7	3.02	4335
Thalamus	—	L	−19	−23	14	3.82	4445
Posterior cingulate	23	M	−7	−37	25	2.29	1152
Cerebellum	—	M	7	−68	−10	2.75	6969
	—	L	−15	−47	−17	2.40	1043
False recollection, young > old							
Ventral ACC	24	M	0	42	1	2.56	1975
Inferior frontal gyrus	44/9	R	52	17	23	2.55	988
	8	L	−45	10	23	3.23	988
Precentral gyrus	4	R	37	−24	66	3.21	12346
Temporal pole	20/21	R	45	7	−29	3.57	2195
	38	L	−30	7	−36	3.33	2689
Parahippocampal gyrus	35/34	R	26	−25	−21	3.43	1646
	35	R	22	−32	−9	3.42	2195
	35/36	L	−26	−35	−8	3.3	1921
Retrosplenial cortex	30	R	22	−49	12	2.56	988
Precuneus	7	R	15	−53	71	2.6	1482
Occipitoparietal/occipital cortex	39/40/19	R	59	−56	23	3.49	5268
Occipitoparietal	19/7	L	−30	−70	34	2.68	1262
False recollection, old > young							
No significant areas of activation							

Key: ACC, anterior cingulate cortex; BA, Brodmann's area; H, hemisphere; L, left; PFC, prefrontal cortex; R, right.
[a] Coordinates from Talairach and Tournoux (1988).

overlap within a more limited network including only ACC., left inferior temporal gyrus, and a small number of sensory processing regions. Taken together, the results suggest that although true and false memories are mediated by similar cognitive operations in young adults, this may not be the case in older adults. Despite this disparity with previous results in younger adults, age differences

Table 4
Neural activity predicted by rate of true and false recollection in older adults

| | BA | H | Coordinates[a] | | | t | mm³ |
			X	Y	Z		
True recollection							
Superior frontal gyrus	10	R	26	56	3	3.48	1427
Inferior parietal	40	R	41	−30	22	4.97	1536
Insula	—	R	37	−12	21	4.33	988
Superior parietal cortex	39	L	−45	−73	34	3.98	2359
False recollection							
Superior frontal gyrus	10	R	30	52	−6	3.01	1427
Precentral gyrus	6	R	67	2	20	4.01	1372
Superior/Middle temporal gyrus	22/42	R	63	−24	4	3.40	1317
	22/42	L	−59	−31	8	4.24	3402
Insula	—	R	45	−9	17	5.24	5158
Precuneus	7	R	19	−80	45	3.38	1207
Occipitoparietal cortex	39	R	41	−52	23	3.72	1262

Key: L, left; R, right.
[a] Coordinates from Talairach and Tournoux (1988).

in true recollection exhibited a pattern typically observed in the literature (posterior-to-anterior shift in aging [PASA]; for a review see Dennis and Cabeza, 2008), with younger adults exhibiting increased activity in largely posterior brain regions, whereas older adults exhibited increased activity in mainly frontal cortices. With regard to false recollection, younger adults exhibited greater activity in a widespread network including ventral ACC., bilateral inferior frontal gyrus, PHG, and occipitoparietal cortex, whereas no region exhibited increased activity in older adults. Finally, exploring the role of individual differences in aging, regression analyses in older adults found true recollection rates predicted activity in frontal and parietal cortices, whereas false recollection rates predicted activity in bilateral middle/superior temporal gyrus, right superior frontal gyrus, and right occipitoparietal cortex. An interpretation of each finding follows.
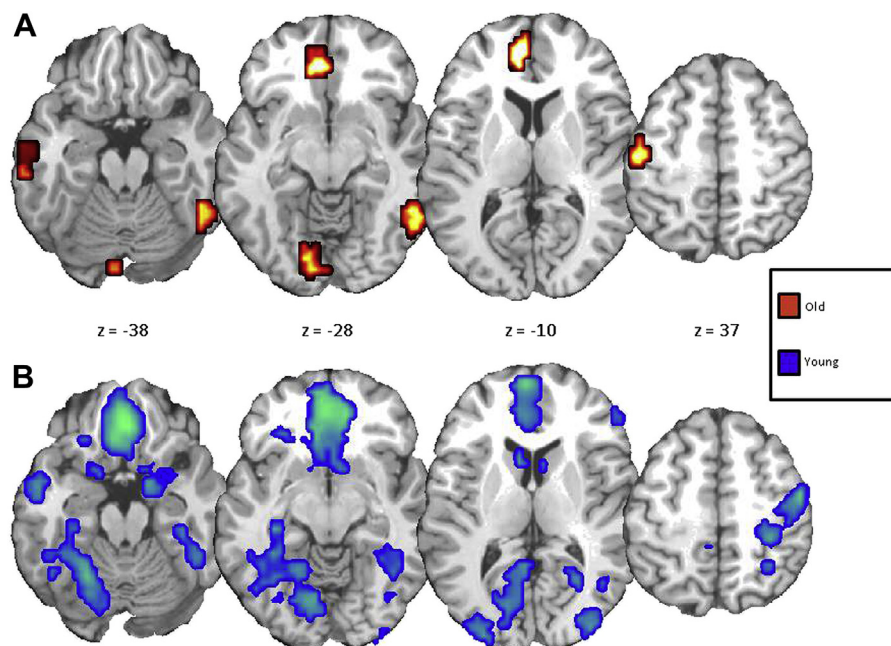
4.1. Common recollection activity in older adults

Consistent with previous literature examining true and false recognition (e.g., Cabeza et al., 2001; Dennis et al., 2012; Garoff-Eaton et al., 2006; Kahn et al., 2004; Schacter et al., 1996, 1997a; Stark et al., 2010), we identified several regions that exhibited common activation for both true and false recollection in older adults, including the ACC., postcentral gyrus, left inferior temporal gyrus, right fusiform gyrus, and early visual cortex. The general network resembles that exhibited by younger adults included in the current age comparisons analyses (Dennis et al., 2012), but the overall extent of this common activation is spatially reduced in the older adult cohort (see Fig. 2). In addition, unlike young adults, older adults did not exhibit any common recollection activity in the MTL. This is simply a qualitative observation (because a quantitative difference cannot be reached given the nature of the conjunction analysis within groups), but the results led us to conclude that although a single cognitive process (i.e., memory-related reconstruction) may underlie both true and false

recollection in young adults (Dennis et al., 2012), the data in older adults (in particular, the lack of common MTL activity) does not warrant a similar conclusion.

Also as predicted, older adults showed common recollection activity in the ACC and late visual cortex, specifically the right fusiform. Although we predicted the presence of ACC activity based on its role in making effortful decisions (e.g., Fleck et al., 2006; Yonelinas et al., 2005), it is also possible that this activity reflects monitoring processes (e.g., Abel et al., 2009) or competition/conflict processing (e.g., Botvinick et al., 2001). All processes are associated with the difficult decision of deciding whether a related item has been previously studied and negotiating retrieved details. With respect to common recollection activity in the right fusiform, this region is part of the late visual processing stream previously shown to exhibit common activity for true and false memories in young adults (Dennis et al., 2012; Garoff-Eaton et al., 2006; Slotnick and Schacter, 2004, 2006). In addition, the right fusiform has also been shown to be sensitive to object repetitions (Buckner et al., 2000), semantic representations of objects and object identity (Martin, 2001; Martin et al., 1996), and general semantic processing (Antonucci et al., 2008; Binder et al., 2009; Mummery et al., 2000). Common recollection-related activity in this region supports our hypothesis that older adults rely on semantic processing and gist acquired at encoding for support of both true and false recollection (e.g., Brainerd and Reyna, 2002; Dennis et al., 2008b; Gutchess and Schacter, 2012; Koutstaal et al., 1999; Tun et al., 1998).

One finding we did not predict was that of common recollection activity in early visual cortex. Previous research in young adults has found activity in this region to differentiate between true and false memories, showing activity only for true memories (whereas late visual cortex was shown to be equally active across both types of retrieval) (Dennis et al., 2012; Slotnick and Schacter, 2004; Stark et al., 2010). The sensory reactivation hypothesis posits that this differentiation reflects reactivation of sensory details

Fig. 2. Common activity for true and false recollection in older and younger adults. Areas common to true and false recollection in older adults (A) include the anterior cingulate, left postcentral gyrus, left inferior temporal cortex, right fusiform gyrus, and early visual cortex. See Table 2 for a complete list of regions and coordinates of peak activation. Common recollection activity in young adults (B) was found in the anterior cingulate, right superior parietal cortex, and bilateral parahippocampal gyrus. For a complete list of regions please see results reported in Dennis et al., 2012.
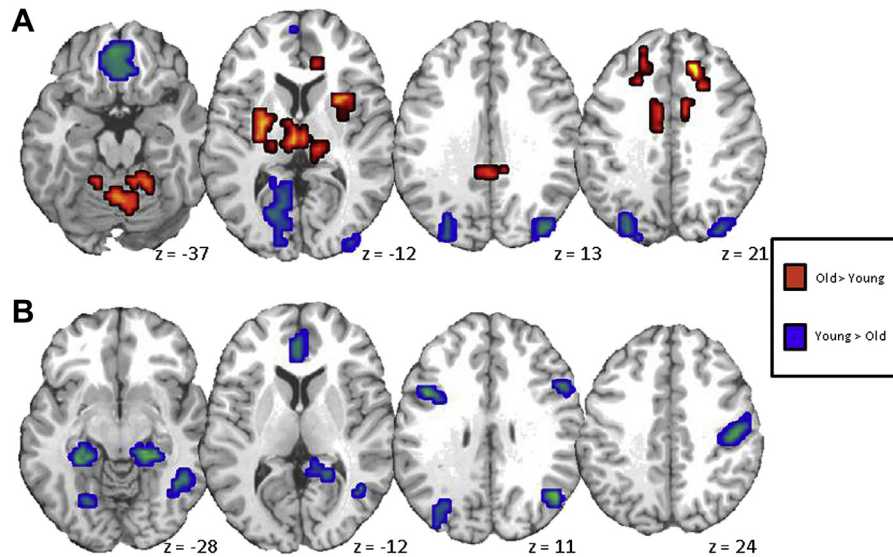
Fig. 3. Age-related differences in (A) true and (B) false recollection. Activity in blue represents regions in which young adults showed greater activity compared with older adults. Activity in red represents regions in which older adults showed greater activity compared to young adults. See Table 3 for complete list of regions and coordinates of peak activation.

associated with the encoding episode, details that are only available and retrieved for truly old items (Cabeza et al., 2001; Dennis et al., 2012; Garoff et al., 2005; for similar results in auditory cortex, see Schacter et al., 1996; Slotnick and Schacter, 2004; Wheeler and Buckner, 2003; Wheeler et al., 2000). We predicted reduced activity in visual cortex for older adults based on previous studies (for a review, see Dennis and Cabeza, 2008), but finding early visual activity associated with false recollection was unexpected. On the basis of previous literature, we offer 2 explanations. In accord with the sensory reactivation hypothesis, early visual cortex activity for false recollection may reflect the visualization and retrieval of sensory details from an encoded item that is evoked in association with the presentation of the perceptually similar related lure. Alternatively, this common activity may reflect dedifferentiation of the early visual cortex in older adults, indicative of age-related decline in the sensory processing systems (Baltes and Lindenberger, 1997; Cabeza et al., 2004; Grady et al., 1994; Lindenberger and Baltes, 1994; Norman and Schacter, 1997). Dedifferentiation in sensory processing domains has been well documented in aging (Carp et al., 2011a, 2011b; Chen et al., 2002; Park et al., 2004, 2012; Reuter-Lorenz et al., 2000; Voss et al., 2008), with studies showing that older adults show attenuation in the selectivity of cortical areas (e.g., fusiform gyrus and parahippocampal gyrus) dedicated to the processing of faces, places, and other object categories. Thus, it follows that the early visual processing regions that support automatic differentiation between old and new items in young adults could be another sensory processing region that is compromised in aging, with this dedifferentiation, in turn, leading to increased false memories to related lures. More research will be needed to differentiate between these proposed explanations.

4.2. Age differences in true and false recollection activity

With regard to age differences in true recollection, results were generally consistent with both our predictions and a large previous literature that finds age-related deficits in posterior processing regions combined with age-related increases in frontal cortices (i.e., the often-observed PASA; for a review of studies, see Dennis and Cabeza, 2008) (see Figure 3). Specifically, age-related deficits

in occipital cortices including left lingual gyrus (i.e., early visual cortex), right fusiform gyrus, and bilateral superior occipital gyrus support our prediction that older adults exhibit deficits in regions associated with retrieval of item-specific details (Anderson et al., 2000; Cabeza et al., 2004; Davis et al., 2008; Dennis et al.,
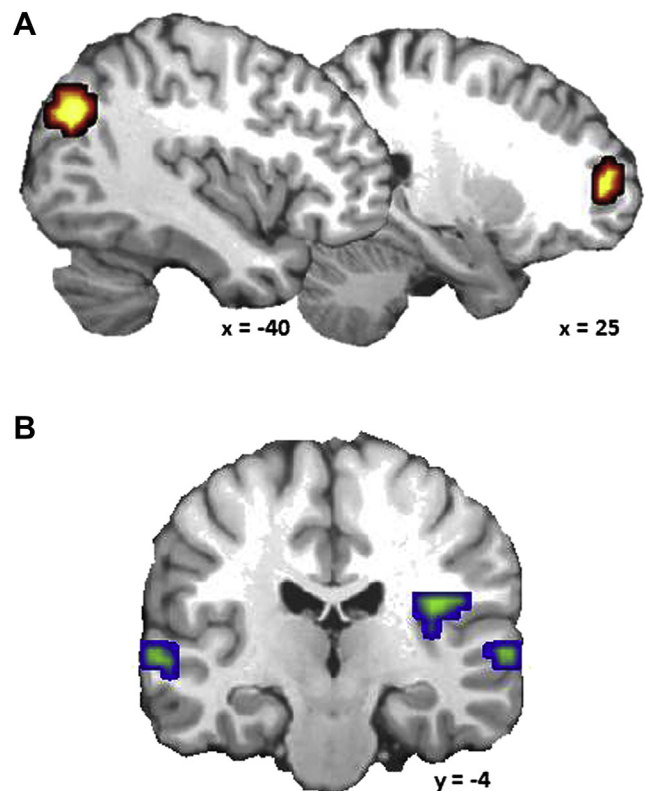
Fig. 4. Individual differences in true and false recollection within older adults. (A) Higher behavioral rates of true recollection in older adults predicted activity in regions including right superior frontal gyrus and left superior parietal cortex. (B) Higher behavioral rates of false recollection predicted activity in bilateral superior/middle temporal gyrus. See Table 4 for coordinates of peak activation.

2007a; Grady et al., 2002; Gutchess et al., 2005). Combined with the aforementioned finding that older adults exhibit common recollection-related activity in early visual cortex and right fusiform gyrus, the current finding supports the theory that older adults experience difficulty utilizing perceptual details during retrieval to support true memories (Koutstaal, 2003).

In conjunction with the foregoing age deficit in sensory processing regions, older adults showed an expected increase in prefrontal activity, including superior prefrontal cortex, and bilateral superior frontal gyrus, supporting true recollection. This PASA pattern has been proposed to reflect an age-related shift from bottom-up perceptual processing to top-down control and attentional guidance (Davis et al., 2008; Madden et al., 2007; Velanova et al., 2007). Given that the current retrieval task requires the need to closely evaluate and monitor memory with respect to retrieval of highly similar objects, the task is made more difficult in older adults when considering impaired perceptual processing. Thus, the need for recruitment of additional top-down attentional and monitoring processes is greater for old compared with young adults. Moreover, the current results add to a growing literature showing that older adults exhibit an increased reliance on such PFC-mediated processes during successful episodic retrieval, particularly in the face of reduced access to, and retrieval of, item-specific details.

Although not common to studies of episodic memory (but see Cabeza et al., 1997), the current study also observed age-related increases in bilateral putamen associated with true recollection. Striatal activity is typically associated with implicit learning (Daselaar et al., 2003a; Knowlton, 2002; Knowlton et al., 1996) and is often suppressed during explicit learning tasks (Poldrack et al., 2001; Poldrack and Packard, 2003; Sherry and Schacter, 1987), yet recent research has suggested that aging may attenuate this relationship. Specifically, research has found a lack of negative connectivity between the 2 learning systems in aging and has shown that the MTL mediates implicit learning in older adults (Dennis and Cabeza, 2011; Rieckmann et al., 2010). The current results support this dedifferentiation of learning systems, finding that older adults also recruit the implicit learning system during an explicit memory task and show a greater reliance on the striatum for true recollection compared to young adults. Alternatively, the observed increase in striatal activity may represent an age-related shift in processing strategy with respect to true recollection. Strategy shifts are not uncommon in aging research (Geary and Wiley, 1991; Touron and Hertzog, 2004); however, it is not clear what alternative processing older adults are utilizing. Future research and replication is necessary to obtain a better understanding of this result.

With regard to age differences in false recollection, results indicated that younger adults exhibited greater activity in several brain regions including ventral ACC., bilateral dorsolateral PFC., bilateral PHG, precuneus, and bilateral occipitoparietal cortices compared with older adults. As noted previously, in younger adults, we attributed activation across the foregoing network to that of reconstruction processes underlying false recollection (Dennis et al., 2012; Gutchess and Schacter, 2012). Age-related deficits in activity across this network point toward an alternative explanation of false recollection in older adults. As noted in the Introduction, we proposed that older adults would exhibit both a deficit in retrieval of true details as well as a greater reliance on gist processing leading to increased false memories. Although age-related deficits in item-specific processes were observed, no region exhibited an age-related increase in false recollection activation. Given the observed age-related increases in the rate of false recollection, this was an unexpected finding. We had predicted that increased reliance on gist would be associated with increased activity in the middle and superior temporal gyri,

regions associated with the processing of semantic information and gist associated with categorical themes (Dennis et al., 2008b, 2007b; Simons et al., 2005a; Wise and Price, 2006). On the basis of the neural differences observed in the age contrast regarding true recollection and the correspondence of these activation maps with that of previous literature (e.g., PASA; see Dennis and Cabeza, 2008, for a review), it is clear that there is sufficient power in the design and difference in the signal-to-noise ratio to detect reliable age differences. The true recollection results also underscore the validity of the current paradigm in showing that the cohort of older and younger adults tested in the current paradigm exhibit age differences in true memories that are consistent with previous research. Thus, the lack of age-related increased observed for false recollection may simply speak to the nature of the neural mechanism supporting false recollection in older compared with younger adults. Furthermore, although the lack of age differences in these regions does not negate the presence of gist processing in older adults, it does suggest that, overall, the reliance on gist processing in aging does not exceed that observed in younger adults (Duarte et al., 2010).

4.3. Individual differences in aging

Although the lack of age-related increases in neural activity associated with false recollection was unpredicted, it may not be surprising given increased variability associated with behavioral responses in aging (e.g., Christensen et al., 1994; Lindenberger and Baltes, 1997; Morse, 1993; Nelson and Dannefer, 1992). Moreover, recent evidence suggests that this behavioral variability is directly related to variability in neural substrates and is a key mediator in identifying task-related neural activity in older adults (e.g., Cabeza et al., 2002; Daselaar et al., 2003b; Duarte et al., 2006; Fabiani et al., 1998; Rosen et al., 2002). Thus, looking for group differences in average neural activity may not always prove to be the best strategy for determining the cause of age-related differences in cognitive performance. In order to overcome this limitation, the current study went beyond the typical analysis by using an individual differences approach when assessing the relationship between behavioral and neural activity in older adults, thereby taking into consideration age-related increases in between-subject variability in behavior when assessing task-related effects of neural activity.

With regard to true recollection, results indicate that individual differences in behavior in aging are associated with increased neural activity in right superior frontal gyrus and bilateral parietal cortex (see Figure 4). This activity is consistent with our predictions that older adults recruit top-down control to support memory processes in the absence of strong support from sensory regions (Davis et al., 2008; Grady et al., 1994). Additionally, the correlation between neural processing in both the prefrontal and superior parietal cortex and true recollection rates supports the theory that activity in these regions is recruited in a compensatory manner, leading to enhanced true recollection (Cabeza and Dennis, in press; Cabeza et al., 2002). However, the results of the regression analysis on false recollection tempers the assertion that increased top-down control is purely beneficial because higher rates of false recollection also predicted greater activity in a nearby (yet not overlapping) region of right middle frontal gyrus as well as right precuneus. Taken together, the present results suggest that superior prefrontal and parietal cortices are critical for recollection yet do not support true recollection specifically. Finally, it should be noted that the regions identified in the regression analysis did not spatially overlap with those identified in the age difference analyses. This suggests that although certain PFC and parietal regions show increased recruitment in aging to support general task

demands, those regions identified in the regression support more specific increments in behavior. As such, the results underscore the value of taking into account individual differences in aging.

Engagement of top-down control processes supporting recollection is a common finding with regard to true recollection in older adults (Daselaar et al., 2006; Duarte et al., 2008, 2010), but it is also supported by recent false recollection results in young adults. That is, when examining hippocampal connectivity associated with both true and false recollection, we recently showed that while true recollection was supported by greater hippocampal connectivity to ventral regions such as occipital cortex, anterior PHG, and orbitofrontal cortex, false recollection was supported by greater hippocampal connectivity with superior PFC and parietal cortices (i.e., regions associated with top-down control processes) (Dennis et al., 2012). Thus, the current results support a growing literature with regard to both age-related neural recruitment regarding true recollection and to false recollection as a controlled cognitive process.

In addition, the current results show that increased activity in left inferior temporal gyrus and bilateral superior and middle temporal gyri was predicted by higher rates of false recollection in older adults (see Figure 4). As mentioned previously, activity in inferior temporal gyrus is associated with semantic processing and the retrieval of semantic labels (i.e., object identity), whereas activity in superior and middle temporal gyrus is associated with semantic gist processing (Simons et al., 2005b; Wise and Price, 2006) and has been shown to support false memories in aging (Dennis et al., 2007b, 2008b; Duarte et al., 2010). Unlike previous studies, which found increased activity in this region for familiarity-based false memories and high-confidence false memories, the current results found this increase to be associated with increases in the rate of false recollection in older adults. Associating semantic gist processing with recollection seems counterintuitive, especially given previous research suggesting that gist most likely contributes to familiarity (and not recollection) processing (Yonelinas, 2002). As such, the current results suggest that one of the factors supporting increased rate of false recollection in aging is retrieval of the gist trace itself. That is, older adults' retrieval of the categorical label (e.g., cat, teddy bear) may be a retrieval detail that supports their false recollection decision. Results also fit within the context of the fuzzy trace theory, which theorizes that false (phantom) recollection is mediated by a strong sense of familiarity elicited by retrieval of the gist trace and the mis-identification of that familiarity/gist retrieval as recollection (Brainerd et al., 2001). The current results support this hypothesis, with stronger gist traces leading to increased rates of false recollection. As such, our results fit within a larger literature of false memory and aging suggesting that older adults' reliance on familiarity and gist traces form the basis of their age-related impairments in false memories (Brainerd and Reyna, 2002; Dennis et al., 2008a, 2008b; Koutstaal and Schacter, 1997; Tun et al., 1998).

The fact that the lateral temporal cortices did not exhibit a significant effect of aging yet did exhibit a significant correlation with false recollection scores is not surprising. As noted, the 2 analyses test fundamentally different hypotheses. Although we expected to find age-related increases in lateral temporal cortices associated with false memories, this hypothesis was based on the theory that high rates of false memories, as typically observed in aging, are based on gist processes. Older adults did show an overall increase in false recollection compared with young adults, but the regression analysis provided a stronger test for this original theory. We further investigated whether this relationship was specific to aging or if it supported false recollection in young adults as well. To do so, we performed two separate analyses. First, we conducted a similar false recollection regression analysis in young adults and

performed a conjunction between age groups. We also extracted the neural activity for each young adult from the peak voxels from the three lateral temporal regions (i.e., left inferior temporal gyrus and bilateral superior and middle temporal gyri) identified in the older adult regression and correlated the activity with false recollection rates. Although no region exhibited overlap in the conjunction, the young adults did exhibit a significant relationship between neural activity and false recollect rates in all three regions. Because it is not possible for us to directly compare this value with that of older adults (due to biased statistical reporting; Vul et al., 2009) we cannot comment on whether this relationship is greater in older compared with younger adults. However, evidence does suggest that activity in bilateral middle/superior temporal gyrus may support increasing rates of false recollection not only in aging but throughout the life span.

4.4. Limitations and future directions

As noted, we identified several findings that ran contrary to our predictions, such as the presence of early visual cortex activity associated with both true and false recollection and the lack of age-related increases in false recollection. Given that the current study is one of only a small number of studies investigating false memory and aging and the first to focus its analysis on false recollection, we recognize the need for more research both to replicate the current results and to provide a stronger basis for the interpretation of the unexpected findings. Specifically, with respect to the unexpected finding regarding the lack of age-related increases associated with false recollection, we feel that a replication is needed not only within the realm of perceptual false memory but across other false memory paradigms as well (e.g., Deese/Roediger-McDermott paradigm, semantic relatedness). Future research in this domain may also look to verify what retrieved details led to the false recollection in an attempt to further elucidate the cognitive process(es) mediating this behavior. With respect to the role of gist and strong familiarity in supporting false recollection, future research is also needed to examine exactly how this mechanism operates. We suggest that there is no single type of gist but that gist can be semantic or perceptual or even conceptual (Koutstaal et al., 2003; Schacter et al., 1997c; Slotnick and Schacter, 2004). Investigation of the distinction between each and the role of each in supporting false memories will also be essential in fully understanding the mechanisms mediating false recollection. With respect to the lack of counterbalancing between categories and images used for unrelated and related lures/targets, we note that future studies should include such a counterbalance to fully rule out the potential effects of stimulus differences within the age × relatedness interaction. Finally, we note that the current conclusions do not preclude the possibility of other mechanisms, such as perceptual gist or general familiarity processing also supporting false recollection in aging. Additional research using both similar and distinct paradigms will be able to fully elucidate the cognitive processes underlying this behavior.

Conclusions

The current study aimed to elucidate the cognitive and neural correlates mediating age-related increases in false recollection in older adults. An initial assessment of recollection-related neural activity common to both true and false recollection in older adults supported the theory that older adults experience dedifferentiation of early visual cortex during retrieval. This lack of distinguishing sensory signal in visual cortex may lead to increased false memories by reducing the distinction between old and new items. In addition, activity in left inferior temporal gyrus was

found to mediate both true and false recollection, indicating a reliance on retrieval of semantic processing for both accurate and erroneous recollection. Although no region exhibited increased activity in older adults associated with false recollection, an individual difference analysis found that increased rates of false recollection predicted activity in left inferior and bilateral middle/superior temporal gyri. Activity in lateral temporal cortex has previously been associated with semantic processing and shown to support false memories associated with high confidence recognition and familiarity (Dennis et al., 2008b; Duarte et al., 2010), but the fuzzy trace theory posits that high levels of gist and familiarity are sufficient to support false recollection because strong gist can be mistaken for recollection. The current study is the first to examine false recollection in older adults, finding that, like more general false recognition, this process may be mediated by gist processing.

Disclosure statement

There are no actual or potential conflicts of interest.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neurobiolaging.2013.08.019.

References

Abel, S., Dressel, K., Kummerer, D., Saur, D., Mader, I., Weiller, C., Huber, W., 2009. Correct and erroneous picture naming responses in healthy subjects. Neurosci. Lett. 463, 167–171.

Ally, B.A., Simons, J.S., McKeever, J.D., Peers, P.V., Budson, A.E., 2008. Parietal contributions to recollection: electrophysiological evidence from aging and patients with parietal lesions. Neuropsychologia 46, 1800–1812.

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. J. Cogn. Neurosci. 12, 775–792.

Antonucci, S.M., Beeson, P.M., Labiner, D.M., Rapcsak, S.Z., 2008. Lexical retrieval and semantic knowledge in patients with left inferior temporal lobe lesions. Aphasiology 22, 281–304.

Balota, D.A., Cortese, M.J., Duchek, J.M., Adams, D., Roediger, H.L., McDermott, K.B., Yerys, B.E., 1999. Veridical and false memories in healthy older adults and in dementia of the Alzheimer's Type. Cogn. Neuropsychol. 16, 361–384.

Baltes, P.B., Lindenberger, U., 1997. Emergence of a powerful connection between sensory and cognitive functions across the adult life span: a new window to the study of cognitive aging? Psychol. Aging 12, 12–21.

Bastin, C., Van der Linden, M., 2003. The contribution of recollection and familiarity to recognition memory: a study of the effects of test format and aging. Neuropsychology 17, 14–24.

Beck, A., Steer, R., 1993. Beck Depression Inventory. The Psychological Corporation, San Antonio, TX.

Benjamin, A.S., 2001. On the dual effects of repetition on false recognition. J. Exp. Psychol. Learn. Mem. Cogn. 27, 941–947.

Binder, J.R., Desai, R.H., Graves, W.W., Conant, L.L., 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. Cereb. Cortex 19, 2767–2796.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.

Brainerd, C.J., Reyna, V.F., 1990. Gist is the gist: the fuzzy-trace theory and new intuitionism. Dev. Rev. 10, 3–47.

Brainerd, C.J., Reyna, V.F., 2002. Fuzzy-trace theory and false memory. Curr. Direct. Psychol. Sci. 11, 164–169.

Brainerd, C.J., Wright, R., Reyna, V.F., Mojardin, A.H., 2001. Conjoint recognition and phantom recollection. J. Exp. Psychol. Learn. Mem. Cogn. 27, 307–327.

Buckner, R.L., Koutstaal, W., Schacter, D.L., Rosen, B.R., 2000. Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. Brain 123, 620–640.

Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R., 2002. Aging gracefully: compensatory brain activity in high-performing older adults. Neuroimage 17, 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. Cereb. Cortex 14, 364–375.

Cabeza, R., Dennis, N.A., 2012. Frontal lobes and aging: Deterioration and compensation. In Stuss, D.T., Knight, R.T. (Eds.). Principles of Frontal Lobe Function, 2nd Edition (pp. 628-652). New York: Oxford University Press.

Cabeza, R., Grady, C.L., Nyberg, L., McIntosh, A.R., Tulving, E., Kapur, S., Jennings, J.M., Houle, S., Craik, F.I., 1997. Age-related differences in neural activity during memory encoding and retrieval: a positron emission tomography study. J. Neurosci. 17, 391–400.

Cabeza, R., Rao, S.M., Wagner, A.D., Mayer, A.R., Schacter, D.L., 2001. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. Proc. Natl. Acad. Sci. U.S.A 98, 4805–4810.

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

Carp, J., Park, J., Hebrank, A., Park, D.C., Polk, T.A., 2011a. Age-related neural dedifferentiation in the motor system. PloS One 6, e29411.

Carp, J., Park, J., Polk, T.A., Park, D.C., 2011b. Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. Neuroimage 56, 736–743.

Chen, J., Myerson, J., Hale, S., 2002. Age-related dedifferentiation of visuospatial abilities. Neuropsychologia 40, 2050–2056.

Christensen, H., Mackinnon, A., Jorm, A.F., Henderson, A.S., Scott, L.R., Korten, A.E., 1994. Age differences and interindividual variation in cognition in community-dwelling elderly. Psychol. Aging 9, 381–390.

Christensen, H., Mackinnon, A.J., Korten, A.E., Jorm, A.F., Henderson, A.S., Jacomb, P., Rodgers, B., 1999. An analysis of diversity in the cognitive performance of elderly community dwellers: individual differences in change scores as a function of age. Psychol. Aging 14, 365–379.

Craik, F.I.M., McDowd, J.M., 1987. Age-differences in recall and recognition. J. Exp. Psychol. Learn. Mem. Cogn. 13, 474–479.

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. Cereb. Cortex 16, 1771–1782.

Daselaar, S.M., Rombouts, S.A., Veltman, D.J., Raaijmakers, J.G., Jonker, C., 2003a. Similar network activated by young and old adults during the acquisition of a motor sequence. Neurobiol. Aging 24, 1013–1019.

Daselaar, S.M., Veltman, D.J., Rombouts, S.A., Raaijmakers, J.G., Jonker, C., 2003b. Neuroanatomical correlates of episodic encoding and retrieval in young and elderly subjects. Brain 126, 43–56.

Davidson, P.S., Glisky, E.L., 2002. Neuropsychological correlates of recollection and familiarity in normal aging. Cogn. Affect. Behav. Neurosci. 2, 174–186.

Davis, S.W., Dennis, N.A., Daselaar, S.M., Fleck, M.S., Cabeza, R., 2008. Que PASA? The posterior-anterior shift in aging. Cereb. Cortex 18, 1201–1209.

Dennis, N.A., Bowman, C.R., Vandekar, S.N., 2012. True and phantom recollection: an fMRI investigation of similar and distinct neural correlates and connectivity. Neuroimage 59, 2982–2993.

Dennis, N.A., Cabeza, R., 2008. Neuroimaging of healthy cognitive aging. In: Salthouse, T.A., Craik, F.E.M. (Eds.), Handbook of Aging and Cognition, third ed. Psychological Press, New York, pp. 1–56.

Dennis, N.A., Cabeza, R., 2011. Age-related dedifferentiation of learning systems: an fMRI study of implicit and explicit learning. Neurobiol. Aging 32, 2318.e17–2318.e30.

Dennis, N.A., Daselaar, S., Cabeza, R., 2007a. Effects of aging on transient and sustained successful memory encoding activity. Neurobiol. Aging 28, 1749–1758.

Dennis, N.A., Hayes, S.M., Prince, S.E., Huettel, S.A., Madden, D.J., Cabeza, R., 2008a. Effects of aging on the neural correlates of successful item and source memory encoding. J. Exp. Psychol. Learn. Mem. Cogn. 34, 791–808.

Dennis, N.A., Kim, H., Cabeza, R., 2008b. Age-related differences in brain activity during true and false memory retrieval. J. Cogn. Neurosci. 20, 1390–1402.

Dennis, N.A., Kim, H.K., Cabeza, R., 2007b. Effects of aging on the neural correlates of true and false memory formation. Neuropsychologia 45, 3157–3166.

Dew, I.T., Buchler, N., Dobbins, I.G., Cabeza, R., 2012. Where is ELSA? The early to late shift in aging. Cereb. Cortex 22, 2542–2553.

Dewhurst, S.A., Knott, L.M., Howe, M.L., 2011. Test-induced priming impairs source monitoring accuracy in the DRM procedure. J. Exp. Psychol. Learn. Mem. Cogn. 37, 1001–1007.

Duarte, A., Graham, K.S., Henson, R.N., 2010. Age-related changes in neural activity associated with familiarity, recollection and false recognition. Neurobiol. 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. Cereb. Cortex 18, 2160–2169.

Duarte, A., Ranganath, C., Trujillo, C., Knight, R.T., 2006. Intact recollection memory in high-performing older adults: ERP and behavioral evidence. J. Cogn. Neurosci. 18, 33–47.

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

Duverne, S., Habibi, A., Rugg, M.D., 2008. Regional specificity of age effects on the neural correlates of episodic retrieval. Neurobiol. Aging 29, 1902–1906.

Fabiani, M., Friedman, D., Cheng, J.C., 1998. Individual differences in P3 scalp distribution in older adults, and their relationship to frontal lobe function. Psychophysiology 35, 698–708.

Fleck, M.S., Daselaar, S.M., Dobbins, I.G., Cabeza, R., 2006. Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. Cereb. Cortex 16, 1623–1630.

Folstein, M.F., Folstein, S.E., McHugh, P.R., 1975. "Mini-Mental State." A practical method for grading the cognitive state of patients for the clinician. J. Psychiatr. Res. 12, 189–198.

Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. Magn. Reson. Med. 33, 636–647.

Garoff-Eaton, R.J., Kensinger, E.A., Schacter, D.L., 2007. The neural correlates of conceptual and perceptual false recognition. Learn. Mem. 14, 684–692.

Garoff-Eaton, R.J., Slotnick, S.D., Schacter, D.L., 2006. Not all false memories are created equal: the neural basis of false recognition. Cereb. Cortex 16, 1645–1652.

Garoff, R.J., Slotnick, S.D., Schacter, D.L., 2005. The neural origins of specific and general memory: the role of the fusiform cortex. Neuropsychologia 43, 847–859.

Gazzaley, A., Cooney, J.W., Rissman, J., D'Esposito, M., 2005. Top-down suppression deficit underlies working memory impairment in normal aging. Nat. Neurosci. 8, 1298–1300.

Geary, D.C., Wiley, J.G., 1991. Cognitive addition—strategy choice and speed-of-processing differences in young and elderly adults. Psychol. Aging 6, 474–483.

Grady, C.L., Bernstein, L.J., Beig, S., Siegenthaler, A.L., 2002. The effects of encoding task on age-related differences in the functional neuroanatomy of face memory. Psychol. Aging 17, 7–23.

Grady, C.L., Maisog, J.M., Horwitz, B., Ungerleider, L.G., Mentis, M.J., Salerno, J.A., Pietrini, P., Wagner, E., Haxby, J.V., 1994. Age-related changes in cortical blood flow activation during visual processing of faces and location. J. Neurosci. 14, 1450–1462.

Grady, C.L., McIntosh, A.R., Craik, F.I., 2005. Task-related activity in prefrontal cortex and its relation to recognition memory performance in young and old adults. Neuropsychologia 43, 1466–1481.

Guerin, S.A., Robbins, C.A., Gilmore, A.W., Schacter, D.L., 2012. Retrieval failure contributes to gist-based false recognition. J. Mem. Lang. 66, 68–78.

Gutchess, A.H., Schacter, D.L., 2012. The neural correlates of gist-based true and false recognition. Neuroimage 59, 3418–3426.

Gutchess, A.H., Welsh, R.C., Hedden, T., Bangert, A., Minear, M., Liu, L.L., Park, D.C., 2005. Aging and the neural correlates of successful picture encoding: frontal activations compensate for decreased medial-temporal activity. J. Cogn. Neurosci. 17, 84–96.

Hultsch, D.F., MacDonald, S.W., Dixon, R.A., 2002. Variability in reaction time performance of younger and older adults. J. Gerontol. B. Psychol. Sci. Soc. Sci. 57, P101–P115.

Jennings, J.M., Jacoby, L.L., 1997. An opposition procedure for detecting age-related deficits in recollection: telling effects of repetition. Psychol. Aging 12, 352–361.

Kahn, I., Davachi, L., Wagner, A.D., 2004. Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. J. Neurosci. 24, 4172–4180.

Kensinger, E.A., Schacter, D., 1999. When true memories suppress false memories: effects of aging. Cogn. Neuropsychol. 16, 399–415.

Knowlton, B.J., 2002. The role of the basal ganglia in learning and memory. In: Squire, L.R., Schacter, D.L. (Eds.), Neuropsychology of Memory, third ed. Guilford Press, New York, pp. 143–153.

Knowlton, B.J., Mangels, J.A., Squire, L.R., 1996. A neostriatal habit learning system in humans. Science 273, 1399–1402.

Koutstaal, W., 2003. Older adults encode—but do not always use—perceptual details: intentional versus unintentional effects of detail on memory judgments. Psychol. Sci. 14, 189–193.

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. J. Exp. Psychol. Learn. Mem. Cogn. 29, 499–510.

Koutstaal, W., Schacter, D.L., 1997. Gist-based false recognition of pictures in older and younger adults. J. Mem. Lang. 37, 555–583.

Koutstaal, W., Schacter, D.L., Galluccio, L., Stofer, K.A., 1999. Reducing gist-based false recognition in older adults: encoding and retrieval manipulations. Psychol. Aging 14, 220–237.

Lampinen, J.M., Meier, C.R., Arnal, J.D., Leding, J.K., 2005. Compelling untruths: content borrowing and vivid false memories. J. Exp. Psychol. Learn. Mem. Cogn. 31, 954–963.

Lindenberger, U., Baltes, P.B., 1994. Sensory functioning and intelligence in old age: a strong connection. Psychol. Aging 9, 339–355.

Lindenberger, U., Baltes, P.B., 1997. Intellectual functioning in old and very old age: cross-sectional results from the Berlin Aging Study. Psychol. Aging 12, 410–432.

Madden, D.J., Spaniol, J., Whiting, W.L., Bucur, B., Provenzale, J.M., Cabeza, R., White, L.E., Huettel, S.A., 2007. Adult age differences in the functional neuroanatomy of visual attention: a combined fMRI and DTI study. Neurobiol. Aging 28, 459–476.

Maldjian, J.A., Laurienti, P.J., Burdette, J.B., Kraft, R.A., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19, 1233–1239.

Martin, A., 2001. Functional neuroimaging of semantic memory. In: Cabeza, R., Kingstone, A. (Eds.), Handbook of Functional Neuroimaging. MIT Press, Cambridge, MA, pp. 153–186.

Martin, A., Wiggs, C.L., Ungerleider, L.G., Haxby, J.V., 1996. Neural correlates of category-specific knowledge. Nature 379, 649–652.

McCabe, D.P., Roediger 3rd, H.L., McDaniel, M.A., Balota, D.A., 2009. Aging reduces veridical remembering but increases false remembering: neuropsychological test correlates of remember-know judgments. Neuropsychologia 47, 2164–2173.

Morse, C.K., 1993. Does variability increase with age? An archival study of cognitive measures. Psychol. Aging 8, 156–164.

Mummery, C.J., Patterson, K., Price, C.J., Ashburner, J., Frackowiak, R.S., Hodges, J.R., 2000. A voxel-based morphometry study of semantic dementia: relationship between temporal lobe atrophy and semantic memory. Ann. Neurol. 47, 36–45.

Naveh-Benjamin, M., 2000. Adult age differences in memory performance: tests of an associative deficit hypothesis. J. Exp. Psychol. Learn. Mem. Cogn. 26, 1170–1187.

Nelson, E.A., Dannefer, D., 1992. Aged heterogeneity: fact or fiction? The fate of diversity in gerontological research. Gerontologist 32, 17–23.

Norman, K.A., Schacter, D.L., 1997. False recognition in younger and older adults: exploring the characteristics of illusory memories. Mem. Cogn. 25, 838–848.

Park, D.C., Polk, T.A., Park, R., Minear, M., Savage, A., Smith, M.R., 2004. Aging reduces neural specialization in ventral visual cortex. Proc. Natl. Acad. Sci. U.S.A 101, 13091–13095.

Park, J., Carp, J., Kennedy, K.M., Rodrigue, K.M., Bischof, G.N., Huang, C.M., Rieck, J.R., Polk, T.A., Park, D.C., 2012. Neural broadening or neural attenuation? Investigating age-related dedifferentiation in the face network in a large lifespan sample. J. Neurosci. 32, 2154–2158.

Parkin, A.J., Walter, B.M., 1992. Recollective experience, normal aging, and frontal dysfunction. Psychol. Aging 7, 290–298.

Poldrack, R.A., Clark, J., Pare-Blagoev, E.J., Shohamy, D., Creso Moyano, J., Myers, C., Gluck, M.A., 2001. Interactive memory systems in the human brain. Nature 414, 546–550.

Poldrack, R.A., Packard, M.G., 2003. Competition among multiple memory systems: converging evidence from animal and human brain studies. Neuropsychologia 41, 245–251.

Reuter-Lorenz, P., Jonides, J., Smith, E.S., Hartley, A., Miller, A., Marshuetz, C., Koeppe, R.A., 2000. Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. J. Cogn. Neurosci. 12, 174–187.

Rieckmann, A., Fischer, H., Backman, L., 2010. Activation in striatum and medial temporal lobe during sequence learning in younger and older adults: relations to performance. Neuroimage 50, 1303–1312.

Rosen, A.C., Prull, M.W., O'Hara, R., Race, E.A., Desmond, J.E., Glover, G.H., Yesavage, J.A., Gabrieli, J.D., 2002. Variable effects of aging on frontal lobe contributions to memory. Neuroreport 13, 2425–2428.

Schacter, D.L., Buckner, R.L., Koutstaal, W., Dale, A.M., Rosen, B.R., 1997a. Late onset of anterior prefrontal activity during true and false recognition: an event-related fMRI study. Neuroimage 6, 259–269.

Schacter, D.L., Israel, L., Racine, C., 1999. Suppressing false recognition in younger and older adults: the distinctiveness heuristic. J. Mem. Lang. 40, 1–24.

Schacter, D.L., Koutstaal, W., Norman, K.A., 1997b. False memories and aging. Trend Cogn. Sci. 1, 229–236.

Schacter, D.L., Reiman, E., Curran, T., Yun, L.S., Bandy, D., McDermott, K.B., Roediger 3rd, H.L., 1996. Neuroanatomical correlates of veridical and illusory recognition memory: evidence from positron emission tomography. Neuron 17, 267–274.

Schacter, D.L., Verfaellie, M., Anes, M.D., 1997c. Illusory memories in amnesic patients: conceptual and perceptual false recognition. Neuropsychology 11, 331–342.

Sherry, D.F., Schacter, D.L., 1987. The evolution of multiple memory systems. Psychol. Rev. 94, 439–454.

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

Simons, J.S., Verfaellie, M., Hodges, J.R., Lee, A.C., Graham, K.S., Koutstaal, W., Schacter, D.L., Budson, A.E., 2005b. Failing to get the gist: reduced false recognition of semantic associates in semantic dementia. Neuropsychology 19, 353–361.

Slotnick, S.D., Moo, L.R., Segal, J.B., Hart Jr., J., 2003. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. Brain Res. Cogn. Brain Res. 17, 75–82.

Slotnick, S.D., Schacter, D.L., 2004. A sensory signature that distinguishes true from false memories. Nat. Neurosci. 7, 664–672.

Slotnick, S.D., Schacter, D.L., 2006. The nature of memory related activity in early visual areas. Neuropsychologia 44, 2874–2886.

Stark, C.E., Okado, Y., Loftus, E.F., 2010. Imaging the reconstruction of true and false memories using sensory reactivation and the misinformation paradigms. Learn. Mem. 17, 485—488.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, Stuttgart, Germany.

Touron, D.R., Hertzog, C., 2004. Distinguishing age differences in knowledge, strategy use, and confidence during strategic skill acquisition. Psychol. Aging 19, 452—466.

Tun, P.A., Wingfield, A., Rosen, M.J., Blanchard, L., 1998. Response latencies for false memories: gist-based processes in normal aging. Psychol. Aging 13, 230—241.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15, 273—289.

Velanova, K., Lustig, C., Jacoby, L.L., Buckner, R.L., 2007. Evidence for frontally mediated controlled processing differences in older adults. Cereb. Cortex 17, 1033—1046.

Voss, M.W., Erickson, K.I., Chaddock, L., Prakash, R.S., Colcombe, S.J., Morris, K.S., Doerksen, S., Hu, L., McAuley, E., Kramer, A.F., 2008. Dedifferentiation in the visual cortex: an fMRI investigation of individual differences in older adults. Brain Res. 1244, 121—131.

Vul, E., Harris, C., Winkielman, P., Pashler, H., 2009. Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. Persp. Psychol. Sci. 4, 274—290.

Watson, J.M., McDermott, K.B., Balota, D.A., 2004. Attempting to avoid false memories in the Deese/Roediger-McDermott paradigm: assessing the combined influence of practice and warnings in young and old adults. Mem. Cogn. 32, 135—141.

Wechsler, D., 1997. Wechsler Memory Scale, third ed. The Psychological Corporation, San Antonio, TX.

Wheeler, M.E., Buckner, R.L., 2003. Functional dissociation among components of remembering: control, perceived oldness, and content. J. Neurosci. 23, 3869—3880.

Wheeler, M.E., Petersen, S.E., Buckner, R.L., 2000. Memory's echo: vivid remembering reactivates sensory-specific cortex. Proc. Natl. Acad. Sci. U.S.A 97, 11125—11129.

Wise, R.J.S., Price, C.J., 2006. Functional imaging of language. In: Cabeza, R., Kingstone, A. (Eds.), Handbook of Functional Neuroimaging of Cognition, second ed. MIT Press, Cambridge, MA, pp. 191—228.

Yassa, M.A., Lacy, J.W., Stark, S.M., Albert, M.S., Gallagher, M., Stark, C.E., 2011. Pattern separation deficits associated with increased hippocampal CA3 and dentate gyrus activity in nondemented older adults. Hippocampus 21, 968—979.

Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. Mem. Lang. 46, 441—517.

Yonelinas, A.P., Otten, L.J., Shaw, K.N., Rugg, M.D., 2005. Separating the brain regions involved in recollection and familiarity in recognition memory. J. Neurosci. 25, 3002—3008.

Yonelinas, A.P., Widaman, K., Mungas, D., Reed, B., Weiner, M.W., Chui, H.C., 2007. Memory in the aging brain: doubly dissociating the contribution of the hippocampus and entorhinal cortex. Hippocampus 17, 1134—1140.