Hippocampal–Cortical Encoding Activity Predicts the Precision of Episodic Memory

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Abstract

■ Our recollections of past experiences can vary in both the number of specific event details accessible from memory and the precision with which such details are reconstructed. Prior neuroimaging evidence suggests the success and precision of episodic recollection to rely on distinct neural substrates during memory retrieval. In contrast, the specific encoding mechanisms supporting later memory precision, and whether they differ from those underlying successful memory formation in general, are currently unknown. Here, we combined continuous measures of memory retrieval with model-based analyses of behavioral and neuroimaging data to tease apart the encoding correlates of successful memory formation and mnemonic precision. In the MRI scanner, participants encoded object-scene displays and later reconstructed features of studied objects using a continuous scale. We observed overlapping encoding activity in inferior prefrontal and posterior perceptual regions to predict both which object features were later remembered versus forgotten and the precision with which they were reconstructed from memory. In contrast, hippocampal encoding activity significantly predicted the precision, but not overall success, of subsequent memory retrieval. The current results align with theoretical accounts proposing the hippocampus to be critical for representation of high-fidelity associative information and suggest a contribution of shared cortical encoding mechanisms to the formation of both accessible and precise memory representations. ■

INTRODUCTION

Our memories are not an exact reproduction of the past but can range from high-fidelity, precise reconstructions of previous experiences to less precise, lower-resolution representations. Behavioral evidence suggests such variation in mnemonic precision to be distinguishable from the general success of memory retrieval (Harlow & Yonelinas, 2016; Richter, Cooper, Bays, & Simons, 2016; Brady, Konkle, Gill, Oliva, & Alvarez, 2013; Harlow & Donaldson, 2013; but see Schurgin, Wixted, & Brady, 2020). Although the likelihood of successful retrieval of information from memory and the precision of the retrieved information correlate across individuals, most variance in each measure is nevertheless unrelated to the other (Richter et al., 2016). Moreover, these two aspects of objective memory performance appear to be associated with separable subjective characteristics (Harlow & Yonelinas, 2016) and are differentially sensitive to various experimental manipulations (e.g., Berens, Richards, & Horner, 2020; Sun et al., 2017; Xie & Zhang, 2017; Sutterer & Awh, 2016) as well as to memory impairments in distinct populations (Korkki, Richter, Jeyarathnarajah, & Simons, 2020; Nilakantan, Bridge, VanHaerents, & Voss, 2018; Cooper et al., 2017), eliciting proposals that they may at least to some degree reflect a dissociable neurocognitive basis.

Indeed, prior neuroimaging evidence indicates the success and precision of episodic recollection to recruit distinct regions of the posterior-medial network during memory retrieval (Richter et al., 2016). Whereas retrieval activity in the hippocampus (HC) has been observed to increase for successful in comparison to unsuccessful retrieval, trial-wise variation in memory precision appears to correlate with retrieval-related activity in the lateral parietal cortex (Richter et al., 2016), although others highlight a role for medial temporal regions also (Montchal, Reagh, & Yassa, 2019; Stevenson et al., 2018). However, despite increased interest in the neural basis of mnemonic precision, the focus of prior studies has been on retrieval mechanisms (e.g., Cooper & Ritchey, 2019; Montchal et al., 2019; Stevenson et al., 2018; Richter et al., 2016), whereas the encoding substrates supporting the formation of precise memory representations, and whether they differ from those supporting successful encoding in general, remain unresolved.

Successful episodic memory formation is typically associated with activity increases in a network of medial temporal, lateral prefrontal, and posterior perceptual regions (Kim, 2011; Spaniol et al., 2009). The HC receives input from content-specific perceptual regions and is thought to bind disparate event features into a coherent memory representation (Cooper & Ritchey, 2020; Ranganath,

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2010; Davachi, 2006; Paller & Wagner, 2002) and allow for the storage of similar experiences in an orthogonalized, or nonoverlapping, manner (Norman & O'Reilly, 2003; O'Reilly & McClelland, 1994). Lateral prefrontal regions, on the other hand, are involved in the strategic and controlled encoding of information into memory via processes such as attentional selection, elaboration, and integration of information relevant for current task goals (Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). The specific neural substrates supporting successful memory formation have been found to exhibit process specificity, varying for instance according to the depth of stimulus processing engaged in at encoding (Park, Uncapher, & Rugg, 2008; Otten & Rugg, 2001) and the type of retrieval process later recruited (Staresina & Davachi, 2006; Ranganath et al., 2004). Moreover, encoding correlates appear sensitive to more subtle differences in the quality of retained representations, including their objective amount of detail (Cooper & Ritchey, 2020; Qin, van Marle, Hermans, & Fernandez, 2011), and subjective ratings of memory vividness or confidence (Kensinger, Addis, & Atapattu, 2011; Qin et al., 2011). However, while beginning to elucidate the encoding mechanisms underlying variation in more qualitative aspects of later retrieval, prior studies have typically been limited by the use of categorical measures of the quantity of details remembered, or participants' subjective reports, which may not directly map onto more graded variations in objective memory precision.

It is possible that, in addition to relying on distinct brain regions during retrieval (Richter et al., 2016), the success and precision of episodic recollection may be supported by at least partly separable neural mechanisms during memory encoding. For instance, the successful retrieval of information from memory may depend on the strength of an association between a retrieval cue and the target memory, thus drawing in particular on associative encoding processes supported by the HC and the prefrontal cortex (Blumenfeld & Ranganath, 2007; Davachi, 2006). In contrast, the precision with which specific mnemonic features can be reconstructed from memory may closely relate to the fidelity of stimulus encoding in posterior perceptual regions (Emrich, Riggall, LaRocque, & Postle, 2013) and/or to hippocampal function supporting the formation of distinct and detailed memory traces that can be later reconstructed with high precision (Moscovitch, Cabeza, Winocur, & Nadel, 2016). Indeed, an association between hippocampal encoding activity and subsequent mnemonic precision would align with prior accounts suggesting the HC to be critical for representation of high-fidelity relational information across perception and memory (Ekstrom & Yonelinas, 2020; Kolarik et al., 2016; Aly, Ranganath, & Yonelinas, 2013; Yonelinas, 2013). Alternatively, it is possible that, contrary to dissociable neural substrates observed during retrieval (Richter et al., 2016), the successful and precise encoding of information into memory may rely on shared neural mechanisms that perhaps act to increase the strength of the memory more generally, rendering it both accessible and precise at retrieval.

In the current study, we employed continuous measures of memory retrieval and model-based analyses of behavioral and neuroimaging data to elucidate the encoding substrates of mnemonic precision. In the MRI scanner, participants encoded visual stimulus displays depicting an object overlaid on a scene background. The location and color of the objects were drawn from circular spaces, and at retrieval, participants recreated these attributes of the studied items using a continuous response dial. This approach allowed us to segregate encoding activity supporting later successful memory retrieval from that supporting subsequent mnemonic precision in a manner not afforded by more typical categorical measures of retrieval performance (e.g., old/new, remember/know), thus providing novel insight into the encoding mechanisms supporting the acquisition of precise episodic memories.

METHODS

Participants

Twenty-one young adults (18–29 years old) participated in the current experiment. All participants were right-handed, native English speakers, and had normal or corrected-to-normal vision, no color blindness, and no current or historical diagnosis of any neurological, psychiatric, or developmental disorder, or learning difficulty. Participants indicated no current use of any psychoactive medication and no medical or other contradictions to MRI scanning. One participant was excluded from all analyses because of excessive movement (>4 mm) in the scanner, leaving 20 participants to contribute to the present analyses (eight men, 12 women; mean age = 22.15 years, SD = 3.10 years). The participants were recruited via the University of Cambridge Psychology Department Sona volunteer recruitment system (Sona Systems, Ltd.) and community advertisements and were reimbursed with £30 for their participation. All participants gave written informed consent in a manner approved by the Cambridge Psychology Research Ethics Committee.

Materials

Stimuli for the memory task comprised 180 images of outdoor scenes and 180 images of distinct everyday objects. The images were obtained from existing stimuli sets (scenes: Richter et al., 2016; objects: Brady et al., 2013) and Google image search. Each object image was randomly paired with a scene image to generate 180 trial-unique study displays (size = 750 × 750 pixels). Across the study displays, we varied the appearance of two object features: color and location. For each display, object color and location were randomly selected from circular

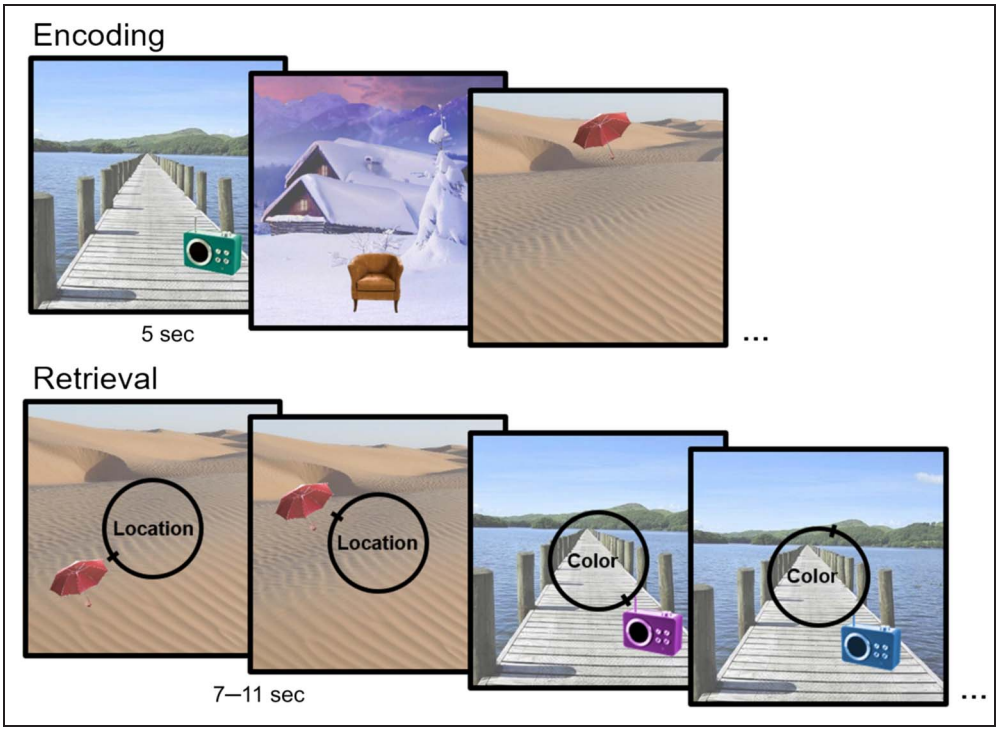

Figure 1. Example study and test trials of the memory task. At study, participants viewed stimuli displays consisting of one object overlaid on a scene background (stimulus duration: 5 sec). The location and color of the objects at study were randomly chosen from circular parameter spaces (0–360°). At test, participants recreated either the location or color of each studied object using a 360° continuous response dial, allowing for a fine-grained assessment of memory fidelity.

parameter spaces (0–360°; cf. Cooper et al., 2017; Richter et al., 2016; see Figure 1). All participants viewed the same study displays in a randomized order.

Design and Procedure

Before the scan, participants read the instructions and undertook practice trials of the memory task. The task was modified from Richter et al. (2016) by reducing the number of objects presented at study and the number of features later tested, to result in one feature retrieval trial per study display. In total, participants completed nine study-test blocks over nine functional runs (one study and one test phase per run). At study, participants sequentially viewed 20 object-background displays (stimulus duration: 5 sec) and were instructed to try and memorize the appearance of each display, including the location and color of the object. The study phase was followed by a 10-sec delay during which a "Get Ready" message was presented on a black screen. After this delay, participants were asked to reconstruct either the location or the color of each object viewed in the preceding study phase (one feature question per each encoding trial, a total of 20 retrieval trials per block). At retrieval, the test object reappeared on its associated background with a central cue word "Location" or "Color" indicating the type of feature tested on that trial. The initial appearance of the tested feature was randomly selected from a circular parameter space (0–360°), whereas the appearance of the untested feature remained unchanged from study to test. In other words, for location trials, the test object reappeared in its original color, but in a randomly selected location, whereas for color trials, the test object reappeared in its original location but in a randomly chosen color. Participants were asked to recreate the object's original features as accurately as they could by moving a slider around a 360° response dial using their middle and index fingers on a button box and were able to confirm their answer by pressing a third key with their thumb. The retrieval phase was self-paced with the constraint of a minimum trial length of 7 sec and a maximum RT of 11 sec. Participants on average produced RTs that were well under this limit (M = 5.64 sec, SD = 0.68 sec), and the percentage of trials where response selection was not confirmed in time was very low (M = 1.36%, SD = 1.77%). Note that if a participant failed to confirm their answer within 11 sec, their last position on the response wheel was recorded as their answer for that trial.

Participants completed 90 location and 90 color trials in total (10 trials of each type per task block). The type of feature tested for each object was randomized across displays but constant across participants so that all participants answered the same feature question for each study display. To ensure that memory was tested for feature values spanning the entire circular space, the randomization was conducted with a constraint of roughly equal number (i.e., 20–25) of target feature values sampled from each quadrant around the circular space for both the location and color conditions. The order of study and test displays was then randomized across participants with the constraint of no more than four encoding or retrieval trials in a row for which the same type of feature was tested. Study and test trials were separated by a fixation cross with jittered duration between 0.4 and 2.4 sec

(mean ISI duration: 1 sec) drawn from a Poisson distribution. After the first five of the nine task blocks, participants were given a 10-min break from the memory task in the scanner, during which a diffusion-weighted structural scan was acquired (analysis of diffusion-weighted data not reported here).

Behavioral Analysis

For each trial, we calculated participants' retrieval error as the angular difference between their response value and the target feature value (0 ± 180°). To distinguish the likelihood of successful memory retrieval from the precision of the retrieved information, we fitted a two-component mixture model (Bays, Catalao, & Husain, 2009; Zhang & Luck, 2008) to each participant's retrieval error data using maximum likelihood estimation (code available at www.paulbays.com/code/JV10/index.php). This mixture model has been shown to characterize long-term memory performance in similar tasks (e.g., Korkki et al., 2020; Richter et al., 2016; Brady et al., 2013) and has been employed to gain insights about the neural basis of the precision of episodic recollection (Cooper & Ritchey, 2019; Stevenson et al., 2018; Richter et al., 2016). The model assumes that two distinct sources of error contribute to participants' retrieval performance across trials: variability, that is, noise, in successful retrieval of target features and the presence of random guess responses where memory retrieval has failed to bring any diagnostic information about the target to mind. These two sources of error are modeled by a von Mises distribution (circular equivalent of a Gaussian distribution) centered at a mean error of 0° from the target value, with a concentration, K, and a circular uniform distribution with a probability, pU, respectively. Precision of memory retrieval can be estimated as the concentration parameter (K; higher values reflect higher precision) of the target von Mises distribution and the likelihood of successful memory retrieval (pT) as the probability of responses stemming from the target von Mises distribution ($pT = 1 - pU$). Consistent with prior studies (Korkki et al., 2020; Richter et al., 2016), this two-component model was found to fit the current data better than an alternative one-component model where participants' responses were assumed to stem from a von Mises distribution around the target feature value only (mean Bayesian information criterion for the one-component model: 386.10; mean Bayesian information criterion for the two-component model: 317.62; models fitted to individual participants' data across the feature conditions).

MRI Acquisition

MRI scanning took place at the University of Cambridge Medical Research Council Cognition and Brain Sciences Unit using a 3-T Siemens Tim Trio scanner with a 32-channel head coil. For each participant, a whole-brain structural image was acquired using a T1-weighted 3-D magnetization prepared rapid gradient echo sequence (repetition time = 2.25 sec, echo time = 3 msec, flip angle = 9°, field of view = 256 × 256 × 192 mm, resolution = 1 mm isotropic, GRAPPA acceleration factor 2). Functional data were acquired over nine runs each comprising one task block (one encoding and one retrieval phase), using a single-shot EPI sequence (repetition time = 2 sec, echo time = 30 msec, flip angle = 78°, field of view = 192 × 192 mm, resolution = 3 mm isotropic). Each volume consisted of 32 sequential oblique-axial slices (interslice gap: 0.75 mm) acquired parallel to the AC–PC transverse plane. Across the participants, the mean number of volumes acquired per functional run was 166.09 (SD = 8.08). The scanning protocol further included a diffusion-weighted structural scan that was acquired after the first five functional runs (not analyzed here).

fMRI Preprocessing

Data preprocessing and analysis were performed with SPM 12 (www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB R2016a (The MathWorks). The first five volumes of each functional run were discarded to allow for T1 equilibration. Furthermore, any additional volumes collected after each task block had finished were discarded for each participant so that the last volume of each run corresponded to a time point of ~2 sec after the last fixation cross. 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 (gray matter, white matter, cerebrospinal fluid). These segmentations were used to create a study-specific structural template image using the DARTEL (Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra) toolbox (Ashburner, 2007). The functional data were normalized to Montreal Neurological Institute space using DARTEL and spatially smoothed with an isotropic 8-mm FWHM Gaussian kernel.

Main fMRI Analyses

To obtain trial-specific estimates of the success and precision of memory retrieval for the fMRI analyses, we fitted the two-component mixture model (von Mises + uniform distribution) to retrieval error data across all participants and feature conditions (3600 trials in total). Using the best-fitting model probability density function, we then calculated the probability of each error belonging to the target von Mises distribution over the uniform distribution and classified errors with at least .05 probability of stemming from the von Mises distribution as "successful" and errors with less than .05 probability of belonging to the

von Mises distribution as "unsuccessful" (cf. Cooper et al., 2017; Richter et al., 2016). In terms of degrees, this corresponded to a subsequent retrieval success cutoff of ±51°, where trials with an absolute error ≤ 51° (range = 0–51°) were classified as "successful" and trials with an absolute error > 51° were classified as "unsuccessful" (range = 52–180°). As done in prior studies (Cooper & Ritchey, 2019, 2020; Cooper et al., 2017; Richter et al., 2016), we used the across-participant model-derived cutoff to ensure that responses of the same error magnitude were consistently classified as successful or unsuccessful across individuals as well as to avoid any bias in the error cutoffs related to differences in individual model fits. We further note that using feature-specific cutoffs, rather than the threshold estimated across all retrieval trials, did not change the significance of our main results. For trials classified as successfully encoded, a trial-specific measure of memory precision was further calculated as 180° minus [participant's absolute retrieval error on that trial] so that higher values (smaller error) reflected higher precision (range = 129–180°; cf. Cooper et al., 2017; Richter et al., 2016).

For each participant, a first-level general linear model was constructed containing three regressors corresponding to each event of interest (successful location encoding, successful color encoding, and unsuccessful encoding) and a fourth regressor modeling the retrieval trials. For the successful encoding trials, the trial-specific estimates of memory precision were 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 effects and were mean centered for each participant. Neural activity was modeled with a boxcar function convolved with the canonical hemodynamic response function, with a duration of 5 sec for the encoding trials and a variable duration (7–11 sec) for the retrieval trials, capturing the duration of the study and test displays, respectively. Six participant-specific movement parameters estimated during realignment (three rigid-body translations, three rotations) were further included as covariates in the first-level model to capture any residual movement-related artifacts. Because of the small number of guessing trials in each functional run, data from all functional runs were concatenated for each participant, and nine constant block regressors were 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 cutoff was used to eliminate low-frequency noise. First-level participant-specific parameter estimates were submitted to second-level random effects analyses.

Contrasts

The contrasts for the fMRI analyses focused on identifying regions where encoding activity positively predicted the subsequent success and/or precision of episodic memory retrieval (i.e., increases in BOLD signal for successful encoding or higher memory precision). To examine encoding activity associated with the subsequent success of memory retrieval, we contrasted encoding trials for which memory retrieval subsequently succeeded against trials for which memory retrieval subsequently failed ("subsequent retrieval success effects"). To identify encoding activity predicting the later precision of memory retrieval, positive associations between BOLD signal and the precision parametric modulator were examined (i.e., linear relationship between BOLD signal and precision parametric modulator; "subsequent precision effects"). We further assessed the overlap between subsequent success and subsequent precision effects using conjunction analyses. Conjunction analyses were conducted testing against the conjunction null hypothesis to ensure that regions identified in this analysis displayed reliable encoding activity associated with each individual contrast, that is, both subsequent success and subsequent precision of memory retrieval (see Nichols, Brett, Andersson, Wager, & Poline, 2005). Moreover, we assessed the specificity of the subsequent success and subsequent precision effects by conducting exclusive masking of each subsequent memory contrast by the other (i.e., subsequent retrieval success masked by subsequent precision contrast and vice versa). For this analysis, the mask image was thresholded at $p < .050$ uncorrected (cf. Uncapher, Otten, & Rugg, 2006; Smith, Henson, Dolan, & Rugg, 2004).

Because of a relatively low number of guess trials per feature condition for some individuals, it was not possible to investigate feature-specific subsequent success effects. Furthermore, analysis of feature-specific subsequent precision effects did not yield any significant differences across the ROIs ($ps > .208$) or the whole brain ($ps > .303$). Thus, our analyses focused on examining BOLD activity predicting the subsequent success and precision of memory retrieval across the feature conditions, consistent with the approach taken in previous studies employing a similar paradigm (Cooper et al., 2017; Richter et al., 2016).

ROIs

The main analyses focused on a small number of a priori ROIs implicated by meta-analytic evidence in supporting the successful formation of episodic memories for visual information (Kim, 2011; Spaniol et al., 2009). Specifically, the ROIs included the HC, the inferior frontal gyrus (IFG), and the fusiform gyrus (FFG). Given evidence for greater consistency of subsequent memory effects in the left hemisphere (Spaniol et al., 2009), left-lateralized ROIs were used, each comprising the left anatomical region as defined by the automated anatomical labeling atlas (Tzourio-Mazoyer et al., 2002). Statistical significance within each anatomical ROI was assessed using small-volume

correction with a peak-level family-wise error (FWE)-corrected (based on random field theory) threshold of $p < .05$, correcting for the number of voxels in each ROI. In addition to the ROI analyses, we sought to identify any additional brain regions displaying a relationship between encoding activity and the subsequent success and/or precision of memory retrieval in exploratory whole-brain analyses conducted at a whole-brain FWE-corrected threshold of $p < .05$, with a minimum extent of 5 contiguous voxels.

Additional Control Analyses

In addition to the main fMRI analyses described above, we conducted two additional analyses to assess whether BOLD signal in any of the ROIs was associated with trial-wise variation in participants' memory error for trials classified as "unsuccessful" based on the model-derived cutoff (absolute error > 51°), that is, when variation in memory error was assumed to be driven by guessing, or when collapsing across all encoding trials without assuming a model-based separation between successful and unsuccessful retrieval. For the first analysis, the first-level general linear model was identical to what was described above, but with the addition of a parametric modulator for unsuccessful trials also that reflected trial-wise variation in participants' subsequent memory error (180° – absolute error; range: 0–128°). For the second, model-free, analysis, all encoding trials in the location and color condition were modeled with one regressor each, and a parametric modulator reflecting trial-wise variation in subsequent memory error (180° – absolute error; range: 0–180°) was added for each condition. Parametric modulators were mean centered, and the contrast of interest investigated linear increases in BOLD signal with decreasing memory error.

RESULTS

Behavioral Results

For each trial, we calculated participants' retrieval error as the angular difference between their response value and the target feature value (0 ± 180°; see Figure 2A). Across participants and feature conditions, overall task performance, as measured by the mean absolute retrieval error, was 30.43° (SD = 15.04°), with a significantly higher mean absolute error in the color (M = 34.48°, SD = 15.90°) in comparison to the location condition (M = 26.37°, SD = 15.80°), $t(19) = 3.63$, $p = .002$, $d = 0.81$. To further decompose the specific sources of error contributing to participants' overall performance, we fitted the two-component mixture model (von Mises + uniform distribution) to each individual participant's retrieval error data using maximum likelihood estimation (Bays et al., 2009). The mean model-estimated probability of successful memory retrieval, defined as the probability of responses stemming from a von Mises distribution centered at the target feature value (pT), was .73 (SD = .18) across participants and feature conditions (see Figure 2B). The mean model-estimated precision of memory retrieval, estimated as the concentration parameter, K, of the target von Mises distribution, was 16.79 (SD = 7.92) across participants and feature conditions (see Figure 2B; note that this value of K is comparable to an SD of approximately 14.20°). Mean memory precision (K) was significantly higher in the location (M = 34.65, SD = 27.24) in comparison to the color condition (M = 10.94, SD = 7.15), $t(19) = 4.04$, $p = .001$, $d = 0.90$, whereas mean probability of successful memory retrieval (pT) did not significantly differ between the two feature conditions (location: M = 0.75, SD = 0.18; color: M = 0.73, SD = 0.20), $t(19) = 0.65$, $p = .524$. Consistent with previous results (Richter et al., 2016), we also observed a moderate positive correlation

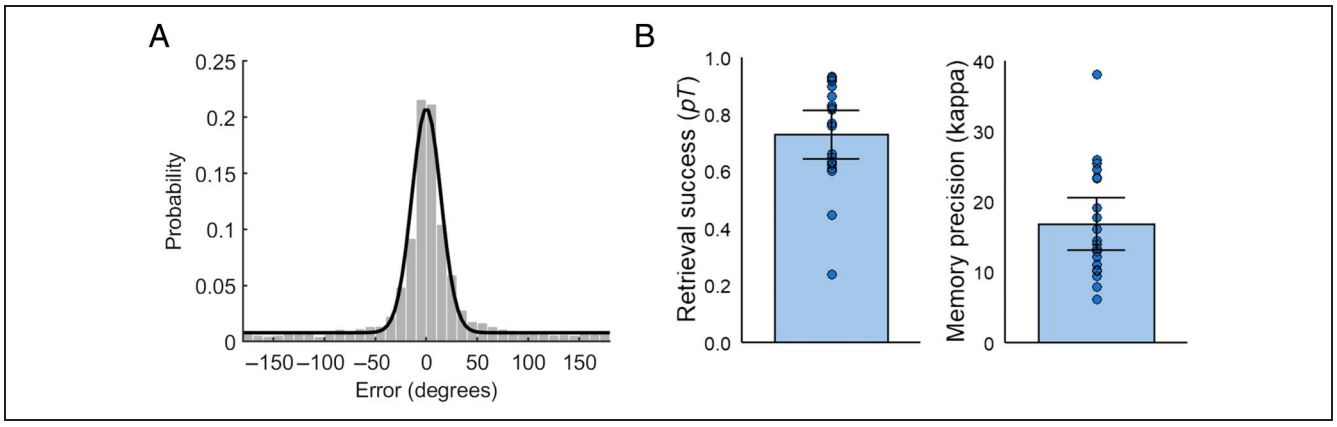

Figure 2. (A) Distribution of retrieval errors (response – target) across all trials and participants. Black line illustrates response probabilities predicted by the two-component mixture model (von Mises + uniform distribution; model fitted to data across all participants for visualization). (B) Mean model-estimated probability of successful memory retrieval (pT) and memory precision (K) across participants. Error bars display 95% confidence interval of the mean and data points of individual participant parameter estimates.

between estimates of the probability of successful memory retrieval and memory precision across participants, $r_s = .54$, $p = .014$.

fMRI Results

Encoding Activity Predicting Subsequent Retrieval Success and Memory Precision in a Priori ROIs

Our ROI analyses focused on examining whether encoding activity in three regions typically displaying subsequent memory effects for visual information, namely, the HC, the IFG, and the FFG, differentially contributes to the later success and precision of episodic memory retrieval. We first examined increases in encoding activity for trials that were subsequently successfully retrieved (absolute retrieval error $\leq 51°$) in contrast to trials that were subsequently forgotten (absolute retrieval error $> 51°$; note that only one object feature, i.e., location or color, was reconstructed for each encoding display). Within our anatomical ROIs, we observed increased encoding activity in the IFG, $t(19) = 6.75$, $p = .001$, peak: −36, 27, 18, and the FFG, $t(19) = 8.88$, $p < .001$, peak: −30, −63, −9, to predict whether object features were later successfully retrieved from memory or forgotten (peak-level FWE-corrected within each ROI; see Figures 3A and 4A). In contrast, no significant subsequent retrieval success effects were detected in the HC ($ps > .151$).

We next examined whether encoding activity in these regions predicted the graded precision with which object features were later successfully retrieved from memory (linear relationship between BOLD signal and precision parametric modulator). In addition to predicting which trials were successfully remembered, encoding activity in the IFG, $t(19) = 5.63$, $p = .011$, peak: −57, 15, 15, and the FFG, $t(19) = 6.27$, $p = .001$, peak: −33, −75, −18, positively correlated with the precision of later memory retrieval (see Figures 3B and 4B). Furthermore, increased encoding activity in the HC, $t(19) = 4.20$, $p = .029$, peak: −33, −30, −9, was associated with greater mnemonic precision for object features (see Figure 3B and C). As a control analysis, we further investigated whether BOLD signal in any of the ROIs predicted trial-wise variation in memory error across trials classified as unsuccessful (i.e., when variation in memory error was assumed to be driven by guessing). No significant associations between BOLD signal and subsequent memory error were detected for trials classified as unsuccessful in any of the ROIs ($ps > .238$).

Thus, results from the ROI analyses suggest encoding activity in the inferior frontal and fusiform cortex to support both the later success and precision of memory retrieval, whereas significant increases in BOLD signal in the HC were observed for subsequent memory precision only. We next sought to assess whether encoding activity predicting these two aspects of later retrieval performance overlapped in any of the ROIs. Conjunction analyses indicated significant overlap between subsequent success and subsequent precision effects in both the IFG, $t(19) = 4.86$, $p = .007$, peak: −42, 3, 27, and the FFG, $t(19) = 6.12$, $p < .001$, peak: −42, −57, −12, whereas no significant overlap was detected in the HC ($ps > .778$). Furthermore, hippocampal encoding activity still predicted the subsequent precision of memory retrieval after exclusive masking with the subsequent retrieval success contrast (mask thresholded at $p > .050$ uncorrected), $t(19) = 4.20$, $p = .029$, peak: −33, −30, −9. On the contrary, significant subsequent retrieval

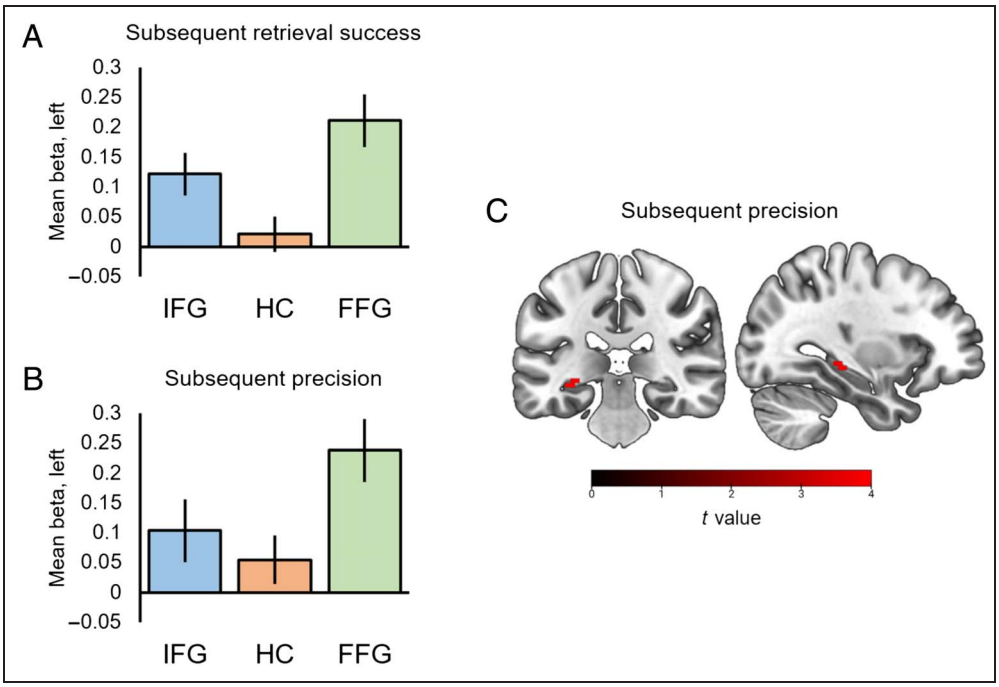

Figure 3. Mean parameter estimates for (A) subsequent success (successful > unsuccessful) and (B) subsequent precision (positive association between BOLD signal and precision parametric modulator) effects in the left IFG, HC, and FFG. Error bars display ±1 *SEM*. (C) Encoding activity correlating with the subsequent precision of memory retrieval in the hippocampal ROI (visualized at an uncorrected threshold of $p < .001$).

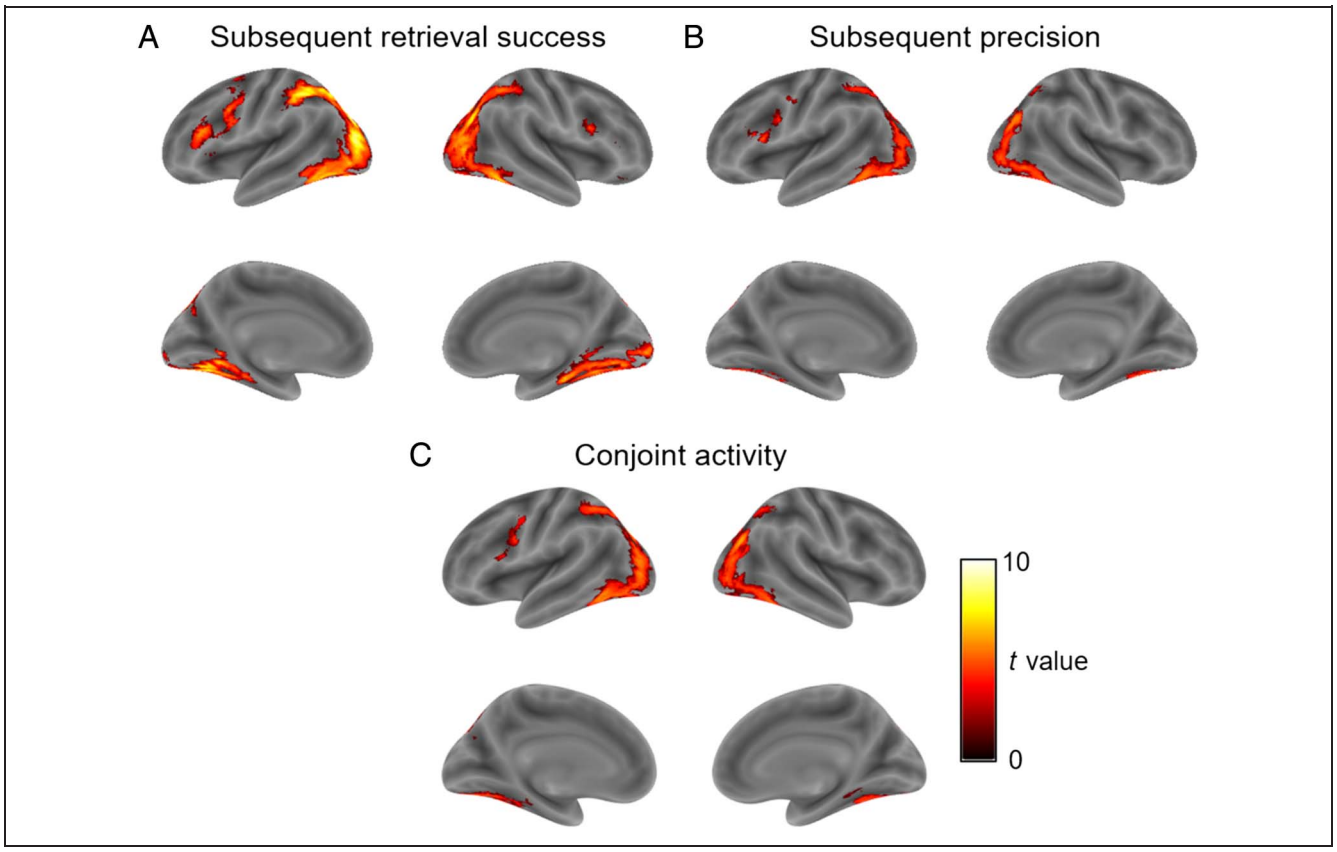

Figure 4. Encoding activity predicting the (A) subsequent success (successful > unsuccessful) and (B) subsequent precision (positive association between BOLD activity and precision parametric modulator) of memory retrieval, and (C) overlap between encoding activity predicting both later success and precision of memory retrieval. Visualized at an uncorrected threshold of $p < .001$, with a minimum cluster of 10 voxels.

success effects were detected in the IFG, $t(19) = 5.76$, $p = .006$, peak = −36, 27, 15, and the FFG, $t(19) = 4.35$, $p = .039$, peak = −18, −45, −12, after exclusive masking with the subsequent precision contrast, consistent with the observation of more widespread subsequent retrieval success than subsequent precision effects in these two regions (see Figure 4). No significant subsequent precision effects were observed in these two regions ($ps > .052$) after exclusive masking with the subsequent retrieval success contrast.

Encoding Activity Predicting Variation in Memory Error across All Encoding Trials in a Priori ROIs

In addition to the model-based analyses described above, we investigated whether trial-by-trial variation in BOLD signal in any of the ROIs was associated with trial-by-trial variation in subsequent memory error across all encoding trials, without assuming a categorical distinction between successful and unsuccessful retrieval. Consistent with the pattern of results observed in the model-based analyses, which indicated encoding activity in the IFG and FFG to be sensitive to both the subsequent success and subsequent precision of memory retrieval, we observed encoding activity in these two regions to also predict the magnitude of subsequent memory error when collapsing across all encoding trials [IFG: $t(19) = 7.03$, $p = .001$, peak: −51, 9, 27; FFG: $t(19) = 12.18$, $p < .001$, peak: −42, −57, −12]. In contrast, trial-wise variation in memory error was not significantly associated with encoding activity in the HC when examining all encoding trials ($ps > .323$).

Encoding Activity Predicting Subsequent Retrieval Success and Memory Precision across the Whole Brain

To identify any additional brain regions, beyond our a priori ROIs, where encoding activity predicted the later success and/or precision of memory retrieval, we further performed complementary whole-brain analyses. Activity in several regions of the dorsal and ventral visual streams, including the middle occipital gyrus, inferior parietal gyrus, FFG, and inferior temporal gyrus, was found to predict which object features were later successfully remembered versus forgotten (see Table 1 and Figure 4A). For subsequent memory precision, no significant voxels survived a whole-brain peak-level corrected significance threshold ($p < .050$ FWE-corrected, $k > 5$), although we note that three clusters spanning the left inferior temporal gyrus, middle occipital gyrus, and cerebellum, $t(19) = 7.08$, $p < .001$, the right middle occipital gyrus and FFG, $t(19) = 5.84$, $p < .001$, and the left IFG, $t(19) =$

Table 1. Encoding Activity Associated with the Subsequent Success (Successful > Unsuccessful) and Subsequent Precision (Positive Relationship between BOLD Activity and Precision Parametric Modulator) of Memory Retrieval in the Whole-Brain Analyses, $p < .050$ FWE-Corrected at Peak Level, $k > 5$

Region	*Voxels*	*x*	*y*	*z*	*t*	*p*
Subsequent retrieval success						
L middle occipital gyrus	355	−36	−87	12	10.50	<.001
L inferior parietal gyrus	87	−33	−45	39	9.41	<.001
R middle occipital gyrus	63	33	−75	30	8.83	.001
R inferior temporal gyrus	15	45	−54	−12	8.27	.003
R middle occipital gyrus	21	42	−81	9	7.95	.005
R FFG	8	30	−27	−21	7.33	.016
Subsequent precision						
No significant voxels						
Conjoint activity						
L middle occipital gyrus	30	−24	−75	30	6.59	.002
R middle occipital gyrus	41	33	−78	24	6.39	.004
L FFG	30	−42	−57	−12	6.12	.008
L middle occipital gyrus	22	−39	−84	6	6.01	.010

L = left; R = right.

5.63, $p < .001$, survived FWE correction at the cluster level (cluster-forming threshold $p < .001$ uncorrected; see Figure 4B for whole-brain results visualized at an uncorrected threshold). Whole-brain conjunction analyses further indicated significant overlap between subsequent success and subsequent precision effects in the middle occipital and fusiform gyri (see Table 1 and Figure 4C). Exclusive masking of each subsequent memory contrast by the other did not reveal any further regions where encoding activity significantly predicted only the subsequent success or the subsequent precision of memory retrieval.

DISCUSSION

Amid growing interest in the neural substrates underlying the precision of episodic memory, prior studies have predominantly focused on retrieval processes (Cooper & Ritchey, 2019; Montchal et al., 2019; Stevenson et al., 2018; Richter et al., 2016), leaving the specific encoding mechanisms supporting the acquisition of high-fidelity memories largely uncharacterized. Here, we employed continuous measures of memory retrieval in combination with model-based analyses of fMRI data to segregate the encoding activity supporting the later success and precision of episodic retrieval. We observed encoding activity in overlapping cortical regions, including the IFG, FFG, and middle occipital gyrus, to predict both which object features were later successfully retrieved from memory versus forgotten and the precision with which they were reconstructed. In contrast, encoding activity in the HC significantly predicted the precision of later memory retrieval only. Together, these findings highlight a hippocampal–cortical basis for the formation of precise memories of perceptual information and provide novel insight into the encoding substrates supporting the accessibility and precision of episodic memory.

The current finding demonstrating a relationship between trial-by-trial variation in hippocampal encoding activity and later memory precision is consistent with previous accounts emphasizing a critical role for this region in supporting detailed episodic memories (Robin & Moscovitch, 2017; Moscovitch et al., 2016). Related to our current findings, prior neuroimaging studies have found hippocampal encoding activity to correlate with measures of later retrieval quality, such as participants' subjective ratings of memory confidence (Kirwan, Wixted, & Squire, 2008; Preston et al., 2008), or the objective amount of detail recalled (Cooper & Ritchey, 2020; Qin et al., 2011). Moreover, trial-wise variation in hippocampal encoding activity has been found to predict the specificity of subsequent neural reinstatement of mnemonic content (Danker, Tompary, & Davachi, 2016; Wing, Ritchey, & Cabeza, 2015), providing support for the idea that hippocampal function at encoding may in part determine the fidelity with which information can

be later recalled. Emerging evidence suggests the posterior HC to be particularly important for supporting the fine-grained representation of perceptual details (Brunec et al., 2018; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013), consistent with our current finding of the peak of the subsequent precision effect being located in the posterior part of the HC.

In contrast, we did not observe significant subsequent retrieval success effects in the HC in our current paradigm. Furthermore, hippocampal encoding activity still predicted the precision of later memory retrieval after exclusive masking with the subsequent retrieval success contrast, suggesting specificity of this effect to memory precision. The lack of significant retrieval success effects in the HC may seem surprising given previous evidence for hippocampal encoding increases for successful versus unsuccessful encoding of associative information (Staresina & Davachi, 2008; Davachi, 2006); however, we note that prior studies have not attempted to distinguish memory precision-related activity from that related to successful encoding in general, both of which may be associated with accurate performance in a categorical memory task. Similar to the pattern of results observed here, others have further observed hippocampal encoding activity to predict graded variation in participants' subjective ratings of memory confidence only for responses above a certain threshold, while not categorically distinguishing between remembered and forgotten items (Shrager, Kirwan, & Squire, 2008). Theoretical accounts postulate that hippocampal involvement across cognitive domains may be explained by requirement for representation of high-fidelity (i.e., highly precise) and high-dimensional (i.e., comprising multiple associations) information (Ekstrom & Yonelinas, 2020; Yonelinas, 2013). This account aligns with our current finding of greater hippocampal encoding activity with greater precision of object feature bindings, although we note that, while requiring binding of multiple event attributes (i.e., object identity to color and spatial location), event complexity was not explicitly manipulated here and participants reconstructed only one feature of each studied object while the untested feature remained unchanged from study to test. Future studies manipulating the number and type of object attributes encoded, and testing memory for multiple features, can more directly evaluate the relationship of hippocampal encoding activity to remembered event complexity. Our findings are further in line with patient evidence demonstrating medial temporal lesions to disproportionately impair both short-term and long-term memory for high-fidelity associations (Nilakantan et al., 2018; Koen, Borders, Petzold, & Yonelinas, 2017) and suggest a potential role for a deficient hippocampal encoding mechanism in such impairments.

A prior study employing a similar paradigm to the one used here found hippocampal retrieval activity to be associated with the success, but not precision, of episodic memory retrieval (Richter et al., 2016). Although likely not directly mapping onto prior distinctions made in the literature, it is possible that this apparent difference between encoding and retrieval effects in the HC could reflect differential demands on hippocampal function during memory encoding and retrieval. More specifically, hippocampal pattern separation during memory encoding may be critical for the storage of differentiated memory representations that can be later retrieved with high precision, in particular when feature overlap is high (i.e., when multiple objects encoded in similar colors or spatial locations; Xie, Park, Zaghloul, & Zhang, 2020; Moscovitch et al., 2016; Yassa & Stark, 2011; Norman & O'Reilly, 2003; Bakker, Kirwan, Miller, & Stark, 2008). At retrieval, hippocampal pattern completion is thought to enable access to stored memory representations when presented with a noisy or partial cue, resulting in a thresholded memory signal where only items above a certain criteria elicit successful retrieval (Norman, 2010; Norman & O'Reilly, 2003). Interestingly, some evidence suggests that hippocampal response during perception may be more graded, supporting fine-grained perceptual discrimination (Elfman, Aly, & Yonelinas, 2014; Aly et al., 2013), a proposal consistent with the pattern of memory-related activity observed here.

Beyond the HC, we observed activity in overlapping cortical regions, including the IFG, FFG, and middle occipital gyrus, to predict both the later success and precision of episodic memory retrieval. Our finding of left inferior frontal involvement in subsequent retrieval success and precision is consistent with previous evidence implicating this region in cognitive control of memory encoding, supporting successful memory formation across a range of encoding tasks and mnemonic content (Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Park & Rugg, 2008, 2011; Murray & Ranganath, 2007; Blumenfeld & Ranganath, 2006). Specifically, ventrolateral regions of the prefrontal cortex have been proposed to support the attentional selection and elaborative encoding of goal-relevant information, leading to formation of strong and distinctive memory traces for specific item features (Blumenfeld, Lee, & D'Esposito, 2014; Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). Such selective encoding processes supported by this region may act to enhance the representation of goal-relevant features in posterior perceptual regions (Sprague, Saproo, & Serences, 2015; Gilbert & Li, 2013; Xue et al., 2013; Chun & Turk-Browne, 2007) and/or modulate hippocampal encoding more directly (Aly & Turk-Browne, 2017; Carr, Engel, & Knowlton, 2013), aiding the formation of durable and precise memory representations.

The current results further emphasize the role of perceptual regions in supporting the formation of accessible and precise memory traces. Specifically, we observed encoding activity in the FFG, a region typically associated with object perception and memory (Vaidya, Zhao, Desmond, & Gabrieli, 2002; Bar et al., 2001; Haxby et al., 2001), to predict both the later success and precision of object feature retrieval. This finding is consistent with

previous studies that have observed memory-related activity increases in the FFG during episodic encoding (reviewed in Kim, 2011; Spaniol et al., 2009), potentially playing an important role in the formation of detailed object representations (Kensinger, Garoff-Eaton, & Schacter, 2007; Garoff, Slotnick, & Schacter, 2005), and with evidence suggesting representational specificity in the occipitotemporal cortex during encoding to predict subsequent memory performance (Gordon, Rissman, Kiani, & Wagner, 2014; Ward, Chun, & Kuhl, 2013; Xue et al., 2010). Beyond our ROIs, we further observed that encoding activity in a wider network of ventral and dorsal visual regions predicted the subsequent success of memory retrieval. Of these regions, conjoint subsequent retrieval success and precision effects were observed in the middle occipital gyrus. The involvement of a broad set of ventral and dorsal visual regions aligns with demands of the current task for processing various visual attributes of the study displays.

We further note that the interpretation of the mixture model parameters as reflecting two distinct sources of memory error in the context of long-term retrieval has recently been challenged (Schurgin et al., 2020). Specifically, Schurgin et al. (2020) suggest errors in visual working memory, and at least under specific constraints also in long-term memory, to be explained by a single-parameter signal detection model when taking the nonlinear relationship between physical and psychological stimulus spaces into account (Schurgin et al., 2020). Although the ability of this model to account for selective changes in retrieval success or precision observed in previous studies of long-term memory (e.g., Nilakantan et al., 2018; Cooper et al., 2017; Nilakantan, Bridge, Gagnon, VanHaerents, & Voss, 2017; Sutterer & Awh, 2016), as well as to generalize to other stimulus spaces, such as spatial locations employed here, remains unclear, we note that our current findings regarding encoding activity in the inferior frontal and ventral visual cortex are not inconsistent with a single-parameter conceptualization. It is possible that the common subsequent success and subsequent precision effects observed in these regions could reflect a single dimension of memory strength or quality. Indeed, encoding activity in these two regions was also found to predict trial-wise variation in memory error when collapsing across all encoding trials, although we note that no such effects were still observed if examining trials classified as unsuccessful only. However, we did not observe hippocampal encoding activity to predict trial-wise variation in memory error when collapsing across all encoding trials (or for trials classified as unsuccessful), suggesting a benefit of the mixture modeling approach for characterizing memory-related activity in the HC. We further note that, although our current approach of using model-derived retrieval success thresholds estimated at the group level ensured consistent classification of trials to conditions across participants, this nevertheless means that our threshold estimate was not sensitive to individual differences in memory precision.

In summary, the current study aimed to elucidate the encoding mechanisms supporting the formation of accessible and precise memory traces. We observed encoding activity in prefrontal and posterior perceptual regions to support both the later success and precision of episodic memory retrieval, suggesting a shared role in the formation of strong and durable memory traces that are readily accessible from memory and can be reconstructed with a high degree of precision. In contrast, activity in the HC was found to significantly predict later memory precision only, consistent with accounts emphasizing the importance of this region in supporting high-fidelity representation of associative information across cognitive domains.

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Author Contributions

Saana M. Korkki: Conceptualization; Formal analysis; Investigation; Methodology; Writing—Original draft, Writing—Review & editing. Franziska R. Richter: Conceptualization; Formal analysis; Investigation; Methodology; Supervision; Writing—Review & editing. Jon S. Simons: Conceptualization; Formal analysis; Funding acquisition; Methodology; Supervision; Writing—Review & editing.

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing

in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .556, W/M = .286, M/W = .063, and W/W = .095.

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