

Age-related changes in neural activity associated with familiarity, recollection and false recognition

Audrey Duarte^{*}, Kim S. Graham¹, Richard N. Henson

Medical Research Council - Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB27EF, UK

Received 1 May 2008; received in revised form 17 September 2008; accepted 25 September 2008

Available online 11 November 2008

Abstract

Older adults often exhibit elevated false recognition for events that never occurred, while simultaneously experiencing difficulty in recognizing events that actually occurred. It has been proposed that reduced recollection in conjunction with an over-reliance on familiarity may contribute to this pattern of results. This explanation is somewhat inconsistent, however, with recent evidence suggesting that familiarity and associated neural activity are reduced in healthy aging. Alternatively, given that illusory memory may be based, in part, on veridical memory processes (recollection/familiarity), one might predict that older adults exhibit enhanced false alarm rates because the neural signatures associated with true recognition (hits) and false recognition (false alarms) are less distinguishable in old than in young adults. Here, we used event-related fMRI to measure the effects of aging on neural activity associated with recollection, familiarity and familiarity-based false alarms for objects in young and older adults. Compared to young adults, older adults exhibited elevated false alarm rates and impaired behavioral indices of recollection and familiarity. Imaging data showed that older adults exhibited reduced recollection effects in the left parietoccipital cortex. Furthermore, while similar regions in frontal, parietal, lateral and inferior temporal cortices contributed to familiarity-based true and false recognition, reduced familiarity-related activity in frontal and inferior temporal regions in the older adults resulted in decreased differentiation between true and false recognition effects in this group. Our results suggest that reductions in neural activity associated with both recollection and familiarity for studied items may contribute to elevated false recognition in older adults, via reduced differentiation between the neural activity associated with true and false memory.

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Keywords: Aging; False memory; Recollection; Familiarity; fMRI

1. Introduction

It is well known that older adults exhibit difficulty remembering previously encountered events as well as young adults (Light, 1991). It is generally believed that this age-related memory loss is primarily restricted to *recollection* for specific contextual details about previously encountered events

while *familiarity*-based recognition, which lacks such details, is relatively preserved (see Spencer and Raz, 1995; Yonelinas, 2002, for reviews). Somewhat paradoxically, older adults are more likely than young adults to falsely recognize events that never occurred, particularly for events that share perceptual and/or conceptual characteristics of events actually experienced (e.g. Balota et al., 1999; Henkel et al., 1998; Norman and Schacter, 1997; Schacter et al., 1997).

Several mechanisms have been proposed to account for the elevated level of false recognition or “false alarms” in older adults. For example, some have suggested that an age-related deficit in recollection for studied events may lead to enhanced false alarms for new events (Balota et al., 1999; Johnson et al., 1993; Norman and Schacter, 1997). Impaired recollection may result in a relatively unopposed sense of familiarity elicited by new items and a subsequently increased level of

^{*} Corresponding author. Present address: School of Psychology, Georgia Institute of Technology, 654 Cherry Street, Atlanta, GA 30332-0170, United States. Tel.: +1 404 894 2349; fax: +1 404 894 8905.

E-mail addresses: audrey.duarte@psych.gatech.edu (A. Duarte), GrahamKS@cardiff.ac.uk (K.S. Graham), rik.henson@mrc-cbu.cam.ac.uk (R.N. Henson).

¹ Present address: Institute of Cognitive Neuroscience and School of Psychology, Cardiff University, Tower Building, Park Place, Cardiff CF10 3AT, UK.

false recognition. This hypothesis is consistent with the idea that recollection is disproportionately affected by aging, as noted above. Another, somewhat related, proposal is that false alarms in older adults reflect an over-reliance on the semantic relatedness or “gist” shared by studied and unstudied items (Balota et al., 1999; Dennis et al., 2008, 2007). Given that familiarity is more likely than recollection to contribute to gist (Yonelinas, 2002), by this account, one might predict that estimates of familiarity for studied items, in addition to unstudied items, would be elevated in older relative to younger adults, consistent with some previous evidence (Bastin and Van der Linden, 2003; Daselaar et al., 2006a,b; Dennis et al., 2008, 2007; Howard et al., 2006).

Some contradictory evidence suggests that neither of these mechanisms can fully account for the elevated levels of false memory in older adults. For example, some behavioral evidence suggests that false alarms can be based on recollection as well as familiarity. Specifically, studies using the “remember-know” procedure – in which participants are instructed to respond “remember” when they recollect details associated with previous events and “know” when the item seems familiar but no contextual details are recollected (Tulving, 1985) – have shown that false alarms can be associated with remember responses (Gallo and Roediger, 2003; Geraci and McCabe, 2006), and that older adults can exhibit enhanced levels of false remembering relative to the young (Jacoby et al., 2005; Norman and Schacter, 1997). Moreover, both young and old adults may misattribute recollected information (e.g. conceptual features) about experienced events to new events (Henkel et al., 1998; Lyle et al., 2006). Collectively, these studies suggest that false recognition may be supported, in part, by illusory recollection in both young and old adults.

Furthermore, other evidence suggests that familiarity, in addition to recollection, may be impaired in older adults. For example, several previous studies using remember-know (Duarte et al., 2006; Light et al., 2000 for review; Prull et al., 2006), “receiver operating characteristic” (ROC) (Healy et al., 2005; Prull et al., 2006) and “inclusion/exclusion” (Davidson and Glisky, 2002) methods, have shown that familiarity for studied information may be impaired in older adults. Despite these decreases in familiarity, false alarms were elevated in old relative to young adults. If an over-reliance on familiarity contributes to enhanced false recognition in older adults, one would predict that false alarm rates should have decreased, not increased, in these previous studies.

Neuroimaging may be useful in elucidating the factors that contribute to false memory in older adults. For example, numerous event-related potential (ERP) and functional magnetic resonance imaging (fMRI) studies have investigated neural activity associated with recognition judgments for studied and unstudied items in young adults (Cabeza et al., 2001; Curran et al., 2001; Dennis et al., 2008; Fabiani et al., 2000; Kahn et al., 2004; Kim and Cabeza, 2007; Okado and Stark, 2003; Slotnick and Schacter, 2004; Wheeler and

Buckner, 2003). Although these studies identified notable differences in both magnitude and location of activity associated with true and false recognition, one consistent finding across these studies was that the patterns of neural activity associated with these effects were highly similar. Specifically, ERPs have been shown to dissociate both hits and false alarms from correctly rejected new items at frontal and parietal electrode locations (Duzel et al., 1997; Nessler and Mecklinger, 2003). Furthermore, some fMRI evidence suggests that lateral frontal, lateral and medial parietal and medial temporal areas distinguish both hits and false alarms from correct rejections (Cabeza et al., 2001; Kim and Cabeza, 2007; Okado and Stark, 2003; Slotnick and Schacter, 2004; Wheeler and Buckner, 2003). This suggests that the same cognitive operations that facilitate successful memory retrieval may also support false recognition of new items. Although these regions have previously been differentially associated with recollection and familiarity processes (e.g. Davachi et al., 2003; Henson et al., 2005; Ranganath et al., 2004; Yonelinas et al., 2005), only one previous study directly investigated recollection-based recognition of both studied and unstudied items, revealing regional overlap (Kahn et al., 2004). Thus, it remains largely unclear whether the neural activity associated with both true recognition of studied items and false recognition of unstudied items is associated with recollection, familiarity or both processes.

These neuroimaging studies suggest that activity associated with false recognition is largely overlapping with activity associated with true recognition and typically observed either in a subset of the regions demonstrating true recognition activity or in the same regions but to a lesser degree (Gonsalves and Paller, 2000; Kahn et al., 2004; Kim and Cabeza, 2007; Wheeler and Buckner, 2003). Thus, although similar cognitive processes may contribute to true and false recognition, young adults’ brain activity may nonetheless distinguish between studied and falsely recognized new items in these overlapping regions, at least when false recognition rates are relatively low. One interesting possibility is that older adults exhibit enhanced false alarm rates because the neural signatures associated with true and false recognition are less distinguishable than they are in the young. Consistent with this hypothesis, one recent ERP study found that while young adults’ ERPs differentiated between hits and false alarms, older adults’ ERPs did not (Gutchess et al., 2007). Such a pattern of decreased distinguishability may occur either by a decrease in activity associated with true recognition and/or an increase in activity associated with false recognition. Two recent fMRI studies suggest that both mechanisms may occur in older adults (Dennis et al., 2008, 2007), although these studies did not directly investigate recollection and familiarity processes.

The current study was designed to address the above issues. We used event-related fMRI to investigate neural activity associated with recollection and familiarity-based recognition of studied and unstudied items in young and older adults. We hypothesized that:

- (1) Recollection would be impaired in the older adults and associated activity in the posterior parietal cortex reduced. This is based on previous behavioral studies and on our previous fMRI findings showing reduced recollection-related activity in this region in older adults with reduced recognition discriminability, due to elevated false alarms (Duarte et al., 2007).
- (2) Familiarity estimates and associated neural activity would be reduced in older adults. This is based on previous behavioral studies, described above, and on our previous ERP study that implemented a similar design and identified impaired behavioral estimates of familiarity and diminished ERPs over frontal and parietal scalp sites in older adults relative to the young (Duarte et al., 2006). Although it is difficult to determine the specific brain regions responsible for generating ERPs, patient lesion and fMRI studies suggest that lateral and medial frontal, posterior parietal and anterior medial temporal lobe (MTL) regions may support familiarity-based recognition (Davachi et al., 2003; Duarte et al., 2005; Henson et al., 2005, 1999a,b; Montaldi et al., 2006; Ranganath et al., 2004; Yonelinas et al., 2005).
- (3) Activity distinguishing familiarity-based false alarms from correctly rejected new items would be represented in similar regions as familiarity for studied items, when collapsing across age groups [Although it was of interest to investigate activity associated with recollection-based false recognition (i.e. illusory recollection), there were not enough trials to investigate this contrast]. Such a pattern would be consistent with theories proposing that false recognition may be supported by the same familiarity signal as true recognition (Yonelinas et al., 1996).
- (4) Finally, we hypothesized that the difference in activity related to true and false recognition would be reduced in older relative to young adults. If so, it was also of interest to determine if this reduced difference in older adults was due to reductions in activity associated with true recognition.

2. Methods

2.1. Participants

17 young adults between 18 and 30 years of age and 27 older adults between 60 and 70 years of age were recruited from local universities, science fairs and the Medical Research Council Cognition and Brain Sciences Unit volunteer panel. 4 young and 7 older adults could not be analyzed because of insufficient numbers of false alarms, resulting in 13 young and 20 older participants. In a previous full analysis of the recollection contrasts for these data, we found reductions in recollection estimates only for the older adults who had worse recognition discriminability (Pr scores than the young adults (“low” performers) (Duarte et al., 2007). Given our present interest in investigating false

Table 1
Group characteristics.

Measure	Young (<i>n</i> = 13)	Old (<i>n</i> = 13)
Age	23.8 (4.1)	62.7 (2.4)
Gender	8/13 female	8/13 female
Education	14.8 (1.5)	15.2 (1.8)
Rey complex figure delayed recall	–	–0.3 (0.89)
WCST (errors)	–	2.15 (0.37)
WMS-R digit span forward	–	1.66 (0.77)
WMS-R digit span backward	–	1.59 (1.0)
WMS-III logical memory immediate	–	1.0 (0.96)
WMS-III logical memory delayed	–	1.15 (0.85)
RMT face recognition	–	0.38 (0.84)
Warrington scene recognition	–	0.59 (1.43)

Note: Standard deviations in parentheses. All neuropsychological tests are reported as *z*-scores according to the age-adjusted published norms for these tests.

recognition in the context of changes in both recollection and familiarity, and the limited number of “high” performing older adults with sufficient false alarm rates (7), we restricted the present analyses to the “low performing” older adults.

Participants were paid for their time and signed consent forms approved by the Cambridge Local Research Ethics Committee. Participants were right-handed, fluent English speakers with normal or corrected-to-normal vision (using MRI-compatible glasses when necessary). None reported cognitive complaint, a history of psychiatric or neurological disorder (including depression and epilepsy), vascular disease (including diabetes) or psychoactive drug use. None of the participants were taking CNS-active medications or anti-hypertensive medications. All MRI scans were screened by a radiologist for abnormalities (excessive white matter lesions, stroke, hydrocephalus, etc.). Group characteristics are shown in Table 1. Groups did not differ for years of education or gender [*p* > 0.9].

2.2. Neuropsychological testing

In order to screen for cognitive deficits below the age-associated norms, all older participants were administered a battery of standardized neuropsychological tests in a separate testing session within 2 months of the MRI scanning session. The battery included tests of working and long-term memory, executive function, and visuospatial ability: Wechsler Memory Scale-Revised (WMS-R) Digit Span Forward and Backward (Wechsler, 1997), Warrington Recognition Memory Test (RMT) face recognition (Warrington, 1984), a topographical scene recognition memory test (Warrington and Whitley, 1978), the Logical Memory test (Wechsler, 1997), the Wisconsin Card Sorting Test (Lezak, 1995) and the Rey Complex Figure Test (Rey, 1941).

2.3. Procedure

Stimuli consisted of 384 grayscale line drawings of nameable concrete objects. Objects were taken from the International Picture Naming Project Database (<http://crl.ucsd.edu/>

~aszekely/ipnp/) and were chosen from the database if they had greater than 70% naming agreement. Objects subtended a maximum vertical and horizontal visual angle of up to 4.16° . A short practice version of the experiment was administered to participants outside of the scanner immediately prior to scanning. Both study and test periods were scanned, but only the data from the test periods are reported here. Participants responded using buttons on a box placed under their right hand.

There were 128 trials in each of 2 study/encoding sessions that were separated by a 5 min MPRAGE scan. This separation was to make the study sessions, or “sets”, more temporally distinct. Half of the objects were presented above a central fixation cross and half were presented below. Objects were presented for 1500 ms in one of 16 possible vertical positions along the midline, with 8 above and 8 below fixation, given that piloting showed this was effective in reducing spatial source accuracy performance from ceiling (and producing a close match to temporal source accuracy). In order to encourage incidental encoding of the spatial/temporal context, participants performed a semantic judgment task on each object, responding whether it would, or would not, fit inside a shoebox. Study trials were separated by a 1500 ms fixation screen.

Study was followed by 4 test/retrieval sessions of 64 studied objects (32 from each study set, half of which previously presented above fixation and half previously presented below) plus 32 unstudied items, presented in a pseudorandom order. For blocks of trials within each test session, participants were cued to either perform the spatial or temporal retrieval task. The spatial and temporal task blocks consisted of 24 trials each. Instructions for the test phase included a description of the appropriate use of the subjective “remember”, “know” and “new” response categories, modeled after previous studies (Gardiner and Java, 1991; Rajaram, 1993), though we replaced the term “know” for the term “familiar” to ease exposition. Objects were all centrally presented above a response cue stating these 3 choices for 3 s. After a 500 ms fixation screen, for 3 s, a new response cue appeared in place of the previous asking the participants to make objective source decisions. In the spatial blocks, participants decided where the object was presented on the screen during the study phase (“top” or “bottom”) and in the temporal blocks, which study set the object was presented in (“set 1” or “set 2”). A third response option of “don’t know” was offered when the relevant context could not be recollected. For all “new” judgments, participants were instructed to respond “don’t know” to the second response cue, in order to balance the number of responses across all conditions. A second 500 ms fixation screen was presented after the objective source decision and before the next trial. A full analysis of both subjective and objective measures of recollection are presented elsewhere (Duarte et al., 2007) and for the purposes of the present manuscript, we collapsed subjective (remember and familiar) decisions across their associated objective (spatial and temporal source) decisions. The Huynh-Feldt correction, reflected

in the *p*-values, was used in the behavioral analyses, where appropriate. Two-tailed *T*-tests were used for pairwise comparisons of the neuropsychological and behavioral data.

2.4. *fMRI acquisition*

Scanning was performed on a 3T Siemens TIM Trio system. Functional data were acquired using a gradient-echo pulse sequence (32 transverse slices oriented along the anterior–posterior commissural axis, repetition time 2 s, echo time 30 ms, $3\text{ mm} \times 3\text{ mm} \times 3.5\text{ mm}$ voxels, 0.8 mm interslice gap). Each encoding session ($n=2$) included 193 volumes and each retrieval session ($n=4$) included 356 volumes. The first 5 volumes per session were discarded to allow for equilibration effects. A high-resolution T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE) image was collected for anatomical localization.

2.5. *fMRI analysis*

Only data from the retrieval period were analyzed and included here. Data were analyzed using SPM2. Images were realigned and the resulting mean EPI image was used to estimate normalization parameters to the standard MNI EPI template, which were then applied to all EPI volumes. Normalized images were resliced to $3\text{ mm} \times 3\text{ mm} \times 3\text{ mm}$ and smoothed with an 8 mm full-width half-maximum isotropic Gaussian kernel. The data were high-pass filtered to a maximum of 1/128 Hz and grand mean scaled to 100.

Statistical analysis was performed in two stages. In the first stage, neural activity was modeled by a sequence of delta functions at onset of the various event types and convolved with a canonical hemodynamic response function. The time-courses were downsampled to the middle slice to form the covariates for the General Linear Model. Temporal autocorrelations within a session were corrected using an AR(1) model. For each participant and session, 6 covariates representing residual movement-related artifacts, determined by the spatial realignment step, were included in the first level model to capture residual (linear) movement artifacts.

Contrasts of the parameter estimates for each participant were submitted to the second stage of analysis (treating participants as a random-effect). A mixed ANOVA model was created for the retrieval period that allowed us to examine both within-group effects as well as condition-by-group interactions. The five conditions were contrasts of: (1) remember responses to studied items (collapsed across objective decisions), (2) familiar responses to studied items (collapsed across objective decisions), (3) new responses to studied items (i.e. “misses”), (4) familiar responses to unstudied items (i.e. “false alarms”), and (5) correct rejections of unstudied items. There were insufficient numbers of “remember” responses to unstudied items to examine them separately and so they were not included in the ANOVA. The between-group factor referred to Young and Old groups. A weighted

least squares estimation procedure was used to correct for inhomogeneity of covariance across within-group conditions and inhomogeneity of variance across groups.

The SPM for the main effect of condition was masked exclusively with the SPM for the group-by-condition interaction, using a liberal uncorrected threshold of $p < 0.05$ for the mask in order to restrict effects to those “common” (i.e. similar size) across groups [Note that a liberal threshold for an exclusive mask is more conservative in excluding regions from the masked SPM]. Inclusive masking was used, where appropriate, to identify regions of overlap between separate contrasts. All inclusive masks were applied using an uncorrected threshold of $p < 0.001$. All main effects of condition (across groups) and group-by-condition interaction SPMs were evaluated using one-tailed T-contrasts under an uncorrected alpha level of 0.001 and a minimum cluster size of 5 contiguous voxels, from which specific regions expected from prior research were identified. Simple effect SPMs (for within-group comparisons) were similarly evaluated under an uncorrected threshold of $p < 0.001$ and a minimum cluster size of 5. For regions of interest (ROI) from prior studies that had clear anatomical delineation, such as hippocampus and parahippocampal cortex, functional activations were examined using $p < 0.05$ corrected for voxels within bilateral masks from the automatic anatomical labeling (AAL) of the MNI brain, using small-volume correction (SVC).

Maxima of significant clusters were localized on individual normalized structural images. Neural activity from these maxima was plotted for recollection-based hits (R), familiarity-based hits (FH) and familiarity-based false alarms (FFA) against a baseline (0) of correct rejections (CR) (consistent with Duarte et al. (2007)). Using one event-type (CRs) as a baseline is necessary in designs like this in which the absence of explicit interstimulus intervals means that overall levels of activity across event-types are not estimated efficiently (so cannot, for example, be compared across groups) (Josephs and Henson, 1999). Neural activity reflected the parameter estimates for the convolved regressors and has arbitrary units.

3. Results

3.1. Neuropsychological test results

Group characteristics and standardized z -scores for neuropsychological tests, according to the published age-adjusted norms, are shown for the older groups in Table 1. As can be seen in the table, older adults were within (and numerically above) the age-adjusted norms for all tests, further supporting our assertion that the older adults were not obviously clinically impaired.

3.2. Behavioral results

The mean proportions of “remember” (R), “familiar” (F) and “new” responses made to studied and unstudied items (i.e. “new” to studied = miss (M) and “new” to unstudied = correct rejection (CR)) and corresponding reaction times (RTs) are shown for both groups in Table 2(A). Although the groups did not differ for proportions of R, F and M responses to studied items [$t < 1$], both R [$t(24) = 2.0$, $p = 0.05$] and F [$t(24) = 2.77$, $p = 0.01$] false alarm rates to unstudied items were greater and CR rates were lower [$t(24) = 4.42$, $p = 0.001$] in old than young adults.

In an attempt to accommodate this apparent bias, the accuracy of R and F judgments were estimated by the Pr measure of discriminability, i.e. subtracting the probability of false alarms (FAs) from the probability of hits. The corresponding estimates of subjective recollection, $p(R, \text{Hit}) - p(R, \text{FA})$, are shown for both groups in Fig. 1. In order to adjust for the potential underestimation of familiarity in the remember-know design, at least according to independence models of recollection and familiarity (Yonelinas and Jacoby, 1995), hit and false alarm probabilities for F judgments were estimated according to $pc(F, \text{Hit}) = p(F, \text{Hit}) / (1 - p(R, \text{Hit}))$ and $pc(F, \text{FA}) = p(F, \text{FA}) / (1 - p(R, \text{FA}))$, respectively. These corrected estimates of subjective familiarity are shown for both groups in Fig. 1. An ANOVA with factors of Measure (Recollection, Familiarity) and Group (Young, Old) revealed a

Table 2

(A) Proportions of remember, familiar and new judgments made to studied and new items at retrieval and corresponding RTs for each group. (B) Estimates calculated using values in part A.

Judgment	Young		Old	
(A)				
Studied items				
Remember (R)	0.53 (0.22)	1442 (282)	0.46 (0.26)	1788 (345)
Familiar (F)	0.34 (0.19)	1754 (300)	0.38 (0.23)	2003 (317)
New (M)	0.13 (0.07)	1632 (371)	0.16 (0.09)	2006 (319)
New items				
Remember	0.02 (0.02)	1541 (297)	0.07 (0.08)	1980 (392)
Familiar	0.14 (0.06)	1915 (312)	0.26 (0.14)	2144 (312)
New (CR)	0.84 (0.07)	1427 (252)	0.67 (0.11)	1777 (254)
(B)				
R bias (Br)	0.07 (0.07)		0.14 (0.15)	
F bias (Br)	0.18 (0.11)		0.30 (0.18)	

Note: standard deviations in parentheses. Abbreviations: CR = correct rejection, M = miss.

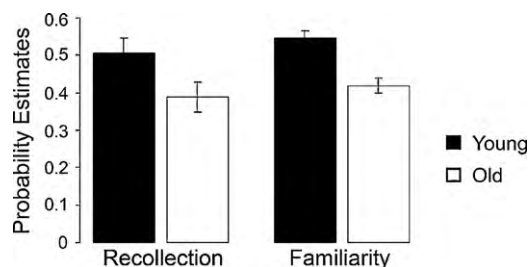


Fig. 1. Recollection and familiarity probability estimates for young and older adults.

significant main effect of Group [$F(1, 24) = 8.7, p = 0.007$] but no interaction, confirming that recollection and familiarity were similarly reduced in the old adults relative to the young [The same analysis using d prime scores from an equal variance signal detection model applied to the independence-corrected F Hit and F FA rates (Kishiyama and Yonelinas, 2003) revealed the same pattern of results].

Given the elevated false alarm rates in the older adults, we wanted to determine whether response biases were more liberal in older than in young adults. We calculated Br estimates of bias for both R and F responses for each group according to: $Br R = p(R, FA) / (1 - (p(R, Hit) - p(R, FA)))$ and $Br F = p(F, FA) / (1 - (p(F, Hit) - p(F, FA)))$ (Snodgrass and Corwin, 1988). These estimates are shown in Table 2(B). An ANOVA with factors of Bias (Br R, Br F) and Group (Young, Old) revealed a significant main effect of Group [$F(1, 24) = 12.8, p = 0.002$] but no interaction, confirming that the older adults exhibited a more liberal response bias than the young for both R and F judgments. Thus, a more liberal response bias may account for at least some of the elevated false alarm responses in the Old relative to the Young group [The same analysis using bias estimates for independence-corrected F hit and F FA rates revealed the same pattern of results].

For all subsequent analyses, we did not include R FAs nor misses (M) due to the low number of trials for both groups. An ANOVA employing factors of Response (R hits, F hits, F FA, CR) and Group (Young, Old) for the RTs shown in Table 2(A) yielded main effects of Response [$F(3, 72) = 23.3, p < 0.001$] and Group [$F(1, 24) = 10.7, p = 0.003$]. As shown in the table, the main effect of Group indicates that older participants were slower to respond to test items than young adults. Pairwise comparisons confirmed that RTs were longer for F FA than all other judgments [$t > 2.9, p < 0.012$], for F hits than R hits and CR judgments [$t > 3.5, p < 0.004$] with no significant differences between R and CR trials [$t < 1$] for both groups.

3.3. fMRI results

To identify regions associated with recollection, we examined the contrast between remember hits (R) and familiar hits (FH), while for familiarity, we used the contrast between familiar hits (FH) and correct rejections (CR). In order to

identify activity related to false recognition, we used the contrast between familiar false alarms (FFA) and correct rejections (CR) (as noted previously, there were insufficient numbers of RFAs to analyze them). In all cases, neural activity was examined that was (1) common to and (2) different between the groups, where common activity was defined using exclusive masking (see Section 2).

3.3.1. Effects common to groups

Recollection: Activity associated with recollection was identified in the right parietoccipital cortex, posterior, lateral and inferior to the parietal areas associated with familiarity (see below). As can be seen in Fig. 2(A), this region exhibited greater activity for R than FH items (in addition to greater activity for FFA than FH items; see below). In contrast, a few regions, such as the right middle temporal gyrus, exhibited greater activity for FH than R items, as shown in Table 3. These latter regions were not predicted, however, and will not be discussed further.

Familiarity: The contrast between FH and CR items revealed an extensive network of regions, in both age groups. As shown in Table 3 and Fig. 2(B), some of these regions, such as the superior medial parietal cortex (extending laterally) and middle frontal gyri, exhibited greater activity for FH items, whereas others, such as the superior temporal gyri (extending into the middle temporal gyri) and extrastriate cortices, showed greater activity for CR items (corresponding to the zero level in the plots). Additionally, ROI analyses (see Section 2) revealed similar patterns of “deactivation” for FH relative to CR items in the parahippocampi, including the rhinal cortex (see Fig. 2(B)), and anterior hippocampi, as can be seen in Table 3.

False recognition: Numerous regions demonstrated significant differences in activity between FFA and CR trials. As shown in Table 3 and Fig. 2(C), some regions, including the superior parietal cortex, dorsomedial prefrontal cortex (PFC) and middle frontal gyri, exhibited greater activity for FFA items. Other regions, such as the superior temporal and fusiform gyri, demonstrated greater activity for CR items (corresponding to the zero level in the plots).

The superior parietal region, including the precuneus shown in Fig. 2(C), extended laterally to the extent that it overlapped with the right parietoccipital region implicated in the recollection contrast. This was confirmed by inclusive masking of the FFA > CR contrast with the R > FH contrast, which revealed a region in right parietoccipital cortex that demonstrated activity associated with both recollection for studied items and false recognition of unstudied items relative to correct rejection of unstudied items (see Figs. 2(A) and (C)).

Similarly, the medial parietal, middle frontal and lateral temporal regions were similar in location to those implicated in the familiarity contrasts (see Fig. 3), consistent with our third prediction in Section 1. Inclusive masking of the FFA > CR contrast with the FH > CR contrast and of the CR > FFA contrast with the CR > FH contrast, separately,

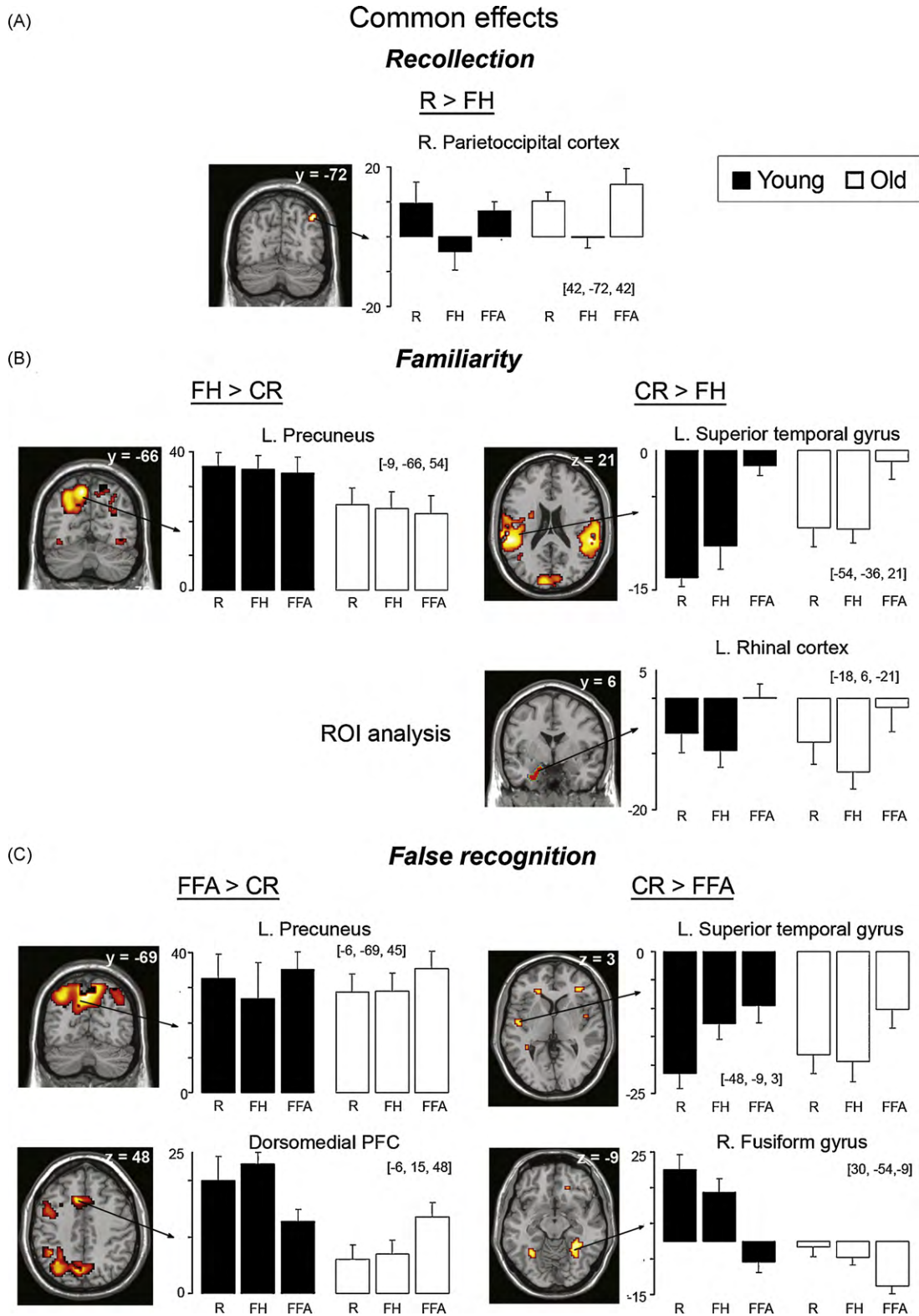


Fig. 2. Memory effects exhibiting common activity across groups, shown in selected regions, displayed on the MNI reference brain. Plots show parameter estimates for the event-related response at the peak maxima of the selected regions for each of the trial types versus correct rejection (CR) trials for each group (units arbitrary). Error bars depict standard error of the mean across participants, for each group. Remember Hits (R), Familiar Hits (FH) and Familiar False Alarms (FFA) [$p < 0.001$, uncorrected, with a 5 voxel extent; exclusively masked by group interactions at $p < 0.05$].

Table 3

Regions showing significant common effects for familiarity, recollection and false recognition across young and older age groups.

Contrast	Region	L/R	MNI coordinates (x, y, z)	BA	T score	Cluster size
Recollection (R > FH)	Parietoccipital cortex (angular/middle occipital gyri)	R	42, -72, 42	19/7/39	4.08	13
Recollection (FH > R)	Middle temporal gyrus	R	69, -36, 6	22	4.03	39
	Lingual gyrus	R	15, -90, -3	18	3.75	20
	Insula	R	33, 12, 12	48	3.68	11
	Posterior inferior frontal gyrus	L	-51, 12, 12	44	3.62	7
		L	-51, -6, 12	44	3.59	8
Familiarity (FH > CR)	Precuneus	L	-9, -66, 54	7	7.52	734
	<i>Inferior parietal lobule</i>	L	-30, -51, 45	40	7.40	
	Angular gyrus	R	30, -54, 48	7	5.80	413
	Middle frontal gyrus	L	-42, 6, 39	6/44	5.11	23
		L	-6, 3, 51	6	5.18	12
		R	27, 0, 51	6	4.99	30
	Inferior frontal gyrus	L	-42, 30, 18	45	3.57	8
	Inferior frontal gyrus	L	-45, 21, 24	48	4.06	12
	Middle occipital gyrus	L	-36, -84, -3	19	4.74	71
	Inferior occipital gyrus	L	-39, -63, -9	37	3.96	24
	Precentral gyrus	L	-30, -6, 54	6	4.95	67
Familiarity (CR > FH)	Superior temporal gyrus	R	57, -36, 21	42/22	7.70	2043
		L	-54, -36, 21	42/22	6.64	2292
	Cuneus	B	-6, -87, 33	18/19	6.78	1116
	Middle cingulate gyrus	B	-15, -30, 45		5.67	405
		L	-6, 3, 39	45	4.83	92
	Anterior cingulate gyrus	R	9, 51, 9	32	4.29	12
	Superior medial frontal (polar) cortex	R	9, 39, 54	8	5.31	163
		R	12, 57, 30	9	4.63	
	Middle frontal gyrus	R	54, -6, 54	6	5.54	50
	Inferior orbital frontal gyrus	R	48, 42, -9	47	5.00	46
		R	21, 12, -21	11	4.73	16
	Paracentral lobule	L	-9, -15, 78	6	5.49	31
	Fusiform gyrus	R	-30, -21, -24	20	4.96	14
	Cerebellum	R	3, -48, -6		4.46	10
	Precentral gyrus	R	27, -18, 75	6	4.06	5
ROI analyses	Parahippocampal gyrus	L	-30, -21, -24	20	4.96	179
	<i>Rhinal cortex</i>	L	-18, 6, -21	28	3.91	
	Parahippocampal gyrus	R	30, -18, -24	20	4.05	157
	Anterior hippocampus	L	-33, -12, -12	20	5.11	215
		R	30, -12, -12	20	5.18	239
False recognition (F FA > CR)	Precuneus	B	0, -69, 48	7	9.37	2032
	<i>Inferior parietal lobule</i>	L	-35, -45, 45	40	8.70	
	Middle frontal gyrus	L	-48, 9, 39	6/44	7.41	2481
	<i>Dorsomedial PFC</i>	B	-9, 9, 60	6	7.34	
	Middle frontal gyrus	L	-33, 51, 24	46	3.74	37
	Middle cingulate gyrus	L	-3, -24, 33	23	4.57	87
	<i>Putamen</i>	L	-15, 9, 3		4.20	37
	Thalamus	L	-12, -21, 9		3.95	23
	Cerebellum	L	-3, -45, -18		3.65	5
		R	33, -60, -33		3.54	6
	Middle temporal gyrus	L	-60, -42, -6	21	3.34	6
False recognition (CR > F FA)	Superior temporal gyrus	R	45, -6, 12	48	4.29	40
		L	-48, -9, 3	48	3.95	31
		L	-51, -30, 9	22	3.70	21
	Fusiform gyrus	R	30, -54, -9	37	4.49	110
		L	-30, -54, -9	37	4.39	51
	Inferior orbital frontal gyrus	L	-18, 36, -3	47/11	4.50	61
	Inferior frontal gyrus	R	36, 36, 6	47	4.09	30
	<i>Inferior orbital frontal gyrus</i>	R	27, 39, -6	11	3.57	

L = left; R = right; B = bilateral. BA = Brodmann's area. R = studied items judged "remember"; FH = studied items judged "familiar" (familiar hits); CR = correctly rejected new items; and F FA = familiar false alarms to unstudied items. Italicized values represent subpeaks of significant clusters.

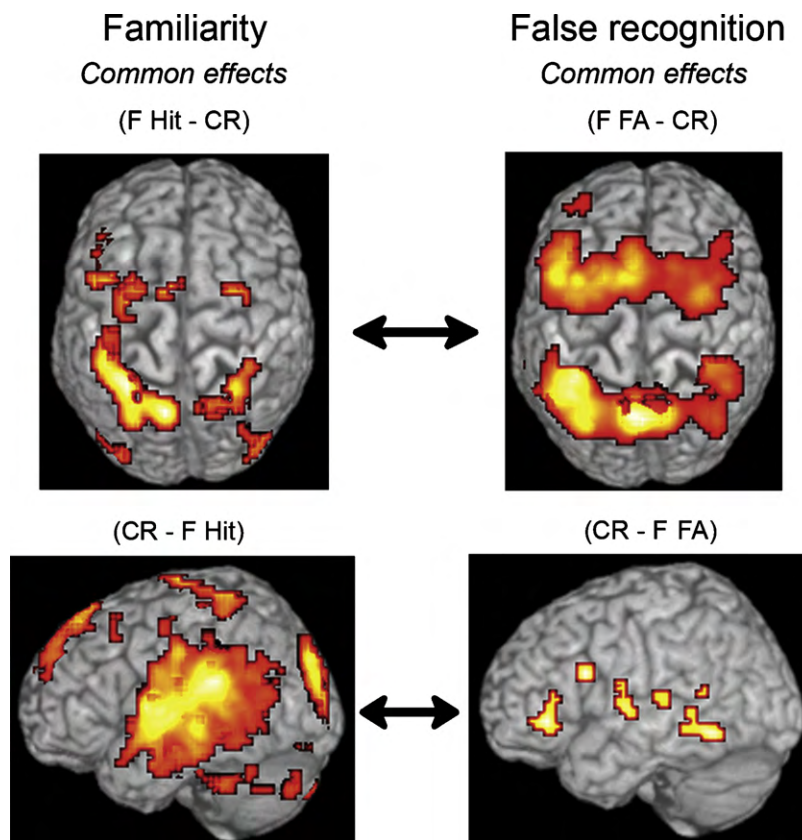


Fig. 3. Familiarity (FH vs. CR) and false recognition (FFA vs. CR) effects common to both age groups shown on the rendered surface of a canonical brain. Arrows are drawn between contrasts where regional overlap was identified. Abbreviations as in Fig. 2 [$p < 0.001$, uncorrected, with a 5 voxel extent; exclusively masked by group interactions at $p < 0.05$].

confirmed that each of these regions exhibited reliable differences between CR trials and both F hits and FFAs.

3.3.2. Differences between groups

Recollection: The comparison of recollection between groups yielded significant differences in the left parietoccipital cortex, as shown in Table 4, and consistent with our first prediction in Section 1. As shown in Fig. 4(A), activity in this region was greater for R than FH items in the young, with no reliable effect in the old group. A few right lateralized frontal regions exhibited the opposite pattern of activity (i.e. R > FH: Old > Young), including a right middle frontal gyrus region also shown in the table and figure. within-group analyses determined that this interaction was due to an FH > R effect in the young but no reliable FH vs. R difference in the older adults.

The left parietoccipital region also appeared to exhibit false recognition activity in both groups, as can be seen in the plot in Fig. 4(A). Inclusive masking of the R > FH: Young > Old interaction with the FFA > CR main effect showed that this region was reliable for both contrasts. Thus, the same parietoccipital region that exhibited comparable familiarity-based false recognition effects for both groups also showed reduced recollection effects in the old relative to the young adults. It should be noted that

although R > FH: Young > Old interaction did not reach significance for the right parietoccipital region described earlier, the patterns of recollection and false recognition effects were similar to that of the left region (see Figs. 2(A) and 4(A)).

Familiarity: Regions showing significantly different familiarity effects between groups are listed in Table 4. Activity in the dorsomedial PFC, left inferior frontal and fusiform gyri was greater for FH than CR items in the young relative to old adults. As can be seen in Fig. 4(B), familiarity effects were greatly reduced in the older adults in the frontal regions, consistent with our second prediction in Section 1. For the fusiform gyri, the group interaction resulted from a “cross-over” effect, where activity was greater for CR (corresponding to the zero level in the plots) than FH trials in the old adults, as can be seen in Fig. 4(B). Within-group analyses determined that both effects were reliable (i.e. FH > CR in young and CR > FH in old). Only one region in the right supramarginal gyrus exhibited the opposite pattern of activity (i.e. FH > CR: Old > Young), as shown in the table.

Note that the dorsomedial PFC and fusiform regions exhibiting significant differences in familiarity effects between groups were similar in location to the regions exhibiting significant differences between FFAs and CR trials across both young and old participants (see Fig. 5). Inclusive

Table 4

Regions showing significant differences between groups for familiarity, recollection and false recognition.

Group	Region	L/R	MNI coordinates (x, y, z)	BA	T score	Cluster size
Recollection (R > FH)						
Young > Old	Parietoccipital cortex (middle occipital/angular gyri)	L	-33, -72, 33	19/39	3.11	32
	Posterior inferior frontal gyrus	L	-45, 15, 27	44	3.35	19
	Fusiform gyrus	R	36, -54, -18	37	3.28	28
Old > Young	Middle frontal gyrus	R	36, 18, 45	46	3.79	33
		R	33, 36, 36	9	3.61	17
	Middle temporal gyrus	R	-54, -9, -12	22	3.37	9
Familiarity (FH > CR)						
Young > Old	Dorsomedial PFC	B	-6, 9, 60	6/8/32	5.24	267
	Superior frontal gyrus	R	24, -6, 57	6	3.61	8
	Inferior frontal gyrus	R	33, 27, 3	47	3.81	12
		L	-33, 21, 3	47	3.79	30
		L	-33, 21, 12	48	3.66	
	Fusiform gyrus	L	-45, 12, 30	44	3.43	5
		R	33, -45, -9	37	4.08	55
		R	27, -66, -3	19	3.83	
	Paracentral lobule	L	-30, -63, -6	37	3.56	9
		L	-9, -24, 66	4/6	4.50	153
		R	21, -60, 57	7	3.44	6
	Cerebellum	R	3, -54, -33	7	3.62	10
L		-24, -93, 21	18	3.39	7	
R		54, -30, 30	48	3.92	17	
Old > Young	Supramarginal gyrus	R	54, -30, 30	48	3.92	17
False recognition (F FA > CR)						
Young > Old	Precuneus	L	-6, -66, 54	7	4.06	21

L = left; R = right; B = bilateral. BA = Brodmann's area. R = studied items judged "remember"; FH = studied items judged "familiar" (familiar hits); CR = correctly rejected new items; F FA = familiar false alarms to unstudied items. Italicized values represent subpeaks of significant clusters.

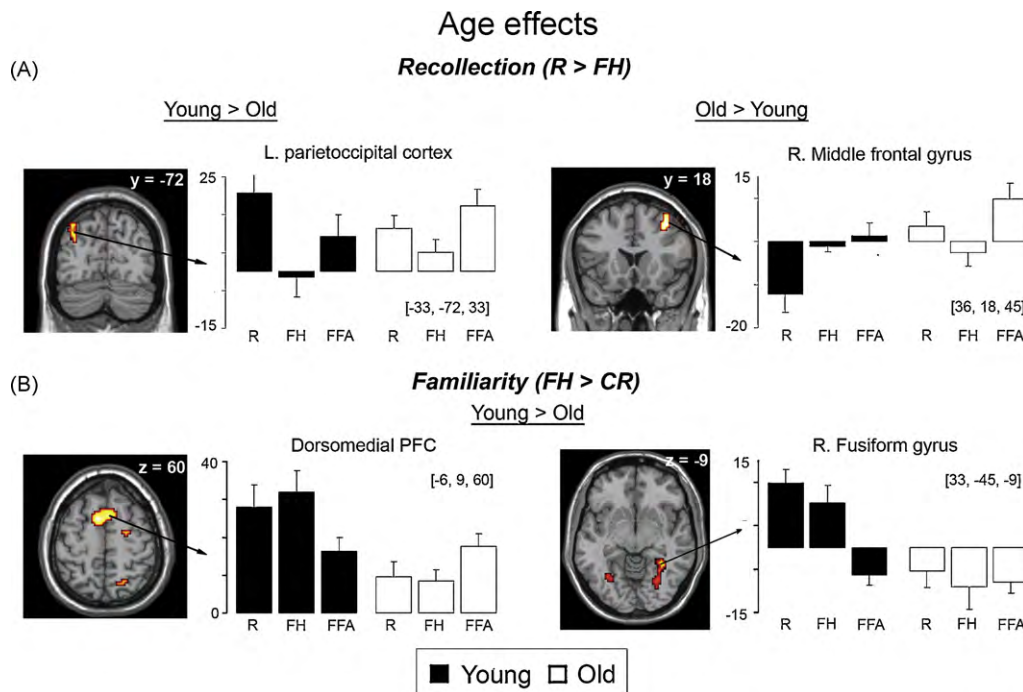


Fig. 4. Memory effects exhibiting group differences, shown in selected regions, displayed on the MNI reference brain. Plots show parameter estimates for the event-related response at the peak maxima of the selected regions for each of the trial types versus correct rejection (CR) trials for each group (units arbitrary). Error bars depict standard error of the mean across participants, for each group. Abbreviations as in Fig. 2 [$p < 0.001$, uncorrected, with a 5 voxel extent].

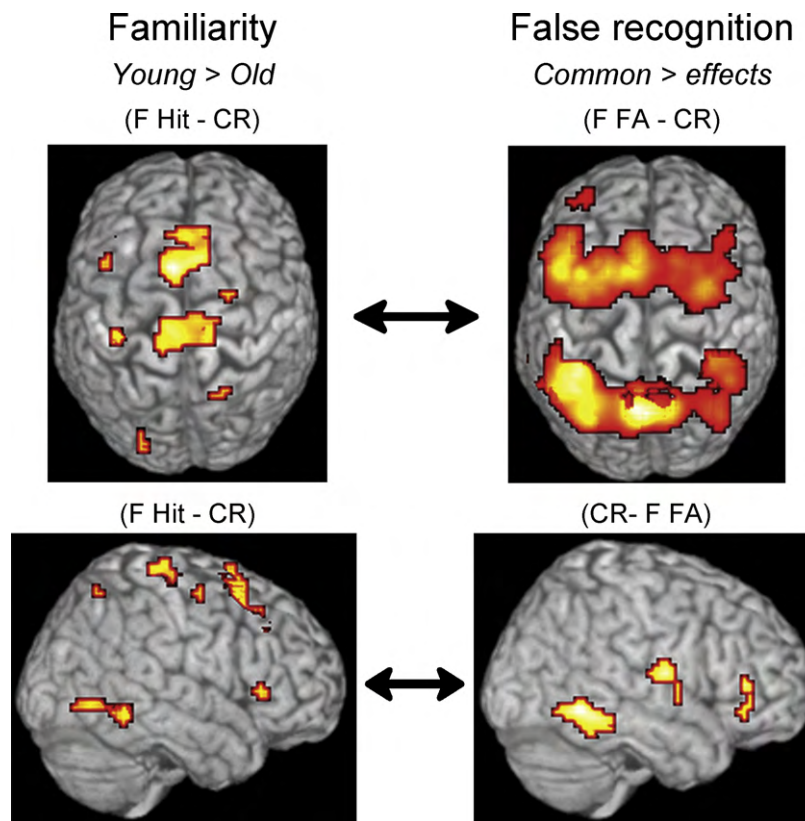


Fig. 5. Familiarity (FH > CR) effects exhibiting group differences and false recognition (FFA vs. CR) effects common to both age groups shown on the rendered surface of a canonical brain. Arrows are drawn between contrasts where regional overlap was identified. Abbreviations as in Fig. 2 [$p < 0.001$, uncorrected, with a 5 voxel extent. False recognition (common) maps exclusively masked by group interactions at $p < 0.05$].

masking of the FH > CR: Young > Old interaction with the FFA > CR and CR > FFA main effects confirmed this observation. Given that familiarity effects were reduced in older adults in these two regions where false recognition effects were of similar magnitude for young and old, it was of interest whether the magnitudes of true and false recognition effects were more similar in the old than in the young. The peak voxel coordinates for the dorsomedial PFC and fusiform regions identified by the inclusive masking were used to compare the magnitudes of familiarity-based false recognition and familiarity-based true recognition effects. A Region (Dorsomedial PFC, Fusiform) \times Memory (True, False recognition) \times Group (Young, Old) ANOVA for the dorsomedial PFC revealed a reliable Memory \times Group interaction [$F(1, 24) = 17.5$, $p < .001$]. As can be seen in Fig. 5, while activity associated with familiarity was greater than activity associated with false recognition in both of these regions in the young [$t(12) > 4.2$, $p < .001$], there was no reliable difference between the magnitude of these effects in the old [$t(12) < 1$], confirming our fourth prediction in Section 1.

False recognition: Only one region in the precuneus exhibited a group difference in false recognition (i.e. FFA > CR: Young > Old), as seen in the table. There were no other group differences associated with this contrast.

4. Discussion

The results yielded several interesting findings regarding the relationship between false recognition and both recollection- and familiarity-based “true” recognition in the young and old. In relation to our four predictions, older adults demonstrated reduced estimates of recollection and recollection-related activity in the left parietooccipital cortex. Second, we replicated our previous findings (Duarte et al., 2006) suggesting that older adults can exhibit impairments in behavioral estimates of familiarity, unlike some previous studies, which was paralleled by altered activity in dorsomedial and inferior frontal and fusiform (but not anterior medial temporal) regions. Third, activity in superior medial parietal (precuneus) and lateral temporal regions was associated with both familiarity-based true recognition of studied items and familiarity-based false recognition of unstudied items, in both young and older adults, consistent with previous behavioral evidence suggesting familiarity contributes to false recognition. Finally, the difference between familiarity-based true and false recognition effects in both dorsomedial frontal and inferior temporal regions was diminished in the older adults relative to the young, due to decreased true recognition activity in the old. These results and their implications are discussed in more detail below.

4.1. *Recollection impairments in older adults*

Consistent with our prediction, older adults exhibited impaired estimates of recollection. The reduced subjective estimates in this group are consistent with a number of previous studies demonstrating similar impairments in older adults (Bastin and Van der Linden, 2003; Daselaar et al., 2006a,b; Howard et al., 2006; Prull et al., 2006; Yonelinas, 2002 for review). It should be noted, however, that the older adults here were chosen on the basis of sufficient false alarm rates, hence exhibited reduced recognition discriminability, and would have been classified as “low performers” in our previous studies (Duarte et al., 2007, 2006). Thus, while the older adults here exhibited impaired estimates of recollection, it is not necessarily true that this generalizes to all older adults [It is worth noting that objective recollection, measured via source memory accuracy, was also impaired and accompanying frontal activity reduced in the older adults, as discussed in a separate manuscript (Duarte et al., 2007). There was no regional overlap between objective recollection and false recognition effects in either group, however (data not shown)].

The current imaging results revealed reduced recollection-related activity in the older adults in the left parietoccipital cortex. A similar region has been associated with recollection in several previous imaging studies, for a variety of stimulus materials and tasks (Cansino et al., 2002; Henson et al., 1999a,b; Johnson and Rugg, 2007; Wheeler and Buckner, 2004). As has been previously suggested (Johnson and Rugg, 2007), this region may either be sensitive to the recovery of information that is common across tasks/conditions or be part of a general “recollection network”. Some recent lesion evidence supports a necessary role for this area in recollection in humans (Berryhill et al., 2007) (but see (Simons et al., 2007) for conflicting results). Furthermore, neuroanatomical evidence from non-human primates (Clower et al., 2001; Lavenex et al., 2002) and functional connectivity studies in humans (Vincent et al., 2006) suggest that the posterior parietal cortex is highly connected with the MTL, including the hippocampus. While we did not observe any direct effects in the MTL, this is not an uncommon finding in retrieval paradigms (reviewed in Rugg and Henson, 2003). Moreover, these previous connectivity studies suggest that an MTL-parietal recollection network may be affected in these older adults, consistent with some previous findings (Daselaar et al., 2006a,b). These changes offer some support for the hypothesis that reductions in recollection may contribute to enhanced false recognition in older adults.

A region in the right middle frontal gyrus showed recollection-related activity in young but not older adults, with familiar hits exhibiting greater activity than remember hits. This pattern has been observed in a similar right dorso-lateral frontal region in at least one previous study (Henson et al., 1999a,b). It has been suggested that the pattern of activity in this region may reflect monitoring processes that act to verify the products of retrieval (Henson et al., 1999a,b, 2000). These processes may be engaged to a greater extent when no

contextual details are retrieved yet the items elicit a feeling of familiarity that leads to further retrieval attempts before a judgment is ultimately made. The lack of activity difference between familiar and remember hits in the older adults monitoring, which may have led to elevated false alarm rates. Such a theory is consistent with the elevated false alarm rates that are typically observed in patients with right frontal lesions (Curran et al., 1997; Schacter et al., 1996)

4.2. *Familiarity impairments in older adults*

Collectively, the behavioral and imaging findings suggest that an over-reliance on familiarity cannot account for the enhanced level of false recognition in these older participants. Behavioral estimates of familiarity were impaired in the older adults relative to the young. This stands in contrast to the widely held belief that familiarity is intact in older participants (see Spencer and Raz, 1995; Yonelinas, 2002, for reviews) and more recently in older rats (Robitsek et al., 2008). As discussed earlier, the older adults presented here represent a subgroup that were chosen on the basis of sufficient false alarm rates, leading into question the impact of group selection upon changes in familiarity and related neural activity. It is worth noting, however, that the older adults not presented here due to insufficient false alarms rates, exhibited intact recognition discriminability but impaired familiarity estimates relative to the young adults and similar changes in familiarity-related neural activity as those observed in the older adults presented here.

Although it has been suggested that the age-related impairment in familiarity may be less than the age-related impairment in recollection (i.e. recollection disproportionately impaired relative to familiarity), this was not true of the current data. What are some potential explanations for this discrepancy? One possibility is that the use of pictures, in contrast to words that have been used in most previous aging studies, affected the estimates of familiarity in either the young or the older adults. However, familiarity for words has also been shown to be impaired in older adults in at least one previous study (Prull et al., 2006), suggesting that stimulus effects alone cannot account for the present results. Furthermore, in some previous studies where recollection was disproportionately affected by aging (e.g. Bastin and Van der Linden, 2003; Parkin and Walter, 1992) familiarity estimates were based upon hit rates alone. Given that false alarm rates, however, often differ between young and older adults, as they do here, it is important to take false alarms into account when comparing familiarity estimates between groups (Roediger and McDermott, 1994) [It should be noted that one recent study identified intact ROC familiarity estimates in older rats in an odor detection task (Robitsek et al., 2008), suggesting that task or species differences may affect age-related familiarity changes]. Another potential reason for the discrepancy is that non-criterial recollection may have inflated familiarity estimates and familiarity may be impaired in the older adults here, in part, due to impaired non-criterial

recollection in the old or to inflated non-criterial recollection in the young (Parks, 2007). The inclusive task instructions, however, in the current study allowed subjective recollection estimates (i.e. “remember” judgments) to be based on any contextual associations, including non-criterial information, making it unlikely that familiarity estimates would have been artificially inflated. Furthermore, as described earlier, several other recent studies have also suggested that familiarity may be more impaired than has previously been believed. For example, one review of numerous behavioral studies using multiple measurement methods found little support for intact familiarity in older adults (Light et al., 2000), suggesting that familiarity deficits may have been underestimated in previous studies. Furthermore, one study directly compared several measurement methods within the same group of participants and found that familiarity estimates (scored under an independence assumption and corrected for false alarm rates as undertaken here) were impaired in older adults, particularly for the remember-know and ROC methods (Prull et al., 2006). Moreover, the familiarity deficit in the older adults in the current study is further supported by the neuroimaging findings, discussed below.

Altered familiarity-related activity in the dorsomedial frontal cortex (BA 6/8/32), inferior frontal (BA 47) and inferior temporal (fusiform) cortices (BA 37) may underlie recognition deficits in older adults. It is noteworthy, however, that activity in the anterior MTL (e.g. perirhinal cortex), which has been associated with a familiarity signal by previous imaging (Henson et al., 2003; Montaldi et al., 2006; Ranganath et al., 2004) and lesion (Bowles et al., 2007) studies, did not appear to be affected by age. This stands in contrast to some recent findings suggesting that behavioral indices of familiarity (measured by ROCs) and associated neural activity in perirhinal cortex were enhanced in older adults relative to the young (Daselaar et al., 2006a,b). One potential reason for the latter finding may relate to the fact that the older participants in the study by Daselaar and colleagues received two study presentations while the young participants received only one; a manipulation that is likely to have enhanced familiarity estimates and related differences in neural activity in their older adults. Another potential reason for this discrepancy across studies could reflect the different stimuli used, i.e. pictures in the present study versus words used by Daselaar and colleagues. Future studies directly comparing familiarity-related activity for words and pictures may be useful in this regard.

The dorsomedial and inferior frontal regions affected in the older adults here has also been associated with familiarity in a few previous studies (Montaldi et al., 2006; Ranganath et al., 2004; Yonelinas et al., 2005). While it is possible that these regions may reflect processes that specifically contribute to familiarity, it is more likely that they are part of a general executive control system that contributes to both memory and non-memory domains. For example, the dorsomedial PFC has been implicated in conflict monitoring (Rushworth et al., 2007) and patients with damage to this

region have difficulty in non-memory tasks containing high levels of response competition (e.g. Stroop tasks) (Stuss et al., 2001). Furthermore, the inferior frontal cortex may contribute to resolving response competition (Badre and Wagner, 2007). Although further study is needed to determine whether these areas are necessary for familiarity-based recognition, some evidence suggests that focal damage to the lateral PFC, including the inferior frontal regions implicated here, produce impairments in behavioral estimates of familiarity (Duarte et al., 2005). Thus, at least some of the processes mediated by frontal regions may be necessary for intact familiarity functioning. The present data suggest that the control processes subserved by these frontal regions are affected in older adults, consistent with the so-called “frontal aging hypothesis” (see Raz, 2000; West, 1996, for reviews), potentially contributing to their familiarity deficits.

Activity in the inferior temporal cortex (fusiform) was greater for familiar hits than correct rejections in the young, with the opposite pattern present in the older adults. This region has been implicated in familiarity previously (Montaldi et al., 2006) and has also been shown to be affected by aging (Daselaar et al., 2006a,b). Furthermore, as discussed below, activity in this region was greater for this true recognition effect than for activity associated with false recognition in the young adults, but not in the older adults. Although this difference in activity between studied and unstudied items could be related to perceptual fluency, which might be intact in the young but not in the old, the difference in activity in the young was in the opposite direction to that typically associated with fluency (viz., reduced activity for studied than unstudied items, or “repetition suppression”) (Henson, 2003). Thus, although it is not clear why young adults showed increased activity for studied items, it is possible that the lack of differential activity between truly (studied) and falsely (unstudied) recognized items in the old reflects reduced perceptual fluency, which may contribute to their impaired estimates of familiarity accuracy.

4.3. *Overlap of true and false recognition effects*

Consistent with our hypothesis that false recognition effects would be observed in many of the same regions as true recognition effects, activity in superior parietal and lateral temporal regions was associated with familiarity-based recognition of both studied (“true”) and unstudied (“false”) items, across both young and older participants. These regions have been implicated in both true and false recognition in some previous studies (Dennis et al., 2007; Kim and Cabeza, 2007; Slotnick and Schacter, 2004), although the present results go beyond these previous studies by demonstrating that this overlap may be confined to familiarity. The superior parietal cortex has been associated with familiarity in several previous studies, in contrast to more lateral and inferior parietal regions implicated in recollection (Henson et al., 2005; Wheeler and Buckner, 2004; Yonelinas et al.,

2005). It should be noted that regions within the superior parietal region (precuneus) have also been associated with recollection in a few previous studies (Henson et al., 1999a,b; Lundstrom et al., 2005). It may be that there are distinct regions within the precuneus that differentially support recollection and familiarity, with superior regions supporting familiarity and more inferior regions supporting recollection, consistent with predictions made for the lateral parietal cortex (Wagner et al., 2005).

It has been hypothesized that activity in the posterior parietal cortex, including the superior regions identified here, may reflect attention toward internal mnemonic representations (Wagner et al., 2005) but also extra-mnemonic functions such as target detection, or response tracking (Herron et al., 2004). It is noteworthy that the activity profile in these regions is consistent with activity associated with an “old” decision, regardless of type of memory judgment (i.e. remember, familiar and false alarms), which is consistent with the response tracking hypothesis. This pattern stands in contrast to that in the superior lateral temporal cortex (superior/middle gyri), where activity was less for hits (recollected and familiar) and, to a lesser extent, false alarms, relative to correctly rejected new items. This decrease may reflect a continuous familiarity signal in this region, which might arise from the degree of fluency in lexico-semantic processing associated with these items, given the known relationship of this area to semantic processing (e.g. Bedny et al., 2008; Friederici et al., 2003; Tyler et al., 2003) [Although not shown in the figures, activity associated with studied items judged to be new (“misses”) did not significantly differ from activity associated with unstudied items judged to be new (“correct rejections”) in the superior parietal region while activity associated with these trial types did differ in the lateral temporal cortex, supporting the response tracking and familiarity hypotheses for the regions, respectively].

One unexpected finding was that activity in the parieto-occipital cortex was associated with both recollection of studied items and familiarity-based false recognition. This is somewhat difficult to explain in light of the absence of familiarity-based true recognition effects in this region. Given that familiarity-based false alarms were associated with relatively long response times, it is possible that activity in this region may reflect attentional processes, rather than successful retrieval, per se (Wagner et al., 2005). Given the absence of familiarity-related true recognition activity in this region, however, despite similarly long response times for F Hits relative to R Hits, it is unlikely that this region is modulated solely by such attentional processes.

Although many brain regions contributed to both true and false recognition, a few were specific to true recognition. As noted above, activity in the anterior medial temporal cortex, including perirhinal cortex, appeared specifically related to true recognition but not recollection or familiarity-based false recognition. Some previous imaging studies suggest that this region supports true recognition only (Dennis et al., 2007; Kim and Cabeza, 2007), while others implicate

a role in both true and false memory processes (Cabeza et al., 2001; Daselaar et al., 2006a,b; Garoff-Eaton et al., 2006), although recollection and familiarity were not examined in these previous studies. One important factor that may contribute to these discrepant results is the fact that the current study did not employ methods specifically to increase false alarms (such as the inclusion of semantically or perceptually similar lures), and false alarm rates were not as high as in these previous studies. It is possible that MTL-mediated retrieval processes would be engaged to a greater extent when unstudied items overtly share such features with studied items and conscious retrieval of item information about studied events is more likely to be elicited by new items (Kim and Cabeza, 2007).

4.4. *Reduced discriminability in the older adults*

The overlap between true and false memory effects is consistent with the idea that similar cognitive processes, particularly those supporting familiarity, contribute to true and false recognition in both young and older adults. Familiarity effects were greater than false recognition effects for both young and older adults in superior medial parietal and lateral temporal brain regions. Thus, although some areas may be sensitive to the perception that an item has been studied, these same regions may be able to discriminate between veridical and illusory recognition. Consistent with our predictions, this difference was less evident in the older adults. Specifically, a difference between true and false familiarity-based recognition effects in the dorsomedial PFC and fusiform gyri that was evident in the young was absent in the older adults. These data suggest that the reduced capacity of frontal and inferior temporal regions to distinguish studied from unstudied items may contribute to the elevated level of false recognition in older adults. A similar loss of differentiation between studied and unstudied items in conjunction with elevated false alarms was identified in older participants in one previous ERP study (Gutchess et al., 2007). The current results go beyond these previous findings, however, by suggesting that reductions, largely in processes contributing to familiarity, contribute to the loss of differentiation between true and false memory correlates in older adults.

Despite the large differences in false recognition rates between young and older participants, there were minimal differences in the neural correlates of false recognition between the groups. These results stand in contrast to one recent study in which activity associated with false memory, in addition to veridical memory, was enhanced in older participants in the lateral temporal cortex (Dennis et al., 2008). These authors argued that their findings supported an over-reliance on semantic gist as the mechanism for elevated false recognition in older adults. Although familiarity and gist memory may not be identical phenomenon, familiarity is more likely than recollection to contribute to gist (Yonelinas, 2002) and consequently, our findings with regard to famil-

ilarity do not support this hypothesis. Instead, reductions in activity associated with familiarity (and recollection) may lead to reduced differentiation between these veridical and illusory memory traces, potentially contributing to the elevated false recognition rates in older adults. An important distinction between the current study and this previous one, however, is that we did not explicitly manipulate the semantic similarity between studied and unstudied items. It may be that this manipulation, or perhaps the inclusion of verbal and not pictorial stimuli, resulted in a greater shift toward familiarity-based processing in older than young adults in this previous study. An interesting question for future research would be whether familiarity processes are differentially engaged in young and older adults under various manipulations of study/test similarity for verbal and pictorial stimuli.

5. Conclusion

In conclusion, the present results offer insight into the effects of aging on the relationship between recollection, familiarity and false recognition. Our data suggest that true and false recognition are supported by similar networks of brain regions, particularly in frontal, parietal, lateral and inferior temporal, but not medial temporal, cortex and that a reduction of familiarity and recollection-related activity within some of these regions may contribute to elevated false recognition in older adults. This evidence argues against the hypothesis that an over-reliance on familiarity contributes to elevated false recognition in older adults but is consistent, however, with the idea that reduced recollection-related processing may contribute to enhanced false memory. We argue that reduced differentiation between veridical and illusory memory traces may be an important contributor to the elevated level of false recognition evident in older adults. Given that only low performing older adults with sufficient false alarms rates were included in this study, however, future studies should investigate the degree to which the behavioral and neural changes observed here generalize to a larger older adult population. Future studies directly comparing familiarity-related activity for various stimulus materials in a larger older population may also be useful in understanding the circumstances in which age-related changes in regions often implicated in familiarity, such as the perirhinal cortex, are observed.

Conflicts of interest

There are no actual or potential conflicts of interest.

Disclosure statement

The study was approved by the Cambridge Local Research Ethics Committee.

Acknowledgements

This research was supported by the Medical Research Council (WBSE U.1055.05.012.00001.01) and the Alzheimer's Research Trust. We thank the staff of the Cognition and Brain Sciences unit for their assistance with data collection, Kate Gough and Hillary Green for their assistance with neuropsychological test assessment and all our participants.

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