Reduced memory precision in older age is associated with functional and structural differences in the angular gyrus

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Abstract

Growing evidence indicates decreased fidelity of mnemonic representations to play a role in age-related episodic memory deficits, yet the brain mechanisms underlying such reductions remain unexplored. Using functional and structural neuroimaging and a continuous report task we examined how changes in two key nodes of the posterior-medial memory network, the hippocampus and the angular gyrus, might underpin loss of memory precision in older age. An age-related reduction in activity reflecting successful memory retrieval was observed in the hippocampus, whereas activity associated with graded variation in memory precision was decreased in the angular gyrus. Grey matter volume of the angular gyrus further predicted individual differences in memory precision in older age, beyond variation in successful memory retrieval. These findings highlight the importance of functional and structural integrity of the angular gyrus in constraining memory precision in older age, advancing current understanding of hippocampal and parietal contributions to age-related episodic memory decline.

Introduction

Human ageing is accompanied with various changes in cognitive function[1,2]. One of the cognitive domains most vulnerable to age-related deterioration is episodic memory[2–4], the long-term memory that enables us to recollect the spatio-temporal, perceptual, and emotional details that constitute a prior experience[5,6]. Growing evidence suggests a critical component of age-related episodic memory loss to be reduced quality and specificity with which information can be encoded into and retrieved from memory[7–10]. Even when able to successfully retrieve similar amounts of information from memory as younger adults, the fidelity, or precision, of the retrieved memories appears to be impoverished in older age[9,11,12]. This decreased precision likely contributes to patterns of memory errors typically observed with ageing, including the increased false recognition of new information sharing perceptual features with studied stimuli[10,13–15].

Neuroimaging findings from younger adults implicate the angular gyrus (AG), a ventrolateral node of the posterior-medial network involved in episodic retrieval[16,17], as critical for supporting the fidelity of episodic recollection. AG activity generally increases with successful episodic retrieval[18], and has been found to correlate positively with both subjective and objective measures of memory detail and quality[19–23]. The role of the AG in episodic retrieval can be conceived as complementary to that of the hippocampus (HC); while hippocampal pattern completion facilitates initial memory access and drives the cortical reinstatement of mnemonic content sufficient for many mnemonic decisions[24–26], the AG is thought to support online maintenance of the reinstated content necessary for more qualitative judgments about the detail of prior experiences[6,27,28]. Consistent with this proposal, multivariate patterns of AG activity during retrieval have been found to represent individual events[19,29] as well as specific event attributes[30,31], enabling a role in fine-grained mnemonic judgements.

While many studies of age-related episodic memory impairments have focused on the role of the HC and the surrounding medial temporal cortices[32–34], it is sometimes overlooked that ageing also impacts integrity of the wider cortico-hippocampal network[35–37]. In particular, age-related reductions in ventrolateral parietal activation during episodic memory retrieval have been commonly observed in prior studies[38], often co-occuring with reductions in hippocampal activity[39]. Despite efforts to disentangle the relative contribution of these two regions to age-related memory deficits, however, the specific role of parietal dysfunction in ageing remains unclear. Considering prior findings from younger adults[22], it is possible that the ventrolateral parietal cortex may be particularly important for maintaining the fidelity of episodic recollection in older age. This possibility has not been directly evaluated in prior

studies that have predominantly relied on categorical assessment of discrete retrieval outcomes (e.g., old/new, remember/know), which do not allow the mapping of brain function or structure to more graded variation in the resolution of mnemonic representations.

In the current study, we employed functional and structural magnetic resonance imaging (MRI) in combination with a continuous report paradigm enabling fine-grained assessment of retrieval fidelity. In the MRI scanner, a sample of healthy young and older adults encoded everyday objects presented in varying locations and colours on a scene background. At retrieval, participants were asked to reconstruct these features of the studied objects using a continuous, analogue scale. A further group of older adults underwent a structural MRI scan and completed the identical memory task outside of the scanner. On the basis of prior findings from younger adults implicating the AG in mnemonic precision[22,40], as well as evidence for age-related alterations in this region[38], we predicted reductions in functional and structural integrity of the AG to contribute to loss of episodic memory precision in older age.

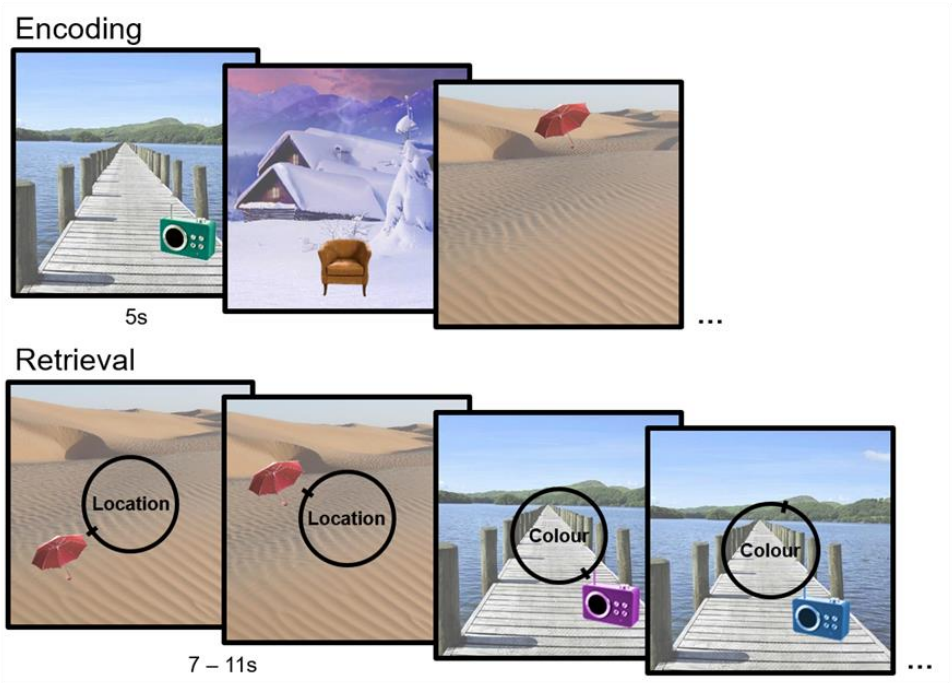

Figure 1. Memory task design. During encoding, participants viewed object-scene displays (stimulus duration: 5s). The location and colour of studied objects were randomly drawn from circular parameter spaces (0-360°). At test, participants were asked to recreate *either* the location *or* the colour of each studied object by moving a slider around a 360° continuous response dial (maximum response time 11s). Retrieval error on each trial was measured as

the angular difference between participants' response value and the original encoded feature value.

Results

Differences in memory performance between young and older adults in the fMRI experiment

All participants completed a memory task that involved studying a series of object-scene displays (see Figure 1, see also refs[22,41,42]). Importantly, the colour and location of each object presented were randomly drawn from circular parameter spaces, allowing us to assess participants' memory for these object attributes using a continuous, analogue scale. We first examined behavioural differences in memory performance between the young (N = 20) and older (N = 19) individuals who took part in the fMRI part of the study. For each trial, retrieval error was calculated as the angular deviation between the participant's response value and the original encoded feature value (response – target, error range: 0 ± 180°, see Figure 2A for distribution of retrieval errors in each age group). The older adults exhibited significantly higher mean absolute retrieval error (*M*: 43.65, *SD*: 8.29) than the younger adults (*M*: 30.43, *SD*: 15.04), $t(37) = 3.38$, $p = .002$, $d = 1.08$, indicating overall poorer memory performance in the older group. To distinguish whether such performance reductions may reflect age-related decreases in the likelihood of successfully retrieving information from memory, or in the precision of the retrieved information, we further fitted a two-component mixture model[43,44] to each individual participant's retrieval error distribution (see Methods for details and Figure 2A for aggregate model fits). Examination of the model parameters indicated that both the probability of successful retrieval of object features (i.e., probability of responses stemming from a von Mises distribution centred at the target object feature, *pT*), $t(37) = 2.30$, $p = .027$, $d = .74$, as well as the precision with which these features were retrieved (i.e., variability in memory error when retrieval was successful, estimated as the concentration parameter, *Kappa*, of the target von Mises distribution), $t(37) = 4.61$, $p < .001$, $d = 1.48$, were reduced in older compared to younger adults (see Figure 2B). Thus, when compared to the younger adults, the older adults demonstrated both reduced success of memory retrieval and reduced mnemonic precision, allowing us to further probe the neural correlates of these behavioural decreases.

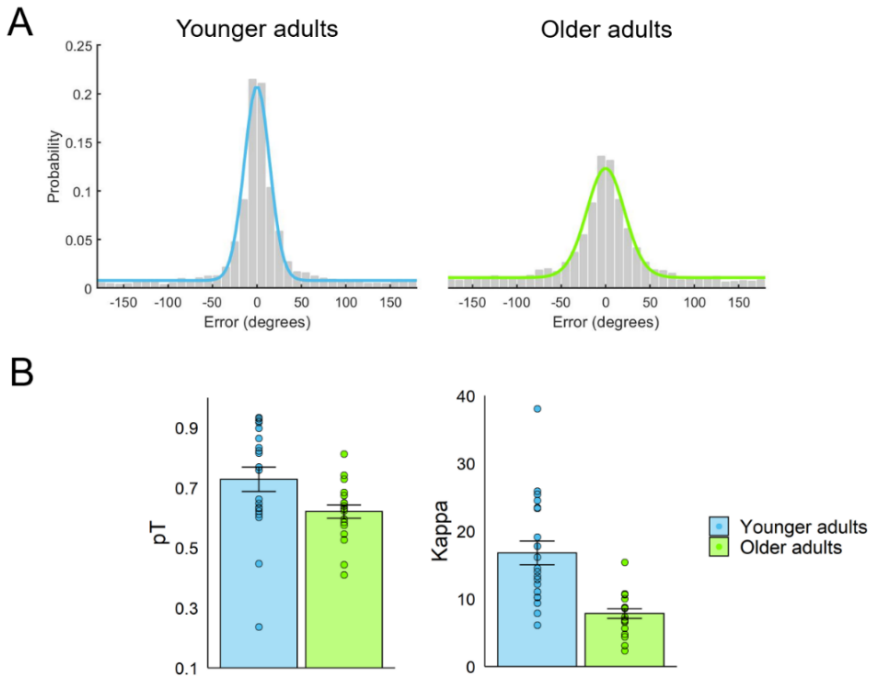

Figure 2. A) Distribution of retrieval errors across young (N = 20) and older participants (N = 19) in the fMRI experiment. Coloured lines indicate fits of the von Mises + uniform mixture model[43,44], fitted to aggregate data in each age group for visualization. B) Mean model-estimated probability of successful memory retrieval (*pT*) and memory precision (*Kappa*) in each age group. Error bars display ± 1 standard error of the mean (SEM).

Age differences in the hippocampus and the angular gyrus during memory retrieval

We next sought to examine age differences in memory-related activation of two key regions of the posterior-medial memory network, the HC and the AG, during retrieval. Across participants, we observed activity in both the HC, $t(37) = 7.25$, $p < .001$, peak: -24, -18, -12, and the AG, $t(37) = 5.27$, $p = .001$, peak: -39, -63, 21, to be significantly increased for successful compared to unsuccessful retrieval. Similarly, across participants, BOLD signal in the HC, $t(37) = 5.63$, $p < .001$, peak: -27, -15, -15, and the AG, $t(37) = 6.13$, $p < .001$, peak: -54, -66, 33, correlated with trial-wise variation in mnemonic precision. Examining age-related differences in BOLD activity associated with these two aspects of memory retrieval, we observed significant age-related reductions in retrieval success effects in the HC, $t(37) = 3.79$, $p = .024$, peak = -18, -6, -12. Although increased hippocampal activity was detected for successful trials in both younger, $t(19) = 6.06$, $p = .001$, peak = -30, -15, -12, and older adults $t(18) = 4.37$, $p = .021$, peak: -24, -18, -12, this effect was reduced significantly in older

age (see Figure 3A). A non-significant trend in the same direction was observed in the AG, $t(37) = 3.23$, $p = .093$, peak = -39, -60, 21, with both young, $t(19) = 5.48$, $p = .003$, peak: -39, -63, 21, and older adults, $t(18) = 4.47$, $p = .020$, peak: -42, -54, 24, nevertheless demonstrating significant retrieval success effects in the AG also.

Conversely, significant age-related reductions in retrieval precision effects were detected in the AG, $t(37) = 3.67$, $p = .033$, peak = -48, -69, 36 (see Figure 3B). Whereas in younger adults AG activity was significantly modulated by the precision of memory retrieval, $t(19) = 5.50$, $p = .003$, peak: -54, -66, 33, no significant precision effects were detected in the older adult group alone (*p*s > .152). Hippocampal activity associated with memory precision, on the other hand, did not significantly differ between the age groups (*p*s > .375). Indeed, significant modulation of hippocampal BOLD signal by memory precision was observed in both young, $t(19) = 4.78$, $p = .008$, peak = -27, -18, -18, and older adults, $t(18) = 4.68$, $p = .012$, peak = -30, -27, -15. No additional age differences in retrieval success or retrieval precision effects survived a whole-brain corrected threshold in exploratory whole brain analyses (*p*s > .077).

Given prior evidence for functional specialization of activity associated with success and precision of episodic memory retrieval[22], we further extracted the mean beta-values corresponding to the retrieval success and retrieval precision effects from the anatomical HC and AG ROI, and subjected them to a 2 (region) x 2 (measure) x 2 (age group) ANOVA (see Figure 3C and 3D). This analysis indicated a significant interaction between region and measure, $F(1,37) = 5.41$, $p = .026$, $\eta_p^2 = .13$, that was driven by greater AG activity associated with memory precision than with retrieval success, $t(38) = 3.12$, $p = .004$, $d = .50$, whereas activity associated with the success and precision of memory retrieval did not significantly differ in the hippocampal ROI ($p = .546$). There was no further 3-way interaction between age group, region, and measure ($p = .120$), although the age-related reduction in memory precision effects in the AG was marginally greater than any age difference observed in the HC for precision-related BOLD signal, $F(1,37) = 3.57$, $p = .067$, $\eta_p^2 = .09$.

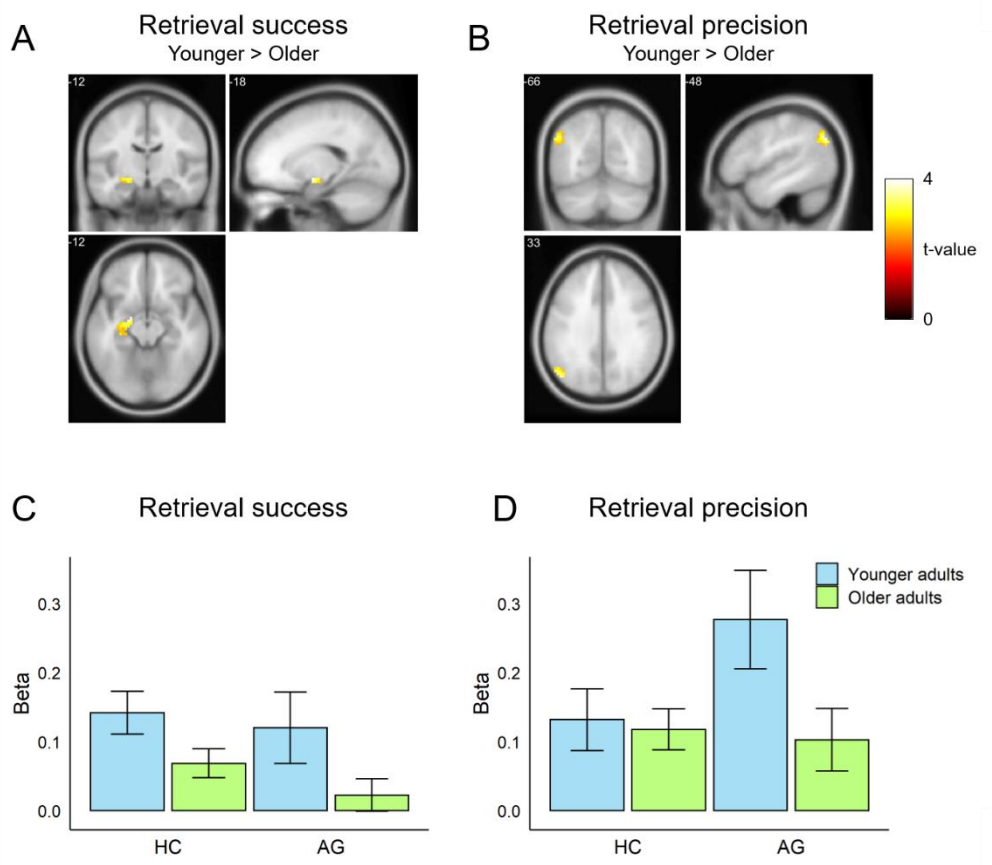

Figure 3. Age-related reductions (younger adults > older adults) in BOLD signal associated with the (A) success and (B) precision of memory retrieval within the (A) hippocampal and (B) angular gyrus ROI, displayed at an uncorrected threshold $p < .01$ for visualization. Mean beta-values for the (C) retrieval success and (D) retrieval precision effects in each age group and anatomical ROI. Error bars display ± 1 SEM.

Relationship between variation in local grey matter volume and memory performance in older age

Examining the full sample of older individuals who took part in the study ($N = 49$; memory task completed in-scanner for 20 individuals and outside of the scanner for 29 individuals), we further investigated whether individual differences in grey matter (GM) volume of the HC and the AG were related to variation in episodic memory performance. Controlling for sex, education, and testing environment, we observed a significant positive association between older age and mean absolute retrieval error on the continuous report task, $r = .33$, $p = .027$, indicating that in addition to detecting differences between young and older adults, the task was sensitive to age-related variation in memory performance within the older adult sample. Examining variation in the model-derived estimates of memory performance, we observed a

significant negative correlation between age and memory precision, $r = -.49$, $p < .001$ (Figure 4B), whereas no significant association between age and retrieval success was detected, $r = -.08$, $p = .619$ (Figure 4A). Indeed, the correlation between age and memory precision was significantly stronger than the association between age and the probability of successful retrieval, $z = 2.36$, $p = .018$.

Moreover, voxel-based morphometry (VBM)[45] analyses indicated a significant association between AG GM volume and individual differences in memory precision, $t(42) = 3.74$, $p = .026$, peak: -46, -68, 24 (Figure 4C and 4D). In contrast, HC volume was not significantly associated with memory precision or the probability of successful memory retrieval within the full older adult sample (*p*s > .133). No significant association between AG GM volume and probability of successful memory retrieval was detected (*p*s > .722). Indeed, when including probability of successful memory retrieval as an additional covariate in the model, we still observed a significant association between AG volume and memory precision, $t(41) = 3.75$, $p = .027$, peak = -46, -68, 24, suggesting specificity of this relationship to mnemonic precision. Exploratory whole-brain analyses did not reveal any further regions where variation in GM volume was associated with either the precision (*p*s > .185) or the success (*p*s > .789) of memory retrieval, although there was a trend toward a positive association between GM volume in the inferior temporal gyrus and memory precision, $t(42) = 5.03$, $p = .061$, peak: 50, -57, -9.

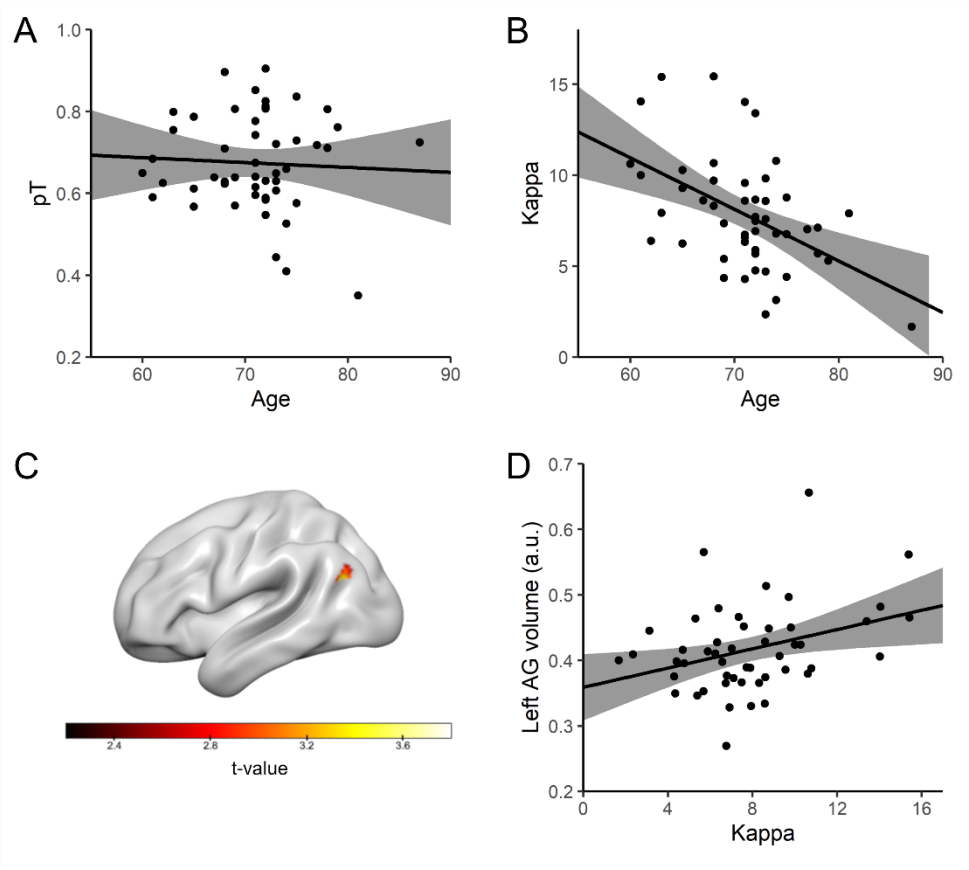

Figure 4. Relationship between age and the model-derived estimates of A) retrieval success and B) retrieval precision in the full older adult sample (N = 49). C) Angular gyrus region displaying an association between grey matter (GM) volume and memory precision in older age, visualized at an uncorrected threshold of $p < .01$. D) Relationship between angular gyrus GM volume and memory precision (GM volume extracted from the cluster showing a relationship to memory precision at $p < .001$ uncorrected).

Discussion

Here, we examined the contribution of two regions of the posterior-medial memory network, the HC and the AG, to age-related memory reductions. Employing model-based analyses of participants' retrieval performance, we observed both the probability of successful memory retrieval and mnemonic precision to be reduced in older compared to younger adults. Of these two measures, memory precision, but not likelihood of successful retrieval, was also negatively associated with age within a larger older adult sample. Analyses of fMRI data acquired during retrieval indicated an age-related reduction in hippocampal activity reflecting successful retrieval of object features, whereas activity associated with memory precision

was reduced in the AG. Moreover, variation in AG GM volume predicted individual differences in mnemonic precision in older age, beyond any association with successful retrieval in general. Taken together, these findings suggest diminished memory precision in older age to be linked with declining structural and functional integrity of the AG.

The current finding of age-related decreases in hippocampal activation aligns with prior evidence emphasizing a contribution of hippocampal dysfunction to memory failures in older age[32,34,46–48]. Specifically, in the older group, we observed diminished, albeit still significant, increases in hippocampal activation for trials resulting in successful recovery of object features when compared to trials that reflected guessing. This finding is consistent with other studies observing age-related reductions in hippocampal recollection success effects[39,49]. Critically, variation in the magnitude of hippocampal signal reflecting successful memory retrieval has been observed to predict inter-individual differences in memory performance across the lifespan[50], as well as longitudinal changes in episodic memory in older age[46], highlighting the functional significance of such effects. It is possible that the hippocampal decreases observed here may in part reflect an age-related deterioration of hippocampal pattern completion, a mechanism by which the HC enables the recovery and reinstatement of a complete encoded memory representation from a partial or noisy cue[24,51]. This interpretation is consistent with prior studies demonstrating reductions in both behavioural and neural indices of pattern completion in ageing[48,52,53]. An additional contribution of extrahippocampal processes to reduced memory accessibility is also possible, based on the current data. In particular, a trend-level reduction in retrieval success effects was evident in the AG in the older group. Given emerging insights about the temporal sequence of hippocampal and parietal retrieval operations, with hippocampal signal reflecting successful retrieval preceding that of the posterior parietal cortex[54,55], it is possible that such a reduction could reflect impoverished input from the HC to the rest of the posterior-medial network in ageing.

In contrast, we did not observe significant age-related reductions in precision-related activity in the HC, where trial-wise variation in BOLD signal during successfully retrieved trials was positively associated with variation in the degree of memory error in both age groups. Instead, the older group displayed diminished precision-related activation in the AG, suggesting that a dysfunction of cortical components of the posterior-medial network may play a greater role in decreased retrieval fidelity in older age. A retrieval-related impairment is consistent with behavioural evidence indicating loss of representational fidelity during perception or working memory to be insufficient to account for age-related decreases in long-term memory precision[9]. The current age-related differences observed in the AG further

align with accounts that emphasize a critical contribution of this region to qualitative aspects of episodic remembering[6,28], including the precision[16,22,40], detail-richness[21,23], and vividness[19,20,29] of memory retrieval. Along with other regions of the default-mode network (DMN), the location of the AG at the apex of a cortical connectivity hierarchy is thought to enable a cross-domain role in representation of internal information that may be untied to immediate sensory input[56,57]. In particular, the AG has been proposed to act as a dynamic, domain-general, 'buffer', supporting the online representation of multi-modal information in a consciously accessible form[27] (see also refs[58,59]). During episodic retrieval specifically, such a role would be complementary to the hippocampus, enabling the sustained maintenance and elaboration of specific event details reinstated in modality-specific cortical regions[6,16,28].

Consistent with prior observations[22,42], BOLD activity in the AG correlated with trial-wise variation in memory precision in the younger group, but no such memory-related modulation was detected in the older group alone. This suggests that the older adults may have been less able to flexibly modulate AG activity to support detailed remembering, aligning with evidence indicating age-related dysregulation of DMN function in response to cognitive demands[60–62]. Given evidence for increased connectivity between medial temporal and parietal regions with increasing precision of memory retrieval[63], it is also possible that the diminished relationship between AG activation and memory precision in older age could in part reflect impoverished inputs from the HC to the AG, even though no local hippocampal age differences relating to memory precision were observed in the present data. Interestingly, contrasting the apparent lack of precision-related modulation of AG activity in the older group observed here, a recent electroencephalography (EEG) study observed parietal event-related-potentials (ERPs) to be sensitive to the accuracy of remembered object locations in older age[64], consistent with earlier findings by the same authors from a younger cohort[65]. However, as no younger control group was included in the first study mentioned[64], it remains unclear whether a similar age-related reduction for parietal ERPs would be observed as for modulation of parietal BOLD signal in the current study. Indeed, consistent with the current findings, other recent evidence suggests age-related reductions in the modulation of parietal ERPs by memory specificity, with such an effect being absent in older age[66].

The VBM analyses involving the full sample of older adults provided further support for a contribution of neural differences in the AG to decreases in memory precision in older age. Specifically, we observed AG GM volume to be positively associated with individual differences in memory precision, even after accounting for variation in the probability of successful memory retrieval. Heteromodal cortical regions, such as the ventrolateral parietal

cortex, appear particularly sensitive to age-related grey matter loss[67–69], highlighting the possibility that such a relationship may in part reflect the degree of age-related deterioration of this region. However, we note that longitudinal data are required to evaluate this interpretation. Moreover, despite the functional age differences observed in the HC, we did not observe any significant associations between hippocampal volume and the success, or precision, of memory retrieval. Given that only mnemonic precision was significantly associated with age within our older adult sample, it is possible that precision may have provided a more sensitive marker of structural brain integrity within the current dataset. Moreover, given the small size and structural complexity of the HC, and the contribution of different hippocampal subfields to distinct mnemonic processes[70], more fine-grained assessment of structural integrity of this region may be required to detect relationships with behaviour. Indeed, both patient[11,71,72] and neuroimaging evidence[41,63,73,74] suggests a contribution of the medial temporal lobes to memory precision, with the HC perhaps playing a particular role at encoding in facilitating the formation of high-fidelity associations between units of information[41,72,75].

While both the probability of successful memory retrieval and mnemonic precision were impaired in the older relative to the younger group, of these two measures only mnemonic precision displayed a significant negative association with age in the full older sample. The association between age and memory precision was stronger than any relationship between age and probability of successful retrieval, highlighting the potential benefit of this measure for detecting early age-related memory deficits. Indeed, the neuroimaging findings implicating the AG in reduced memory precision in older age are also interesting considering the locus of early accumulation of age-associated pathology in the brain, with amyloid-β accumulation detected early in heteromodal cortical regions, and the DMN in particular[76,77]. Future research is required to assess whether continuous measures of long-term memory retrieval, such as the task used here, could be advantageous for detecting early signs of pathological memory changes in ageing. Indeed, within working memory assessment, similar paradigms have been shown to capture variation in short term memory performance related to genetic risk of developing dementia[78–80] (although the extent to which this link might extend to long-term memory is unclear[81]).

The age-related decreases in behavioural memory precision observed here and in previous studies[9,11,12] parallel neuroimaging evidence indicating age-related reductions in the specificity of neural representations during both memory encoding and retrieval[48,82–86]. An interesting question for future studies to address is whether reduced fidelity of neural representations in the AG during retrieval may in part explain the reductions in memory

precision seen in ageing. Such a contribution would align with recent evidence indicating reduced memory reinstatement specificity in the AG to predict unique variance in episodic memory performance in older age, beyond hippocampal activation at retrieval[48]. Interestingly, work in younger adults has also demonstrated transcranial magnetic stimulation of the posterior-medial memory network via the AG to specifically enhance the precision of episodic recollection[40], suggesting a potential avenue for boosting the fidelity of episodic memory in older age also.

Despite common findings of age-related reductions in ventrolateral parietal activation during episodic retrieval[38], the functional significance of such reductions has remained unclear. Here, we provide converging evidence for a contribution of both functional and structural integrity of the AG to age-related reductions in memory precision; an emerging key component of age-related memory decline. Further research is needed to assess whether such measures may also be useful for detecting pathological memory changes in older age.

Methods

Participants

Twenty-one younger (18-29 years old) and 53 healthy older adults (60-87 years old) took part in the current study. Two older participants failed to complete the full study and were therefore excluded. Functional and structural imaging data were acquired for all younger participants and for 21 of the older individuals, whereas 30 older individuals took part in a structural scan only and completed an identical memory task outside of the scanner. All participants were right-handed, native English-speakers, had normal or corrected-to-normal vision, no colour blindness, and no current or historical diagnosis of any neurological, psychiatric, or developmental disorder, or learning difficulty. Participants further indicated no current use of any psychoactive medication, and no medical or other contradictions to MRI scanning. Data from two older individuals was excluded from all analyses due to behavioural performance > 3 *SD*s from the group mean. For analyses of the fMRI data, one younger and one older adult were further excluded due to excessive movement in the scanner (> 4mm). Thus, the final sample sizes for the current analyses consisted of 20 younger and 19 older adults for the fMRI analyses and of 49 older adults for the structural VBM analyses (see Table 1 for participant demographic information). All older participants scored within the healthy range (≥ 26, *M*: 28.51, *SD*: 1.34) on the Montreal Cognitive Assessment (MoCA) screening tool[87]. The young and older adults taking part in the fMRI experiment did not differ

in terms of the number of years of formal education completed, $t(37) = 0.44$, $p = .664$, whereas the older adults had significantly higher scores on the Shipley Institute of Living Vocabulary Score (SILVS)[88] measure of crystallized intelligence, $t(37) = 4.03$, $p < .001$, $d = 1.29$, as typically observed in ageing studies[89]. Moreover, the groups of older adults taking part in the fMRI scan and the structural part of the study only did not significantly differ in terms of age, education, MoCA or Shipley scores (*p*s > .119).

All participants were recruited via the University of Cambridge Memory Lab volunteer database, University of Cambridge Psychology Department Sona volunteer recruitment system (Sona Systems, Ltd), and community advertisements. Volunteers were reimbursed £30 for their participation and for any travel expenses incurred, and gave written informed consent in a manner approved by the Cambridge Psychology Research Ethics Committee.

Table 1. *Participant demographic information.*

	Younger adults	Older adults
N	20	49
Age	22.15 (3.10)	70.94 (5.32)
Gender (N)	8 M, 12 F	18 M, 31 F
Years of education	16.90 (2.79)	16.29 (4.75)
SILVS	32.50 (3.91)	36.98 (1.91)
MoCA	n/a	28.51 (1.34)

Note. M = males, F = females.

Materials

The memory task stimuli consisted of 180 images of everyday objects and 180 images of outdoor scenes that were randomly paired to form a set of 180 trial-unique encoding displays (size: 750 x 750 pixels) (see Figure 1). The location and colour of the object on each display were randomly sampled from circular parameter spaces (0-360°). All participants learned the same encoding displays.

Design and procedure

The continuous report task has been described in detail in Korkki et al.[41]. A total of 9 study-test blocks were completed (see Figure 1). For the participants in the fMRI part of the study, each block was completed during one functional run (i.e., 9 functional runs in total, one study and one test phase per run). In each task block, participants first encoded 20 stimulus displays in a row (stimulus duration: 5s). After a 10s delay, they were asked to recreate *either* the location *or* the colour of each of the objects previously studied (one feature question per object, total of 20 retrieval trials per block). In the test phase, each object was presented on its original associated background. For location questions, the test object was presented in its original colour but in a location randomly drawn from the circular parameter space, whereas for colour questions the test object was presented in its original location but in a randomly chosen colour. Participants were instructed to recreate the location or the colour of the object as accurately as they could by moving a slider around a 360-degree response dial using their middle and index finger on a button box and confirmed their answer by pressing a third key on the button box with their thumb. The retrieval phase was self-paced but with a minimum trial length of 7s and a maximum response time of 11s. This maximum response time was based on older adults' mean reaction time + 2 *SD*s in a fully self-paced pilot version of the task. If a participant failed to confirm their answer within the maximum allotted time, their last position on the response wheel was recorded as their answer for that trial.

In total, participants completed 90 location and 90 colour retrieval trials (10 trials of each type in each block). The feature questioned for each display was randomized, but kept constant across participants. Allocation of object-scene displays to task blocks and their study and test orders were randomized across participants with the constraint of no more than four sequential encoding or retrieval trials within the same feature condition. A fixation cross with a jittered duration ranging between 0.4s and 2.4s (mean: 1s) drawn from an approximate Poisson distribution was presented between each encoding and retrieval trial. For participants in the fMRI part of the study, a diffusion-weighted structural scan was acquired between functional runs five and six.

All participants completed instructions and a practice version of the memory task prior to the main task. For younger volunteers in the fMRI part of the study, the SILVS[88] was completed after the functional scan. For the older fMRI volunteers, the SILVS[88] and the MoCA[87] were completed in a separate behavioural testing session. The older adults completing the structural scan only completed the continuous report task and the other behavioural measures on the same day as their structural scan.

Analysis of behavioural performance

On each trial, retrieval error was calculated as the angular deviation between participants' response and the original encoded target feature value (error range: 0 ± 180°). To examine the sources of memory error contributing to participants' performance, we fitted a two-component probabilistic mixture model consisting of a target von Mises distribution and a circular uniform distribution[43,44] to each participant's retrieval error data using maximum likelihood estimation (code available at: https://www.paulbays.com/code/JV10/index.php). This model assumes that trial-wise variation in participants' performance arises from two different components of memory error: variability, or noise, in successful retrieval of the target features from memory, and the presence of guess responses where memory retrieval has failed to bring any diagnostic information about the target to mind. Variability in successful memory retrieval is modelled by a von Mises distribution (circular equivalent of a Gaussian distribution) centred at the target feature value (i.e., mean retrieval error of zero), whereas the likelihood of guessing responses is captured by the probability of responses stemming from the circular uniform distribution. From this model, two parameters of memory performance can be estimated for all participants: the precision of memory retrieval, corresponding to the concentration parameter, *Kappa*, of the von Mises distribution, and the likelihood of successful memory retrieval, corresponding to the probability of responses stemming from the target von Mises over the uniform distribution ($pT = 1 - pU$).

Although alternative models can also capture the distribution of errors in continuous report tasks well[90–92], the selection of this model was motivated by prior work demonstrating differential effects of age on the two mixture-model components[9,12], as well as differential neural correlates of these components in younger adults[22]. Indeed, while agnostic to the specific mechanisms underpinning errors resembling variability in the accuracy of target retrieval and random guessing, we note that this model provides a good descriptive account of data generated in continuous report tasks[93], and has been widely applied in both behavioural and neuroimaging studies of long-term memory retrieval[22,42,63,73,94,95]. For completeness, we further replicated the functional and structural neuroimaging analyses using model-free metrics of behaviour (i.e., raw retrieval error) and have reported these in the Supplementary material. No significant age differences in functional activity, or relationships between grey matter volume and memory performance, were observed when employing model-free metrics of memory performance, suggesting a benefit of the mixture modelling approach for characterizing age- and performance-related variation in the current dataset.

MRI acquisition

MRI scanning was performed at the University of Cambridge Medical Research Council Cognition and Brain Sciences Unit using a 3T Siemens Tim Trio scanner (Siemens, Germany) with a 32-channel head coil. For each participant, a high-resolution whole brain anatomical image was acquired using a T1-weighted 3D magnetization prepared rapid gradient echo (MPRAGE) sequence (repetition time (TR): 2.25s, echo time (TE): 3ms, flip angle = 9°, field of view (FOV): 256 x 256 x 192mm, resolution: 1mm isotropic, GRAPPA acceleration factor 2). The functional data were acquired over 9 runs using a single-shot echoplanar imaging (EPI) sequence (TR: 2s, TE: 30ms, flip angle° = 78, FOV: 192 x 192mm, resolution: 3mm isotropic). Each functional volume consisted of 32 sequential oblique-axial slices (interslice gap: 0.75mm) acquired parallel to the anterior commissure – posterior commissure transverse plane. The mean number of volumes acquired per functional run was 167.39 (*SD*: 7.49) and did not significantly differ between the age groups (younger adults: 166.09, *SD*: 8.08, older adults: 168.75, *SD*: 6.77, $t(37) = 1.11$, $p = .273$). The scanning protocols also included additional imaging sequences not analysed here.

fMRI preprocessing and analyses

Preprocessing and analysis of both the functional and structural images were performed with Statistical Parametric Mapping (SPM) 12 (https://www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB R2021b. The first five volumes of each functional run were discarded to allow for T1 equilibration. Any additional volumes acquired after each task block had finished were also discarded so that the last volume of each run corresponded to a time point of ~2s after the last fixation cross for each participant. The functional images were spatially realigned to the mean image to correct for head motion and temporally interpolated to the middle slice to correct for differences in slice acquisition time. The anatomical image was coregistered to the mean EPI image, bias-corrected and segmented into different tissue classes (grey matter, GM; white matter, WM; cerebrospinal fluid, CSF). These segmentations were used to create a study-specific structural template image using the DARTEL (Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra) toolbox[96]. The functional data was normalized to MNI space using DARTEL and spatially smoothed with an isotropic 8mm full-width at half-maximum (FWHF) Gaussian kernel.

To gain trial-specific estimates of the success and precision of memory retrieval for the fMRI analyses, the two-component mixture model (von Mises + uniform distribution) was fitted to

all retrieval errors across all participants (7020 trials in total) to calculate a cut-off point at which the probability of participants' responses stemming from the target von Mises distribution was less than .05 and responses thus likely reflected guessing[22,41,42]. This cut-off point of ± 59 degrees was then used to classify each retrieval trial as successful (absolute retrieval error ≤ 59 degrees) or unsuccessful (absolute retrieval error > 59 degrees). For successful retrieval trials, a trial-specific measure of memory precision was further calculated as 180 – participant's absolute retrieval error on that trial so that higher values (smaller error) reflected higher precision (range: 121 – 180). A measure of memory precision was not considered for the unsuccessful trials as responses in this condition were approximately randomly distributed and thus were not expected to carry meaningful information about memory quality. Indeed, in a control analysis that included an additional parametric regressor reflecting trial-wise variation in memory error for trials classified as unsuccessful, we did not observe any significant associations between BOLD activity and memory error in either of the two ROIs, or across the whole brain (see Supplementary material).

First-level General Linear Model (GLM) for each participant contained four separate condition regressors corresponding to successful location retrieval, successful colour retrieval, unsuccessful retrieval, as well as encoding. As done in previous work[22,42], unsuccessful trials were modelled across the two feature conditions, due to low numbers of guessing responses per feature condition for some participants. For successful retrieval trials, trial-specific estimates of memory precision were further included as parametric modulators comprising two additional regressors in the model. The precision parametric modulators were rescaled to range between 0 and 1 to facilitate the direct comparison of success and precision-related activity, and mean-centred for each participant. Neural activity corresponding to the regressors of interest was modelled with a boxcar function convolved with the canonical hemodynamic response function (HRF), with event duration corresponding to the duration of the retrieval display on the screen (i.e., duration of 7s if participant's RT on that trial was under 7s, and duration equal to participant's RT if the RT exceeded 7s). Six participant-specific movement parameters estimated during realignment (3 rigid-body translations, 3 rotations) were included as covariates in the first-level model to capture any residual movement-related artefacts. Due to the small number of guessing trials in each functional run, data from all functional runs were concatenated for each participant, and 9 constant block regressors included as additional covariates. Autocorrelation in the data was estimated with an AR(1) model and a temporal high pass filter with a 1/128 Hz cut-off was used to eliminate low frequency noise. First-level subject-specific parameter estimates were submitted to second-level random effects analyses.

Contrasts for the fMRI analyses focused on examining retrieval activity that varied with the success and precision of memory retrieval. To examine retrieval activity associated with the success of memory retrieval, we contrasted successful retrieval trials (absolute retrieval error ≤ 59 degrees) to trials where memory retrieval failed (absolute retrieval error > 59 degrees; *retrieval success effects*). To identify retrieval activity associated with the precision of memory retrieval, we examined positive associations between BOLD signal and trial-wise variation in memory error on trials classified as successful (i.e., positive linear relationship between BOLD signal and precision parametric modulator; *retrieval precision effects*).

VBM preprocessing and analyses

Preprocessing of the structural images for the VBM analyses included segmentation of the anatomical images into GM, WM and CSF. These segmentations were then used to create a structural template image using the DARTEL toolbox[96], and normalised to MNI space using DARTEL. The normalized GM images were spatially smoothed with an isotropic 8mm FWHF Gaussian kernel, with modulation applied to preserve the total amount of GM within each voxel. For each participant, total intracranial volume (TIV) was computed as the sum of total GM, WM and CSF estimates.

Two separate GLMs were constructed to examine the relationship of GM volume to memory performance within the full older adult sample: one including model-derived estimates of the probability of successful retrieval *(pT*) as the covariate of interest, and the other including memory precision (*K*) as the covariate of interest. For both models, participant age, gender, education level, and TIV were included as covariates of no interest. When comparing the two groups of older adults who took part in the fMRI scan versus the structural scan only, we observed lower probability of successful memory retrieval in the group of participants who performed the memory task inside the MRI scanner (*M*: 0.63, *SD*: 0.10) than in those participants who performed the task outside of the scanner (*M*: 0.71, *SD*: 0.12), $t(47) = 2.53$, $p = .015$, $d = 0.73$, perhaps reflecting an impact of the MRI scan environment on memory performance[97]. Memory precision, on the other hand, did not significantly differ between these two groups of participants (in-scanner *M*: 7.78, *SD*: 3.01, outside of the scanner *M*: 7.91, *SD*: 3.20), $t(47) = 0.14$, $p = .888$. To account for the differences in retrieval success, testing environment was added as an additional covariate in all VBM analyses.

Regions of interest

The functional and structural neuroimaging analyses focused on two key regions of the posterior medial memory network: the HC and the AG. The selection of these regions was motivated by prior evidence suggesting a degree of functional specialization during episodic retrieval[22], as well as common findings of age-related alterations in both regions[38,98]. Left-lateralized ROIs were created with the Automated Anatomical Labelling (AAL) atlas, given evidence for left-lateralization of episodic retrieval effects[99]. Statistical significance within each anatomical ROI was assessed using small-volume correction with a peak-level familywise error (FWE) corrected threshold of $p < .05$, correcting for the number of voxels in each ROI. In addition to the ROI analyses, we performed exploratory whole brain analyses to identify any additional regions displaying age differences in memory-related retrieval activity, or an association between grey matter volume and memory performance, at a whole-brain corrected threshold of $p < .05$ FWE-corrected.

Data availability

Data and materials are available from the corresponding authors on reasonable request.

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