



Recollection and prior knowledge recruit the left angular gyrus during recognition

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Abstract

The human angular gyrus (AG) is implicated in recollection, or the ability to retrieve detailed memory content from a *specific* episode. A separate line of research examining the neural bases of more *general* mnemonic representations, extracted over multiple episodes, also highlights the AG as a core region of interest. To reconcile these separate views of AG function, the present fMRI experiment used a Remember-Know paradigm with famous (prior knowledge) and non-famous (no prior knowledge) faces to test whether AG activity could be modulated by both task-specific recollection and general prior knowledge within the same individuals. Increased BOLD activity in the left AG was observed during both recollection in the absence of prior knowledge (recollected > non-recollected or correctly rejected non-famous faces) and when prior knowledge was accessed in the absence of experiment-specific recollection (famous > non-famous correct rejections). This pattern was most prominent for the left AG as compared to the broader inferior parietal lobe. Recollection-related responses in the left AG increased with encoding duration and prior knowledge, despite prior knowledge being incidental to the recognition decision. Overall, the left AG appears sensitive to both task-specific recollection and the incidental access of general prior knowledge, thus broadening our notions of the kinds of mnemonic representations that drive activity in this region.

Keywords Default mode network · Episodic memory · fMRI · Parietal · Semantic memory

Introduction

The angular gyrus (AG) is reliably implicated in our ability to remember past events (Wagner et al. 2005; Cabeza et al. 2012a; Levy 2012; Shimamura 2014; Ramanan et al. 2017;

Sestieri et al. 2017; Rugg and King 2018; Simons et al. 2022). In particular, evidence from neuroimaging suggests that the AG, particularly in the left hemisphere, is engaged during recollection—the retrieval of details from a *specific* past episode (Rugg and Vilberg 2013; Frithsen and Miller 2014). In line with recollection-based accounts, activity in the left AG tracks how precisely a representation in memory matches the original properties of the encoded stimulus (Richter et al. 2016; see also Korkki et al. 2022), such that physical stimulus properties can be decoded from memory-related activity (Kuhl and Chun 2014; St-Laurent et al. 2015; Lee and Kuhl 2016; Thakral et al. 2017b; Lee et al. 2018). Access to these precise episode-specific representations can be temporarily modulated using non-invasive stimulation targeting the AG, further supporting its direct involvement in recollection (Bonnici et al. 2016; Nilakantan et al. 2017; Thakral et al. 2017a; Wang et al. 2014; Yazar et al. 2017).

The left AG, however, is not exclusively involved in recollecting episode-specific details nor episodic memory as a whole. Accessing semantic memory, or general knowledge abstracted over multiple past experiences, has also been argued to recruit the left AG (Binder et al. 2009; Price 2010;

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Binder and Desai 2011; Seghier 2013; Skipper-Kallal et al. 2015; Kim 2016; Amer et al. 2019; c.f., Humphreys et al. 2022). Similarly, access to semantics can be causally modulated using non-invasive brain stimulation (Capotosto et al. 2016; Price et al. 2016). Some studies have even argued that activity in the AG can reduce the likelihood of remembering specific episodic details (van der Linden et al. 2017), consistent with a role in representing across-episode generalities (Wagner et al. 2015).

These separate lines of evidence implicate the left AG in (1) the representation of sensory-rich, idiosyncratic details pertaining to *specific* past experiences (i.e., recollection) and (2) more generalized mnemonic representations that are not linked to a specific past episode. It is unclear how these two accounts of AG function, one emphasizing specificity and another generality, can be reconciled. Episode-specific details (episodic memory) and across-episode generalities (semantic memory) are considered two ends of a continuum in memory (Renoult et al. 2012, 2019; Irish and Vatansever 2020) that rely on separable learning systems and neural substrates (McClelland et al. 1995; Squire 1986; Tulving 1972; Winocur et al. 2010). While the stark distinction between these two aspects of human memory is under reconsideration (Renoult et al. 2012, 2019; Irish and Vatansever 2020; Renoult and Rugg 2020), the literature examining how these accounts coincide within the AG remains an active debate (Seghier 2013; Humphreys and Lambon Ralph 2014; Ramanan et al. 2017; Rugg and King 2018; Humphreys et al. 2021). Therefore, an explicit comparison between these two accounts of AG function is a necessary step towards clarifying the underlying component processes that drive activity in this region. One possibility is that activity in the AG is driven by the amount of detail retrieved from memory, irrespective whether the details are truly episode-specific (i.e., recollection) or derived across multiple past episodes (e.g., prior knowledge). In some sense, this can be seen as an extension of multimodal integrator accounts of AG function (Shimamura 2011; Bonner et al. 2013; Ben-Zvi et al. 2015; Price et al. 2015a; Bonnici et al. 2016; Ramanan et al. 2017; Yazar et al. 2017; Tibon et al. 2019), such that the integration process extends beyond the sensory domain to combine mnemonic content across specific recollections and general prior knowledge in service of remembering past experiences in rich detail (Irish and Piguet 2013; Ramanan and Bellana 2019; Simons et al. 2022).

Here, we sought to determine whether the left AG was uniquely sensitive to (i) *episode-specific* recollection, (ii) more generalized mnemonic content, derived *across multiple episodes*, or (iii) *both* kinds of representations. Several empirical studies have examined the relation between the neural responses to recognizing stimuli learned in-lab and those evoking pre-experimental knowledge (Denkova et al. 2006; Trinkler et al. 2009; Renoult et al. 2015; Liu et al.

2016; Vatansever et al. 2021), but few of these studies have focused on the response profiles within the posterior parietal cortex (Bonnici et al. 2016; Humphreys et al. 2022). To this end, we used fMRI with a cytoarchitecture-based region of interest (ROI) approach centered on the inferior parietal cortex to directly probe the AG and surrounding lateral posterior parietal cortex in terms of their sensitivity to different kinds of mnemonic content. We tested participants' recognition memory for faces of famous and non-famous individuals using a Remember-Know paradigm in the scanner, allowing us to isolate recognition trials associated with explicit recollection of study-specific context as indicated by the participant. Considering that famous faces are associated with multiple past episodes, and that semantic person knowledge is rapidly accessed upon presentation of the face (Bruce and Young 1986; Ramon and Gobbini 2017), famous faces provide an ideal stimulus class for eliciting prior knowledge. Importantly, the presence or absence of prior knowledge is orthogonal to any recognition decision in the context of a standard Remember-Know paradigm (Tulving 1985); thus, allowing us to capture independently the effects of prior knowledge and episode-specific recollection.

It is important to note that while famous faces elicit prior knowledge, this knowledge is not restricted to semantic information. In the context of famous faces, prior knowledge is likely to contain a mixture of semantic content (e.g., the individual's name, profession and other general facts) and episodic content (e.g., past events when you watched their movies, or had conversations about them with friends). This episodic content, however, is likely different from more lab-based examples of episode-specific recollection, where a study item is yoked to one particular study episode (e.g., studying a list of words and then remembering seeing the word during study while performing a recognition test). The episodic content incidentally cued up upon seeing a famous face likely draws upon multiple past episodes. For this reason, if one considers episode-specific details (episodic memory) and across-episode generalities (semantic memory) as two ends of a single continuum (Renoult et al. 2012; Irish and Vatansever 2020), then the incidental prior knowledge elicited upon recognition of a famous face should lie closer to the semantic end of the continuum than the recollection of a recently studied item. Therefore, rather than examining the contributions of the AG in episodic or semantic memory, here we use prior knowledge to test whether recollection, in this strict sense, is *necessary* to drive activity in the AG.

Additionally, to determine whether recollection-related activity in the left AG was sensitive to differences in the amount of recollected content (Hutchinson et al. 2014; Rugg and King 2018; Ciaramelli et al. 2020), we manipulated encoding duration, as longer study should afford more time to encode episodic details (Vilberg and Rugg 2009a, 2009b; Leiker and Johnson 2014). Using this paradigm, we

were able to test directly the separate effects of recollection and prior knowledge on activity in the left AG and the surrounding inferior parietal lobe. We also directly tested the hypothesis that activity in the left AG tracked recollection and prior knowledge simultaneously during recognition, consistent with its aforementioned role in integrating these separable aspects of memory in service of phenomenologically rich remembering. Specifically, we predicted that the left AG should track both recollection and prior knowledge, thereby providing evidence for its sensitivity to the amount of mnemonic content retrieved, irrespective of whether retrieval was via recollection.

Materials and methods

Participants

Twenty-nine young adults between 19 and 30 years of age participated in the experiment. Participants were recruited from the University of Toronto and the surrounding area and were compensated a total of \$50 for a testing session that lasted an average 2.5 h. Five participants did not meet our inclusion criteria for the final sample and were excluded from subsequent analyses (one did not recognize at least 50% of famous stimuli, and four had excessive movement or drowsiness during scanning). Our final sample included 24 participants (years of age: $M = 22.5$, $SD = 2.4$; years of education: $M = 16.5$, $SD = 1.9$; $n_{\text{female}} = 11$). This sample size was chosen so as to be comparable to previous fMRI studies examining memory-related effects in the posterior parietal cortex (e.g., Bonnici et al. 2016; Hutchinson et al. 2014; Thakral et al. 2015; Vilberg et al. 2009a, 2009b). All participants were screened to be healthy, right-handed, free of health problems (psychiatric, neurological, or vascular conditions) and/or medications that may influence cognitive functioning or brain activity. The study was approved by the Research Ethics Board at the University of Toronto and informed consent was given by each participant before participating.

Stimuli

Images were obtained from the Internet using Google image search to create an initial pool of 400 stimuli. Two-hundred images were of famous celebrities and 200 were of non-famous people. Both famous and non-famous pools were balanced for sex, with 100 male and 100 female images each. Faces were neutral to slightly positive in expression. Non-famous faces were each manually matched for age, race and other distinctive features with a corresponding famous face to ensure no overall differences across stimulus pools. Furthermore, images of non-famous people were selected to be

“famous-like”, such that they were often found on various modelling agency websites and their image quality was comparable to those of the famous celebrities. The faces were manually centered and cropped from the full image using an oval frame in Adobe Photoshop and resized to 475×595 pixels. Images were set to black and white and their luminance was matched using SHINE toolbox (Willenbockel et al. 2010). A scrambled version of each face was also generated using custom scripts in MATLAB (MathWorks, Natick, MA, USA), such that each image was divided into 5-pixel clusters and then randomly shuffled. These scrambled images were used for null trials in the fMRI experiment.

An online pilot study was conducted to collect normative subjective ratings on the stimuli. All 400 face stimuli were incorporated into a survey via Qualtrics (Qualtrics, Provo, Utah, USA), and seven separate ratings were collected for each face. The seven rating tasks included in the survey were as follows: (1) recognition and nameability, and 5-point ratings of (2) fame, (3) facts known about the person pictured, (4) personal memories associated with the person pictured, (5) emotionality, (6) facial expression, and (7) attractiveness (for details, see Bellana et al. 2021). The survey was administered in-lab and online using Amazon’s Mechanical Turk (Amazon, Seattle, WA, USA), and included a total of 225 participants between the ages of 19 and 28. Participants were all either in Canada or the USA when completing the survey and gave their consent before participating. Each participant was presented with a randomly selected subset of 100 faces, 50 famous and 50 non-famous, and was required to perform all seven ratings per face. One catch trial per rating task was included, instructing participants to make a specific rating, serving as a quality-check to ensure all participants were following instructions. Data from participants with an incorrect catch trial in any of the seven rating tasks were excluded entirely from all subsequent analyses. Ratings from 190 participants survived this strict exclusion criterion, which amounted to ratings from 47 to 58 participants per face.

Only famous faces that were reliably recognized (i.e., evoked prior knowledge) across participants were included in the stimulus pool for the main recognition experiments. Recognition was operationalized as: ($\%$ of participants who recognized a given face) – ($\%$ of participants who did not recognize a given face). Positive values indicate the majority of participants recognized the face, while negative values indicate the majority of participants did not. The final stimulus pool consisted of 128 faces that were the most recognizable ($M = 68\%$, $SD = 20\%$) and their age and race-matched non-famous counterparts ($M = -78\%$, $SD = 12\%$) for a total of 256 faces. Both famous and non-famous stimulus pools used for recognition were balanced in terms of sex ($n_{\text{male}} = 64$, $n_{\text{female}} = 64$, for both famous and non-famous pools). Independent samples *t*-tests were used to compare average ratings across the final famous and non-famous stimulus pools, with

Bonferroni adjusted p -values for multiple comparisons. The famous and non-famous faces were comparable in terms of attractiveness ($M_{\text{famous}} = 2.8$, $M_{\text{non-famous}} = 2.7$; $t(254) = 2.25$, $p > 0.1$, $d = 0.28$), but robustly differed in terms of fame ($M_{\text{famous}} = 3.8$, $M_{\text{non-famous}} = 1.4$; $t(254) = 39.9$, $p < 0.0001$, $d = 4.99$), facts known ($M_{\text{famous}} = 3.3$, $M_{\text{non-famous}} = 1.3$; $t(254) = 44.69$, $p < 0.0001$, $d = 5.59$), personal memories ($M_{\text{famous}} = 2.6$, $M_{\text{non-famous}} = 1.2$; $t(254) = 28.23$, $p < 0.0001$, $d = 5.59$), and emotionality ($M_{\text{famous}} = 2.7$, $M_{\text{non-famous}} = 1.7$; $t(254) = 36.71$, $p < 0.0001$, $d = 3.53$). These robust differences were by design, as the measures with large differences were on rating scales that tapped into aspects of prior knowledge. Relative to prior knowledge, a modest difference was also found in facial expression ($M_{\text{famous}} = 2.6$, $M_{\text{non-famous}} = 2.3$; $t(254) = 3.85$, $p = 0.0009$, $d = 0.48$), suggesting the famous faces were perceived to be slightly more expressive.

Experimental procedure

Overall, participants underwent an eyes-open resting state scan (7 min, 8 s), then performed four experimental recognition memory blocks (7 min, 8 s each), followed by a structural scan (7 min, 10 s), four experimental recognition memory blocks, and a final eyes-open resting state scan for a total time of approximately 80 min in the scanner. After scanning, participants underwent a final surprise self-paced delayed recognition test outside of the scanner (*Mean duration of post-scan test* = 20 min, 45 s). The total session, including consent, instructions, practice, scanning preparation and debriefing, was completed within 2.5 h.

In the scanner, we assessed memory using a Remember-Know paradigm on a total of 128 famous and 128

non-famous faces (96 targets, 32 foils each). For a schematic overview of the experiment, see Fig. 1A. Remember-Know is a commonly used recognition memory paradigm to capture recollection (Tulving 1985; Yonelinas 2002). In addition to making an old-new decision during recognition, participants introspect about the subjective quality of their recognition. Participants select the Remember option (R) if their recognition is accompanied by recall of contextual information from the study episode. Know (K) is selected if recognition is not accompanied by any contextual information from study. Accuracy (i.e., hits—false alarms) was calculated for both R and K responses, where recollection was defined as $R_{\text{hit}} - R_{\text{fa}}$, or the proportion of studied trials that received an R response (i.e., *hit*) minus the proportion of new trials that received an R response (i.e., false alarms; *fa*).

The experimental paradigm consisted of eight blocks, each of which contained a study and recognition phase (Fig. 1). Prior knowledge was manipulated at the block level such that 4 of the blocks were entirely composed of famous stimuli and the remaining four blocks of non-famous stimuli, in a fixed interleaved order which was counterbalanced across participants. Each block corresponded to a separate functional scan. This block-level manipulation was employed to reduce any potential influence of prior knowledge on the criteria participants used to make Remember (R), Know (K), or New (N) decisions within a given block. During each encoding phase, participants explicitly studied a fixed, pseudorandom sequence of 24 face trials. Each trial began with a red fixation cross presented for 500 ms, followed by a face stimulus presented centrally onscreen. Half of the face stimuli were presented for 1 s and half for 4 s to provide a manipulation of encoding duration, followed by an inter-trial interval ranging between 1500 and 2750 ms

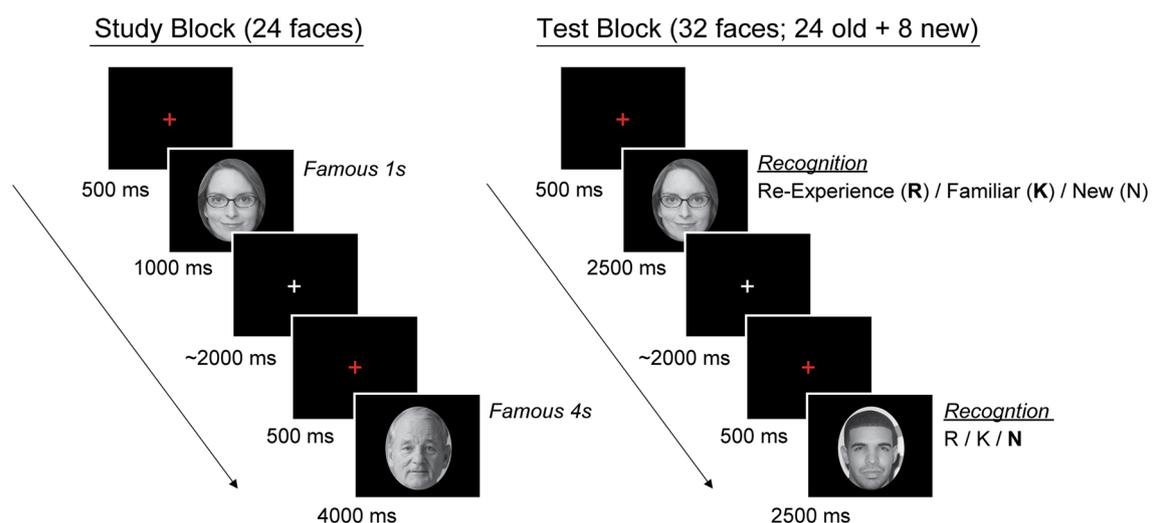


Fig. 1 Schematic example of one in-scan study-test block from the famous condition. In this example, the faces of Tina Fey and Bill Murray are studied, while Tina Fey (old target) and Drake appear at test (novel foil). For details, see Procedure

($M = \sim 2$ s). Participants were asked to study each face in as much detail as possible as their memory would be tested immediately after each study phase. No explicit response was required during study, though eye-movement was monitored by the experimenter via eye-tracking to ensure participants were fixating on the faces. Participants were also instructed that each block was independent from the others and contained unique face stimuli. In addition to the target face trials, 12 additional null trials were also interspersed during the study phase. Null trials consisted of scrambled face stimuli from the experiment, 6 of which were presented for 1 s and 6 for 4 s. These trials were not to be encoded.

The first recognition trial was presented 20 s after the termination of the last study trial. During this 20 s period, participants were instructed that the test would begin shortly and were asked to fixate on a central cross. For each recognition phase, participants were presented with a fixed, pseudorandom sequence of 32 faces, 24 of which were from the previous study list and 8 were novel foils (i.e., old/new ratio of 75/25). Each trial began with a red fixation cross presented for 500 ms, followed by the face stimulus presented centrally onscreen. Each face was presented for 2.5 s during which time participants were required to make a R/K/N response using a fMRI compatible response box followed by an inter-trial interval ranging between 1500 and 2750 ms ($M = \sim 2$ s). Participants used their right hand to make responses, with the index and middle finger used to respond *R* or *K*, and the ring finger used to respond *N*. The mapping of index and middle finger to the *R* and *K* response option was counterbalanced across participants. Given the importance of baselines in fMRI, particularly when interpreting activity in regions like the AG (Humphreys et al. 2021), 12 additional null scramble trials were also interspersed during the recognition phase. Participants were asked to press any of the three response keys for these null trials, with no demands on recognition. Note that the short delay between study and test (20 s) was used to increase the number of *R* responses, a central component of our theoretical question. This procedure, however, necessarily reduced the number of *K* responses and limited our ability to model neural responses associated with *K* trials.

After the eight study-test blocks were completed, participants exited the scanner and were briefly interviewed regarding their experience and memory strategies. Lastly, participants were asked to perform a surprise delayed recognition memory test. All 256 faces from the previous 8 blocks of the experiment (i.e., both studied targets and novel foils) in addition to 32 entirely novel unstudied faces (16 famous and 16 non-famous) were presented in a random order during the delayed test. Trials were self-paced and participants responded with the index fingers of both hands using the buttons *Q* or *P* on the keyboard with response mapping counterbalanced across participants. Each trial began with a 500 ms

red fixation cross, followed by the presentation of a face in the centre of the screen. Participants were first required to indicate whether the face was old (i.e., a target or foil previously seen in the experiment) or new (i.e., entirely novel, not seen in the experiment). Next, participants were asked to indicate whether they believed the face was of a famous or non-famous individual, based on their personal experience. For faces judged as famous, participants were then required to indicate how much they knew about the individual on a scale of 1 (very little) to 5 (a great deal) using the number pad on the keyboard. Participants then indicated whether or not they could name the famous individual via a yes or no button response.

Behavioural analysis

To characterize the effect of our experimental manipulations (i.e., prior knowledge and encoding duration) on memory accuracy, we performed two sets of analyses on participants' behavioural performance. First, we examined how prior knowledge and encoding duration affected overall recognition accuracy using a 2 (prior knowledge: famous, non-famous) \times 2 (encoding duration: 1 s, 4 s) repeated measures ANOVA. Recognition accuracy was defined as the proportion of accurately recognized targets after subtracting the proportion of false alarms on novel foils (hits—false alarms), per participant. This measure characterizes overall recognition while collapsing over subjective distinctions in recognition quality, namely, Remember or Know. Next, we examined the subjective quality of recognition by submitting hit—false alarm estimates to a 2 (prior knowledge: famous, non-famous) \times 2 (encoding duration: 1 s, 4 s) \times 2 (response type: Remember, Know) repeated measures ANOVA.

fMRI data acquisition

MRI images were acquired using a Siemens Prisma 3 T scanner with a 32-channel head coil at the Toronto Neuroimaging (ToNI) centre located at the University of Toronto. Structural MRI images were collected using a T1-weighted high-resolution scan with a standard 3-dimensional magnetization-prepared rapid-acquisition gradient echo (MPRAGE) pulse sequence [160 slices; field of view (FOV) = 256 \times 256 mm; 1 mm isotropic resolution; echo time (TE) = 2.4 ms; repetition time (TR) = 2000 ms; flip angle = 9°; for a total duration of 430 s]. For the functional MRI images (both task and rest), blood oxygenation level-dependent (BOLD) signal was measured using a T2-weighted multiband echo planar imaging (EPI) acquisition procedure [39 slices; FOV = 216 \times 216 mm; 3 mm isotropic resolution; TE = 31 ms; TR = 1000 ms; flip angle = 45°; multiband factor = 3, with a total of 428 volumes collected]. Head movements were limited by inserting

soft cushions into the head coil. Eye movements were monitored using an in-scan MRI-compatible EyeLink 1000 plus (SR research, Ltd.). Visual stimuli were presented by E-Prime software (version 2, Psychology Software Tools, Inc.), presented on an MRI-compatible LCD screen and viewed with a mirror mounted on the head coil. Responses were collected with an MRI-compatible response box.

Data preprocessing

Preprocessing of MRI images was conducted using a combination of functions from AFNI (Cox 1996; <https://afni.nimh.nih.gov/>) and FSL (Smith et al. 2004; <https://fsl.fmrib.ox.ac.uk/fsl/fslwiki>). The pipeline included the following steps: DICOM to NII (AFNI: Dimon), spatial realignment (AFNI: 3dvolreg), co-registration (FSL: epi_reg), subject-specific tissue segmentation (FSL: FAST) and spatial normalization to MNI space (FSL: FLIRT). The final functional images were resampled to 2 mm isotropic voxels (AFNI: 3dresample), spatially smoothed using a Gaussian kernel with the full-width at half maximum of 5 mm (AFNI: 3dmerge). An additional motion scrubbing procedure was added to the end of our preprocessing pipeline (Campbell et al. 2013). Using a conservative multivariate technique, volumes that were outliers in both the six rigid-body motion parameter estimates and BOLD signal intensity were removed and replaced by interpolating the BOLD signal across neighbouring volumes. Motion scrubbing further minimizes any effects of motion-induced spikes on the BOLD signal, over and beyond standard motion regression (which was included in the subsequent analysis step), without leaving sharp discontinuities due to the removal of outlier volumes (for details, see Campbell et al. 2013). Images were manually inspected throughout the preprocessing pipeline to ensure data quality.

Defining regions of interest

Since our hypotheses were specific to the left AG, a region of interest (ROI)-based approach at the group-level was most appropriate. Considering the structural and functional heterogeneity of the inferior parietal lobe (Caspers et al. 2006, 2013; Nelson et al. 2010), we chose to use a fine-grained ROI definition based on cytoarchitectural probability maps from the Jülich Histological Atlas (Eickhoff et al. 2005) as implemented in FSL. The inferior parietal lobe consists of the supramarginal gyrus (anteriorly) and the angular gyrus (posteriorly), which roughly correspond to Brodmann's area 40 and 39. More recent studies of cytoarchitecture suggest that the inferior parietal lobe consists of seven separable regions, listed in the anterior to posterior direction: PFop, PFt, PFcm, PF, PFm, PGa and PGp (see Caspers et al. 2006, 2013). Tissue probability maps for these seven regions

across both left and right hemispheres were selected from the Jülich Histological Atlas (Eickhoff et al. 2005) and thresholded at 40% as a conservative approach to form our ROIs (see Fig. 4A, and Supplementary Materials: S3). These maps were further exclusively masked, from posterior to anterior, to ensure all ROIs were non-overlapping. From these masks, regions PGa and PGp are the most posterior and fall within the vicinity of the AG. Notably, the more posterior PGp has robust structural connectivity with the hippocampus while the PGa does not (Uddin et al. 2010). Furthermore, a Neurosynth (Yarkoni et al. 2011) reverse inference meta-analytic map based on the term “episodic memory” (<http://neurosynth.org/analyses/terms/episodic%20memory/>; derived from 270 studies, FDR corrected at $p < 0.01$, 2 mm isotropic voxel resolution) produced a total of 350 voxels overlapping with the left AG (i.e., defined as a combined mask of the left PGa and PGp), such that 68% of these fell within the PGp and the remaining 32% within the PGa. For additional context, only 37 voxels associated with episodic memory fell in subregions anterior to the left PGa. Therefore, we selected the left PGp as our primary focus for subsequent analyses.

fMRI analysis

A general linear model (GLM), via AFNI's 3dDeconvolve, with a gamma response function timelocked to stimulus onset was used to estimate BOLD activity for each trial type per participant during retrieval. The GLM included 12 regressors of interest: (1) recollected (i.e., remember response) famous trials with 4 s exposure at encoding, (2) recollected famous trials with 1 s exposure at encoding, (3) recollected non-famous trials with 4 s exposure at encoding, (4) recollected non-famous trials with 1 s exposure at encoding, (5) non-recollected (i.e., know response or miss) famous trials with 4 s exposure at encoding, (6) non-recollected famous trials with 1 s exposure at encoding, (7) non-recollected non-famous trials with 4 s exposure at encoding, (8) non-recollected non-famous trials with 1 s exposure at encoding, (9) correctly rejected new famous trials, (10) correctly rejected new non-famous trials, (11) scrambled null trials, and (12) button presses across all trials. Given differences in performance on the task, the number of trials included in each regressor varied. The average number of trials included in each regressor can be found in Table 1. Note that regressors 1–4 include only accurately recollected trials by definition. Accurate “Know” and Miss trials were combined into a “non-recollected” regressor due to a low trial count. Collapsing over “Know” and “Miss” complicates the interpretation of this regressor with respect to recognition accuracy, however, it still allows for the contrast of trials where a studied face was associated with the subjective experience of recollection with trials where it was not. Averaged timecourses from subject-specific white matter and

Table 1 Average number of trials included as regressors in fMRI analysis. Standard deviation is listed in parentheses

Trial type	Recollected (remember hits)		Non-recollected (know hits or misses)		Correct rejections
	4 s	1 s	4 s	1 s	
Famous	37.7 (6.1)	35.2 (6.3)	8.2 (6.1)	10.7 (6.4)	27.5 (4.0)
Non-famous	30.8 (6.1)	24.5 (7.9)	15.5 (6.3)	15.5 (6.3)	25.4 (5.0)
Null trials	96				
Button presses	356				

cerebrospinal fluid masks (thresholded at 90% probability) alongside 6 rigid-body motion parameters were included as the baseline model. Furthermore, 1–4th order polynomial trends were included in the baseline model to account for scanner drift and other extraneous changes in the signal over time. To ensure that we were manipulating prior knowledge accurately within our participants, we only modeled trials that were accurately judged as famous or non-famous by our participants according to post-scan fame judgements (mean number of omitted trials = 13/256, or 5%; mean fame recognition accuracy for famous = 0.93, and non-famous faces = 0.96). To account for the low trial counts in the non-recollected famous conditions, estimates were collapsed over duration in all applicable subsequent group analyses. Relevant voxelwise beta estimates were then averaged within each ROI, per participant, and then submitted to subsequent group-level analyses of variance (ANOVA), pairwise t-tests and trend analyses.

Our fMRI analyses are summarized below: (1) an ROI analysis, centered on the left PGp, using repeated measures ANOVAs to examine how recollection and prior knowledge modulate activity in the left AG; (2) an ROI analysis, where we performed direct contrasts examining effects of recollection and prior knowledge in 7 cytoarchitecturally separable ROIs from the inferior parietal lobes, in each hemisphere; and (3) a whole-brain voxelwise linear trend analysis testing the possibility of effects across both recollection strength and prior knowledge. To further supplement these gamma response-based analyses and to take advantage of our multi-band imaging sequence, we conducted an additional GLM using a finite impulse response (FIR) approach to visualize the timecourse of activity in the PGp. FIRs were estimated using an 18-parameter tent function in AFNI's 3dDeconvolve (*TENT_{zero}*) from 1 s before stimulus onset to 17 s after and were thus aligned to our 1 s TR grid. Note that our scrambled null trials (regressor 11, described above) were included in our FIR analysis to act as a descriptive baseline, allowing for the visual comparison of recollection and prior knowledge effects against AG activity in the absence of retrieval demands. The results from this model were used for visualization only. Whole-brain results were visualized using BrainNet Viewer (Xia et al. 2013; <http://www.nitrc.org/projects/bnv/>).

Results

Behavioural results

Prior knowledge and encoding duration improve overall recognition

Recognition accuracy was defined as the proportion of accurately recognized targets after subtracting the proportion of false alarms on novel foils (hits—false alarms), irrespective of any differences in the subjective experience of recognition (i.e., Remember or Know), per participant. The effect of prior knowledge and encoding duration on recognition accuracy was measured using a 2 (prior knowledge: famous, non-famous) × 2 (encoding duration: 1 s, 4 s) repeated measures ANOVA. Group-averaged accuracy across conditions is presented in Fig. 2A. Significant main effects of both prior knowledge [$F(1,23) = 41.72$, $p < 0.0001$, $partial \eta^2 = 0.64$] and encoding duration [$F(1,23) = 64.1$, $p < 0.0001$, $partial \eta^2 = 0.74$] were observed, indicating that the presence of prior knowledge and a longer encoding opportunity during study both improved subsequent recognition accuracy (Bellana et al. 2021). A significant interaction between prior knowledge and encoding duration was also observed [$F(1,23) = 8.97$, $p = 0.006$, $partial \eta^2 = 0.28$]. Simple effects using pairwise *t*-tests demonstrated that the benefit of longer encoding duration was most prominent during encoding of non-famous ($M_{1s} = 0.64$, $M_{4s} = 0.72$, $SD_{diff} = 0.05$; $t(23) = 7.75$, $p < 0.0001$, *Cohen's d* = 1.58) relative to famous faces ($M_{1s} = 0.84$, $M_{4s} = 0.88$, $SD_{diff} = 0.05$; $t(23) = 4.12$, $p = 0.0004$, *d* = 0.84).

Prior knowledge and encoding duration increase likelihood of recollection

The subjective quality of recognition was then examined by submitting hit—false alarm estimates to a 2 (prior knowledge: famous, non-famous) × 2 (encoding duration: 1 s, 4 s) × 2 (response type: Remember, Know) repeated measures ANOVA. Group-averaged estimates for Remember and Know recognition accuracy across conditions are presented in Fig. 2B, C. A significant 3-way interaction between prior knowledge × encoding duration × response type was

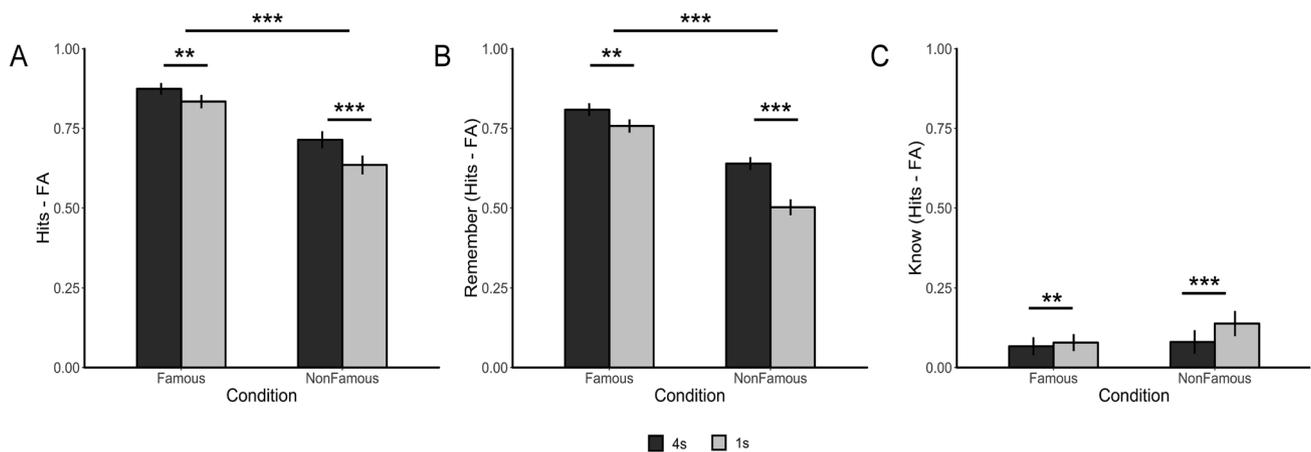


Fig. 2 Behavioural performance. Effect of prior knowledge (famous, non-famous) and encoding duration (1 s, 4 s) on **A** overall recognition (i.e., hits—false alarms), **B** Remember accuracy (i.e., proportion of Remember hits—proportion of Remember false alarms), and **C**

Know accuracy (i.e., proportion of Know hits—proportion of Know false alarms). Darker bars represent the 4 s encoding duration, while lighter bars represent 1 s. Error bars represent standard error of the mean. *** $p \leq .001$, ** $p \leq .01$, * $p \leq .05$

observed [$F(1,23) = 7.11$, $p = 0.01$, partial $\eta^2 = 0.24$]. This interaction was decomposed by examining the effect of prior knowledge and encoding duration on Remember (R) and Know (K) separately. For R accuracy, significant main effects of prior knowledge [$F(1,23) = 151.8$, $p < 0.0001$, partial $\eta^2 = 0.87$] and encoding duration [$F(1,23) = 51.93$, $p < 0.0001$, partial $\eta^2 = 0.69$] were observed, alongside a significant interaction between the two factors [$F(1,23) = 12.45$, $p = 0.002$, partial $\eta^2 = 0.35$]. Again, simple effects using pairwise t -tests demonstrated that the benefit of longer encoding duration on R accuracy was most prominent during encoding of non-famous ($M_{1s} = 0.50$, $M_{4s} = 0.64$, $SD_{diff} = 0.10$; $t(23) = 6.6$, $p < 0.0001$, *Cohen's d* = 1.35) relative to famous faces ($M_{1s} = 0.76$, $M_{4s} = 0.81$, $SD_{diff} = 0.07$; $t(23) = 3.57$, $p = 0.002$, *d* = 0.73). For K accuracy, a significant main effect of encoding duration was observed [$F(1,23) = 13.12$, $p = 0.001$, partial $\eta^2 = 0.36$], though in the opposite direction, with higher accuracy for 1 s as compared to 4 s of encoding. The main effect of prior knowledge and the interaction between the two factors were not significant (all p 's > 0.1). A pronounced benefit of prior knowledge on recollection has been reported previously using this paradigm (for details, see Bellana et al. 2021). For additional behavioural results examining the role of prior knowledge on memory, see Supplementary Materials: S1-S2.

fMRI results

Recollection and prior knowledge modulate activity in the left AG

The primary question of interest was to determine whether activity in the left AG could be modulated both by

task-specific recollection and prior knowledge in the same participants with the same paradigm. We, therefore, submitted participant-specific parameter estimates averaged across all voxels in the left PGp to a 2 (prior knowledge: famous, non-famous) \times 2 (recollection: recollected, correct rejection) repeated measures ANOVA. Parameter estimates for recollection trials were averaged across those presented for 4 s and 1 s at study to first test the effect of recollection regardless of encoding duration. Timecourses of activity based on FIR models of left PGp activity across all trials of interest are presented in Fig. 3A, B. Group-averaged parameter estimates across conditions are presented in Fig. 3C. Main effects of recollection [$F(1,23) = 6.26$, $p = 0.02$, partial $\eta^2 = 0.21$] and prior knowledge [$F(1,23) = 13.03$, $p = 0.001$, partial $\eta^2 = 0.36$] were observed. The interaction between recollection and prior knowledge was not statistically significant [$F(1,23) < 1$]. Overall, this suggests that the left AG (1) responds to recollection irrespective of whether the face was previously known or novel, and (2) responds to prior knowledge irrespective of whether the trial was accurately recollected or correctly rejected.

Next, we sought to characterize the response profile of the left AG to previously studied targets where recollection was successful against when recollection failed (i.e., know response or miss). To this effect, participant-specific parameter estimates from the left PGp were submitted to a 2 (recollection success: recollected, non-recollected) \times 2 (prior knowledge: famous, non-famous) repeated measures ANOVA (Fig. 3D). Estimates were again collapsed over trials with 1 and 4 s encoding duration to increase the number of trials in the famous non-recollected condition. Main effects of recollection success [$F(1,23) = 43.75$, $p < 0.0001$, partial $\eta^2 = 0.66$] and prior knowledge [$F(1,23) = 20.85$,

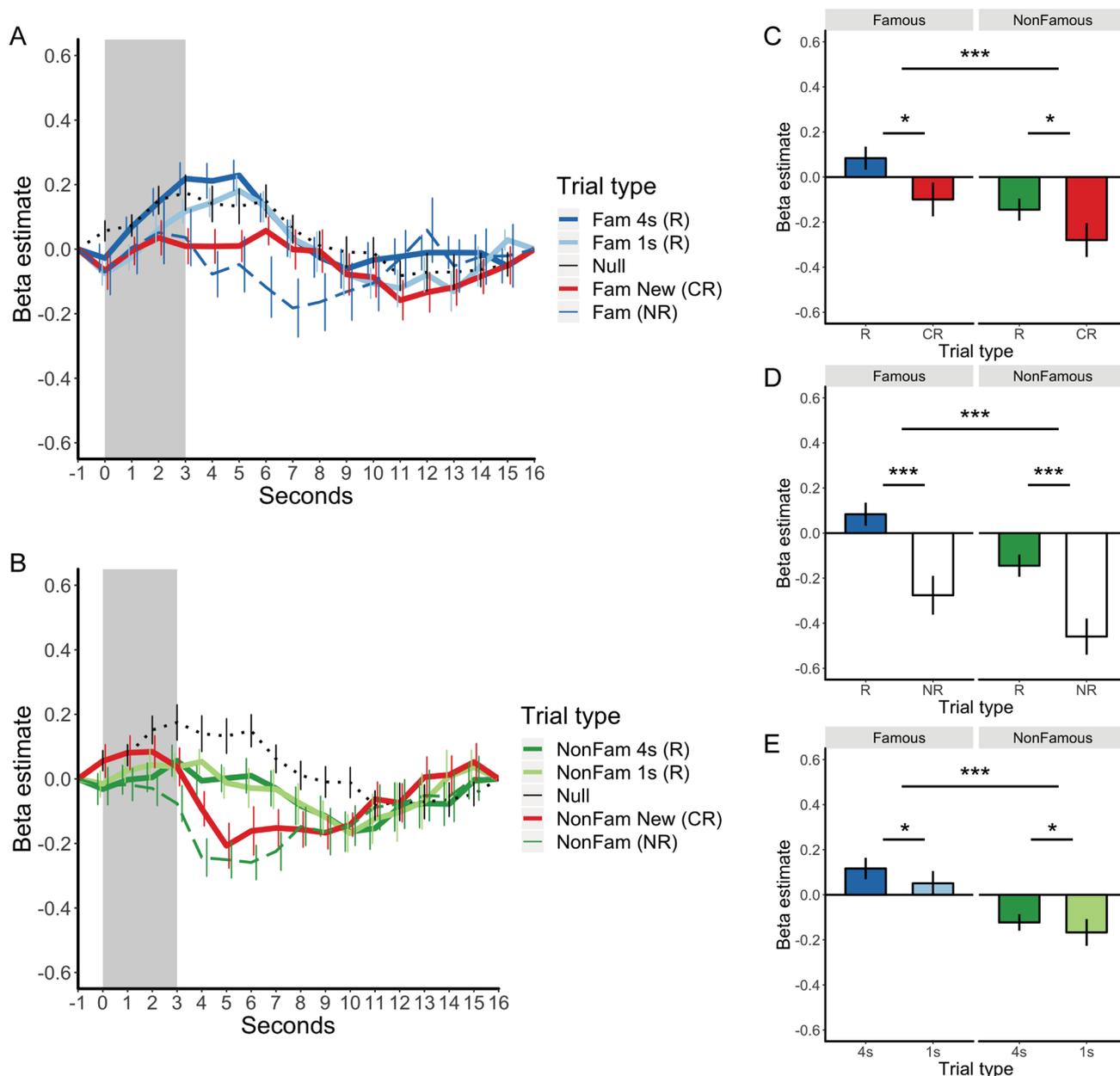


Fig. 3 Time-course of left PGp activity based on a finite impulse response model, visualizing trial-average activity patterns for **A** famous (blue) and **B** non-famous (green) trials separately. New famous and non-famous trials are plotted in red. Dotted line in black represents the timecourse for null trials. Zero represents stimulus onset. *R* Recollected target (i.e., remember hits). *CR* Correct rejection, *NR* Non-recollected target (i.e., know or miss). **C** Group-level univariate results: Activity in the left PGp for R and CRs, depicting an effect of both recollection and prior knowledge. Activity was mod-

elled using a standard gamma function. **D** Activity in the left PGp for recollection success (R, NR) × prior knowledge (famous, non-famous), while collapsing over encoding duration. R trials showed greater activity than NR trials, and the magnitude of the recollection response increased with prior knowledge. **E** Activity in the left PGp for recollection strength via encoding duration (4 s, 1 s) × prior knowledge (famous, non-famous). R trials with longer encoding durations (i.e., 4 s) show greater activity than those that were encoded for 1 s. *** $p \leq .001$, ** $p \leq .01$, * $p \leq .05$

$p = 0.0001$, partial $\eta^2 = 0.48$] were again observed, whereas the interaction between these factors was not statistically significant ($p > 0.5$). The left AG shows a robust recollection success effect during retrieval, consistent with previous reports (Rugg and King 2018; Vilberg and Rugg 2008).

Furthermore, the left AG shows greater activity in response to previously studied faces with prior knowledge irrespective of whether recollection succeeds. This again indicates that the effect of prior knowledge is independent of recollection success, modulating the strength of recollection and

non-recollection responses in the left AG. Furthermore, though an ROI approach was best suited to our theoretical question, additional voxelwise results are reported in the Supplementary Materials (S4-5), revealing direct overlap between the independent contrasts of recollection and prior knowledge within the left PGp.

Activity in the left AG has been suggested to track recollection strength, or the amount of details recollected, over and above an overall response to recollection (Hutchinson et al. 2014; Rugg and King 2018; Ciaramelli et al. 2020). We sought to replicate this effect by testing whether the magnitude of the recollection response in the left AG would increase with longer exposure at study, in line with experimental evidence supporting a recollection strength account (Leiker and Johnson 2014; Vilberg and Rugg 2009a, b). To this effect, participant-specific parameter estimates from the left PGp were submitted to a 2 (prior knowledge: famous, non-famous) \times 2 (encoding duration: 1 s, 4 s) repeated measures ANOVA, using recollected trials only (Fig. 3E). The main effect of prior knowledge [$F(1,23) = 14.38, p = 0.0009$, partial $\eta^2 = 0.38$] was significant, but critically, a modest effect of duration was also observed [$F(1,23) = 4.55, p = 0.044$, partial $\eta^2 = 0.17$] in which faces studied for 4 s showed a greater recollection response than those studied for 1 s. The interaction between prior knowledge and encoding duration was not statistically significant ($p > 0.7$). Overall, we report evidence consistent with notions of recollection strength in the left AG, specifically in the same region that shows sensitivity to prior knowledge more generally.

Effect of recollection and prior knowledge across the inferior parietal lobe

We report evidence that the left AG, specifically within the cytoarchitecturally distinct region of the PGp, responds to both recollection and prior knowledge within the same subjects. To compare the response profile of the PGp with other regions of the inferior parietal lobe, we extracted participant-specific parameter estimates from each of the seven cytoarchitectural subregions of the inferior parietal lobe (i.e., PFop, PFt, PFcm, PF, PFm, PGa and PGp; see Caspers et al. 2006, 2013), across both hemispheres, for three contrasts of interest: (1) recollected targets > correctly rejected foils, without prior knowledge (i.e., non-famous), (2) recollected > non-recollected targets, without prior knowledge, and (3) correctly rejected foils with prior knowledge (i.e., famous) > without prior knowledge (i.e., non-famous). Contrasts (1) and (2) isolate recollection effects in the absence of prior knowledge, whereas contrast (3) captures the effect of prior knowledge in the absence of any task-specific recollection. Group-averaged estimates are presented in Fig. 4B–D. Subject-specific parameter estimates were submitted to a one-way repeated measures ANOVA examining the effect

of subregion (PFop, PFt, PFcm, PF, PFm, PGa, PGp, per hemisphere), separately for each of the three contrasts. For exploratory purposes, additional one-sample t -tests were used to compare the parameter estimates against 0 for each ROI separately. Both uncorrected and FDR-corrected (per hemisphere) p -values are reported below. The results of the left PGp are reported first, followed by the other subregions of the IPL. To determine whether the response profile of the left PGp was distinct relative to the broader bilateral IPL, direct comparisons between left PGp and all other IPL subregions are reported in Supplementary Materials: S6 and 7.

For contrast 1), which isolates the effect of recollection relative to correct rejections for trials in the absence of prior knowledge, a significant main effect of subregion was observed [$F(13,299) = 5.90, p < 0.001$, partial $\eta^2 = 0.20$]. This indicates that the subregions of the IPL showed statistically dissociable response profiles from one another. One-sample t -tests against 0 revealed the left PGp as the only region with a marginal effect of recollection [$t(23) = 1.34, p = 0.059$], which did not survive FDR correction ($p_{FDR} = 0.137$) (Fig. 4B). The remaining regions of the bilateral inferior parietal lobe either did not differ from 0 (i.e., Left PFcm, PF, PFm, and PGa; Right PFt, PFcm, and PF; all $ps > 0.1$, uncorrected) or showed greater activity for correct rejections than recollection [Left PFop: $t(23) = 3.02, p = 0.006, p_{FDR} = 0.029$; Left PFt: $t(23) = 2.89, p = 0.008, p_{FDR} = 0.029$; Right PFop: $t(23) = 2.22, p = 0.037, p_{FDR} = 0.07$; Right PFm: $t(23) = 2.39, p = 0.025, p_{FDR} = 0.07$; Right PGa: $t(23) = 3.36, p = 0.003, p_{FDR} = 0.019$; and Right PGp: $t(23) = 2.17, p = 0.04, p_{FDR} = 0.07$].

For contrast (2), which isolates the effect of recollection relative to non-recollected trials (i.e., know or miss responses) in the absence of prior knowledge, a significant main effect of subregion was observed [$F(13,299) = 8.22, p < 0.001$, partial $\eta^2 = 0.26$]. One-sample t -tests against 0 revealed a significant response to recollection in the left PGp [$t(23) = 6.09, p < 0.0001, p_{FDR} < 0.0001$] (Fig. 4C). The left [$t(23) = 4.27, p = 0.0003, p_{FDR} = 0.001$] and right PFcm [$t(23) = 3.82, p = 0.0009, p_{FDR} = 0.002$] also showed greater activity for recollection success. The remaining regions of the bilateral inferior parietal lobe either did not differ from 0 (i.e., Left PFop, PFt, PF, PFm, and PGa; Right PFop, PFt, PF and PGp; all $ps > 0.1$) or showed greater activity for recollection failures [Right PFm: $t(23) = 4.03, p = 0.0005, p_{FDR} = 0.002$; Right PGa: $t(23) = 3.93, p = 0.0007, p_{FDR} = 0.002$].

For contrast (3), which isolates the effect of prior knowledge in the absence of task-specific recollection, a significant main effect of subregion was observed [$F(13,299) = 2.58, p = 0.002$, partial $\eta^2 = 0.10$]. One-sample t -tests against 0 revealed the left PGp was again statistically significant [$t(23) = 2.64, p = 0.015$], though the effect did not survive FDR correction ($p_{FDR} = 0.1$).

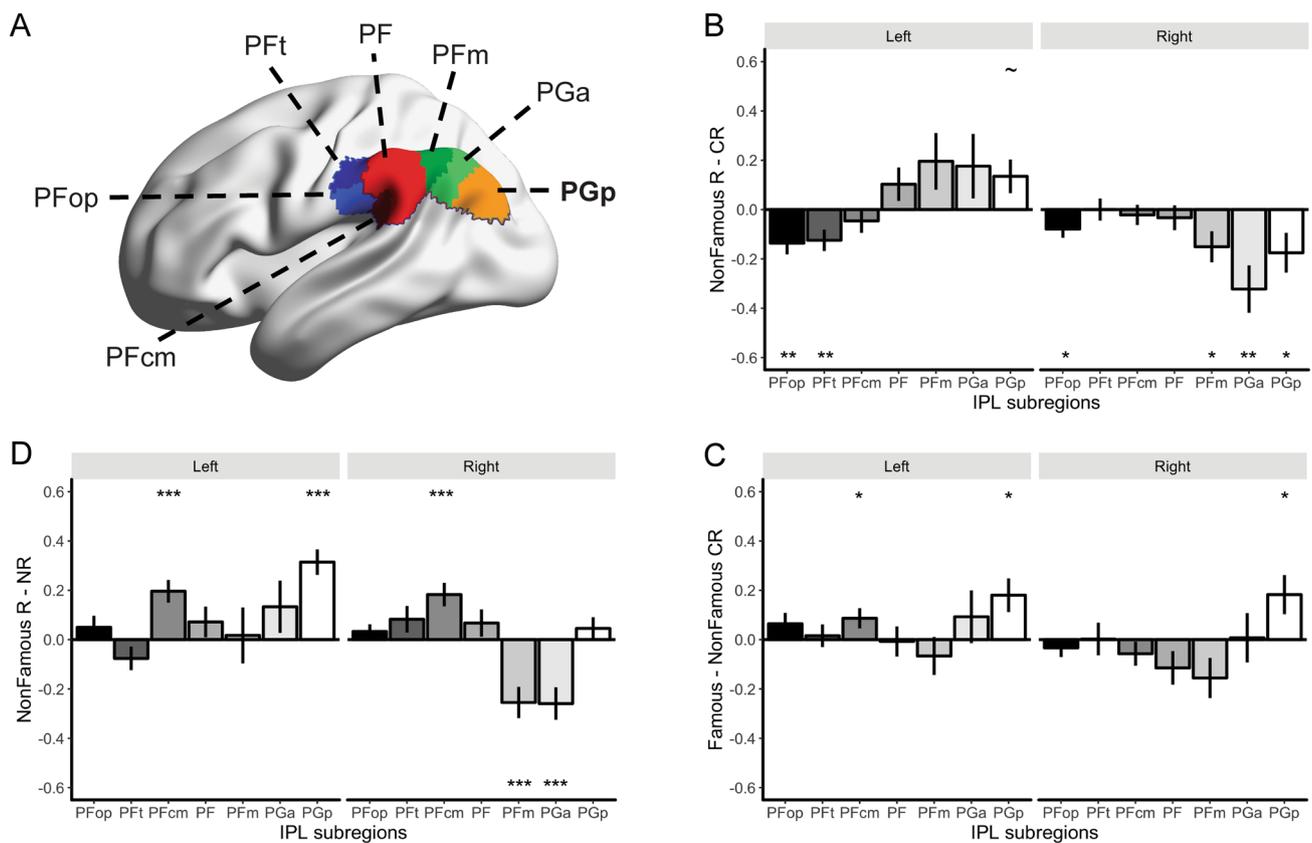


Fig. 4 **A** Cytoarchitecture-based parcellation of the inferior parietal lobe from Caspers et al. (2006) as implemented in the Julich Histological Atlas. Probability maps were thresholded at 40% and exclusively masked to be non-overlapping. Left hemisphere depicted. **B** Group-level contrast examining the effect of R relative to CR in the absence of prior knowledge (i.e., non-famous trials only). Results from contrast are plotted across all subregions in the bilateral inferior parietal lobe. **C** Contrast examining the effect of R relative to NR,

in the absence of prior knowledge (i.e., non-famous trials only). **D** Contrast examining the effect of prior knowledge in the absence of any demands on recollection (i.e., CR only). *** $p \leq .001$, ** $p \leq .01$, * $p \leq .05$, $\sim p \leq .06$, uncorrected. Error bars represent standard error of the mean. For voxel counts in each IPL subregion ROI, see Supplementary Materials: S3. For voxelwise overlap between recollection and prior knowledge in the IPL, see Supplementary Materials: S4-5

The left PFcm [$t(23) = 2.11$, $p = 0.045$, $p_{FDR} = 0.16$] and the right PGp [$t(23) = 2.30$, $p = 0.031$, $p_{FDR} = 0.22$] also showed some evidence for increased activity in response to prior knowledge (Fig. 4D). The remaining regions of the bilateral inferior parietal lobe largely did not differ from 0 (i.e., Left PFop, PFt, PF, PFm, and PGa; Right PFop, PFt, PFcm, PF, and PGa; all $ps > 0.06$, uncorrected).

Overall, the left PGp is the only region of the inferior parietal lobule to show numerically greater activity in the hypothesized direction across all three contrasts. Despite higher mean estimates, the PGp was not statistically dissociable from the neighboring left PGa of the posterior IPL across any of the specified contrasts in our sample. These data highlight the role of the posterior IPL, in the broader vicinity of the AG, in responding to both recollection and prior knowledge during retrieval.

Integrating evidence across recollection and incidental prior knowledge

The left AG, centered on subregion PGp, shows the most pronounced response to both recollection and prior knowledge relative to other regions of the bilateral inferior parietal lobe. We hypothesize that the magnitude of activity in this region may scale with the amount of information available at the time of recognition, collapsing over the idiosyncrasies of a specific episode, as indexed by recollection, and more general mnemonic content not linked to any specific past experience, namely, prior knowledge. To test the idea that an increase in activity should accompany how much related information across recollection and prior knowledge is available for each trial, we tested for a linear trend at the voxel level examining whether trials with more

cumulative exposure were associated with greater activity. Here, cumulative exposure is defined as a measure of how much experience a participant had with a given stimulus, where the degree to which a stimulus is exposed increases with any opportunity a participant had to encounter this stimulus during their lifetime. Critically, this definition of cumulative exposure explicitly combines both experience from the experiment itself with pre-experimental knowledge, providing an ideal measure to examine their integration in the brain (see also, Duke et al. 2017). For example, a recognizable famous face necessarily has more cumulative exposure than a non-famous face by nature of being known pre-experimentally. Also, a face presented for 4 s at encoding also has more cumulative exposure than one that was presented for only 1 s, as the participant has precisely four times more exposure while studying the former. Similarly, both types of studied faces have more cumulative exposure than a novel foil by virtue of being studied at all. Concretely, a linear increase in brain activity accompanying increased cumulative exposure was operationalized at the voxel level using the following linear weighted contrast: Famous 4 s R > Famous 1 s R > Famous correct rejection > Non-famous 4 s R > Non-famous 1 s R > Non-famous correct rejection (corresponding contrast weights: 5, 3, 1, -1, -3, -5). This contrast highlights voxels where retrieval activity linearly scales with the cumulative exposure associated with a given face, summing across experience from both the experimental episode and pre-experimental knowledge. It is important to note that our contrast treats prior knowledge as a categorical variable, such that prior knowledge is either present (famous) or absent (non-famous). Therefore, the precise amount of cumulative exposure is not properly captured, only whether one condition should be associated with more or less exposure than another. In other words, according to this contrast, the cumulative exposure between 4 and 1 s of study is the same as that between a correctly rejected famous face and a non-famous face that was studied for 4 s. For additional results in which participant-specific prior knowledge for famous faces is treated as a parametric modulator, see Supplementary Materials: S10-11. Also, for the sake of simplicity, non-recalled trials were excluded from this analysis as their appropriate position on a vector of cumulative exposure is not clear.

Whole-brain results are presented in Fig. 5 for voxels surviving a false discovery rate (FDR) correction of $p < 0.01$. Of the surviving voxels, 342 fell within the left inferior parietal lobe (i.e., combined mask of all 7 subregions), most commonly within the left PGp subregion (43.6%). Percentage of voxels showing a significant linear response in activity to cumulative exposure from other left IPL subregions are as follows: PF (23.8%), PFCm (13.7%), PGa (9.3%), PFM (1.6%), PFT (1%) and PPop (0.5%). Critically, in addition to the left AG, our voxelwise analysis revealed a distributed

set of regions showing a similar linear increase in activity across both recollection and prior knowledge (warm coloured regions in Fig. 5; for coordinates and supporting results, see Supplementary Materials: S6–9). Ventromedial prefrontal cortex, posterior cingulate, precuneus, lateral temporal cortex, right AG, posterior parahippocampal gyrus and the hippocampus, regions commonly known to form the default mode network (DMN), also showed activity scaling positively with increased cumulative exposure. Notably, when reducing the threshold to an FDR correction of $p < 0.05$, activation extended to the anterior medial temporal lobe, including regions of the perirhinal cortex, as previously observed in other studies of cumulative exposure (Duke et al. 2017). A separate set of regions, including fusiform gyrus, superior parietal lobe, anterior insula and dorsal anterior cingulate, showed a negative relationship with cumulative exposure suggesting activity in these regions scales up with stimulus novelty.

Discussion

We provide novel evidence that the left AG is not exclusively sensitive to recollection. Instead, prior knowledge—more general memory representations, derived across multiple episodes rather than a single past episode—can also modulate univariate activity in this region. These data stand in contrast to theoretical accounts that emphasize the unique importance of recollection in AG function (e.g., Rugg and Vilberg 2013). While we replicate the involvement of the left AG in the retrieval of experiential details from a specific past episode, the AG was also sensitive to the contrast of famous against non-famous faces that differed only in terms of general pre-experimental familiarity. As prior knowledge of this kind lies outside a traditional definition of recollection, a more accurate model of AG function must consider its role in the retrieval of this broader range of mnemonic representations.

Furthermore, recollection-specific activity in the left AG was heightened for faces with prior knowledge and for those with longer opportunity for study, consistent with accounts of recollection strength (i.e., amount of retrieved detail) modulating retrieval-related activity in this region (Rugg and King 2018). The observed strength effect does not appear to be restricted to recollection, as activity in the left AG, alongside a distributed set of regions in the DMN, scaled up with cumulative exposure across both domains of within-experiment recollection and pre-experimental knowledge. This increase in AG activity in response to within-episode recollection and across-episode prior knowledge highlights the common neural representation of these two ostensibly separate aspects of memory (Tulving 1972; Irish and Vatansever 2020; Renoult and Rugg

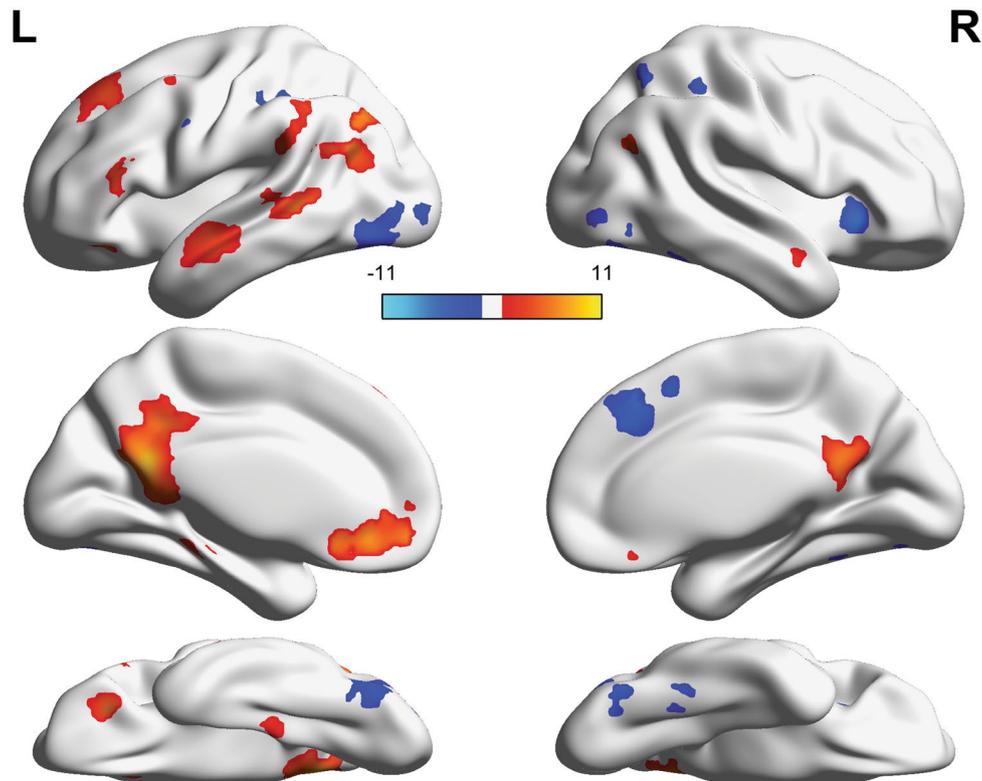


Fig. 5 Whole-brain voxelwise linear trend analysis corresponding to cumulative exposure (i.e., Famous 4 s R > Famous 1 s R > Famous Correct Rejection > Non-famous 4 s R > Non-famous 1 s R > Non-famous Correct Rejection; with corresponding contrast weights of: 5, 3, 1, -1, -3, -5). Warm coloured clusters show a positive linear trend such that magnitude of activity increases with cumulative exposure. Cool coloured clusters show a negative relationship with

cumulative exposure. Results are thresholded at a false discovery rate (FDR) correction of $p < 0.01$, with a minimum cluster extent of 20 voxels. For voxel counts in IPL subregions, see Supplementary Materials: S8. For whole-brain coordinates, see Supplementary Materials: S9. For related parametric modulation analysis, where participant-specific ratings of prior knowledge for each face were included in the model, see Supplementary Materials: S10, S11

2020), particularly in the higher order cortical regions of the DMN. At face value, these results run contrary to some previous findings of distinct neural substrates underlying task-specific recollection on one hand and pre-experimental knowledge on the other (e.g., Trinkler et al. 2009). We believe, however, that our theory-driven ROI approach and linear trend analysis afforded us more sensitivity to detect any potential cumulative effects across both kinds of mnemonic evidence. Overall, the data collected in the current study extend our understanding of AG function by emphasizing one critical point: any *complete* functional account of the left AG during retrieval *must* extend beyond the recollection of specific episodic details to incorporate its concurrent sensitivity to more general prior knowledge. Therefore, we argue that the left AG may be better characterized by its sensitivity to the amount of details retrieved from memory, as opposed to where those details lie on the continuum between episodic and semantic. This relative insensitivity to the distinction between episode-specificity and across-episode generalities may ideally position the AG to integrate these kinds of details in service of

remembering past experiences in rich detail (Ramanan and Bellana 2019).

Angular gyrus, recollection and prior knowledge

Various theoretical accounts have posited that the left AG is involved in our ability to access specific past experiences from memory (e.g., Berryhill 2012; Cabeza et al. 2012a; Ciaramelli et al. 2008; Gilmore et al. 2015; Levy 2012; Shimamura 2011; Simons et al. 2010; Vilberg and Rugg 2008; Wagner et al. 2005). An alternate line of evidence argues for its role in representing general semantic knowledge (Geschwind 1972; Binder et al. 2009; Binder and Desai 2011; Seghier 2013; Skipper-Kallal et al. 2015; Amer et al. 2019). Previous meta-analyses have suggested overlap across semantic and episodic memory in the AG (Humphreys and Lambon Ralph 2014; Kim 2016), but direct comparisons within the same individuals have highlighted distinctions when retrieving these two kinds of mnemonic content (Bonnici et al. 2016; Humphreys et al. 2022; Vatansever et al. 2021). Some studies go beyond spatial separation and

emphasize that the AG has opposing response profiles when retrieving details from a specific episode or across-episode generalities, in some cases supporting episodic retrieval but not generalities (Humphreys et al. 2022) while others show the reversed pattern (van der Linden et al. 2017). In the present study, we began unpacking this complex set of findings by testing the specificity of the AG response to episodic information. In other words, consider episodic and semantic memory as two ends of a continuum, from specific details from a single past episode to the generalities extracted across multiple past episodes (Renoult et al. 2012, 2019; Irish and Vatansever 2020). Does the AG exclusively respond to the strongest case of episodic memory: recollection? Or might it also show sensitivity to more general kinds of mnemonic content, derived across multiple past episodes, like prior knowledge? To this end, we provide evidence that activity in the left AG, especially in the vicinity of PGp, was independently modulated by both recollection and prior knowledge within the same individuals. Critically, the left AG was the only region in the bilateral posterior parietal lobes to show this response profile. These data provide an important caveat to semantic and episodic models of AG function: activity in this region may not be well characterized by theories derived from either domain alone. While this study does not conclusively contrast episodic memory against ‘pure’ semantic memory, it does demonstrate that retrieval of details from a specific past episode (i.e., recollection), a hallmark of episodic memory, is not necessary to drive AG activity. Instead, the incidental retrieval of prior knowledge upon presentation of a famous face, which consists of associations that are likely derived across several episodes, can similarly drive activity in the AG.

A question worth considering is what precisely makes up prior knowledge. Is it truly across-episode generalities, or might the presentation of a famous face automatically elicit specific recollections of past episodes, which would allow an exclusively episodic account of AG function to explain the present results? Alternatively, might famous faces elicit rich sensory representations that require integration, and thus, across-episode generalities are not what drives AG activity, but a multisensory integration process instead (Ben-Zvi et al. 2015; Bonnici et al. 2016; Yazar et al. 2017; Tibon et al. 2019)?

In the present experiment, the left AG was recruited during the correct rejection of novel famous faces relative to non-famous faces. Participants had 2.5 s to select between three response options (i.e., *R/K/N*) and were exposed to 128 famous faces over the course of the experiment. Critically, prior knowledge was incidental to task performance. Under these circumstances, we consider it unlikely that participants were consistently recalling specific past episodes each time a famous face was presented

during recognition (e.g., “Oh that’s Beyoncé. That reminds me of that time Britt, Vince and I watched *Lemonade* at our old apartment!”; “Oh, that’s the actor from that movie I saw a few months back...”). Instead, we suspect that participants were more likely focusing on making the memory decision, and while instances of explicit recollection likely occurred, we think it unlikely that they occurred more reliably than the incidental retrieval of more general associations, derived across multiple past episodes (Bruce and Young 1986; for analogous results with familiar scenes, see Robin et al. 2019). Similarly, it is possible that famous faces elicited multisensory associations (e.g., how they sound; how they may have looked at other times), but in the absence of any explicit demands to elaborate on these sensory details in particular, it is unclear why multisensory integration would drive AG activity in this task. While we cannot definitively rule out these possibilities, we contend that our results demonstrate that the left AG is sensitive to the incidental access of mnemonic content, whether episodic or semantic, while correctly rejecting a famous face. These findings, at the very least, require us to consider a wider range of mnemonic representations that can drive activity in this region beyond strict recollection.

Moreover, there is considerable evidence that the left AG represents abstract, conceptual knowledge without obvious dependencies on sensory representations or episodic memory. A study by Bonner and colleagues found activity in the left AG when contrasting abstract words (e.g., doctrine) and pseudowords in the context of a lexical decision task (c.f., Graves et al. 2017). Similarly, the AG has been reported to show evidence of successful cross-classification across modalities (i.e., using neural representation of the word “apple” to classify a photo of an apple; Fairhall and Caramazza 2013), consistent with a role in representing abstract, higher-order concepts (Fernandino et al. 2015; Price et al. 2015a, b, 2016). Therefore, the role of the left AG in integration may not be dependent on processing multisensory information or recalling specific past episodes. Instead, we argue that our data provide evidence that recollection-sensitive regions of left AG can also be recruited when accessing related knowledge, in the absence of explicit demands on multisensory integration or episodic retrieval, consistent with a concurrent role in representing higher order concepts in semantic memory (Binder et al. 2009; Kim 2016; Price 2010). Rather than limiting the integration process to sensory information, it may be that AG activation is driven by a domain-general integration process, combining abstract conceptual information with detailed perceptual and mnemonic content in the service of retrieving rich memories (Shimamura 2011; Wagner et al. 2015; Bonnici et al. 2016; Fernández and Morris 2018; Rugg and King 2018; Simons et al. 2022).

Angular gyrus and evidence accumulation

Activity in the left AG can be modulated by the amount of information recollected during retrieval. For example, recollection responses in the left AG are heightened for trials with longer relative to shorter presentation at encoding (Vilberg and Rugg 2009a, b), a pattern that we replicated (Fig. 3E). Similarly, this region has been reported to track stimulus repetition (Guerin and Miller 2011; Nelson et al. 2013; Gilmore et al. 2015; Ciaramelli et al. 2020), amount of source information at retrieval (Hutchinson et al. 2014), degree of cortical reinstatement from encoding (Jonker et al. 2018; Kuhl and Chun 2014; Leiker and Johnson 2014; Thakral et al. 2017b), and subjective memory strength (Thakral et al. 2015; Rissman et al. 2016). This recent evidence is broadly consistent with the mnemonic accumulator hypothesis (Wagner et al. 2005), which states that activity in the posterior parietal cortex tracks the amount of available evidence for an old response during recognition. Magnitude of activity, or strength of mnemonic evidence, is then compared against a decision criterion ultimately leading to recognition. It is unclear, however, why damage to an evidence accumulator would spare recognition memory performance, as observed in patients with lesions to the inferior parietal lobe (Berryhill 2012; Rugg and King 2018; c.f., Ben-Zvi Feldman et al. 2021). Results from our voxelwise linear trend analysis, however, demonstrate that increased activity in the AG corresponded to a linear vector representing cumulative exposure, combining recollection strength and prior knowledge on a common scale (Brown et al. 2018). Critically, this was true despite prior knowledge being incidental to recognition decisions in our paradigm. Therefore, the retrieval-related activity in the left AG may track mnemonic evidence beyond what is necessary for recognition, consistent with previous evidence separating AG activity from the decision process itself (Guerin and Miller 2011). Activity may instead reflect access to a cascade of wide-ranging associations related to the attended target, including contextual details from past episodes and broader semantic associations (Ramanan and Bellana 2019). Therefore, damage to the AG should only affect memory decisions to the degree that this broad ‘associative context’ is necessary. This hypothesis coincides with lesion evidence, in which damage to the AG specifically impairs performance on complex memory tasks, such as those probing recollection (Davidson et al. 2008), memory confidence (Simons et al. 2010; Hower et al. 2014), or recall of multimodal details (Ben-Zvi et al. 2015; Ciaramelli et al. 2017, 2020).

Overall, we provide evidence that retrieval-related activity in the left AG is sensitive to both experiment-specific recollection and pre-experimental mnemonic content. In fact, the AG may be particularly suited to integrate recent experiences with prior knowledge. Recent work on temporal

receptive windows, or the length of time during which an incoming signal is affected by its previous response history (Hasson et al. 2015), highlight the long temporal receptive window in the AG (i.e., history-dependence over minutes). This property is ideal for integrating incoming information with extended past experience (Chen et al. 2016; Akrami et al. 2018; Kaefer et al. 2022). Similarly, regions of the DMN (AG, ventromedial prefrontal cortex, posterior cingulate, precuneus, lateral temporal cortex, posterior parahippocampal gyrus and hippocampus) are also characterized by a history-dependence on the order of minutes (Chen et al. 2016), highlighting their unique sensitivity to past experience relative to the rest of the neocortex. DMN regions are also the most anatomically segregated from early sensory cortices (Margulies et al. 2016; Murphy et al. 2018) and thus are ideally situated to support complex internal representations removed from immediate sensory input (Mesulam 1998). Therefore, regions of the DMN, including the left AG, may be modulated by either recollection or prior knowledge when separated experimentally, but are perhaps best characterized by their ability to integrate recent past experience with pre-experimental knowledge in support of complex internal models of an attended target, consistent with their contributions to accessing conceptual knowledge (Binder et al. 1999), episodic memories (Bellana et al. 2017; Rugg and Vilberg 2013), schemas (Liu et al. 2016; Gilboa and Marlatt 2017) and cumulative exposure (Duke et al. 2017). Future research exploring the dissociable functional properties of regions within the DMN is necessary.

A note on task difficulty

The AG and broader regions of the DMN have long been associated with the label “task-negative”, due to their inverse relationship with task difficulty (Raichle et al. 2001; Fox et al. 2005). Subsequent work has argued against this model of DMN function, demonstrating mnemonic content can drive activity in the DMN irrespective of task difficulty (Spreng 2012; Andrews-Hanna et al. 2014; Spreng et al. 2014; Konishi et al. 2015; Murphy et al. 2018). Though this account may have been ultimately incorrect in the context of episodic memory, there remains controversy regarding whether the semantic activations in the AG can be explained by task difficulty alone (Graves et al. 2017; Humphreys and Ralph 2017; Humphreys et al. 2021). In this study, famous faces were better recognized than non-famous faces, making it difficult to disentangle prior knowledge from task difficulty during retrieval. However, during encoding, activity in the AG is known to show a reversed pattern, such that higher activity is associated with encoding failure rather than success (Huijbers et al. 2009, 2012; Sestieri et al. 2017; for a replication of this pattern in the present data, see Supplementary Materials: S12). If one speculates that successfully

encoded trials are ‘easier’ than trials when encoding fails, then the negative relationship between encoding activity and subsequent recollection may complicate an account of relying entirely on task difficulty. These trials likely differ along several other dimensions as well, making it difficult to rule out the contributions of task difficulty.

It is worth noting that Fig. 3A, B does reveal a highly comparable timecourse of PGP activity, during retrieval, across remembered Famous faces and null trials (i.e., scrambled images), in which no stimulus-related recollection or prior knowledge should be available. As we cannot infer what was going on in the minds of our participants during these null trials, we cannot provide a conclusive explanation for this pattern. It may provide, however, some initial insight into the *kinds* of cognitive demands that drive activity in the AG. For example, when a task is very easy, as is the case for our null trials, participants may engage in various kinds of diffuse kinds of cognition, such as mind-wandering. Mind-wandering is a complex set of cognitive processes and has been demonstrated to recruit the left AG, in addition to (though not exclusively) the broader DMN (Binder et al. 1999; Mason et al. 2007; Christoff et al. 2009; Andrews-Hanna et al. 2010; Stawarczyk et al. 2011; Fox et al. 2015; Ellamil et al. 2016; Van Calster et al. 2016; Bellana et al. 2017). It may be that the left AG and DMN are sensitive to common features underlying the generative and diffuse processing associated with remembering specific episodes, accessing prior knowledge, and mind-wandering (Axelrod et al. 2017; Gorgolewski et al. 2014; Smallwood and Schooler 2015; Van Calster et al. 2016). Future research probing this possibility will provide crucial insights into the role of these brain regions in memory and cognition more broadly.

Functional heterogeneity in inferior parietal lobe

While our theoretical interests centered on the left AG, our results additionally highlight the functional heterogeneity within the inferior parietal lobe (Nelson et al. 2010; Humphreys and Lambon Ralph 2014). Notably, we replicated the left-lateralization commonly reported in neuroimaging studies exploring retrieval effects in the AG (Bellana et al. 2016; Guerin and Miller 2009), where regions surrounding the right AG did not show the recollection effects observed in the left hemisphere (see Fig. 4B, C). As language processes tend to be left lateralized in right-handed individuals (Knecht et al. 2000), the degree of verbal processing required in a given task may predict left-lateralization. While famous faces are associated with names and this verbal information may be activated automatically during retrieval, Fig. 4B, C highlight this left-lateralization when recollecting non-famous faces, which are less likely to elicit such verbal code. Further work is needed

to characterize the nature of this lateralization during memory retrieval and why it occurs.

Beyond laterality, differences in response profile can be observed across the cytoarchitecturally separable subregions of the IPL. For example, when contrasting Remember trials against correct rejections, recollection effects appear most prominently in posterior rather than anterior regions of the left IPL (Fig. 4B). However, when recollection is defined relative to non-recollected trials instead (i.e., Know and misses), bilateral PFCm also showed some sensitivity (Fig. 4C). Despite its relatively anterior position in the IPL, previous studies have often reported the involvement of the supramarginal gyrus, which can include the PFCm, in episodic memory retrieval (Ciaramelli et al. 2008, 2010, 2020; Cabeza et al. 2012a; Hutchinson et al. 2014). Its specific role in retrieval remains unclear, although some studies have argued for a role in bottom-up attentional capture of salient memories (Ciaramelli et al. 2008, 2010, 2020).

Limitations

It is important to explicitly state that our conclusion, that the left AG responds to *both* recollection and prior knowledge, hinges on the assumption that rejecting a novel famous face does not reliably elicit recollection. We cannot definitively rule out this possibility in the present dataset. Nonetheless, we contend that the incidental access of mnemonic content that is elicited while correctly rejecting a famous face, whether episodic or semantic or a mixture of both, forces us to broaden our assumptions regarding the kinds of mnemonic content that drive activity in the left AG beyond a traditional definition of recollection (Renoult et al. 2012; Irish and Vatansever 2020). Furthermore, the idea that the AG activity may be driven by mnemonic content outside of strict recollection is consistent with the results of our parametric modulation analysis, where faces for which participants reported to have more prior knowledge were associated with greater activity in the AG and broader DMN (see Supplementary Materials: S8, S9). Similarly, this more general role in memory is in line with the AG’s purported involvement in semantics (Geschwind 1972; Binder et al. 2009; Binder and Desai 2011; Seghier 2013; Fairhall and Caramazza 2013; Fernandino et al. 2015; Price et al. 2015a, b; 2016; c.f., Humphreys et al. 2022) and its position as a hub in the DMN, ideally situating the AG to support the integration of both recent and remote experiences (Chen et al. 2016; Hasson et al. 2015; Kaefer et al. 2022).

Conclusions

We provide novel evidence that the left AG is sensitive to both experiment-specific recollection and access to pre-experimental knowledge within the same individuals. These

results argue that a broader array of mnemonic representations can drive activity in this region than previously considered. Perhaps most importantly, we believe that this broader account of AG function is consistent with its anatomical profile, alongside the broader DMN, which may be ideally situated to support complex internal mnemonic representations removed from immediate sensory input (Margulies et al. 2016; Mesulam 1998; Murphy et al. 2018; Ramanan and Bellana 2019), irrespective of their episodic or semantic nature.

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Data availability All data are available from the corresponding authors upon reasonable request. The data are not publicly available at this time as they contain information that could compromise research participant privacy and signed consent.

Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

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