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2 recall during visual imagery

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15 **Running title:** Distinct representations for encoding and recall

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Abstract

During memory recall and visual imagery, reinstatement is thought to occur as an echoing of the neural patterns during encoding. However, the precise information in these recall traces is relatively unknown, with previous work primarily investigating either broad distinctions or specific images, rarely bridging these levels of information. Using ultra-high-field (7T) fMRI with an item-based visual recall task, we conducted an in-depth comparison of encoding and recall along a spectrum of granularity, from coarse (scenes, objects) to mid (e.g., natural, manmade scenes) to fine (e.g., living room, cupcake) levels. In the scanner, participants viewed a trial-unique item, and after a distractor task, visually imagined the initial item. During encoding, we observed decodable information at all levels of granularity in category-selective visual cortex. In contrast, information during recall was primarily at the coarse level with fine level information in some areas; there was no evidence of mid-level information. A closer look revealed segregation between voxels showing the strongest effects during encoding and those during recall, and peaks of encoding-recall similarity extended anterior to category-selective cortex. Collectively, these results suggest visual recall is not merely a reactivation of encoding patterns, displaying a different representational structure and localization from encoding, despite some overlap.

Keywords: 7T fMRI, encoding-recall similarity, objects, representational similarity analyses, scenes

39

Introduction

40 When we visually recall an object or scene, our memory contains rich object and spatial
41 information (Bainbridge et al. 2019). During such recollection, our brain is thought to reinstate
42 neural patterns elicited by the initial perception (McClelland et al. 1995; Buckner and Wheeler
43 2001; Tompary et al. 2016; Dijkstra et al 2019). One common view is that the hippocampus
44 indexes populations of neocortical neurons associated with that memory (Teyler and Rudy
45 2007; Danker and Anderson 2010; Schultz et al. 2019). Under this view, representations in
46 hippocampus are largely independent of a memory's perceptual content (Davachi 2006; Liang
47 et al. 2013; Huffman and Stark 2014). In contrast, the neocortex is thought to show sensory
48 reinstatement, where the same regions show the same representations during recall as during
49 encoding (Wheeler et al. 2000; Kahn et al. 2004; Staresina et al. 2012; Ritchey et al. 2013; Lee et
50 al. 2012; O'Craven and Kanwisher 2000; Dijkstra et al. 2017). However, prior work has focused
51 on specific levels of information (e.g. broad stimulus class, specific image) and the extent to
52 which representations during recall reflect the same information as during perception, at all
53 levels of granularity (from individual exemplar up to broad stimulus category), is unclear. Here,
54 using ultra-high-field (7T) fMRI, we conducted an in-depth investigation of the content of
55 encoded and recalled representations of objects and scenes across cortex, hippocampus, and
56 the medial temporal lobe, assessing the granularity of detail in the representations of individual
57 items.

58 First, we employed a hierarchically organized stimulus set (Figure 1a) with three levels
59 of granularity from coarse (scenes/objects) to mid (e.g., natural/manmade scenes) to fine (e.g.,
60 bedrooms/conference rooms) level. Prior work comparing encoding and recall have primarily

61 investigated memory content at opposite ends of this granularity spectrum. At a coarse level,
62 recall of stimulus classes (faces, scenes, objects) have been reported to reactivate high-level
63 visual regions (Polyn et al. 2005; Johnson et al. 2009; Reddy et al. 2010; LaRocque et al. 2013)
64 and produce differentiable responses in hippocampus (Ross et al 2018). At the fine level, other
65 work has shown reinstatement for individual images, with specific visual stimuli decodable in
66 high-level visual cortex (Dickerson et al. 2007; Buchsbaum et al. 2012; Lee et al. 2012; Kuhl and
67 Chun 2014) and medial temporal lobe (Zeineh et al. 2003; Gelbard-Sagiv et al. 2008; Chadwick
68 et al. 2010; Wing et al. 2015; Mack and Preston 2016; Tompary et al. 2016; Lee et al. 2019).
69 Decoding for specific images (Thirion et al. 2006; Naselaris et al. 2015), positions (Stokes et al.
70 2011) and orientations (Klein et al. 2004; Albers et al. 2013) is even present in early visual
71 cortex during visual imagery. However, it is often unclear what information is driving
72 discrimination across the brain: fine-level image-specific information, coarse-level perceptual
73 category information, or information unrelated to stimulus content such as memory strength.
74 For example, while recalled grating orientation is decodable from early visual cortex (V1-V3),
75 reinstatement strength but not content is decodable from the hippocampus (Bosch et al. 2014).
76 Further, few studies have investigated the ability to detect reinstatement of mid-level
77 information (e.g., is it a natural or manmade scene, a big or small object) during recall, even
78 though such information is known to be decodable during perception (e.g., Park et al. 2011;
79 Kravitz et al. 2011; Konkle et al. 2012). Our approach using nested levels of stimulus
80 information reveals what granularity of information is contained in regions across the visual
81 processing pathway, and whether reinstatement is simply an echo of the same response from
82 encoding to recall.

83 Second, to isolate the activity specific to recall, we adopted a visual imagery task
84 focusing on recall of individual items without requiring the learning of cue-stimulus
85 associations, which have commonly been used (e.g., Ganis et al. 2004; Kuhl et al. 2012; Zeidman
86 et al. 2015a; Jonker et al. 2018). Recalled representations in associative tasks are likely to
87 contain information not only about the recalled item, but also the cue and the association itself.
88 Further, there are differences in neocortex when performing an associative versus item-based
89 memory task (Staresina and Davachi 2006). In fact, the neural representation of a target may be
90 largely dependent on what cue it is associated with (Xiao et al. 2017). Here, we employ an item-
91 based recall task in which participants encode trial-unique images, and following a distractor
92 task, recall that specific image. This approach allows us to investigate the recall of individual
93 items, without the learning of associations.

94 Using this direct recall task and nested stimulus structure, we find striking differences in
95 the representational structure and spatial localization for visual encoding and recall, suggesting
96 recall patterns are not just a repetition of patterns during encoding, despite some similarities.

97

98 Materials and Methods

99 *Participants*

100 Thirty-four adults were recruited for the experiment. All participants were healthy,
101 right-handed, and had corrected or normal vision. Twelve participants were unable to complete
102 the experiment due to discomfort in the 7T scanner, drowsiness, or scanner malfunction, and
103 their data were excluded from the study. This level of participant dropout is not unusual for 7T
104 scans, given that nausea and vertigo occasionally occur, and the bore is more restrictive than

105 the more standard 3T scanners. The final set of participants included twenty-two adults (fifteen
106 female; mean age: 24 years, standard deviation: 3.4 years, range: 19-35 years). All participants
107 provided consent following the guidelines of the National Institutes of Health (NIH) Institutional
108 Review Board (National Institute of Mental Health Clinical Study Protocol NCT00001360, 93M-
109 0170), and were compensated for their participation.

110

111 *Stimuli*

112 Stimulus images comprised 192 images with nested categorical structure (Figure 1a).
113 We refer to the different levels of information as coarse, mid, and fine. At a coarse level, 50% of
114 the stimuli were objects and 50% scenes.

115 At a mid-level, the objects and scenes were varied according to factors known to show
116 differential responses in the brain during perception. The objects were made up of four object
117 types, varying along two factors: 1) small / big objects (Konkle et al. 2012), and 2) tool / non-
118 tool objects (Valyear et al. 2007; Mahon et al. 2007; Beauchamp and Martin 2007). Big objects
119 were selected as objects generally larger than a 1-foot diameter and small objects were those
120 smaller than a 1-foot diameter. Tools were defined as objects commonly grasped by one's
121 hands using a power grip (e.g., Grèzes et al. 2003), although note that there are multiple ways
122 tools are defined in the field (Lewis 2006). Similarly, the scenes were made up of four scene
123 types, varying along two factors: 1) natural / manmade (Park et al. 2011), and 2) open / closed
124 (Kravitz et al. 2011). Natural scenes were defined as those primarily made up of natural objects
125 (i.e., plants, rocks, sand, ice), while manmade scenes were primarily made of artificial objects
126 (i.e., buildings, furniture). Open scenes were defined as those with an open spatial extent, while

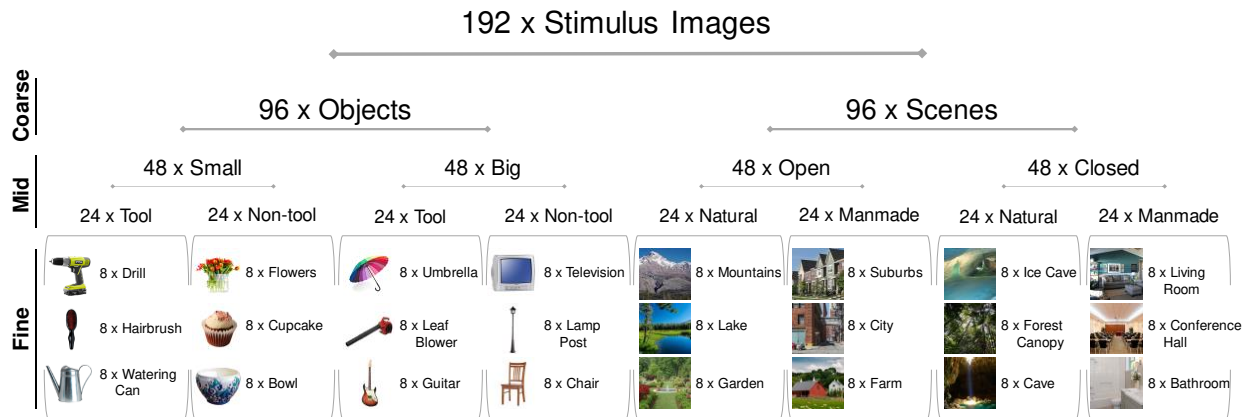
127 closed scenes were defined as those in which the viewer is enclosed by boundaries (Park et al.
128 2011).

129 At a fine-level, each object or scene type contained three categories, with eight
130 exemplars for each object or scene category (e.g., small, non-tool objects: bowl, cupcake,
131 flowers; closed, manmade scenes: bathroom, conference hall, living room; see Figure 1a for all
132 fine-level categories). Images were all square 512 x 512 pixel images presented at 8 degrees of
133 visual angle, and objects were presented cropped in isolation on a white background.

134

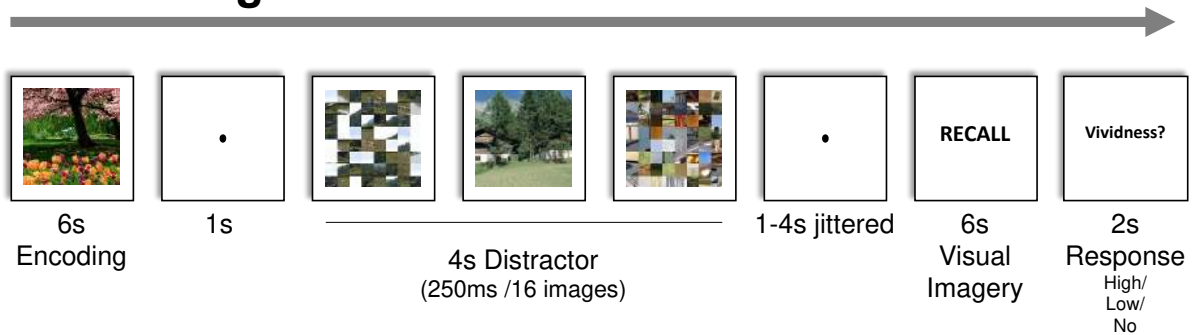
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136 a)



138 b)

Trial Timing



140 **Figure 1. Experimental stimuli and task.** (a) Nested structure of stimuli and example images. 192 trial-unique
141 images were encoded and recalled by participants, arranged under nested structure based on the *coarse* level
142 (object / scene), *mid* level (e.g., open / closed or natural / manmade scene), and *fine* level (mountains / lake) of
143 stimulus organization. Each fine-level category contained 8 different exemplar images (e.g., 8 different lake
144 photographs). (b) The timing of each trial. Participants studied an image for 6 s, performed a distractor task
145 requiring detection of an intact image amongst scrambled images for 4 s, and then after a randomized jitter of 1-4
146 s, recalled the original image through visual imagery for 6 s. Finally, they indicated the vividness of their memory
147 with a button press.

148

149 *In-scanner recall task and post-scan recognition task*

150 Participants first completed a single run of a 7-min 6-sec block-design localizer scan to
151 identify scene- and object-selective regions. In this localizer, participants viewed 16-sec blocks
152 of images of objects, scenes, faces, and mosaic-scrambled scenes and identified consecutive
153 repeated images. All images used in the localizer were distinct from those used in the main
154 experiment. Participants then completed eight runs of an item-based memory recall task
155 requiring visual imagery (Figure 1b). In each trial, participants studied a trial-unique stimulus
156 image for 6 s. After a 1 s fixation, they performed a distractor task in which they viewed a
157 stream of 16 quickly presented images (250 ms each) and had to press a button as soon as they
158 saw the sole intact image in a stream of mosaic-scrambled images. Scrambled and intact target
159 images were taken from a separate stimulus set, and were chosen to be of the same coarse
160 level (i.e., object or scene) as the studied image in order to keep general visual properties
161 consistent (i.e., not switching from one type of stimulus to another). These distractor images
162 were taken with random mid and fine levels, unrelated to the stimulus being encoded and
163 recalled. Intact object images were presented as an intact object against a mosaic-scrambled
164 background, so that participants would have to fixate the object to successfully perform the
165 task (rather than identify white edges). The distractor task lasted for 4 s total and was followed
166 by a 1-4 s jittered interval in which participants were instructed to wait and maintain fixation.
167 The word “RECALL” then appeared on the screen for 6 s, and participants were instructed to
168 silently visually imagine the originally studied image in as much detail as possible. Finally,
169 following the “RECALL” phase, participants were given 2 s to press a button indicating the
170 vividness of their memory as either no memory, low vividness, or high vividness. The next trial

171 then continued after a 1 s delay. Participants were instructed that the task was difficult, and
172 they should focus on reporting their vividness truthfully. On average, participants reported
173 ‘high vividness’ on 60.8% of trials (SD=16.9%), ‘low vividness’ on 29.9% of trials (SD=12.8%), and
174 ‘no memory’ on 9.31% of trials (SD=8.38%). Trials in which participants indicated “no memory”
175 were not included in any of the main analyses of the data. Each run contained 24 trials, lasting 8
176 min 38 s, and participants completed 8 runs total. Each run included three “catch trials” that
177 skipped the recall phase, in order to keep participants vigilant, to discourage them from pre-
178 emptively recalling the target image, and to better separate encoding from distractor and recall
179 phases during deconvolution. Each fine-level stimulus category (e.g., guitar, cupcake) was
180 shown once per run, and each stimulus exemplar image was only used once in the entire
181 experiment, so that there would be no memory effects on subsequent presentations of the
182 same image.

183 After the scan, participants performed a post-scan recognition task to test their memory
184 for the images studied in the scanner. Participants were presented with all 192 images studied
185 in the scanner randomly intermixed with 192 foil images of the same fine-level stimulus
186 categories and were asked to indicate for each image whether it was old or new. Two
187 participants were unable to complete the post-scan recognition task due to time constraints.
188 Analyses on the post-scan recognition data as well as vividness ratings are reported in the
189 Supplementary Material (SM1, SM2).

190

191 *MRI acquisition and preprocessing*

192 The experiment was conducted at the NIH, using a 7T Siemens MRI scanner and 32-
193 channel head coil. Whole-brain anatomical scans were acquired using the MP2RAGE sequence,
194 with 0.7 mm isotropic voxels. Whole-brain functional scans were acquired with a multiband EPI
195 scan of in-plane resolution 1.2 x 1.2 mm and 81 slices of 1.2 mm thickness (multiband factor =
196 3, repetition time = 2 s, echo time = 27 ms, matrix size = 160 x 160, field of view = 1728 x 1728,
197 flip angle = 55 degrees). Slices were aligned parallel with the hippocampus and generally
198 covered the whole brain (when they did not, sensorimotor parietal cortices were not included).
199 Functional scans were preprocessed with slice timing correction and motion correction using
200 AFNI and surface-based analyses were performed using SUMA (Cox 1996; Saad and Reynolds
201 2012).

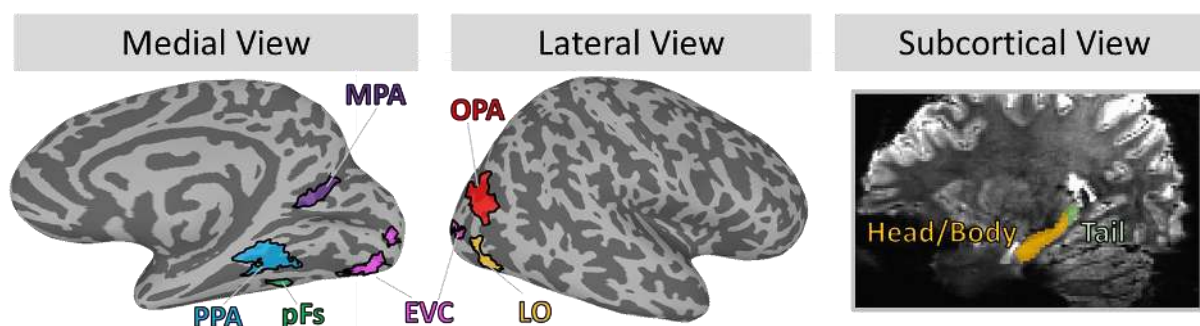
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203 *fMRI Region of Interest (ROI) Definitions*

204 For each participant, key ROIs for early visual cortex, object selective cortex, scene
205 selective cortex, and hippocampus were determined *a priori* and defined using functional and
206 anatomical criteria (Figure 2). Using the independent functional localizer, we identified three
207 scene-selective regions with a univariate contrast of scenes > objects: PPA (Epstein & Kanwisher
208 1998), medial place area (MPA; Silson et al. 2016), and occipital place area (OPA; Dilks et al.
209 2013). We localized object-selective regions lateral occipital (LO) and posterior fusiform (pFs)
210 with a univariate contrast of objects > scrambled images (Grill-Spector et al. 2001). Finally, we
211 localized early visual cortex (EVC) with a univariate contrast of scrambled images > baseline.
212 With each contrast, the functional ROIs were defined as the contiguous set of at least 20 voxels
213 showing significant activation for the contrast, located within the broader anatomical areas

214 described in the literature (e.g., PPA should be in and around the collateral sulcus, Epstein and
215 Baker 2019; LO should be within lateral occipital regions). For all contrasts, we first identified
216 these contiguous sets of voxels with a univariate contrast with a False Discovery Rate (FDR)-
217 corrected threshold of $q=0.001$. When a contiguous set of voxels could not be identified, we
218 looked at increasingly liberal thresholds of $q=0.005$, $q=0.01$, $q=0.05$, $p=0.001$, $p=0.005$, $p=0.01$,
219 and $p=0.05$ until a contiguous set of 20 voxels passing that threshold was identified. If no
220 contiguous set of voxels was identified at this threshold, then the ROI was determined missing
221 for that given participant. Left and right ROIs were combined to create bilateral ROIs in the
222 analyses. Overlapping voxels between scene- and object-selective regions were discarded from
223 any ROI. LO, pFs, PPA, and EVC were identified in 22 participants, OPA in 21 participants, and
224 MPA in 20 participants. Anatomical ROIs were localized using FreeSurfer's recon-all function
225 using the hippocampal-subfields-T1 flag (Iglesias et al. 2015), and then visually inspected for
226 accuracy. This hippocampus parcellation function splits the hippocampus into the head/body
227 (Hip-HB) and tail (Hip-T), and within the head/body region further segments the hippocampus
228 into different subfields (dentate gyrus, CA1, CA3, and subiculum; Iglesias et al. 2015). We did
229 not find meaningful differences across subfields (all subfields either showed identical results to
230 the Hip-HB or Hip-T), but report those results in the Supplementary Material (SM3). This
231 FreeSurfer parcellation also localized the perirhinal cortex (PRC) and parahippocampal cortex
232 (PHC) within the medial temporal lobe (MTL). PHC was determined as a participant's
233 anatomically defined PHC minus voxels already contained with their functionally defined PPA.
234 For the main body of the text, we report the results from the Hip-HB (with subfields combined),

235 Hip-T, PRC, and PHC. A table of ROI sizes by participant is provided in the Supplementary
236 Material (SM4).



238 **Figure 2. Main regions of interest (ROI).** The current study focused on a set of visual and memory-related ROIs.
239 Visual regions consisted of early visual cortex (EVC), object-selective regions of the lateral occipital (LO) and the
240 posterior fusiform (pFs), and scene-selective regions of the parahippocampal place area (PPA), medial place area
241 (MPA), and occipital place area (OPA). Visual regions were individually localized using functional localizers in each
242 participant; shown here are probabilistic ROIs of voxels shared by at least 12% of participants. Memory-related
243 regions consisted of the hippocampus divided into anterior (head and body) and posterior (tail) subregions, as well
244 as the perirhinal cortex (PRC, not shown) and parahippocampal cortex (PHC, not shown). These ROIs were
245 segmented automatically using anatomical landmarks.

246

247

248 *Whole-Brain Univariate Analyses*

249 We conducted whole-brain univariate contrasts using a general linear model (GLM) that
250 split the trials into six regressors along two factors: 1) encoding / distractor / recall, and 2)
251 scenes / objects. Six additional regressors for movement were also included. Additionally, trials
252 in which participants indicated they had “no memory” for the item were modeled separately as
253 three regressors (for the encoding, distractor, and recall periods) in the GLM to avoid them
254 contributing to either target stimulus responses or an implicit baseline. We then performed

255 whole-brain t -contrasts of scenes vs. objects separately during encoding and recall. All whole-
256 brain contrasts were projected onto the cortical surface using AFNI surface mapper SUMA
257 (Saad and Reynolds 2012).

258 With these whole-brain analyses, we located and compared the peak voxels of
259 activation during encoding and recall. For each participant, we localized the peak voxel within
260 each broad visual ROI definition (e.g., for PPA, voxels in and around the collateral sulcus,
261 Epstein and Baker 2019) separately for encoding and recall. We extracted the MNI coordinates
262 for each participant for the voxels with the highest object activation near LO and pFs, and the
263 highest scene activation near PPA, MPA, and OPA. The peaks of encoding and recall were
264 directly compared across participants with a paired Wilcoxon signed rank test, comparing the
265 median anterior-posterior coordinates between encoding and recall.

266

267 *Representational Similarity Analyses and Discrimination Indices*

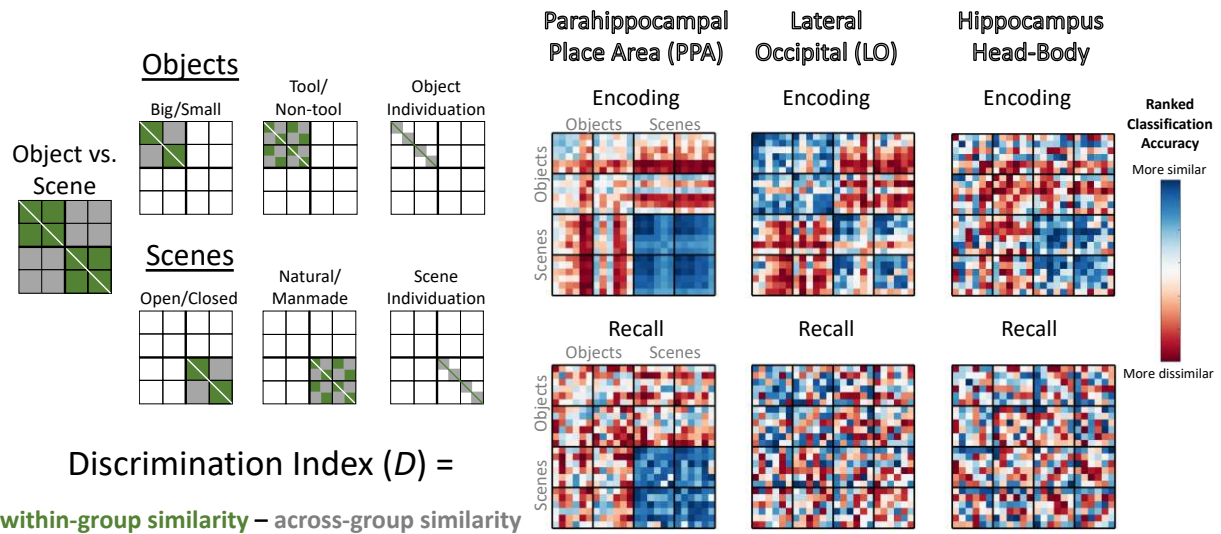
268 Multivariate analyses were conducted to look at the representations of different
269 stimulus information during encoding and recall, across brain regions. For these analyses, the
270 experimental data were first split into two independent halves – even runs and odd runs. For
271 each split half, a GLM was calculated, modeling separate regressors for each fine-level category
272 (e.g., cupcake) for the encoding period (6 s boxcar function), distractor period (4 s boxcar), and
273 recall period (6 s boxcar). Each event (e.g., encoding a cupcake) thus had two resulting beta
274 estimates: one across even runs, and one across odd runs. As in the univariate analysis GLM,
275 trials in which participants indicated they had no memory for the image were captured with
276 three additional regressors for the encoding period, the distractor period, and the recall period.

277 The estimated motion parameters from the motion correction were included as six further
278 regressors.

279 We then investigated the similarity between different types of stimulus information
280 during encoding, recall, and distractor periods, using representational similarity analyses (RSA;
281 Kriegeskorte et al. 2008). For each ROI, we created a representational similarity matrix (RSM)
282 comparing the similarity of all pairs of fine-level stimulus category (e.g., cupcake vs. guitar).
283 Similarity was calculated as the Pearson's correlation between the voxel values (t-statistic) in an
284 ROI for one fine-level category (e.g., cupcake) from one half of the runs (e.g., odd runs), with
285 the voxel values for another category (e.g., guitar) from the other half (e.g., even runs).
286 Specifically, pairwise item similarity was taken as the average of the correlation with one split
287 (odd runs for item A, even runs for item B) and correlation with the opposite split (even runs for
288 item A, odd runs for item B). This metric indicates the similarity in the neural representations of
289 two categories, and importantly, because the comparisons use separate halves of the data, we
290 can observe a category's similarity to itself across runs. This self-similarity measure thus
291 quantifies the degree to which a given region shows similarity across exemplars within category
292 (i.e., are cupcakes similar to other cupcakes). Correlation coefficients were all corrected with
293 Fisher's Z-transformations. We focused our main analyses on three RSMs: 1) correlations of the
294 encoding responses (Encoding RSM), 2) correlations of the recall responses (Recall RSM), 3)
295 correlations of the encoding responses with the recall responses (Cross-Discrimination RSM).
296 These different classifications allow us to see what stimulus information exists separately
297 during encoding and recall, as well as what information is shared between encoding and recall.

298 From these RSMs, we conducted discriminability analyses, which show the degree to
299 which each ROI can discriminate the different conditions of fine-, mid-, and coarse-level
300 information (e.g., do the responses in PPA discriminate natural vs. manmade scenes?). For each
301 comparison of interest, we computed a discrimination index D , calculated as the difference of
302 the mean across-condition correlations (e.g., scenes with objects) from mean within-condition
303 correlations (e.g., scenes with other scenes; Kravitz et al. 2011; Cichy et al. 2014; Harel et al.
304 2013; Harel et al. 2014; Henriksson et al. 2015). The intuition behind this index is that if an ROI
305 contains information about that comparison, then within-condition similarity should be higher
306 than across-condition similarity (e.g., if the PPA *does* discriminate natural vs. manmade scenes,
307 then natural scenes should be more similar to other natural scenes than manmade scenes).
308 Discriminability analyses at all levels of stimulus granularity were calculated from the same
309 underlying correlation matrix, and there were close to the same number of trials contributing
310 to the calculation of each cell in the matrix (only differing due to the exclusion of no-memory
311 trials). However, do note that the comparisons of different granularity use different proportions
312 of the matrix; e.g., the coarse level of objects versus scenes utilizes the whole matrix, while the
313 mid level of natural versus manmade only looks within scenes. We compared these
314 discrimination indices versus a null hypothesis of 0 discrimination using one-tailed t-tests. While
315 multivariate analyses may often violate the assumptions of parametric statistics (Allefeld et al.
316 2016), in practice, one-tailed t-tests to evaluate discrimination indices are not meaningfully
317 different from non-parametric methods (Nili et al. 2020). However, we confirmed all results
318 hold when also calculating significance with a permutation test across 1,000 RSM permutations
319 (Supplementary Material SM5). Mid-level discriminability was only computed within same-

320 coarse-level items (e.g., only scenes were used for the natural vs. manmade comparison), and
 321 fine level discriminability was only computed within same-mid-level items (e.g., when looking at
 322 the discriminability of living rooms, they were only compared to other closed, manmade
 323 scenes). Refer to Figure 3 for a depiction of these discrimination indices and to see example
 324 RSMs. All statistics reported are FDR-corrected within each ROI across all 21 discriminations
 325 (the seven discriminations shown in Figure 3, each for encoding, recall, and cross-
 326 discrimination) at a value of $q < 0.05$.
 327



328
 329 **Figure 3 – Calculating information discriminability from representational similarity matrices.** (Left) Depictions of
 330 the cells of the representational similarity matrices (RSMs) used to calculate discrimination indices for key regions
 331 of interest (ROIs). The RSMs represent pairwise Pearson’s correlations of stimulus groupings calculated from ROI
 332 voxel t-values, compared across separate run split halves (odd versus even runs). These depictions show which
 333 cells in the matrices are used in the calculation of discriminability of different properties, with green cells indicating
 334 within-condition comparisons, which are compared with grey cells indicating across-condition comparisons. For all
 335 discriminability calculations except fine-level discrimination of individual categories, the diagonal was not included.

336 All operations were conducted on the lower triangle of the matrix, although both sides of the diagonal are shown
337 here for clarity. (Right) Examples of encoding and recall RSMs from the data in the current study, specifically the
338 rank-transformed average RSM for the parahippocampal place area (PPA), lateral occipital (LO), and the
339 hippocampus head and body. Blue cells are more similar, while red cells are more dissimilar.

340

341 *Discrimination-based Searchlight Analyses*

342 We also conducted discriminability analyses using spherical searchlights (3-voxel radius)
343 in two ways. First, we conducted discriminability analyses (as described above) for searchlights
344 centered on voxels in the ROIs. For each searchlight, we obtained a scene-object
345 discriminability metric during encoding and one during recall, allowing us to examine the
346 relationship between encoding and recall information in these ROIs. Note that while the center
347 voxel in the searchlight was located within each given ROI, peripheral voxels could fall outside
348 of an ROI's boundaries. This is to ensure that searchlights are of equal volume throughout the
349 ROI and will result in only a small amount of smoothing of the ROI's borders (e.g., 3 voxels at
350 maximum).

351 Second, we conducted discriminability analyses in searchlights iteratively moved
352 through each individual's brain, to examine ability to discriminate information outside of our
353 pre-defined ROIs. Group maps were combined with a one-tailed t-test comparing group
354 discrimination indices versus no discrimination (0). Group maps were thresholded at $p < 0.005$
355 uncorrected for visualization purposes however we also provide unthresholded maps. We
356 conducted these searchlights looking at both discriminability of information within memory
357 process type (encoding or recall), as well as ability to cross-discriminate information between
358 encoding and recall. We also identified the locations of peak voxels for encoding, recall, and

359 cross-discrimination, using the same methods as described in the *Whole-Brain Univariate*
360 *Analyses*.

361

362 *Encoding-recall correlation and overlap analyses*

363 In order to directly compare encoding and recall information within ROIs, we conducted
364 two separate analyses. We specifically focused on coarse level discrimination of objects versus
365 scenes, as this discrimination is reliably found across regions for both encoding and recall (see
366 Results).

367 First, we calculated the correlation between encoding and recall discrimination indices
368 in the searchlights within each ROI (see previous section). For each searchlight centered within
369 an ROI, we Spearman rank correlated its coarse level discrimination index (scenes vs. objects)
370 between encoding and recall. This analysis reveals the degree to which voxels that represent
371 encoding information also represent recall information. High correlations indicate that voxels
372 that can discriminate objects versus scenes during encoding can also discriminate them during
373 recall, while low correlations provide evidence for no relationship between encoding and recall
374 discriminability. Significance was calculated using a non-parametric Wilcoxon signed rank test,
375 comparing the rank correlations against a null median of 0.

376 Second, given the relatively low correlations we observed, we conducted an overlap
377 analysis to determine the degree to which the most discriminative voxels are the same
378 between encoding and recall. To perform this analysis, for each ROI, we took the top 10%
379 discriminating encoding voxels and compared their overlap with the top 10% discriminating
380 recall voxels. Chance level of overlap was calculated with permutation testing, by taking two

381 random sets of searchlights (rather than the top ranked searchlights) consisting of 10% of the
382 ROI size. Across 100 permutations per ROI per participant, we calculated the overlap between
383 these two shuffled sets, and then took the average across all permutations as the chance level
384 for each participant. This permuted level of chance ultimately resolves to 10% across all ROIs,
385 which matches the computed chance level for this analysis - if you take two random sets of 10%
386 of voxels, by chance, 10% of those voxels should overlap. Significance was calculated with a
387 non-parametric paired Wilcoxon rank sum test comparing the true overlap percentage with the
388 permuted random overlap percentage.

389

390

Results

391 In the following sections, we examine the relationship between representations elicited
392 during encoding and recall. First, we compare granularity of stimulus content representations in
393 object- and scene-selective visual ROIs and the hippocampus. We observe reduced information
394 during recall, particularly for mid-level information. Second, to directly compare encoding and
395 recall representations, we conduct searchlight analyses to investigate the distribution of voxels
396 showing the strongest discrimination during encoding, recall and cross-discriminability between
397 these two phases, both within and outside the ROIs. We observe little correlation between
398 discrimination during encoding and recall and find that the voxels that represent recalled
399 information are frequently distinct from those that represent encoding information, with the
400 strongest representations during recall anterior to the category-selective regions traditionally
401 studied during perception.

402

403 **Decoding stimulus content from scene- and object-selective visual regions and medial**
404 **temporal lobe**

405 What aspects of a visual memory are represented in scene- and object-selective areas
406 and medial temporal lobe during encoding and recall? We asked this question by discriminating
407 stimulus information from the patterns of blood oxygen level dependent (BOLD) responses at
408 various scales of stimulus granularity, ranging from a coarse level (scenes, objects), to a mid-
409 level (e.g., natural/manmade scene, big/small object), to a fine level (e.g., cupcake, guitar). This
410 discrimination was conducted across independent exemplars, never including the same images
411 in the training and testing sets of the decoding model. This allowed us to see what levels of
412 information are represented in these regions, separate from an ability to distinguish identical
413 images. Discrimination indices and their corresponding p -values (see Methods) for all ROIs are
414 reported in Supplementary Material SM6. Here, in the text we only describe statistics that pass
415 FDR correction, but all values including those where $p < 0.05$ but p does not pass FDR correction
416 are included in this table.

417

418 *Visual ROIs: Detailed information during encoding, limited information during recall*

419 We investigated discriminability in object-selective regions LO and pFs, scene-selective
420 regions PPA, MPA, and OPA, and early visual cortex (Figure 4, refer to Supplementary Material
421 SM6 for discrimination indices and individual statistics).

422 We first examined what information was discriminable during the encoding period. All
423 object- and scene-selective regions could discriminate coarse level information (objects vs.
424 scenes), all $p < 10^{-4}$. For mid-level object information, tool/non-tool could be discriminated in

425 object-selective regions LO ($p = 0.009$) and pFs ($p = 0.012$), but object size did not show
426 significant discriminability in any region. For mid-level scene information, open/closed could be
427 discriminated in LO ($p = 0.009$), pFs ($p = 0.002$), and PPA ($p = 0.001$), while manmade/natural
428 could be discriminated in LO ($p = 0.001$), PPA ($p = 0.003$), and MPA ($p = 4.76 \times 10^{-4}$). Finally, fine-
429 level object information could be discriminated in all regions except MPA (all $p < 0.001$), while
430 the fine level for scenes could be discriminated in scene-selective regions PPA ($p = 7.64 \times 10^{-4}$)
431 and OPA ($p = 0.002$). In addition, response patterns in the encoding period for all visual ROIs
432 was predictive of reported memory vividness, and patterns in the LO, PPA, and OPA were
433 predictive of subsequent recognition (Supplementary Material SM1, SM2). Overall, these
434 results confirmed the findings of prior studies (e.g., Valyear et al. 2007; Walther et al. 2009;
435 Park et al. 2011; Kravitz et al. 2011; Troiani et al. 2012), in which during encoding and
436 perception, responses in scene- and object-selective regions can be used to distinguish various
437 levels of information about visually presented scenes and objects.

438 We next investigated the information present in these ROIs during recall. Discrimination
439 of coarse-level information was significant in all visual regions (all $p < 0.001$). However, no
440 region showed significant discriminability for any mid-level information (big/small, tool/non-
441 tool for objects and open/closed, natural/manmade for scenes; all $p > 0.10$). Also, no region
442 showed fine-level object information during recall. However, significant fine-level information
443 during recall of scenes was present in pFs ($p = 0.009$) as well as scene regions PPA ($p = 0.011$)
444 and MPA ($p = 0.008$). In addition, response patterns from all visual areas during recall were
445 predictive of recall vividness, although not predictive of subsequent recognition
446 (Supplementary Material SM1, SM2). These results reveal that while visual regions maintain

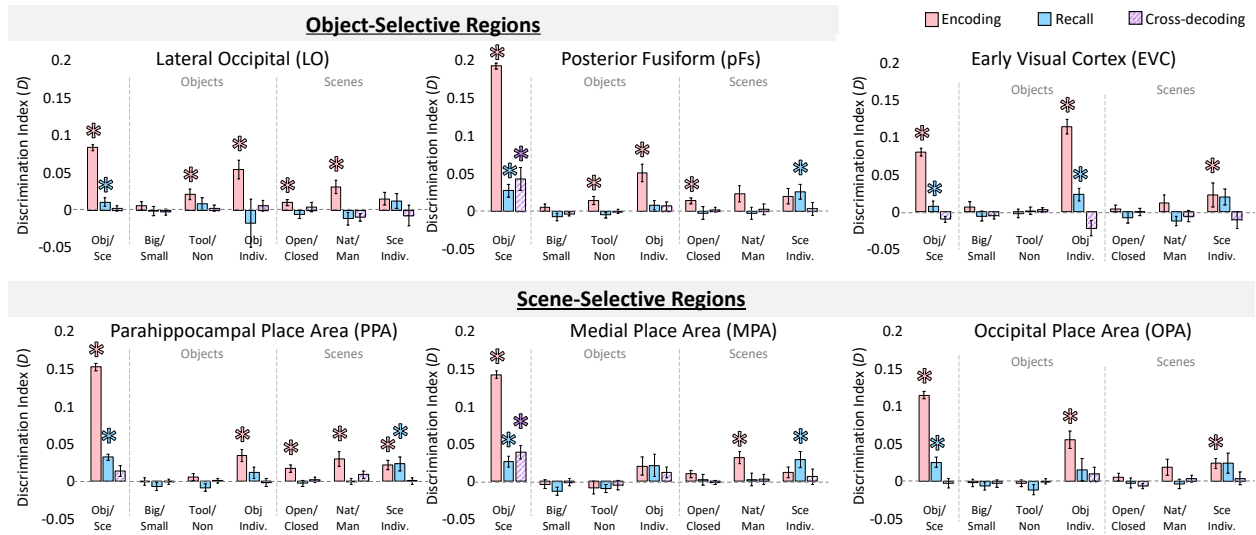
447 coarse-level information during recall, we find no evidence for mid-level stimulus information.
448 Despite the lack of mid-level information, however, there is fine-level information in some
449 regions.

450 To investigate which regions show a shared neural representation during encoding and
451 recall, we conducted a cross-discrimination analysis identifying the degree to which a region
452 shows similar patterns between encoding and recall. The only significant cross-discrimination
453 was for the coarse level (objects versus scenes), which was found in pFs ($p = 0.006$) and MPA (p
454 $= 1.59 \times 10^{-4}$). Significant cross-discrimination did not emerge for any mid-level information in
455 any ROI (all $q > 0.05$), nor at the fine level in any ROI (all $q > 0.05$). These findings imply that
456 encoding and recall may differ in their representational structure across different levels of
457 information.

458 Given these effects in object- and scene-selective regions, we conducted a follow-up
459 analysis to look at visual responses outside of category selective cortex, namely early visual
460 cortex (EVC; Figure 4, Supplementary Material SM6). During encoding, EVC showed significant
461 discrimination at the coarse level ($p = 4.43 \times 10^{-7}$), but no discrimination at the mid-level for
462 scenes or objects (all $q > 0.05$). However, EVC did show significant discrimination of the fine-
463 level for both objects ($p = 5.13 \times 10^{-7}$) and scenes ($p = 0.005$). During recall, EVC again showed
464 significant coarse-level discrimination ($p = 0.004$), no significant mid-level discrimination (all $p >$
465 0.10), and significant fine-level discrimination for objects ($p = 0.008$) although not for scenes
466 ($p > 0.05$). EVC did not show significant cross discrimination at any level (all $p > 0.20$). These
467 results suggest that retinotopic information—driven by the visual features of different object
468 categories and their differences from scenes—is likely discriminable during recall. However,

469 mid-level information did not show differences in early visual processing during encoding, and
 470 was not discriminable during recall.

471



472

473 **Figure 4 – Information discriminability in scene- and object-selective regions.** Discriminability for visual regions of
 474 interest (ROIs) for each stimulus property was calculated from the RSMs (as in Figure 3). Bar graphs indicate mean
 475 discrimination index for different comparisons across ROIs, are split by coarse stimulus class, and show three levels
 476 of discrimination: 1) the coarse level (objects versus scenes), 2) the mid level (objects: big/small, tools/non-tools;
 477 scenes: open/closed, natural/manmade), and 3) the fine level (specific object and scene categories). The y-axis
 478 represents the average discrimination index (D), which ranges from -1 to 1. Significance (*) indicates results from a
 479 one-tailed t-test versus 0, with a FDR-corrected level of $q < 0.05$ (applied to all 21 comparisons within each ROI).

480 Values that do not pass FDR correction can still be seen in Supplementary Material SM6. Pink bars indicate
 481 discriminability during encoding trials, blue bars indicate discriminability during recall trials, and hatched purple
 482 bars indicate cross-discriminability (i.e., there is a shared representation between encoding and recall). Error bars
 483 indicate standard error of the mean.

484

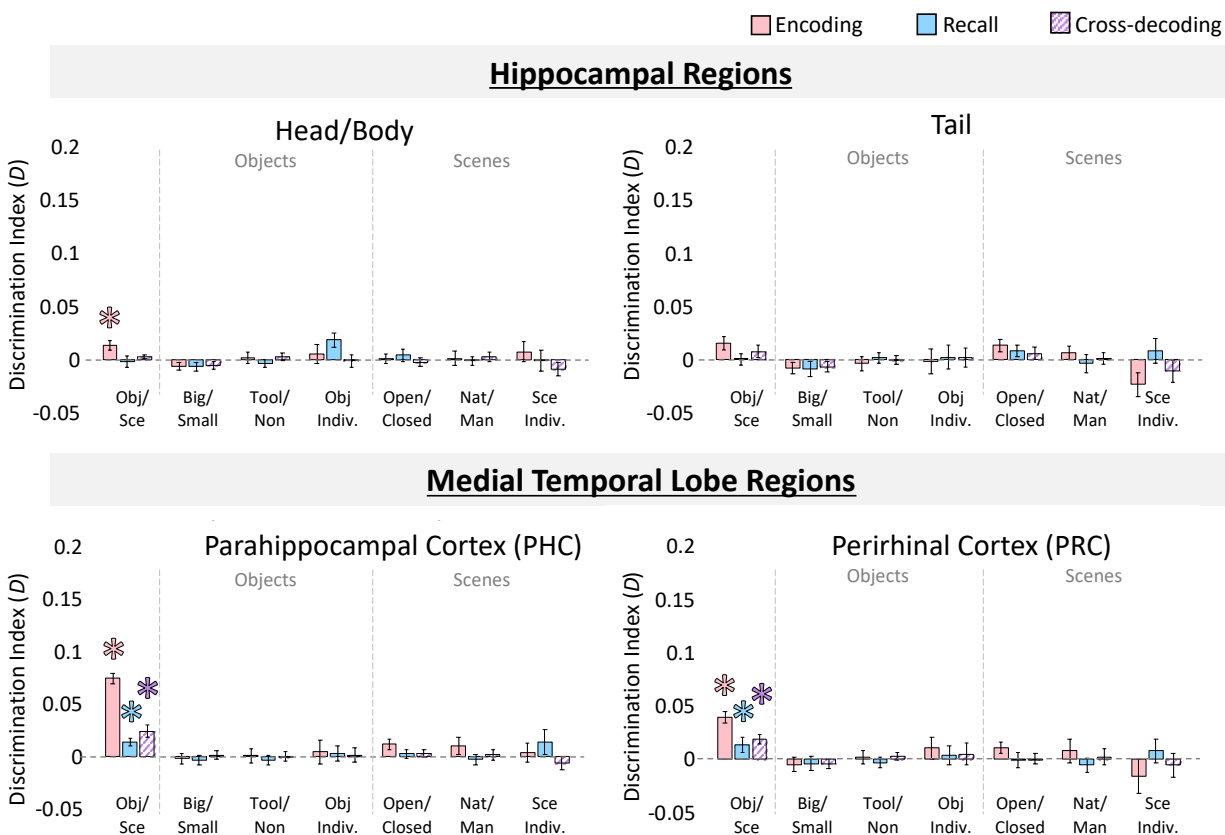
485 *Hippocampus and Medial Temporal Lobe Show Coarse Level Information During Encoding*

486 We conducted the same analyses in the hippocampus and medial temporal lobe regions
487 (MTL) consisting of the perirhinal cortex (PRC) and parahippocampal cortex (PHC) (Figure 5).
488 We primarily focused on the segregation of the hippocampus into anterior (Hip-HB) and
489 posterior (Hip-T) regions, but results for the individual subfields can be found in the
490 Supplementary Material (SM3).

491 During encoding, significant coarse-level discrimination of objects versus scenes was
492 present in Hip-HB ($p = 3.28 \times 10^{-4}$), PRC ($p = 5.74 \times 10^{-5}$), and PHC ($p = 4.62 \times 10^{-6}$), but not Hip-T
493 ($p = 0.108$). There was no mid-level information present in any of these regions (all $q > 0.05$),
494 nor was there fine-level information (all $q > 0.05$). During recall, coarse-level information was
495 not detected in the hippocampus (Hip-HB: $p = 0.82$; Hip-T: $p = 0.48$), but was discriminable in
496 PRC ($p = 0.004$) and PHC ($p = 0.003$). No mid- or fine-level information was present during recall
497 in any of these regions (all $p > 0.20$). Finally, significant cross-discriminability between encoding
498 and recall was found in the PRC (2.53×10^{-4}) and PHC (3.99×10^{-4}), but not in the hippocampus
499 (Hip-HB: $p = 0.082$; Hip-T: $p = 0.10$). No mid-level or fine-level information was cross-
500 discriminable in these regions (all $p > 0.10$).

501 Although hippocampus did not show content-related information beyond the coarse
502 level during encoding, additional analyses revealed other discriminable information present in
503 the hippocampus. Patterns during recall in the hippocampus were significantly predictive of
504 reported memory vividness, although patterns during encoding were not (Supplementary
505 Material SM1, SM2). Further, an analysis comparing the representational structure in different
506 ROIs revealed that while visual areas were very dissimilar from the hippocampus during the

507 encoding period, their patterns become more similar to those of the hippocampus during recall
 508 (Supplementary Material SM7, SM8).
 509



510
 511 **Figure 5 – Information discriminability in the hippocampus and medial temporal lobe.** Discriminability for
 512 hippocampal ROIs, perirhinal cortex (PRC), and parahippocampal cortex (PHC) for each stimulus property was
 513 calculated from the RSMs. Bar graphs are displayed in the same manner as Figure 4, and indicate mean
 514 discrimination index for comparisons of different levels of stimulus information (coarse, mid-, and fine levels for
 515 objects and scenes). Pink bars indicate discriminability during encoding trials, blue bars indicate discriminability
 516 during recall trials, and hatched purple bars indicate cross-discriminability (i.e., there is a shared representation
 517 between encoding and recall). Error bars indicate standard error of the mean. Asterisks (*) indicate significance at
 518 a FDR corrected level of $q < 0.05$.
 519

520 *Discrimination of Information During the Distractor Period*

521 To ensure any ability to discriminate information during recall was not due to bleed-
522 over from the encoding period or active visual working memory strategies, we computed
523 discrimination indices during the distractor period. Distractor stimuli differed by coarse level
524 category (scenes, objects), and indeed coarse level information was available in LO
525 (discrimination index $D = 0.02$, $p = 5.94 \times 10^{-5}$), PPA ($D = 0.02$, $p = 5.00 \times 10^{-5}$), and OPA ($D =$
526 0.02 , $p = 6.13 \times 10^{-5}$), although not in pFs, MPA, Hip-HB, PRC, or PHC ($q > 0.05$), all of which
527 showed discrimination during the encoding and recall periods (with the exception of the Hip-
528 HB). Mid-level and fine level information was not discriminable in any ROI during the distractor
529 period ($q > 0.05$), despite the presence of such information during the encoding period.
530 Importantly, the lack of fine-level information during the distractor period contrasts with the
531 stronger and significant fine-level information in pFs, PPA, and MPA during the recall period.
532 Thus, it is highly unlikely that information measured during recall reflects carry over from the
533 encoding period or active visual working memory strategies.

534

535 In sum, the analyses in this section reveal that while during encoding information can be
536 discriminated in many of these ROIs from all levels of stimulus granularity (fine, mid, and
537 coarse), there is limited information available during recall. Namely, while coarse- and fine-level
538 information is available in many of the ROIs, mid-level information was not detected in any ROI.
539 Significant cross-discrimination between encoding and recall was also only present at the
540 coarse level of information. These results suggest distinct representational structure during

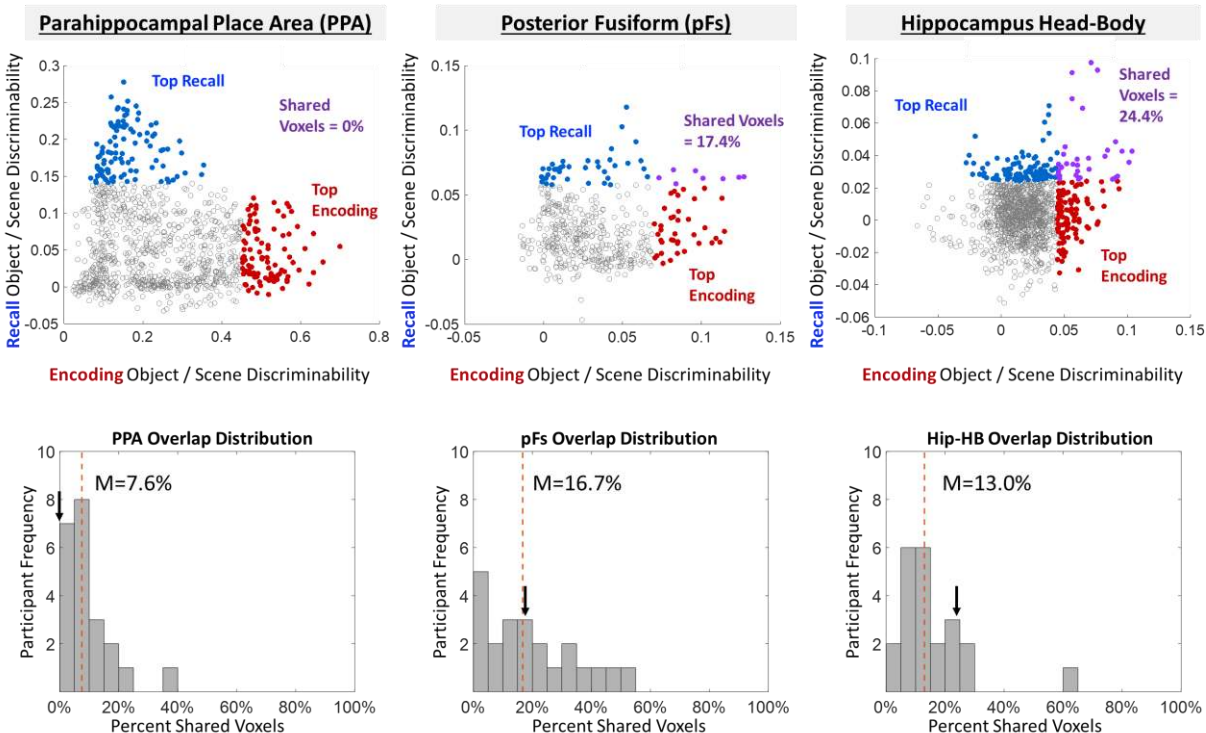
541 encoding and recall, and motivate a direct comparison between encoding and recall
542 representations at the sub-ROI level.

543

544 **Direct comparison of encoding and recall discriminability within ROIs**

545 We observed cross-discrimination in some regions (pFS, MPA, PRC, PHC), but not in
546 others (LO, PPA, OPA, Hip-HB, Hip-T), providing mixed evidence for shared neural substrates for
547 encoding and recall across these regions. To further investigate the relationship between
548 encoding and recall discrimination, we directly compared discrimination indices across each
549 region. Because only coarse-level information showed cross-discrimination in any region, we
550 focused our analyses here on the coarse discrimination of objects versus scenes. For each ROI,
551 we computed Spearman rank correlations between encoding and recall discrimination
552 searchlights (see Methods). While some regions showed significant correlations between
553 encoding and recall discriminability (MPA: Median Spearman's rank correlation $\rho = 0.210$,
554 Wilcoxon signed rank test: $Z = 2.52$, $p = 0.012$; LO: $\rho = 0.104$, $Z = 3.17$, $p = 0.002$; pFs: $\rho = 0.200$,
555 $Z = 2.26$ $p = 0.024$; Hip-HB: $\rho = 0.065$, $Z = 2.09$, $p = 0.036$; PHC: $\rho = 0.244$, $Z = 3.72$, $p = 2.01 \times 10^{-4}$),
556 others did not (PPA: $\rho = -0.006$, $Z = 1.31$, $p = 0.189$; OPA: $\rho = 0.030$, $Z = 1.28$, $p = 0.200$; Hip-T:
557 $\rho = -0.045$, $Z = 0.02$, $p = 0.987$; PRC: $\rho = 0.168$, $Z = 1.79$, $p = 0.074$). However, even in those cases
558 where we found significant effects, the correlations tended to be weak, and every ROI had 22%
559 (5 out of 22) or more of the participants who showed negative correlations between encoding
560 and recall. Moreover, the distribution of the plotted data often revealed an L-shape distribution
561 with greatest similarity between encoding and recall for the voxels with the lowest
562 discrimination scores (Figure 6).

563 To compare encoding and recall discriminability further, we focused on the top 10% of
564 searchlights that showed encoding discriminability and compared their overlap with the top
565 10% of searchlights that showed recall discriminability within each ROI (Figure 6, Methods). If
566 the same voxels perform encoding and recall discrimination, we should find significantly higher
567 overlap than chance (approaching 100%). Conversely, if encoding and recall information
568 comprise distinct sets of voxels, we should find equal or lower overlap compared to chance
569 (~10%, estimated by 100 permuted shuffles). PPA showed significantly lower overlap than
570 chance (Median = 9.15%, Wilcoxon rank sum test: $Z = 1.96$, $p = 0.050$), while pFs showed
571 significantly higher overlap ($M = 19.14\%$, $Z = 2.05$, $p = 0.040$). All other regions showed no
572 significantly different overlap than predicted by chance (MPA: 16.9%; OPA: 11.2%; LO: 14.03%;
573 Hip-HB: 15.6%; Hip-T: 15.4%; PRC: 13.3%; PHC: 20.2%; all $p > 0.10$). These results suggest a
574 limited relationship between encoding and recall across all visual and memory regions. pFs
575 shows high overlap and significant correlation between encoding and recall searchlights, in
576 addition to significant cross-discrimination across encoding and recall, suggesting some shared
577 neural substrate. In contrast, PPA shows no correlation and significantly low overlap in addition
578 to an absence of cross-discrimination, suggesting distinct neural substrates between encoding
579 and recall. The remaining ROIs show mixed evidence, with relatively low correlations between
580 encoding and recall and no difference in overlap from chance, suggesting limited shared
581 information between encoding and recall.



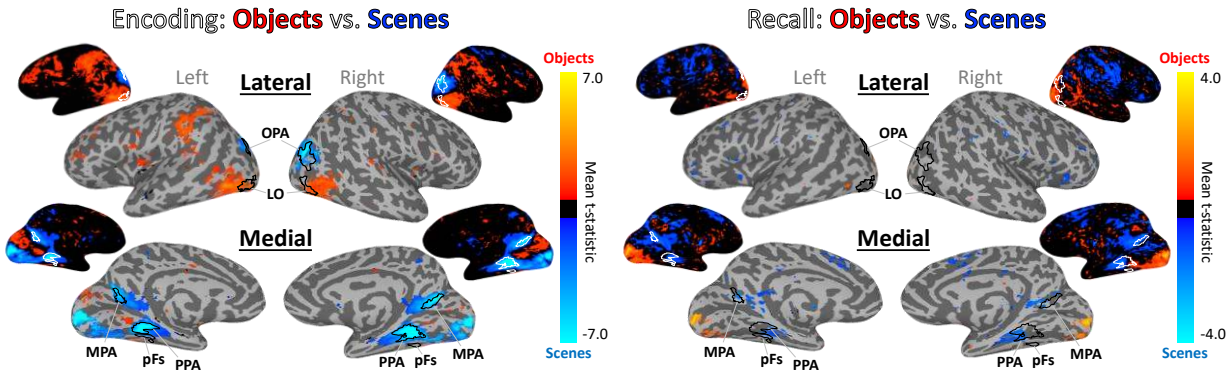
582

583 **Figure 6 – Comparing encoding and recall discriminability within the ROIs.** (Top) Example ROIs from a single
584 participant, where each point represents a voxel-centered spherical searchlight in that ROI and is plotted by the
585 object/scene discrimination index during encoding (x-axis) versus the object/scene discrimination index during
586 recall (y-axis). The 10% of searchlights showing strongest recall discriminability are colored in blue, while the 10%
587 of searchlights showing strongest encoding discriminability are colored in red. Searchlights that overlap between
588 the two (those that demonstrate both encoding and recall discrimination) are colored in purple. The patterns in
589 this participant mirror the patterns found across participants—PPA shows low (in this case no) overlap, while pFs
590 shows higher overlap. (Bottom) Histograms for these ROIs showing participant distribution of the percentage of
591 overlap between the top 10% of encoding discriminating and top 10% of recall discriminating voxels. The arrow
592 represents the participant's data plotted above, while the dashed red line shows the median overlap percentage
593 across participants.

594

595 Whole-Brain Investigation of Encoding and Recall Effects

596



597

598 **Figure 7 – Whole-brain activation of objects and scenes during encoding and recall.** Univariate whole-brain t-
599 statistic maps of the contrast of objects (red/yellow) versus scenes (blue/cyan) in encoding (left) and recall (right).
600 Contrasts show group surface-aligned data (N=22), presented on the SUMA 141-subject standard surface brain
601 (Saad and Reynolds 2012). Outlined ROIs are defined by voxels shared by at least 25% participants from their
602 individual ROI definitions (using independent functional localizers), with the exception of the pFs and OPA which
603 were defined by 13% overlap (there were no voxels shared by 25% of participants). The encoding maps are
604 thresholded at FDR corrected $q < 0.05$. For the recall maps, no voxels passed FDR correction, so the contrast
605 presented is thresholded at $p < 0.01$ for visualization purposes. Smaller surface maps show unthresholded results.

606

607 Given the differences we observed between encoding and recall within ROIs, we
608 conducted follow-up analyses at the whole-brain level. Looking at a group univariate contrast of
609 objects versus scenes during encoding (Figure 7), we confirm that stimulus class selectivity is
610 strongest in ROIs predicted by the literature: LO and pFs show high sensitivity to objects, while
611 PPA, MPA, and OPA show high sensitivity to scenes (e.g., Epstein and Kanwisher 1998; Grill-
612 Spector et al. 2001). Interestingly, in EVC we observe stronger responses for scenes during
613 encoding and stronger responses for objects during recall. This may explain the negatively
614 trending cross-discrimination between encoding and recall in EVC. However, a group univariate
615 contrast of objects versus scenes during recall reveals that recall scene-selectivity appears

616 strongest in areas anterior to PPA and MPA, and recall object-selectivity appears strongest in
617 areas anterior to LO and in early visual cortex. We quantified this observation by comparing the
618 locations of the peak encoding voxel and the peak recall voxel around each ROI for every
619 participant. Recall peaks were significantly anterior to encoding peaks across participants
620 bilaterally in PPA (Left Hemisphere: Wilcoxon signed rank test $Z = 2.32$, $p = 0.020$; Right
621 Hemisphere: $Z = 2.65$, $p = 0.008$) and OPA (LH: $Z = 2.52$, $p = 0.012$; RH: $Z = 2.91$, $p = 0.004$), and
622 in the left pFs ($Z = 2.68$, $p = 0.007$), left MPA ($Z = 2.45$, $p = 0.014$), and right LO ($Z = 2.71$, $p =$
623 0.007). Even in those hemispheres showing non-significant effects the same numeric trend was
624 observed, with recall peaks anterior to encoding peaks. In sum, rather than the peaks of
625 recalled stimulus class overlapping with those of encoding, the greatest scene-object
626 differences occur in a spatially separate set of voxels largely anterior to those during encoding.

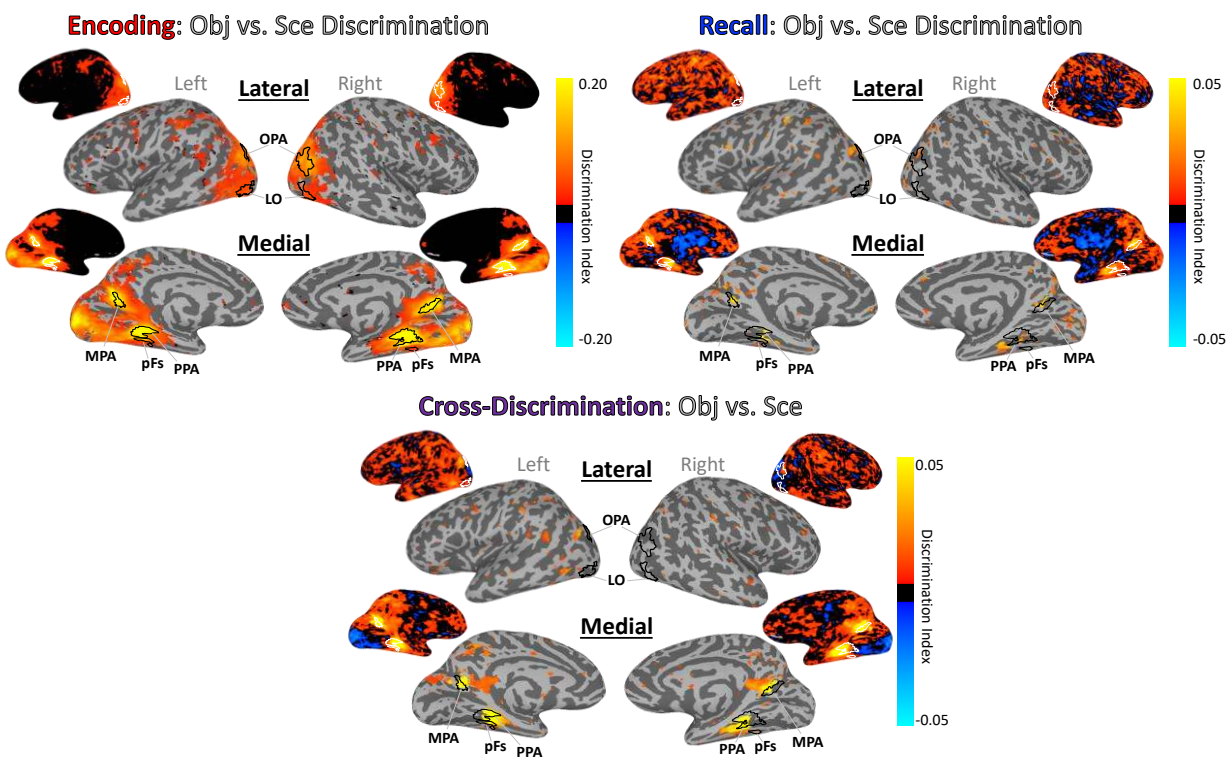
627 A searchlight analysis looking at information discriminability across the brain replicates
628 this spatial separation (Figure 8). During encoding, scenes and objects are most discriminable in
629 the same regions identified by the independent perceptual localizer (LO, pFS, PPA, MPA, OPA).
630 However, during recall, peak discriminability visibly occurs in voxels anterior to these encoding-
631 based regions. A comparison of the peak voxel locations between encoding and recall
632 confirmed that recall was significantly anterior to encoding in several regions (right PPA: $Z =$
633 2.06 , $p = 0.039$; left OPA: $Z = 3.20$, $p = 0.001$; left LO: $Z = 2.61$, $p = 0.009$; right LO: $Z = 2.06$, $p =$
634 0.039 ; left pFs: $Z = 2.21$, $p = 0.027$), and numerically showing the same trend in others (left PPA,
635 left and right MPA, right OPA). Next, we employed a cross-discrimination searchlight to identify
636 regions with shared stimulus representations between encoding and recall. Again, areas
637 anterior to those most sensitive during encoding showed highest similarity between encoding

638 and recall representations. This anterior shift was significant in bilateral PPA (LH: $Z = 3.30$, $p =$
639 9.83×10^{-4} ; RH: $Z = 2.39$, $p = 0.017$), bilateral OPA (LH: $Z = 3.59$, $p = 3.34 \times 10^{-4}$; RH: $Z = 3.43$, $p =$
640 6.15×10^{-4}), left pFs ($Z = 2.38$, $p = 0.017$), right LO ($Z = 2.97$, $p = 0.003$) and numerically showed
641 the same trend in left LO, right pFs, and right MPA.

642 These results suggest a spatial separation between encoding and recall with strongest
643 reinstatement occurring outside of scene- and object-selective regions typically localized in
644 visual tasks.

645

646



647

648 **Figure 8 – Whole-brain discrimination analyses for encoding, recall, and cross-decoding of information.** Whole-
649 brain searchlight analyses investigating discrimination of objects versus scenes during encoding (top left), recall
650 (top right), and cross-discrimination (bottom). Brighter yellows indicate higher discrimination indices. Outlined

651 ROIs are defined using independent stimuli in an independent localizer run. All maps are thresholded at $p < 0.005$
652 uncorrected, and unthresholded maps are also shown. The cross-discrimination searchlight shows regions that
653 have a shared representation between encoding and recall.

654

655

Discussion

656 In this work, we conducted an in-depth investigation of how and where recalled
657 memory content for complex object and scene images is represented in the brain. First, we
658 observed a striking difference in the representational structure between encoding and recall.
659 While information in cortex during encoding reflected multiple levels of information, during
660 recall we observed clear evidence for coarse-level information (objects versus scenes) as well as
661 some fine-level scene information. No region showed mid-level information during recall (e.g.,
662 natural/manmade for scenes, tool/non-tools for objects), even though such information was
663 often stronger than fine-level information during encoding. In hippocampus, we only observed
664 coarse-level discrimination and only during encoding. Medial temporal lobe regions perirhinal
665 cortex and parahippocampal cortex also only showed coarse-level discrimination, although this
666 information was discriminable during both the encoding and recall periods. Second, a direct
667 comparison between encoding and recall discriminability within ROIs found only weak
668 correlations that were significant in a limited number of ROIs. When we further examined just
669 the top discriminating voxels for encoding and recall, most regions showed no overlap between
670 them, with only pFs showing higher overlap than chance. Finally, a whole brain comparison of
671 encoding and recall discriminability revealed that the peaks for recall as well as the strongest
672 encoding-recall similarity were spatially anterior to the peaks during encoding. Collectively, our

673 results reveal key spatial and representational differences between encoding and recalling
674 stimulus content.

675 The ability to decode scenes versus objects during recall is consistent with several
676 findings showing broad stimulus class decodability during recall (Polyn et al. 2005; Reddy et al.
677 2010; Boccia et al. 2019; O'Craven and Kanwisher 2000). Similarly, the ability to decode fine-
678 level information of individual scene categories is consistent with prior work showing decoding
679 of specific stimulus images (e.g., Dickerson et al. 2007; Buchsbaum et al. 2012; Lee et al. 2012;
680 Kuhl and Chun 2014). Additionally, we replicate several findings observing discriminability of
681 different levels of information during perception (e.g., Mahon et al. 2007; Walther et al. 2009;
682 Kravitz et al. 2011; Park et al. 2011). We did not find discriminability of object size in visual
683 areas (Konkle et al. 2012) as expected, but this may reflect the range of sizes we selected, which
684 were not as far apart as in prior work. We also find a significant ability to decode memory
685 vividness and future recognition success from many cortical regions as shown in prior work
686 (Supplementary Material S1, S2; Brewer et al. 1998; Wais 2008; Dijkstra et al. 2017; Fulford et
687 al. 2018). However, at face-value the limited decoding we find during recall as well as the low
688 encoding-recall similarity in category-selective cortex appear to be at odds with prior findings.
689 We discuss each of these issues in turn in the paragraphs below.

690 While we were able to discriminate coarse-level information in most areas and fine-level
691 information in some areas during recall, we found no evidence for recall of mid-level
692 information in any region. Prior work has primarily focused on these coarse- and fine-levels,
693 and this absence of mid-level information suggests that imagery-based representations in
694 cortex do not contain more information that generalizes across categories. Participants may be

695 recalling limited image features, sufficient for fine-level classification of some specific image
696 categories (e.g., retinotopic features shared across exemplars of a category), and sufficient for
697 classification at the coarse level of scenes versus objects (given large differences between their
698 features). However, the representations during recall may not contain more abstract
699 information, such as features shared by items at a similar mid-level (e.g., size, function, qualities
700 of a scene). This pattern of results is reflected not only in many category-selective areas, but
701 also in early visual cortex, which is unlikely to represent these more abstract features.

702 In terms of encoding-recall similarity, our results also appear to be inconsistent with
703 some previous findings of sensory reinstatement, in which the neurons or voxels sensitive
704 during encoding have been reported to show the same patterns during recall (Wheeler et al.
705 2000; Danker and Anderson 2010; Buchsbaum et al. 2012; Johnson and Johnson 2014; Tomparny
706 et al. 2016; Schultz et al. 2019). In several visual and memory-related regions, we observed
707 limited overlap between the sub-regions with peak encoding and those with peak recall
708 information, with the strongest encoding-recall similarity in more anterior regions. However,
709 some studies do report encoding-recall similarity within scene- and object-selective cortex (e.g.,
710 O'Craven and Kanwisher 2000; Johnson and Johnson 2014) which may be attributable to key
711 methodological differences from the current study. First, as noted above, we targeted
712 recollection of stimulus content rather than individual items. While scene- and object-selective
713 regions may maintain item-specific visual information during both encoding and recall, our
714 results suggest a difference in representations during encoding and recall at more generalized
715 levels of information. Second, we employed an item-based recall task, rather than associative
716 tasks commonly used to study recall (e.g., Ganis et al. 2004; Zeidman et al. 2015a; Xiao et al.

717 2017; Jonker et al. 2018). This allowed us to ensure that information we decoded was not
718 related to other factors such as decoding a cue or association. One potentially interesting
719 question for future work is how strength of the memory representation (e.g., reported
720 vividness) or task may modulate the degree of overlap between encoding and recalled
721 representations.

722 Our findings suggest a posterior-anterior gradient within cortical regions, in which
723 recalled representations extend anterior to encoding or perceptual representations. These
724 results agree with recent research showing that regions involved in scene memory are anterior
725 to those involved in scene perception, with the possibility of separate perception and memory
726 networks (Baldassano et al. 2016; Burles et al. 2018; Chrastil 2018; Silson et al. 2019a). This
727 anterior bias for recall may reflect top-down refreshing of a memory representation in contrast
728 to the largely bottom-up processes that occur during perception (Mechelli et al. 2004; Johnson
729 et al. 2007; Dijkstra et al. 2019). Indeed, recent work using electroencephalography (EEG) has
730 identified a reversal of information flow during object recall as compared to encoding (Linde-
731 Domingo et al. 2019). Alternatively, other research has suggested a gradient within the
732 neocortex that reflects a split of conceptual information represented anterior (or downstream)
733 to perceptual information (Peelen and Caramazza 2012; Borghesani et al. 2016; Martin 2016).
734 While recent work shows highly detailed visual content within recalled memories (Bainbridge et
735 al. 2019), it is possible recalled memories may be more abstracted and conceptual compared to
736 their encoded representations. This recalled memory could thus contain less mid-level
737 perceptual information or be abstracted into a different representation, explaining why we can
738 decode memory strength but not fine-grained perceptually-defined distinctions (e.g., natural

739 versus manmade) during recall. Collectively, our results support these two possible accounts for
740 anterior-posterior gradients of memory/perception or conceptual/perceptual information in
741 the brain, in contrast with other accounts claiming an identical representation between
742 encoding and recall (e.g., Schultz et al. 2019).

743 The current work also provides further support for a content-independent role of the
744 hippocampus in memory. During encoding, we observe broad content selectivity in the
745 hippocampus, as has been observed in other recent work claiming a perceptual role for the
746 hippocampus (Zeidman et al. 2015b; Hodgetts et al. 2017). However, we do not observe strong
747 evidence of any other content representations during encoding or recall; the hippocampus does
748 not show sensitivity to more fine-grained information, and during recall, it does not even show
749 differences at the broadest distinction of objects versus scenes. These results lend support for
750 the notion that the hippocampus is largely content-independent (Davachi 2006; Danker and
751 Anderson 2010; Liang et al. 2013; Schultz et al. 2019), with individual item decoding in previous
752 work possibly driven by decoding of indexes within the hippocampus connected to fuller
753 representations in the neocortex, or a coding of memory strength (e.g., Teyler and Rudy, Jonker
754 et al. 2018). In fact, while stimulus content during recall is not discriminable, we find that
755 memory strength is decodable from the hippocampus, mirroring similar results finding strength
756 but not content representations in the hippocampus for oriented gratings (Bosch et al. 2014).
757 There is also evidence to suggest that the hippocampus may require longer delays (e.g., several
758 hours to a week) to develop decodable representations of memory content (Tomparny and
759 Davachi 2017; Lee et al. 2019), and so a similar experiment conducted with longer delays
760 between study and test (e.g., days) may find decodable stimulus content from the

761 hippocampus. These results in the hippocampus also serve as an interesting counterpoint to
762 our findings in PRC and PHC within the medial temporal lobe. While these regions also do not
763 show any mid- or fine-grained information, they show significant discrimination of coarse-level
764 information during encoding, recall, and cross-discriminable representations between the two.
765 These results support prior findings of category selectivity within these regions (e.g., Murray &
766 Richmond 2001; Buckley & Gaffan 2006; Staresina et al. 2011) as well as work suggesting similar
767 representations between perception and recall (Schultz et al. 2019).

768 The current study combining nested categorical structure for real-world images and an
769 item-based recall approach allows us to observe different levels of stimulus representations
770 across the brain; however, there are limitations to this methodology that could be addressed in
771 future work. In particular, the limited information and null findings during recall could partly
772 reflect a lack of power reflecting the weaker signals during recall compared to encoding.
773 However, from a combination of our results, we think issues of power alone cannot explain our
774 findings. First, several regions during encoding show stronger mid-level discriminability than
775 fine-level discriminability (e.g., PPA, pFs, and MPA for natural/manmade). However, these same
776 regions show significant fine-level discriminability but not mid-level discriminability during
777 recall, suggesting that the nature of the information present during recall is different, not just
778 diminished. Second, our ability to decode recall vividness from most visual regions suggests
779 decodable patterns of information are present during recall (Supplementary Material S1, S2).
780 Third, our analyses uncovering separate peaks of encoding and recall also suggest that
781 significant recall discriminability does exist, but in regions somewhat distinct from these
782 perceptually-based ROIs. Finally, the current sample size (N=22) and number of trials (192

783 stimuli) fall in the higher range compared to related studies (e.g., Lee et al. 2012: N=11;
784 Johnson and Johnson 2014: N=16; Schultz et al. 2019: N=16). Another limitation of our current
785 study is our inability to assess discriminability for individual images – our current methodology
786 was designed to allow us to powerfully test stimulus content divorced from memory for
787 individual items. Future studies should investigate whether individual item representations are
788 identical between encoding and recall, even if more general content representations are not.
789 Such findings could have meaningful implications on the nature of representations during
790 recall, suggesting the imagery for an individual item is vivid enough to be item-specific, but
791 results in a limited level of abstraction. Another question for future research will be a deeper
792 examination of the different factors influencing encoding-recall similarity for each ROI. While
793 the conjunction of our results in addition to the whole-brain analyses suggests a clear
794 difference between encoding and recall, high encoding-recall correlations or low overlap in
795 isolation could be attributed to alternate explanations. For example, high correlations between
796 encoding and recall could be due to anatomical influences on voxel activity. On the other hand,
797 at-chance overlap between encoding and recall could be due to high noise within an ROI.
798 Finally, it will be important to see whether these newly defined anterior recall regions show
799 more fine-grained representations of stimulus content during recall, and whether there may be
800 region-specific differences (e.g., the MPA in particular has been a key target for comparisons of
801 scene perception and scene recall; Burles et al. 2018; Chrastil 2018; Silson et al. 2019b).

802 Examining item-based recall and representations of memory content in the brain has
803 ultimately unveiled a rather complex, nuanced relationship of encoding and recall, with
804 strongest encoding-recall similarity occurring largely anterior to scene- and object-selective

805 visual cortex. In the study of memory, it is important to examine not only how we remember,
806 but *what* we are remembering, and this study reveals that the way in which this content is
807 manifested may vary greatly between encoding and recall.

808

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