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PII: S1053-8119(22)00048-9
DOI: https://doi.org/10.1016/j.neuroimage.2022.118918
Reference: YNIMG 118918

To appear in: *NeuroImage*

Received date: 8 November 2021
Revised date: 12 January 2022
Accepted date: 15 January 2022

Please cite this article as: Mingzhu Hou , Erin D. Horne , Marianne de Chastelaine , Michael D. Rugg , Divided attention at retrieval does not influence neural correlates of recollection in young or older adults, *NeuroImage* (2022), doi: https://doi.org/10.1016/j.neuroimage.2022.118918

Divided attention at retrieval does not influence neural correlates of recollection in young or older adults

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Abstract

Age-related decline in episodic memory has been partially attributed to older adults' reduced domain general processing resources. In the present study, we examined the effects of divided attention (DA) - a manipulation assumed to further deplete the already limited processing resources of older adults - on the neural correlates of recollection in young and older adults. Participants underwent fMRI scanning while they performed an associative recognition test in single and dual (tone detection) task conditions. Recollection effects were operationalized as greater BOLD activity elicited by test pairs correctly endorsed as ‘intact’ than pairs correctly or incorrectly endorsed as ‘rearranged’. Detrimental effects of DA on associative recognition performance were identified in older but not young adults. The magnitudes of recollection effects did not differ between the single and dual (tone detection) tasks in either age group. Across the task conditions, age-invariant recollection effects were evident in most members of the core recollection network. However, while young adults demonstrated robust recollection effects in left angular gyrus, angular gyrus effects were undetectable in the older adults in either task condition. With the possible exception of this result, the findings suggest that DA did not influence processes supporting the retrieval and representation of associative information in either young or older adults, and converge with prior behavioral findings to suggest that episodic retrieval operations are little affected by DA.

Keywords: aging, episodic memory, dual task, fMRI, core recollection network

1. Introduction

Cognitively healthy adults typically demonstrate a decline in episodic memory performance beginning around 60 years of age. This decline is held to be largely accounted for by ineffective encoding resulting, in part, from insufficient neurocognitive resources (e.g., Craik

& Rose, 2012; Friedman & Johnson, 2014; Old & Naveh-Benjamin, 2008). However, as we discuss below, the importance of encoding for age-related memory decline does not rule out a concurrent role for age differences in retrieval processing. Notably, to the extent that a retrieval process is resource limited (Mitchell & Johnson, 2009; Rugg, 2004), one might expect it to be vulnerable to aging given the evidence that domain general processing resources are depleted with increasing age (Craik, 2020; Craik & Byrd, 1982).

Experimental studies of the effects of resource depletion on cognitive performance frequently employ a divided attention (DA) approach. For example, one might contrast memory performance according to whether the 'primary' task, such as a study task or a memory test, is performed alone or concurrently with a secondary task. Numerous studies employing a variety of DA procedures have demonstrated that episodic encoding is highly vulnerable to resource depletion (e.g., Anderson et al., 1998; Craik et al., 1996; for review, see Naveh-Benjamin, 2002); indeed, it has been proposed that the disruption to encoding in young adults caused by DA approximates the conditions under which older adults encode information when their attention is undivided (Craik & Rose, 2012).

Here, we focus on the effects of DA during retrieval. Studies employing young participants have consistently reported little, if any, decline in performance when memory is tested under DA, at least for secondary tasks that compete with the retrieval test for domain general cognitive resources (e.g., Baddeley et al., 1984; Craik et al., 1996, 2018; Lozito & Mulligan, 2006; Naveh-Benjamin et al., 1998; see Fernandes & Moscovitch, 2000 for an example of domain specific interference, and see Kilb & Naveh-Benjamin, 2014 for review). These findings have been interpreted as evidence that memory retrieval is in some sense 'protected', such that cognitive resources are allocated 'automatically' to retrieval processing (Craik et al., 1996; but see Craik et al., 2018).

As noted above, a potential contributor to age-related memory decline is the reduction in domain general neurocognitive resources that accompanies aging (Craik, 2020; Craik & Byrd, 1982). Consistent with this account, several studies of the effects of DA at retrieval have reported that secondary task performance suffers to a greater extent in older than in young adults (Anderson et al., 1998; Craik & McDowd, 1987; Fernandes & Moscovitch, 2003; Park et al., 1989; Whiting & Smith, 1997; for review, see Klib & Naveh-Benjamin, 2014). However, the effects of DA on retrieval accuracy have typically been age-invariant, with some studies reporting similar performance declines in young and older adults under DA (Fernandes & Moscovitch, 2003; Park et al., 1989; Whiting & Smith, 1997), and others reporting little or no effect of DA in either age group (Anderson et al., 1998; Nyberg et al., 1997).

In a recent study, Horne et al. (2021) employed fMRI to examine the effects of DA on the neural correlates of retrieval monitoring - processes that act on the outcome of a retrieval attempt in service of the retrieval goal - during associative recognition in young and older adults. Neural correlates of monitoring were operationalized as greater fMRI BOLD signal for test pairs endorsed as 'rearranged' than for pairs correctly endorsed as 'intact', under the assumption that the former class of judgments places heavier demands on monitoring than the latter class [see de Chastelaine et al. (2016) and Horne et al. (2021) for justification of this assumption]. The authors predicted that DA would further deplete the already limited domain general resources available to support monitoring in older adults, leading to an age-dependent monitoring impairment and a concomitant decline in the magnitude of monitoring-related neural activity. Indeed, DA led to an age-specific reduction in associative recognition memory performance and, in addition, to the elimination in the older age group of the robust relationship between monitoring-related activity and memory performance that was evident when attention was undivided. Crucially, though, the magnitudes of neural 'monitoring effects' did not differ between the divided and full attention conditions in either age group. This null finding prompted the authors to conjecture that the decline in older adults' memory performance under DA did not result from a monitoring impairment but, instead, from impairment of memory processes operating 'upstream' of monitoring.

In the present study, we report the results of further analysis of the data acquired by Horne et al. (2021). Rather than examining neural monitoring effects, here we examined the effects of DA on neural correlates of recollection (hereafter, 'recollection effects') – that is, the enhanced neural activity elicited by retrieval cues associated with successful as opposed to unsuccessful recollection that we and others assume to reflect processes supporting the retrieval and representation of episodic information (e.g., Benoit & Schacter, 2015; Rugg & Vilberg, 2013). Recollection effects have been extensively examined for more than two decades in a variety of experimental paradigms (see Kim 2010, 2013 and Rugg & Vilberg, 2013 for reviews). Successful recollection has consistently been associated with enhanced BOLD activity (hereafter, 'recollection effects') in a 'core recollection network' that comprises medial prefrontal cortex (MPFC), posterior cingulate (PCC)/retrosplenial cortex, hippocampus, parahippocampal gyrus (PHC), left middle temporal gyrus (MTG) and left angular gyrus (AG) (King et al., 2015; Rugg & Vilberg, 2013). Of importance in the present context, recollection effects in these regions scale with the amount of information recollected about the study event (e.g., Hutchinson et al., 2014; Rugg and Vilberg, 2013; Thakral et al., 2015; Yu et al., 2012a, b).

Here, we report what to our knowledge is the first study to examine the influence of DA at retrieval on recollection effects in young and older adults (see Anderson et al., 2000 and Fernandes et al., 2006 for early studies of the effects of DA on retrieval that employed blocked experimental designs). Given the findings from a previous aging study that employed the same associative recognition memory task (de Chastelaine et al., 2016), we predicted that we would identify robust and largely age-invariant recollection effects across the core recollection network when the task was performed under full attention. The key questions concerned the impact on these effects of dividing attention between memory retrieval and a secondary task, and whether any such impact is moderated by age. In relation to the first question, we note that while Horne et al. (2021) reported null effects of DA on associative recognition performance in their younger sample (replicating numerous prior findings – see above), it is unknown whether such null behavioral findings extend to the neural correlates of successful memory retrieval. For example, the insensitivity of memory performance to DA in young adults might be accompanied by a reduction in the amount or richness of retrieved information that is too subtle to be reflected in typical behavioral measures; this would however be expected to show up as a reduction in the magnitude of recollection effects in members of the core recollection network (see above). Alternately, preserved performance under DA might depend on the allocation of additional neural resources to the processing of the retrieval cues, reflected perhaps in an enhancement of the neural activity elicited by both recollected and unrecollected test items. Moreover, if the deleterious effect of DA on older adults' memory performance reported by Horne et al. (2021) reflects interference with processes supporting the retrieval and representation of episodic information, then DA should be associated with the emergence or exaggeration of age differences in recollection or cue processing effects.

2. Methods

A detailed description of the methods can be found in the prior publication where the behavioral and monitoring-related fMRI data from the present study were first reported (Horne et al., 2021). The study was approved by the Institutional Review Boards of UT Dallas and The University of Texas Southwestern Medical School. All participants provided written informed consent prior to undertaking the experiment and received remuneration of $30/hr. The recollection-related fMRI findings reported below have not been described previously.

2.1 Participants

Participants were 28 young adults aged between 18-30 years and 28 older adults aged 65-76 years. They were recruited from the UT Dallas and surrounding metropolitan Dallas communities. They were right-handed, had normal or corrected-to-normal vision, and scored a minimum of 27 on the Mini-Mental State Examination (MMSE). Inclusion and exclusion criteria are described in detail in Horne et al. (2021).

A standard battery of neuropsychological tests was administered to participants on a separate day prior to the experimental session. See Horne et al. (2021) for details.

2.2 Materials

Experimental stimuli consisted of 320 semantically unrelated word pairs. The pairs were randomly divided into five lists, which were counterbalanced across participants such that each pair provided items for each category of test pair (see below). For the study phase, critical stimuli were word pairs from four of the lists. For the test phase, critical stimuli consisted of 192 intact pairs (words presented together at study), 64 rearranged pairs (words paired with different words at study), and 64 new pairs (words not presented at study). The test items were intermixed with 104 null trials. At both study and test the different categories of word pairs were pseudo-randomized so that no more than three pairs from the same category occurred successively. Two buffer pairs were inserted at the beginning and the middle of all experimental task blocks.

A randomly determined sequence of low (400 Hz) and high (900 Hz) frequency auditory tones were presented concurrently with each test list. Tones were presented with a stimulus onset asynchrony (SOA) ranging between 1000-3000 ms such that one to three tones occurred during each trial. To avoid the possibility of cross-modal perceptual interference, tone onsets did not occur concurrently with the red fixation cross presented immediately prior to each word pair, nor during the first 500 ms of each word pair presentation. ‘Target’ and ‘non-target’ tones (see below) were presented in a 30:70 ratio. The frequency of the target tones (high or low) was counterbalanced across participants.

2.3 Experimental Procedure

The experiment consisted of a study phase and a test phase. The study phase was administered outside the scanner on a laptop computer. There were two blocks separated by a brief rest. Each word pair was presented for 2000 ms and was preceded by a red fixation cross for 500 ms. A white fixation cross was then presented for 1000 ms. The task was to judge which of the two objects denoted by the words would more likely ‘fit’ into the other and to respond via a button press. To encourage relational encoding of the word pairs, participants were instructed to generate a vivid visual image or verbal story to determine which item would fit into the other. Participants were aware of the subsequent associative recognition test. Following the study session, participants were escorted to the scanner and prepared for the test phase.

Participants undertook the scanned retrieval test approximately 25 minutes after completion of the study session. The retrieval test extended across four test blocks, separated from one another by short rest periods. In each block, word pairs were presented for a duration of 2000 ms and were preceded by a red fixation cross for 500 ms. A white fixation cross followed for 2000 ms. Null trials consisted of a white fixation cross displayed for the same duration as a critical trial (4.5 s). A rest period of 30 s was inserted at the halfway point of each test block. Test blocks alternated between single task (associative memory task only) and dual task (associative memory plus tone detection) conditions. In the single task condition, participants were instructed to ignore the tones and focus on the retrieval test. In the dual task condition, participants were required to perform the retrieval and tone detection tasks concurrently under instructions to give equal emphasis to each task. The retrieval test required participants to indicate via a button press, using the index, middle and ring fingers of one hand, whether each test pair was ‘intact’, ‘rearranged’, or ‘new’. The tone detection task required participants to signal with the index finger of the other hand whenever a target tone occurred. Hand assignments, response-finger mapping and the ordering of the task conditions were counterbalanced across participants. For both the primary and secondary tasks, participants were instructed to respond as quickly but also as accurately as possible.

Practice on the study and retrieval tasks was given prior to the start of the experiment. As part of the practice, participants performed the tone detection task in the absence of test items. Accuracy and response time (RT) from this session were used to define baseline performance for the secondary tone task. Tone detection performance, and the procedures employed to ensure that participants were able to comfortably perceive the tones in the scanner, are described in Horne et al. (2021).

2.4 fMRI Acquisition

Participants were scanned using a 3 Tesla Philips Achieva MRI scanner (Philips Medical Systems) equipped with a 32-channel receiver head coil. T1-weighted images were acquired with a 3D magnetization-prepared rapid gradient echo (MP-RAGE) pulse sequence (FOV 256 x 256, 1x1x1 mm voxel size, 176 slices, sagittal acquisition). Functional data were obtained using a T2*-weighted echo-planar imaging (EPI) sequence (270 volumes, 33 axial images per volume, TR = 2 s, TE = 30 ms, flip angle 70°) with 3 mm thick slices (1 mm interslice gap, 3x3 mm in-plane resolution). Functional data were acquired in ascending order with a sensitivity encoding (SENSE) reduction factor of 2. The first 5 volumes of each block were discarded to allow tissue magnetization to reach equilibrium.

2.5 fMRI Preprocessing

The data were preprocessed and analyzed using SPM12 (http://www.fil.ion.ucl.ac.uk). Functional images were realigned, motion and slice-time corrected, and spatially normalized to a sample-specific template. The normalized images were then smoothed using an 8 mm full-width half-maximum (FWHM) Gaussian kernel. The functional data from the different test blocks were concatenated using the spm_concatenate.m function before being entered into the first-level GLMs (see below).

2.6 Statistical analyses

Critical trial types utilized in the analysis of the fMRI data were ‘associative hits’ (intact pairs correctly endorsed as intact), ‘associative misses’ (intact pairs endorsed as rearranged) and ‘associative correct rejections’ (rearranged pairs correctly endorsed as rearranged). Due to insufficient trial numbers for some participants, associative misses and associative correct rejections were collapsed at the first level to create a single trial type. Justification for this procedure is provided by the findings that an age group (young, older) x memory judgment (associative misses, associative correct rejections) mixed-design ANOVA conducted on a large independent data sample (de Chastelaine et al., 2016) failed to identify any significant effects of memory judgment (all ps > 0.1) in our *a priori* defined regions of interest (ROIs, see below). Thus, although it is possible for rearranged test pairs to be identified as such through a 'recall-to-reject' strategy (recollection of the studied pair-mate of one or both items, e.g. Rotello et al., 2000) this does not appear to be the case for the associative recognition procedure implemented in our laboratory. Hereafter, we refer to associative hits as 'intact' judgments and the combination of associative misses and associative correct rejections as 'rearranged' judgments. Note that the results reported below were essentially identical when we contrasted associative hits with associative misses in subgroups of the participants with sufficient trial numbers (see Supplementary Materials).

Statistical analyses were conducted with SPSS 27.0, JASP 0.14.0.0 and R software (R Core Team, 2018). The Greenhouse-Geisser correction was applied to ANOVA contrasts where appropriate. Significance levels for all tests were set at $p < 0.05$. For the behavioral and ROI analyses described below, Bayes factors were estimated to assess the evidence supporting findings arising from null hypothesis significance tests. We report BF_{10} values for t-tests and BF inclusion (BF_{incl}) values for ANOVAs. BF_{10} values estimate how many times more likely the data are to favor the alternative hypothesis over the null. BF_{incl} values provide an estimation of how many times more likely a particular effect is to account for variance in the data than not to do so. For both BF_{10} and BF_{incl}, values > 1 support the alternative hypothesis, while values < 1 support the null hypothesis. BF_{10} and BF_{incl} values between 0.33 and 1 are conventionally considered to provide anecdotal evidence, between 0.1 and 0.33 moderate evidence, and between 0 and 0.1 strong evidence in favor of the null hypothesis. By contrast, BF_{10} and BF_{incl} values between 1-3, 3-10 and 10-30 provide anecdotal, moderate and strong evidence respectively in favor of the alternative hypothesis (Jeffreys, 1961; Lee & Wagenmakers, 2013).

2.6.1 Behavioral analysis

We tested the influence of DA on accuracy and mean response time (RT) measures derived from the associative recognition and tone detection tasks. Associative memory performance (pR) was calculated as the difference between the proportion of associative hits and the proportion of associative false alarms (rearranged pairs erroneously endorsed as intact). Tone detection performance was calculated as the proportion of responses to target tones (hits) - proportion of responses to non-target tones (FAs) separately for the baseline (tone practice phase) and the dual task condition. Both measures were subjected to 2 (task: single, dual) x 2 (age group: young, older) ANOVAs. To assess whether young and older adults adopted different response criteria when making associative recognition judgments we also estimated response bias (Br, Snodgrass and Corwin, 1988), using the formula Br = p(associative false alarms)/[1-(p(associative hits)-p(associative false alarms))]. Br was also examined using a 2 (task: single, dual) x 2 (age group: young, older) ANOVA. Participant-wise mean RTs from the associative memory task were entered into a 2 (task) x 2 (age group) x 2 (memory judgment: intact, rearranged) ANOVA. RTs to target tones were subjected to a 2 (task: baseline, dual) x 2 (age group: young, older) ANOVA.

2.6.2 fMRI analyses

To examine the influence of DA on recollection effects we conducted ROI analyses directed at members of the core recollection network. An exploratory whole brain analyses was also conducted to complement the ROI analyses and to identify effects outside these *a priori* defined brain regions. These analyses are described in more detail below.

2.6.2.1 ROI analyses (single-trial GLM)

For each participant, we estimated single-trial beta estimates with a first level GLM that implemented the least squares all (LSA) approach (Abdulrahman & Henson, 2016; Mumford et al., 2012). Neural activity elicited by test pairs was modeled as a delta function and convolved with a canonical hemodynamic response function (HRF). Each test pair from the single and dual tasks was modeled as a separate event of interest; the 30-s rest periods that occurred midway through each block, the six motion regressors, and the constants modeling the mean BOLD signal in each block were modeled as covariates of no interest.

Mean across-trial parameter estimates for intact and rearranged judgments were extracted from 5 mm spheres (3 mm spheres for ROIs in the medial temporal lobe) centered on the members of the 'core recollection network' described by Rugg and Vilberg (2013) along with the MTG (a later addition to the network, King et al., 2015). ROI coordinates (see Table 1) were the same as those employed in de Chastelaine et al. (2016) and represented the centers of mass of the conjunctions of recollection effects derived from two other, independent, datasets (Elward et al., 2015; Wang et al., 2016).

In light of the extensive attention that has been paid to the hippocampus and left AG in prior fMRI studies of memory retrieval, and the theoretical prominence of these regions in the cognitive neuroscience of recollection (for hippocampus, see for example Eichenbaum et al., 2007; Moscovitch et al., 2016; for left AG, see Cabeza et al., 2012; Humphrey et al., 2021; Rugg & King, 2018), we analyzed the hippocampus and left AG independently of the remaining ROIs. Parameter estimates from the left and right hippocampus were subjected to a 2 (task) x 2 (age group) x 2 (memory judgment) x 2 (hemisphere) mixed-design ANOVA. For the left AG, an analogous ANOVA (factors of task, age group, memory judgment) was implemented. Parameter estimates extracted from the remaining regions (left MPFC, PCC, PHC and MTG) were analyzed with a 2 (task) x 2 (age group) x 2 (memory judgement) x 4 (region) mixed-design ANOVA. ANOVAs that yielded significant interactions involving the factor of age group were followed up with an ANCOVA to control for the potentially confounding effect of age differences in associative memory performance (cf. de Chastelaine et al., 2016). To determine whether DA impacted trial-wise variability of recollection-related neural activity, we employed an analogous approach to examine across-trial standard deviations of the single-trial parameter estimates as a function of task, age group, memory judgment and region. Since these analyses failed to identify any effects of task, we relegate their description to the Supplementary Materials.

Table 1. Regions of interest for analyses of recollection.

ROI	Peak_MNI (x, y, z)
Left PHC	-21, -37, -17
Left AG	-51, -70, 37
Left MTG	-57, -55, 16
Left MPFC	-3, 56, 13
Left PCC	-6, -46, 37
Left hippocampus	-24, -13, -20
Right hippocampus	27, -16, -20

2.6.2.2 Trial-wise generalized mixed-effects analyses

To anticipate the results, the ROI analyses described above failed to identify significant left AG recollection effects in older adults. Because of the potential theoretical significance of this finding, we went on to employ generalized linear mixed-effects models to further examine recollection effects in this region. A model was constructed to assess whether trial-wise estimates of retrieval-related AG activity were predictive of associative recognition judgments, and whether any such relationship varied across age group. The model employed trial-wise binarized associative recognition outcomes (i.e., intact vs. rearranged) as the dependent variable. Age group, left AG BOLD activity (AG_{BOLD}) and the two-way interaction between these variables were entered as the fixed effects predictors. Participant-wise intercept and slope terms were entered into the model as random effects. The generalized mixed-effects model was estimated in R (R core Team 2018) using the glmer function in the lme4 package (Bates et al., 2015). Syntax of the model was as follows:

$$\text{Memory} = \text{Age group} + AG_{BOLD} + \text{Age Group} \times AG_{BOLD} + (1 + AG_{BOLD} \mid \text{Subject})$$

2.6.2.3 Whole brain analysis

For the reasons noted above, we also conducted an exploratory whole brain analysis of the fMRI data. The analysis proceeded in two stages. In the first stage, separate GLMs were constructed for each participant. Neural activity elicited by test pairs was modeled as a delta function and convolved with a canonical hemodynamic response function (HRF) and a second, ‘delayed’ HRF generated by shifting an orthogonalized canonical HRF one TR (2s) later in time (the results for the delayed regressor did not reveal any theoretically significant effects beyond those identified with the canonical HRF and are not reported). Events of interest (intact, rearranged and correctly rejected new trials) were separately modeled for the single and dual tasks. Covariates of no interest included events of no interest, the 30-s rest breaks, the six motion regressors, four constants modeling the mean BOLD signal for each test block, and spike regressors modeling volumes showing a transient displacement of > 1mm or > 1 degree in any direction.

In the second stage of the whole brain analyses, participant-specific parameter estimates for each event of interest were subjected to a 2 (age group: young, older) x 2 (task: single, dual) x 3 (memory judgment: intact, rearranged, correct rejection) ANOVA. The ANOVA was subjected to a height threshold of $p < 0.001$ combined with a cluster extent threshold of $p < 0.05$ after FWE correction.

3. Results

3.1 Behavioral Results

The behavioral data were reported in detail in Horne et al. (2021). For the convenience of the reader, we re-present the data in Tables 2-4 and briefly describe the outcomes from their analysis.

3.1.1 Associative Memory Performance

Table 2 shows the proportions of accurate judgments to intact, rearranged and new pairs, along with associative memory performance (pR) for the single and dual task conditions. One sample t-tests indicated that pR exceeded the chance value of 0 in both young and older adults in each task condition (ts > 8.01, ps < 0.001, Cohen's ds > 1.51, BF_{10}s > $1.0e^6$). A 2 (age group) x 2 (task) ANOVA of pR estimates revealed main effects of task [$F(1, 54) = 11.88$, $p < 0.001$, partial $\eta^2 = 0.18$, $BF_{incl} = 24.31$] and age group [$F(1, 54) = 35.32$, $p < 0.001$, partial $\eta^2 = 0.40$, $BF_{incl} = 5.51e^4$]. The task x age group interaction was not significant [$F(1, 54) = 2.13$, $p = 0.150$, partial $\eta^2 = 0.04$, $BF_{incl} = 0.62$)]. In light of the pre-experimental predictions, planned pairwise t-tests were conducted nevertheless to examine task effects in each age group. Younger adults' associative memory performance did not significantly differ between the two task conditions [$t(27) = 1.59$, $p = 0.123$, Cohen's $d = 0.30$, $BF_{10} = 0.62$], whereas pR was significantly lower in the dual than in the single task condition in the older adults [$t(27) = 3.14$, $p = 0.005$, Cohen's $d = 0.58$, $BF_{10} = 9.91$].

Further examination of the associative hit and false alarm rates revealed that hit rates did not differ as a function of task condition in either age group [for young, $t(27) = 0.94$, $p = 0.354$, Cohen's $d = 0.18$, $BF_{10} = 0.30$; for older, $t(27) = 0.89$, $p = 0.381$, Cohen's $d = 0.17$, $BF_{10} = 0.29$]. Older adults demonstrated higher associative false alarm rates in the dual than in the single task condition [$t(27) = 2.54$, $p = 0.017$, Cohen's $d = 0.48$, $BF_{10} = 2.91$], but there was no significant task effect in young adults [$t(27) = 1.07$, $p = 0.292$, Cohen's $d = 0.20$, $BF_{10} = 0.34$]. Analyses of the associative hit and false alarm rates collapsed across task revealed lower hit rates ($M_{young} = 0.70$, $SD_{young} = 0.15$, $M_{older} = 0.57$, $SD_{older} = 0.18$) and higher false alarm rates ($M_{young} = 0.19$, $SD_{young} = 0.10$, $M_{older} = 0.30$, $SD_{older} = 0.18$) in the older group, ts > 2.73, ps < 0.01, Cohen's ds > 0.72, BF_{10}s > 5.42.

We also examined estimates of response bias using the Br metric. Mean Br in the young adults was 0.39 (SD = 0.21) and 0.41 (SD = 0.19) for the single and dual tasks respectively. Br estimates for older adults were 0.38 (SD = 0.22) in the single task and 0.43 (SD = 0.23) in the dual task. A 2 (age group) x 2 (task) ANOVA failed to identify any significant effects: for the main effect of age group, $F(1, 54) = 0.01$, $p = 0.942$, partial $\eta^2 < 0.001$, $BF_{incl} = 0.42$; for the main effect of task, $F(1, 54) = 3.47$, $p = 0.068$, partial $\eta^2 = 0.06$, $BF_{incl} = 0.90$; for the age group x task interaction, $F(1, 54) = 0.80$, $p = 0.374$, partial $\eta^2 = 0.02$, $BF_{incl} = 0.37$.

Table 2. Mean proportions (SD) of intact, rearranged, and new judgments given to intact, rearranged, and new test pairs and pR for each age group and task condition. Correct judgments in bold font.

	Young		*Older*	
	Single task	Dual task	Single task	Dual task
Intact judgments				
Intact pairs	**0.71 (0.15)**	**0.70 (0.16)**	**0.58 (0.16)**	**0.56 (0.21)**
Rearranged pairs	0.18 (0.12)	0.20 (0.11)	0.27 (0.18)	0.33 (0.19)
New pairs	0.04 (0.05)	0.04 (0.05)	0.10 (0.09)	0.12 (0.11)
Rearranged judgments				
Intact pairs	0.17 (0.09)	0.18 (0.12)	0.28 (0.13)	0.27 (0.15)
Rearranged pairs	**0.56 (0.14)**	**0.57 (0.13)**	**0.45 (0.16)**	**0.37 (0.15)**
New pairs	0.22 (0.14)	0.22 (0.13)	0.28 (0.12)	0.27 (0.16)
New judgments				
Intact pairs	0.12 (0.09)	0.12 (0.07)	0.14 (0.06)	0.17 (0.10)
Rearranged pairs	0.26 (0.12)	0.23 (0.09)	0.29 (0.14)	0.30 (0.15)
New pairs	**0.74 (0.15)**	**0.73 (0.16)**	**0.62 (0.16)**	**0.61 (0.19)**
pR	0.53 (0.19)	0.49 (0.18)	0.31 (0.14)	0.22 (0.15)

3.1.2 RTs to test items

Mean RTs for the critical trial types are shown in Table 3. A 2 (age group) x 2 (task) x 2 (memory judgment: intact, rearranged) ANOVA revealed main effects of task [F(1, 54) = 15.99, $p < 0.001$, partial $\eta^2 = 0.23$, $BF_{incl} = 62.27$], memory judgment [F(1, 54) = 200.10, $p < 0.001$, partial $\eta^2 = 0.79$, $BF_{incl} = 4.29e^{38}$], and an age group x memory judgment interaction [F(1, 54) = 7.97, p = 0.007, partial $\eta^2 = 0.13$, $BF_{incl} = 122.79$]. In each age group, mean RTs for both memory judgments were faster during dual task blocks. Independent sample t-tests revealed that the age group x memory judgment interaction reflected slower RTs for intact judgments in older relative to young adults in both task conditions (ts > 2.10, ps < 0.040, Cohen's ds > 0.55, BF_{10}s > 1.66). No age difference was identified for rearranged judgments [for the single task, t(54) = 0.03, p = 0.973, Cohen's d = 0.01; $BF_{10} = 0.27$, for the dual task, t(54) = 0.21, p = 0.833, Cohen's d = 0.06; $BF_{10} = 0.28$].

Table 3. Mean RT (SD) for the associative memory task by age group and critical trial types for fMRI analyses. Intact: intact judgments to intact pairs (associative hits), Rearranged: rearranged judgments to intact or rearranged pairs (associative misses and associative correct rejections).

	Young		*Older*	
	Single task	Dual task	Single task	Dual task
Intact	1608 (311)	1546 (294)	1790 (333)	1716 (308)
Rearranged	2131 (424)	2028 (407)	2128 (347)	2049 (325)

3.1.3 Secondary task performance

Secondary task performance is summarized in Table 4. Below, we present a comparison of tone detection performance at baseline vs. dual task. The 2 (task: baseline, dual) x 2 (age group: young, older) ANOVA conducted on the tone detection performance (Hit – FA) identified a main effect of task [F(1, 54) = 35.13, $p < 0.001$, partial $\eta^2 = 0.39$, $BF_{incl} = 1.25e^{6}$], but no effects of age group [F(1, 54) = 1.36, p = 0.248, partial $\eta^2 = 0.03$, $BF_{incl} = 0.39$] nor an age group x task interaction [F(1, 54) = 1.48, p = 0.229, partial $\eta^2 = 0.03$, $BF_{incl} = 0.61$]. Thus, tone detection performance during dual task blocks relative to baseline was significantly lower for both groups. The 2 (task: baseline, dual) x 2 (age group: young, older) ANOVA of mean RTs to target tones revealed main effects of task [F(1, 54) = 386.01, $p < 0.001$, partial $\eta^2 = 0.88$, $BF_{incl} = 5.66e^{26}$] and age group [F(1, 54) = 6.80, p = 0.012, partial $\eta^2 = 0.11$, $BF_{incl} = 4.49$], as well as a task x age group interaction [F(1, 54) = 5.74, p = 0.020, partial $\eta^2 = 0.10$, $BF_{incl} = 2.74$]. Both groups were slower to respond to target tones under dual task conditions, relative to baseline RT. Further analyses revealed that older adults were significantly slower to respond to target tones than younger adults in the dual task [t(54) = 2.88, p = 0.006, Cohen's d = 0.77, $BF_{10} = 7.38$] but not at baseline [t(54) = 1.50, p = 0.141, Cohen's d = 0.40, $BF_{10} = 0.68$].

Table 4. Performance on the tone detection task (SD) by age group and task condition.

	Hit - FA (tones)		*Mean RT to target tones*	
	Baseline	Dual task	Baseline	Dual task
Young	0.99 (0.02)	0.90 (0.13)	451 (97)	709 (157)
Older	0.99 (0.01)	0.85 (0.17)	486 (77)	816 (118)

3.2 fMRI Results

3.2.1 Hippocampal recollection effects

Parameter estimates from the left and right hippocampus were subjected to a 2 (task) x 2 (age group) x 2 (memory judgment) x 2 (hemisphere) ANOVA. As is evident from Table 5 and Fig 1, significant main effects of memory judgment and hemisphere were identified, reflecting greater BOLD activity for intact than rearranged judgments, and greater activity in the left than the right hippocampus. The main effect of task was also significant, but this effect interacted with age group. Further analyses revealed that, for older adults only, hippocampal activity was greater in the dual than in the single task [t(27) = 3.11, p = 0.004, Cohen's d = 0.59, $BF_{10} = 9.26$; for young adults, t(27) = 0.28, p = 0.786, Cohen's d = 0.05, $BF_{10} = 0.21$]. Neither the main effect of age group nor any other interaction effect attained significance.

When we repeated the ANOVA with an ANCOVA to control for the associative recognition performance in the single and dual tasks, the task x age group interaction failed to attain significance [F(1, 52) = 2.85, p = 0.097, partial $\eta^2 = 0.05$]. This null finding is however strongly qualified by the associated Bayes factor ($BF_{incl} = 3.43$) which offers moderate evidence in favor of the alternative hypothesis. Regardless of the status of this interaction, the original ANOVA failed to reveal any evidence of an interaction between the factors of age group and memory judgment, or for the three-way interaction between these factors and task (see Table 5).

Thus, we found no evidence that hippocampal recollection effects differed according to age group or task condition.

Table 5. ANOVA results for parameter estimates extracted from left and right hippocampus. Significant effects in bold font. Task (single, dual), age group (younger, older), memory judgment (intact, rearranged), hemisphere (left hippocampus, right hippocampus). BF_{incl} values are provided for nonsignificant results.

Source	F (1, 54)	p.value	partial η^2	BF_{incl}
task	**6.11**	**0.017**	**0.10**	**8.05**
age group	0.22	0.644	0.004	0.23
memory judgment	**40.51**	**< 0.001**	**0.43**	**$5.33e^6$**
hemisphere	**10.43**	**0.002**	**0.16**	**$2.21e^3$**
task x age group	**4.41**	**0.041**	**0.08**	**3.26**
task x memory judgment	3.65	0.062	0.06	0.41
task x hemisphere	1.92	0.172	0.03	0.54
age group x memory judgment	0.05	0.830	0.001	0.15
age group x hemisphere	1.43	0.238	0.03	0.61
memory judgment x hemisphere	0.63	0.432	0.01	0.16
task x age group x memory judgment	0.001	0.977	< 0.001	0.20
task x age group x hemisphere	1.59	0.213	0.03	0.51
task x memory judgment x hemisphere	0.04	0.834	0.001	0.21
age group x memory judgment x hemisphere	0.22	0.641	0.004	0.20
hemisphere x task x memory judgment x age group	2.13	0.151	0.04	0.31

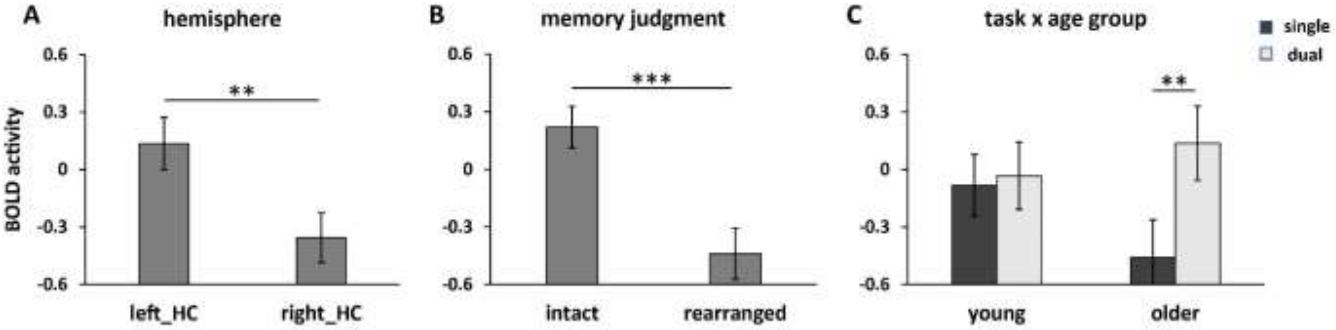

Fig 1. Significant effects in the hippocampus for (A) hemisphere, (B) memory judgment and (C) the age group x task interaction. BOLD activity is in arbitrary units, error bars represent standard error of the mean. ** $p < 0.01$; *** $p < 0.001$.

3.2.2 AG recollection effects

As is evident from Table 6, the ANOVA conducted on the parameter estimates from the left AG revealed significant main effects of age group and memory judgment. A significant age group x memory judgment interaction was also identified, indicating that recollection effects differed according to age group (see Fig 2A). Follow-up analyses revealed a significant recollection effect in the young adults [t(27) = 5.04, $p < 0.001$, Cohen's d = 0.952, BF_{10} = 848.04], while no such effect was evident in the older adults [t(27) = 0.61, $p = 0.548$, Cohen's d = 0.12, BF_{10} = 0.24]. Despite the absence of a significant task x memory judgment x age group interaction, we tested for recollection effects in the older adults in each task separately: t-tests failed to reveal a significant effect in either task [single task, t(27) = 1.61, $p = 0.120$, Cohen's d = 0.30, BF_{10} = 0.63; dual task, t(27) = 0.28, $p = 0.781$, Cohen's d = 0.05, BF_{10} = 0.21; for young adults, ts > 3.58, ps < 0.002, Cohen's ds > 0.67, BF_{10}s > 26.84, see Figs 2B and C].

When we repeated the ANOVA after controlling for associative recognition performance in the single and dual tasks, the age group x memory judgment interaction remained significant [F(1, 52) = 7.49, $p = 0.008$, partial $\eta^2 = 0.13$, BF_{incl} = 5.16]. Consistent with the above-mentioned results, simple-effects analyses revealed a significant recollection effect only in young adults ($M_{difference}$ = 0.88, $p < 0.001$; for older adults, $M_{difference}$ = 0.06, $p = 0.757$). In summary, we found no evidence for an influence of task on recollection effects in either group. Moreover, reliable AG recollection effects could be identified in the young adults only.

Table 6. ANOVA results for parameter estimates extracted from left AG. Significant effects in bold font. Task (single, dual), age group (younger, older), memory judgment (intact, rearranged). BF_{incl} values are provided for nonsignificant results.

Source	F (1, 54)	p.value	partial η^2	BF_{incl}
task	0.23	0.634	0.004	0.19
age group	**14.56**	**< 0.001**	**0.21**	**70.66**
memory judgment	**17.12**	**< 0.001**	**0.24**	**20.36**
task x age group	0.51	0.477	0.01	0.28
age group x memory judgment	**11.02**	**0.002**	**0.17**	**4.98**
task x memory judgment	2.93	0.092	0.05	0.33
task x memory judgment x age group	0.02	0.891	< 0.001	0.25

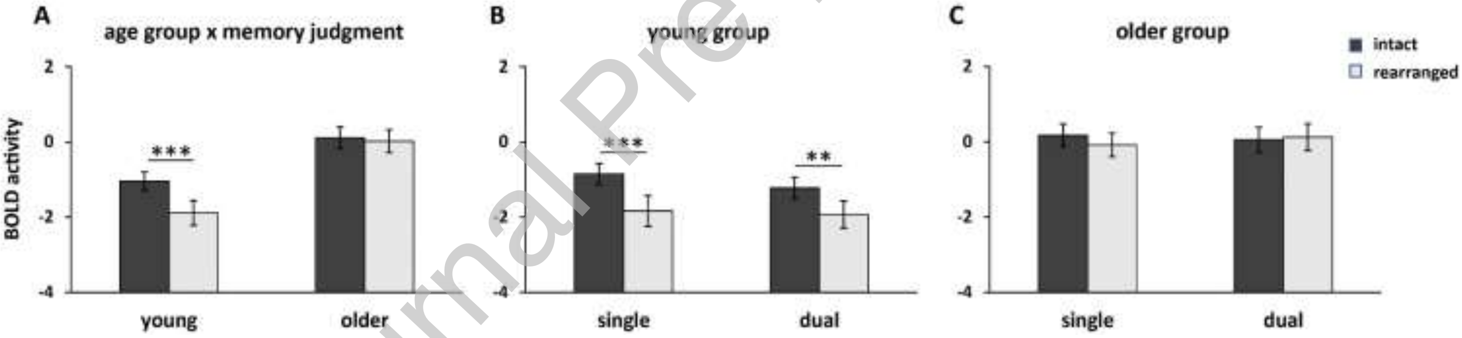

Fig 2. Plots illustrating (A) the age group x memory judgment interaction in the left AG, and the comparison between intact and rearranged judgments for each task in (B) young adults and (C) older adults. BOLD activity is depicted in arbitrary units, error bars represent standard error. ** $p < 0.01$; *** $p < 0.001$.

3.2.3 Recollection effects in other core recollection regions

Parameter estimates from the remaining ROIs were entered into a 2 (task) x 2 (age group) x 2 (memory judgment) x 4 (region: left MPFC, PHC, PCC, MTG) ANOVA. As is evident from Table 7 and Fig 3, all of the main effects except task were significant. Of importance, both age group and region significantly interacted with memory judgment. In addition, significant age group x region and task x age group x region interactions were identified. No other effects were significant.

As is evident from Fig 3A, the age group x memory judgment interaction indicated that recollection effects were generally weaker in the older adults. Nonetheless, pair-wise t-tests identified significant recollection effects in both young and older adults (ts > 5.36, ps < 0.001, Cohen's ds > 1.14, BF_{10}s > $1.91e^3$).

The region x memory judgment interaction is plotted in Fig 3B. As is evident from the figure, recollection effects were larger in the MPFC than in the other regions. Despite the different magnitudes of recollection effects across regions, however, pairwise contrasts between memory judgments conducted on each region identified significant recollection effects in each case (ts > 4.29, ps < 0.001, Cohen's ds > 0.57, BF_{10}s > 298.51).

The significant task x age group x region interaction indicated that the age group x task interaction varied across regions. To unpack this three-way interaction, a 2 (task) x 2 (age group) ANOVA was conducted for each region. Complete results of these analyses are presented in the Supplementary Materials. In brief, in MPFC, the main effect of age group was significant, indicating greater mean BOLD activity in older than in young adults. In PCC and PHC, age group significantly interacted with task. Further analyses revealed that in older adults, mean BOLD activity was greater in the dual than in the single task in both regions. By contrast, no significant task effect was evident in young adults. A significant main effect of task was evident in MTG, indicating greater mean BOLD activity in the dual than in the single task (see also Supplemental Fig 1).

We repeated the initial ANOVA as an ANCOVA model controlling for associative recognition performance in the single and dual tasks. With the addition of these covariates, the age group x memory judgment interaction did not attain significance [$F(1, 52) = 1.50$, $p = 0.226$, partial $\eta^2 = 0.03$, $BF_{incl} = 0.77$]. By contrast, the task x age group x region interaction remained significant, albeit unsupported by the accompanying Bayes factor [$F(2.50, 129.78) = 3.37$, $p = 0.028$, partial $\eta^2 = 0.06$, $BF_{incl} = 0.76$]. An ANCOVA was conducted in each ROI to follow up this interaction. With the additional covariates, both the main effect of age group in MPFC and the age group x task interaction in PHC (but not the PCC) remained significant (see Supplementary Materials for complete results).

In summary, recollection effects in MPFC, PCC, PHC and MTG did not differ between task conditions. Older adults demonstrated an overall weaker recollection effect in these regions than young adults, but this age difference was nonsignificant after controlling for individual differences in associative recognition performance.

Table 7. ANOVA results for parameter estimates extracted from MPFC, PCC, PHC and MTG. Significant effects in bold font. Task (single, dual), age group (younger, older), memory judgment (intact, rearranged), region (left MPFC, PCC, PHC, MTG). BF_{incl} values are provided for the nonsignificant results.

Source	df	df error	F	p.value	partial η^2	BF_{incl}
task	1	54	1.23	0.273	0.02	0.25
age group	**1**	**54**	**19.27**	**< 0.001**	**0.26**	**230.48**
memory judgment	**1**	**54**	**68.12**	**< 0.001**	**0.56**	**$1.17e^{9}$**
region	**2.50**	**135.05**	**66.88**	**< 0.001**	**0.55**	**$7.08e^{75}$**
task x age group	1	54	2.32	0.134	0.04	1.02
task x region	2.54	137.23	1.03	0.372	0.02	0.03
task x memory judgment	1	54	2.28	0.137	0.04	0.25
age group x memory judgment	**1**	**54**	**5.78**	**0.020**	**0.10**	**0.94**
age group x region	**2.50**	**135.05**	**7.25**	**< 0.001**	**0.12**	**$2.24e^{8}$**
memory judgment x region	**2.69**	**145.09**	**9.98**	**< 0.001**	**0.16**	**0.49**
task x age group x memory judgment	1	54	0.25	0.620	0.01	0.15
task x age group x region	**2.54**	**137.23**	**3.44**	**0.025**	**0.06**	**0.71**
task x memory judgment x region	2.38	128.70	2.08	0.120	0.04	0.04
age group x memory judgment x region	2.69	145.09	1.14	0.332	0.02	0.04
task x age group x memory judgment x region	2.38	128.70	1.25	0.294	0.02	0.08

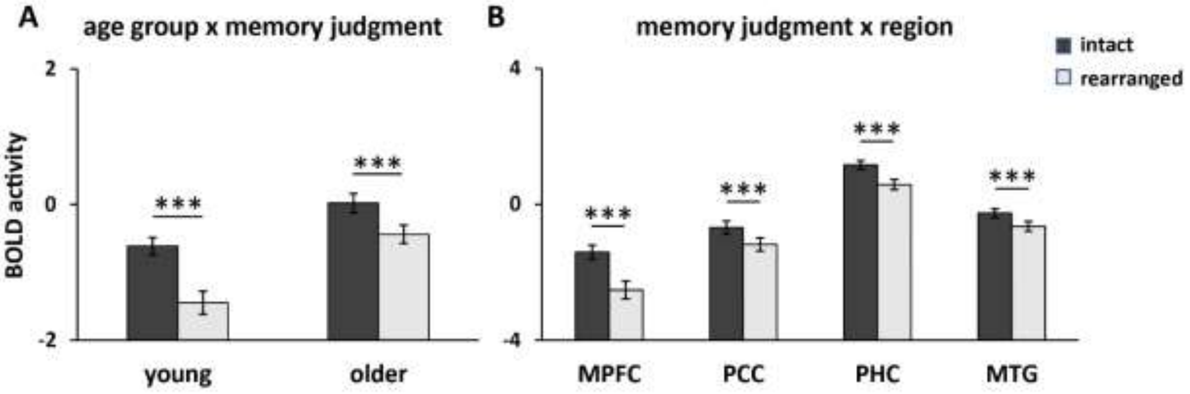

Fig 3. Plots for significant (A) memory judgment x age group, and (B) memory judgment x region interaction effects evident in left MPFC, PCC, PHC and MTG. BOLD activity is depicted in arbitrary units, error bars represent standard error. *** $p < 0.001$.

3.2.4 Linear mixed-effects analysis on the AG data

We constructed a generalized linear mixed-effects model to examine the relationship between trial-wise BOLD activity in the left AG (i.e., AG_{BOLD}) and associative memory judgments (see Methods). As is evident from Table 8, both age group and AG_{BOLD} significantly predicted the odds of an 'intact' judgment. Crucially, the age group x AG_{BOLD} interaction was also significant. [When we included task and the two and three-way interactions involving task as additional predictors of memory judgments, no predictors involving the task factor attained significance (ps > 0.585)].

Table 8. Generalized linear mixed effect regression results for the left AG bold activity predicting associative memory accuracy. Significant effects in bold font.

term	logit odds	std.error	z	p.value	95% CI
intercept	**0.74**	**0.12**	**6.05**	**< 0.001**	**0.50 — 0.97**
age group	**-0.39**	**0.17**	**-2.29**	**0.022**	**-0.73 — -0.057**
AG_{BOLD}	**0.04**	**0.01**	**4.85**	**< 0.001**	**0.03 — 0.06**
age group x AG_{BOLD}	**-0.03**	**0.01**	**-2.63**	**0.009**	**-0.06 — -0.009**

Note: rearranged trials, young adults and the dual task treated as reference conditions.

To follow-up the age group x AG_{BOLD} interaction, we repeated the analyses for each age group separately. As can be seen in Table 9 and Fig 4, while greater AG activity was related to an increased likelihood of an intact judgment in young adults, no such relationship was evident in older adults.

Table 9. Generalized linear mixed effect regression results for the left AG bold activity predicting associative memory accuracy in each age group. Significant effects in bold font.

	term	logit odds	std.error	z	p.value	95% CI
Young						
	intercept	**0.74**	**0.09**	**7.92**	**< 0.001**	**0.56 – 0.92**
	AG_{BOLD}	**0.05**	**0.01**	**4.50**	**< 0.001**	**0.03 – 0.06**
Older						
	intercept	**0.34**	**0.14**	**2.36**	**0.018**	**0.06 – 0.62**
	AG_{BOLD}	0.01	0.01	0.69	0.493	-0.01 – 0.02

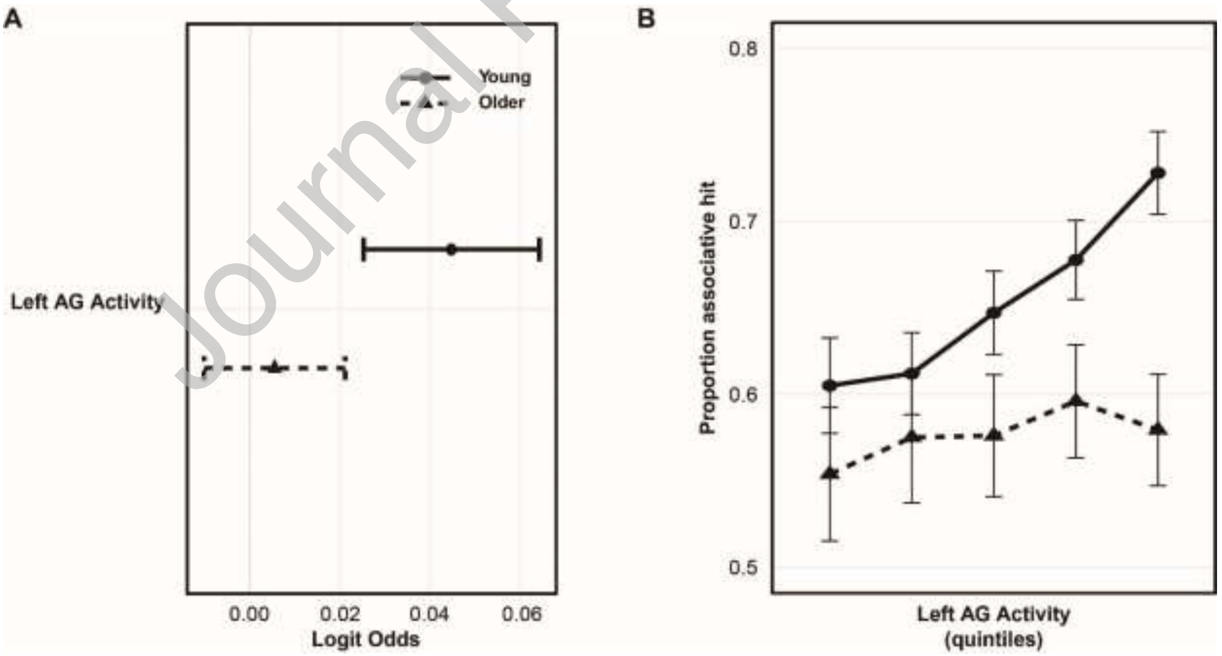

Fig 4. A: Logit odds and 95% confidence intervals are plotted for left AG activity separately for each age group. B: Trial-wise left AG activity sorted within-participant into quintiles (bars represent standard

error). Increasing trial-wise AG activity predicted an increasing proportion of correct associative memory judgments in young adults only.

3.2.5 Recollection effects in the anatomically defined left AG

In light of the lack of evidence for an AG recollection effect in older adults in the ROI analyses described above, we went on to examine possible effects across the entire extent of the left AG (see Supplementary Materials for results of whole brain analyses examining the recollection effects as a function of age group and task condition). We employed an anatomically defined ROI that encompassed both the anterior (PGa) and posterior (PGp) sub-regions of the AG as defined by the Anatomy toolbox v3.0 (Eickhoff et al., 2005, 2006, 2007, see also Rugg & King, 2018). Examination of the recollection effects in the anatomical ROI was conducted using the whole brain analysis approach described in the Methods combined with a small volume correction confined to the ROI (using a voxel-wise FWE corrected threshold of $p < 0.05$). A significant age group (young, older) x memory judgment (intact, rearranged) interaction was revealed in a cluster of 21 voxels (peak: -51, -64, 41). Of importance, the identified cluster included a subpeak (-48, -70, 38) that was closely adjacent to the *a priori* defined AG ROI (see Table 1). Follow-up voxel-wise comparisons between the intact and rearranged judgments conducted within the anatomically defined ROI in each age group revealed a significant recollection effect in young but not in older adults. Thus, consistent with the findings from the functional ROI analysis, a left AG recollection effect was only detectable in the young adults.

4. Discussion

The present study examined the effects of divided attention at retrieval on the neural correlates of recollection in young and older adults. In both age groups, neither recollection effects nor recollection-related differences in across-trial BOLD variability differed significantly as a function of the DA manipulation. Regardless of task condition, age-invariant recollection effects were identified in left and right hippocampus and, after controlling for individual differences in associative recognition performance, in left MPFC, MTG, PHC and PCC. Strikingly, recollection effects in the left AG were robust in young participants, but undetectable in older adults.

The primary goals of the present study were to examine whether DA impacted recollection-related neural activity and to identify any moderating effects of age group. Focusing on the well-characterized core recollection network (Rugg & Vilberg, 2013) we failed to detect an influence of DA on recollection effects or recollection-related BOLD variability in either young or older adults. These null findings were supported by the outcome of an exploratory whole brain analysis, which also failed to find evidence for an effect of DA on recollection-related activity. Together, these findings add to much behavioral evidence (see Introduction) in suggesting that, regardless of age, the efficacy of the processes supporting the retrieval and representation of a prior episode are largely immune to resource depletion caused by DA. Of note, the null findings for DA on fMRI recollection effects in the young group suggest that in addition to having no detectable effect on memory performance in these participants, DA did not impact the amount of information recollected about the study events (see Introduction).

Why then did DA impair associative recognition performance in our older adults[1]? A clue comes from the finding that the impairment was driven exclusively by an elevated associative false alarm rate. Therefore, following Horne et al. (2021), we think it unlikely that the lower associative memory performance of the older group under DA is attributable to disrupted processing of the retrieval cues. Together with the fMRI findings reported in that paper, the present findings suggest that the functional locus of the impact of DA on older adults' memory performance was upstream of the processes supporting such functions as the retrieval, representation or monitoring of associative information. The specific locus of this effect, and the reason why it selectively elevated false alarms, are unclear (see below, and Horne at al., 2021 for further discussion).

As was first reported and discussed by Horne et al. (2021), RTs for both intact and rearranged judgments were reliably faster in the dual than the single task condition in both age groups. This finding constitutes compelling evidence of an influence of the task manipulation on performance during the memory test and mitigates concerns that the weak effects of the manipulation on fMRI recollection effects might merely reflect the choice of a dual task that interfered minimally with performance on the primary task. As was noted by Horne et al. (2021), reduced test RTs in the dual task condition might reflect the requirement to rapidly switch attention between the two tasks (and their respective sensory modalities), leading participants to allocate less time to the memory test in the dual task condition because of the need to monitor and respond to the tones (cf. Craik et al., 2000). The finding that, for the young adults at least, this speed-up in RT was not accompanied by a concomitant reduction in accuracy suggests that these participants were not adhering to the instruction to respond as quickly as they could without sacrificing accuracy in the single task condition. By contrast, in the older group the speed-up might offer a clue as to why the dual task condition was associated with an elevated false alarm rate.

Prior studies have employed functional neuroimaging to examine the neural correlates of the effects of DA on episodic encoding in young adults (Iidaka et al., 2000; Kensinger et al., 2003; Uncapher & Rugg, 2005, 2008), with two studies contrasting these effects between age groups (Anderson et al., 2000; Kim & Giovanello et al., 2011a). To our knowledge, the present study is however the first attempt to use fMRI to examine the impact of DA on the neural correlates of successful episodic retrieval, or to contrast these correlates across samples of younger and older adults. We elected to employ a secondary task (tone detection) that would compete with the retrieval test for domain general rather domain specific resources. This choice was driven by our hypothesis that post-retrieval monitoring depends heavily on such resources (see Introduction). We note however that prior studies of DA, both at encoding (e.g. Kim & Giovanello et al., 2011a, b) and retrieval (e.g. Fernandes & Moscovitch, 2000, 2002, 2003), have reported that deleterious effects of DA tend to be greater when the secondary task competes for domain specific resources (notably, Kim & Giovanello, 2011a reported that relative to item encoding, associative encoding was uniquely impacted by a ‘relational’ secondary task). Whether the present findings extend to circumstances where retrieval is paired with secondary tasks that compete for domain specific resources, such as those engaged by relational processing, is an interesting question for future research.

We identified robust age-invariant recollection effects in the hippocampus in both task conditions. Analogous findings were reported in Dulas and Duarte (2012, 2016) and Wang et al. (2016), where it was also reported that hippocampal recollection effects were age-invariant. By contrast, despite employing the same associative recognition task as here, de Chastelaine et al. (2016) reported an age-related attenuation of associative recollection effects. The age difference did not persist, however, after controlling for individual differences in associative memory performance. Together with the prior findings, the present results suggest that healthy older and young adults recruit the hippocampus to an equivalent extent when retrieving episodic information.

Older adults also demonstrated reliable recollection effects in MPFC, MTG, PHC and PCC, although these effects were weaker than those evident in the young participants. Echoing the findings of de Chastelaine et al. (2016) described above, these age differences were however nonsignificant after controlling for memory performance. The findings are consistent with those of prior studies that also reported limited or null effects of age on extra-hippocampal recollection effects, especially when memory performance was matched or statistically equated across age groups (de Chastelaine et al., 2016; Dulas & Duarte, 2012; Wang & Giovanello, 2016; Wang et al., 2016; but see Angel et al., 2013 for contrasting findings). The findings raise the possibility that age differences in recollection effects manifested in these core recollection regions are a reflection not of age-related reductions in the functional integrity of the regions but, rather, of the negative association between age and memory performance. That is, the magnitudes of older adults' recollection effects approximate those of young participants demonstrating the same level of memory performance (see Hou et al., 2021 for a review of studies examining age effects on recollection-related activity before and after controlling for memory performance). Overall, together with prior reports, our results suggest that recollection effects in these core recollection regions are only modestly, if at all, affected by age.

In striking contrast, an age-related reduction in recollection effects in the left AG was evident both before and after controlling for memory performance. Furthermore, AG recollection effects were not only attenuated, but were undetectable, in the older age group. These null findings were corroborated by a trial-wise, generalized LME analysis and by voxel-wise analysis of recollection-related activity in an anatomically defined cortical parcel corresponding to the left AG. To our knowledge, a seemingly complete absence of left AG recollection effects in older adults is almost unprecedented (cf. Duarte et al., 2010); typically, such effects have been reported to be robust and either equivalent in magnitude to those of younger adults (de Chastelaine et al., 2016; Trelle et al., 2019; Wang et al., 2016) or attenuated but seemingly statistically significant (Daselaar et al., 2006). Of course, we cannot rule out the possibility that the present findings reflect an idiosyncrasy of this specific sample of older adults, and hence have no implications for furthering the understanding of the functional role of the AG in memory retrieval. This possibility seems unlikely, however, in light of the robust recollection effects identified in the same sample in other core recollection ROIs, not least the hippocampus. Rather, we conjecture that the absent AG recollection effects in our older adults was the result of interference from the tones presented during both the single and the dual task conditions. One prominent account of the functional significance of AG recollection effects is especially consistent with this possibility. According to the 'attention to memory' (AtoM) account (Cabeza et al., 2012; Ciaramelli et al., 2008), these effects reflect the role of this cortical region in 'bottom-up' attention, whereby successful recollection automatically elicits attentional re-orienting towards the recollected content. From this perspective, the present findings for our older adults reflect the 'capture' of this orienting mechanism by the tones that were presented in both task conditions. This proposal receives support from prior evidence that older adults are more distractable, and thus find it more difficult to maintain attention on a single source of information, than young participants (e.g., Schmitz et al., 2010; Tsvetanov et al., 2013; for reviews, see Campbell et al., 2020; Hasher, 2015; see Hasher et al., 1999 for a review of early findings). By this argument, our older participants were distracted by the tones even when they were not task relevant, and this led to a failure to orient automatically to recollected test pairs.

Despite the seemingly absent left AG recollection effects in the older sample, these participants exhibited robustly above chance associative memory performance in both task conditions. Thus, the effects (at least as they are indexed by fMRI BOLD responses) do not appear to reflect processes that play a necessary role in successful recollection. These findings are consistent with reports of patients with parietal lesions encompassing the AG (Berryhill et al., 2009; Ciaramelli et al., 2017; Simons et al., 2010) who demonstrated intact or near-intact associative and source memory performance. It should be noted, however, that compared with healthy controls, memory judgments of patients with parietal lesions tend to be associated with lower levels of subjective recollection ('Remember' judgments) and confidence (Ally et al., 2008; Ciaramelli et al., 2017; Davidson et al., 2008; Hower et al., 2014; Simons et al., 2010). Thus, the present findings leave open the possibility that the angular gyrus plays a necessary role in subjective memory judgments, as has been suggested previously (Bonnici et al., 2018; Ciaramelli et al., 2017; Hower et al., 2014).

Although we only identified limited effects of age group on fMRI recollection effects, item-related BOLD responses (responses elicited by both intact and rearranged pairs relative to baseline) varied robustly as a function of age group in left MPFC. Similar age differences were reported by Wang et al. (2016) for item-related BOLD responses in MPFC and hippocampus, and by Hou et al. (2021) for item-related responses across the entire core recollection network. In both of these prior studies, older adults demonstrated comparable recollection effects to young adults in these same regions. The present findings converge with these prior results, adding to the evidence that the magnitudes of item-related activity and recollection effects in young and older adults are fully dissociable. The functional significance, if any, of these age differences in item-related activity is obscure.

In both age groups, item-related activity in the MTG was elevated in the dual relative to the single task condition (an analogous effect was also evident in the PHC, albeit for older adults only). The functional significance of these findings is also uncertain, but it is tempting to ascribe them to an upregulation of neural activity in response to the increased cognitive challenge associated with the dual task requirement (see Introduction). Regardless of the validity of this conjecture, these findings demonstrate that DA not only impacted behavioral performance on the associative recognition test (see prior discussion of the RT findings), but also modulated task-related neural activity, further suggesting that null findings associated with the task manipulation were not a consequence of an ineffectual secondary task.

There are several limitations to the present study. First, the modest sample sizes signal the need for caution in accepting null findings. Notably, sample size limitations might have restricted our ability to detect subtle DA effects. Second, the employment of a cross-sectional rather than a longitudinal experimental design means that we cannot distinguish between the influences of age and of age-related confounds such as cohort effects or selection bias (Rugg, 2017). Third, the estimates of neural activity that were employed (fMRI BOLD signals) might have been confounded with age differences in vascular factors mediating between neural activity and the BOLD signal (e.g., Liu et al., 2013; Lu et al., 2011; Tsvetanov et al., 2015), although the regional heterogeneity in the influence of age on recollection effects makes it unlikely the findings are solely attributable to vascular factors. Last, our DA manipulation required participants either to ignore (single task condition) or to discriminate between (dual task condition) tones presented during the associative recognition test. While this design has the advantage of exactly matching stimulus conditions across the two tasks, it raises the possibility that, by virtue of their distractibility, older participants were effectively dividing their attention in both task conditions (we have already alluded to this possibility when discussing the absent angular gyrus recollection effects in these participants). Nonetheless, as we have already noted, RTs to the test pairs and item-related BOLD responses were impacted to an equivalent extent in the young and older groups by the secondary task requirement and, in the older group only, there was also a deleterious effect on memory performance. Thus, while the two age groups might have experienced differential attentional demands in the single task condition, it is clear that the secondary task imposed additional demands regardless of age. Thus, there seems to be little reason to think that the insensitivity of the older adults' recollection effects to the task manipulation was a result of these participants being equivalently attentionally challenged in the two task conditions.

5. Conclusion

We were unable to identify any effects of divided attention at retrieval on the neural correlates of successful recollection in either young or older adults. Thus, the present findings suggest that the weak or null findings for the effects of DA on episodic retrieval reported in numerous prior behavioral studies extend to its neural correlates.

Footnote

1. We note that the ANOVA contrasting associative recognition according to age group and task condition did not give rise to a significant interaction between the two factors. As was noted in the results and discussed at more length in Horne et al. (2021), the decision nevertheless to examine the effects of task condition in each age group separately was motivated by the pre-experimental predictions that, in the older participants, DA would lead to a reduction in associative recognition performance, and that this reduction would be driven exclusively by an elevated associative false alarm rate. These predictions were fulfilled, and the associated Bayes factors provide reassurance that the findings are unlikely to be Type I errors.

Credit Author Statement

Mingzhu Hou: Methodology, Software, Validation, Formal Analysis, Data Curation, Writing – Original Draft, Review & Editing, Visualization.

Erin D. Horne: Methodology, Software, Validation, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Review & Editing, Project Administration.

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Michael D. Rugg: Conceptualization, Methodology, Validation, Formal Analysis, Resources, Writing – Original Draft, Review & Editing, Supervision, Project Administration, Funding Acquisition.

Data code availability revision

The data generated by this study are undergoing additional analyses. The data that support the findings of this study are available from the authors on request subsequent to a formal data sharing agreement. Unthresholded group maps from the whole brain analyses described in the paper are available through NeuroVault (https://identifiers.org/neurovault.collection:11991). The software, functions, formula and syntax of model that we used to generate the results are specified in the Methods section.

Acknowledgements

This work was supported by the National Institute on Aging [grant numbers R21AG054197, RF1AG039103].

Declaration of Competing Interest

None

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