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Parietal representations of stimulus features are amplified during memory retrieval and flexibly aligned with top-down goals

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23 Abstract

24 In studies of human episodic memory, the phenomenon of reactivation has traditionally
25 been observed in regions of occipitotemporal cortex (OTC) involved in visual perception.
26 However, reactivation also occurs in lateral parietal cortex (LPC), and recent evidence
27 suggests that stimulus-specific reactivation may be stronger in LPC than in OTC. These
28 observations raise important questions about the nature of memory representations in LPC
29 and their relationship to representations in OTC. Here, we report two fMRI experiments
30 that quantified stimulus feature information (color and object category) within LPC and
31 OTC, separately during perception and memory retrieval, in male and female human
32 subjects. Across both experiments, we observed a clear dissociation between OTC and
33 LPC: while feature information in OTC was relatively stronger during perception than
34 memory, feature information in LPC was relatively stronger during memory than
35 perception. Thus, while OTC and LPC represented common stimulus features in our
36 experiments, they preferentially represented this information during different stages. In
37 LPC, this bias toward mnemonic information co-occurred with stimulus-level reinstatement
38 during memory retrieval. In Experiment 2, we considered whether mnemonic feature
39 information in LPC was flexibly and dynamically shaped by top-down retrieval goals.
40 Indeed, we found that dorsal LPC preferentially represented retrieved feature information
41 that addressed the current goal. In contrast, ventral LPC represented retrieved features
42 independent of the current goal. Collectively, these findings provide insight into the nature
43 and significance of mnemonic representations in LPC and constitute an important bridge
44 between putative mnemonic and control functions of parietal cortex.

45

46 **Significance Statement**

47 When humans remember an event from the past, patterns of sensory activity that were
48 present during the initial event are thought to be reactivated. Here, we investigated the role
49 of lateral parietal cortex (LPC), a high-level region of association cortex, in representing
50 prior visual experiences. We find that LPC contained stronger information about stimulus
51 features during memory retrieval than during perception. We also found that current task
52 goals influenced the strength of stimulus feature information in LPC during memory. These
53 findings suggest that, in addition to early sensory areas, high-level areas of cortex like LPC
54 represent visual information during memory retrieval, and that these areas may play a
55 special role in flexibly aligning memories with current goals.

56

57 Introduction

58 Traditional models of episodic memory propose that sensory activity evoked during
 59 perception is reactivated during recollection (Kosslyn, 1980; Damasio, 1989). There is
 60 considerable evidence for such reactivation in occipitotemporal cortex (OTC), where visual
 61 information measured during perception is observed during later memory retrieval, though
 62 degraded in strength (Wheeler et al., 2000; O'Craven and Kanwisher, 2000; Polyn et al.,
 63 2005). Recent human neuroimaging work has found that reactivation also occurs in higher-
 64 order regions such as lateral parietal cortex (LPC) (Kuhl and Chun, 2014; Chen et al.,
 65 2016; Lee and Kuhl, 2016; Xiao et al., 2017). Though these findings are consistent with
 66 older observations of increased univariate activity in LPC during successful remembering
 67 (Wagner et al., 2005; Kuhl and Chun, 2014), they also raise new questions about whether
 68 and how representations of retrieved memories differ between LPC and OTC.

69 Univariate fMRI studies have consistently found that, in contrast to sensory regions, ventral
 70 LPC exhibits low activation when perceptual events are experienced but high activation
 71 when these events are successfully retrieved (Daselaar, 2009; Kim et al., 2010). The idea
 72 that LPC may be relatively more involved in memory retrieval than perception has also
 73 received support from recent pattern-based fMRI studies. Long, Lee, and Kuhl (2016)
 74 found that reactivation of previously learned visual category information was stronger in
 75 the default mode network (which includes ventral LPC) than in OTC (see also Chen et al.,
 76 2016), whereas the reverse was true of category information during perception. Similarly,
 77 Xiao and colleagues (2017) found that stimulus-specific representations of retrieved stimuli
 78 were relatively stronger in LPC than in high-level visual areas, whereas stimulus-specific
 79 representations of perceived stimuli showed the opposite pattern.

80 Collectively, these studies raise the intriguing idea that reactivation—defined as consistent
 81 activation patterns across perception and retrieval—may not fully capture how memories
 82 are represented during recollection. Rather, there may be a systematic transformation of
 83 stimulus information from sensory regions during perception to higher-order regions
 84 (including LPC) during retrieval. Critically, however, previous studies have not measured or
 85 compared OTC and LPC representations of stimulus *features* during perception and
 86 memory retrieval. This leaves open the important question of whether the same stimulus

features represented in OTC during perception are represented in LPC during retrieval, or whether these regions represent different stimulus dimensions across processing stages (Xiao et al., 2017). Finally, consideration of feature-level representations in LPC is also important because subregions of LPC may play a role in flexibly aligning retrieved features of a stimulus with behavioral goals (Kuhl et al., 2013; Sestieri et al., 2017). Given the proposed role of dorsal frontoparietal cortex in top-down attention (Corbetta and Shulman, 2002), a bias toward goal-relevant stimulus features may be particularly likely to occur in dorsal LPC.

We conducted two fMRI experiments designed to directly compare visual stimulus representations during perception and memory in OTC and LPC. Stimuli were images of common objects with two visual features of interest: color and object categories (Fig. 1). In both experiments (Fig. 2A), human subjects learned word-image associations prior to a scan session. During scanning, subjects completed separate perception and memory retrieval tasks (Fig. 2B). During perception trials, subjects viewed the image stimuli. During memory trials, subjects were presented with word cues and recalled the associated images. The key difference between Experiments 1 and 2 occurred during scanned memory trials. In Experiment 1, subjects retrieved each image as vividly as possible, whereas in Experiment 2 subjects retrieved only the color feature or only the object feature of each image as vividly as possible. Using data from both experiments, we evaluated the relative strength of color and object feature information in OTC and LPC during stimulus perception and memory. We also compared the strength of feature-level and stimulus-level reinstatement in these regions. Using data from Experiment 2, we evaluated the role of top-down goals on mnemonic feature representations, specifically testing for differences in goal-sensitivity across LPC subregions.

Material and Methods

Subjects

Forty-seven male and female human subjects were recruited from the New York University (Experiment 1) and University of Oregon (Experiment 2) communities. All subjects were right-handed native English speakers between the ages of 18 and 35 who reported normal

116 or corrected-to-normal visual acuity, normal color vision, and no history of neurological or
 117 psychiatric disorders. Subjects participated in the study after giving written informed
 118 consent to procedures approved by the New York University or University of Oregon
 119 Institutional Review Boards. Of the 24 subjects recruited for Experiment 1, seven subjects
 120 were excluded from data analysis due to poor data quality owing to excessive head motion
 121 ($n = 3$), sleepiness during the scan ($n = 2$), or poor performance during memory scans ($n =$
 122 2 , $< 75\%$ combined vivid memory and weak memory responses). This yielded a final data
 123 set of 17 subjects for Experiment 1 (19 - 31 years old, 7 males). Of the 23 subjects
 124 recruited for Experiment 2, two subjects withdrew from the study prior to completion due to
 125 either a scanner error ($n = 1$) or discomfort during the scan ($n = 1$). An additional four
 126 subjects were excluded from data analysis due to: an abnormality detected in the acquired
 127 images ($n = 1$), poor data quality owing to excessive head motion ($n = 2$), or poor
 128 performance during memory scans ($n = 1$, $< 75\%$ combined vivid memory and weak
 129 memory responses). This yielded a final data set of 17 subjects for Experiment 2 (18 - 31
 130 years old, 8 males).

131 Stimuli

132 Stimuli for Experiment 1 consisted of 32 unique object images (Fig. 1). Each stimulus had
 133 two visual features of interest: object category (backpacks, cups, fish, flowers, fruit, hats,
 134 insects, or shoes) and color category (blue, green, red, or yellow). We chose object
 135 category as a feature dimension because there is long-standing evidence that object
 136 information can be robustly decoded from fMRI activity patterns (Haxby et al., 2001). We
 137 chose color category as a feature because it satisfied our requirement for a second feature
 138 that could be orthogonalized from object category and also be easily integrated with object
 139 category to generate unique stimulus identities. Finally, we were motivated to select color
 140 category as a feature because of prior evidence for color decoding in visual cortex
 141 (Brouwer and Heeger, 2009; Brouwer and Heeger, 2013) and for flexible color
 142 representations in monkey parietal cortex (Toth and Assad, 2002).

143 Each of the 32 stimuli in our experiments represented a unique conjunction of one of the
 144 four color categories and one of the eight object categories. In addition, the specific color
 145 and object features of each stimulus were unique exemplars of that stimulus's assigned

categories. For example, the blue, green, red, and yellow backpack stimuli were all different backpack exemplars. The rationale for using unique exemplars was so that we could measure generalizable information about color and object categories rather than idiosyncratic differences between stimuli. That is, we wanted to measure a representation of ‘backpacks’ as opposed to a representation of a specific backpack. Thirty-two closely matched foil images with the same color and object category conjunctions were also used in the behavioral learning session to test memory specificity. Stimuli for Experiment 2 were identical to those from Experiment 1, with the exception of the fruit object category, which was replaced with a bird object category. All images were 225 x 225 pixels, with the object rendered on a white background. Word cues consisted of 32 common verbs and were the same for both experiments.

Tasks and procedure

Experiment 1. The experiment began with a behavioral session, during which subjects learned 32 unique word-image associations to 100% criterion. A scan session immediately followed completion of the behavioral session. During the scan, subjects participated in two types of runs: 1) perception, where they viewed the object images without the corresponding word cues and 2) memory, where they were presented with the word cues and recalled the associated object images (Fig. 2A, B). Details for each of these phases are described below.

Immediately prior to scanning, subjects learned 32 word-image associations through interleaved study and test blocks. For each subject, the 32 word cues were randomly assigned to each of 32 images. During study blocks, subjects were presented with the 32 word-image associations in random order. On a given study trial, the word cue was presented for 2 s, followed by the associated image for 2 s. A fixation cross was presented centrally for 2 s before the start of the next trial. Subjects were instructed to learn the associations in preparation for a memory test, but no responses were required. During test blocks, subjects were presented with the 32 word cues in random order and tested on their memory for the associated image. On each test trial, the word cue was presented for .5 s and was followed by a blank screen for 3.5 s, during which subjects were instructed to try to recall the associated image as vividly as possible for the entire 3.5 s. After this period

176 elapsed, a test image was presented. The test image was either the correct image (target),
177 an image that had been associated with a different word cue (old), or a novel image that
178 was highly similar (same color and object category) to the target (lure). These trial types
179 occurred with equal probability. For each test image, subjects had up to 5 s to make a
180 yes/no response indicating whether or not the test image was the correct associate. After
181 making a response, subjects were shown the target image for 1 s as feedback. After
182 feedback, a fixation cross was presented centrally for 2 s before the start of the next trial.
183 Lure trials were included to ensure that subjects formed sufficiently detailed memories of
184 each image so that they could discriminate between the target image and another image
185 with the same combination of features. Subjects alternated between study and test blocks
186 until they completed a minimum of 6 blocks of each type and achieved 100% accuracy on
187 the test. The rationale for overtraining the word-image associations was to minimize
188 variability in retrieval success and strength during subsequent scans.

189 Once in the scanner, subjects participated in two types of runs: perception and memory
190 retrieval. During perception runs, subjects viewed the object images one at a time while
191 performing a cover task of detecting black crosses that appeared infrequently on images.
192 We purposefully avoided using a task that required subjects to make explicit judgments
193 about the stimuli. The rationale for this was that we wanted to measure the feedforward
194 perceptual response to the stimuli without biasing representations toward task-relevant
195 stimulus dimensions. On a given perception trial, the image was overlaid with a central
196 white fixation cross and presented centrally on a gray background for .5 s. The central
197 white fixation cross was then presented alone on a gray background for 3.5 s before the
198 start of the next trial. Subject were instructed to maintain fixation on the central fixation
199 cross and monitor for a black cross that appeared at a random location within the borders
200 of a randomly selected 12.5% of images. Subjects were instructed to judge whether a
201 target was present or absent on the image and indicate their response with a button press.
202 Each perception run consisted of 32 perception trials (1 trial per stimulus) and 8 null
203 fixation trials in random order. Null trials consisted of a central white fixation cross on a
204 gray background presented for 4 s and were randomly interleaved with the object trials
205 thereby creating jitter. Every run also contained 8 s of null lead in and 8 s of null lead out
206 time during which a central white fixation cross on a gray background was presented.

207 During memory runs, subjects were presented with the word cues one at a time, recalled
 208 the associated images, and evaluated the vividness of their recollections. In contrast to our
 209 task choice for the perception runs, here we chose a task that would maximize our ability
 210 to measure subjects' internal stimulus representations (i.e., the retrieved images) as
 211 opposed to feedforward perceptual responses. On each memory trial, the word cue was
 212 presented centrally in white characters on a gray background for .5 s. This was followed by
 213 a 2.5 s recall period where the screen was blank. Subjects were instructed to use this
 214 period to recall the associated image from memory and to hold it in mind as vividly as
 215 possible for the entire duration of the blank screen. At the end of the recall period, a white
 216 question mark on a gray background was presented for 1 s, prompting subjects to make
 217 one of three memory vividness responses via button box: "vividly remembered", "weakly
 218 remembered", "not remembered". The question mark was replaced by a central white
 219 fixation cross, which was presented for 2 s before the start of the next trial. Responses
 220 were recorded if they were made during the question mark or the ensuing fixation cross.
 221 As in perception runs, each memory run consisted of 32 memory trials (1 trial per stimulus)
 222 and 8 null fixation trials in random order. Null trials consisted of a central white fixation
 223 cross on a gray background presented for 6 s, and as in perception runs, provided jitter.
 224 Each run contained 8 s of null lead in and 8 s of null lead out time during which a central
 225 white fixation cross on a gray background was presented.

226 For both perception and memory tasks, trial orders were randomly generated for each
 227 subject and run. Subjects alternated between perception and memory runs, performing as
 228 many runs of each task as could be completed during the scan session (range = 7-10, $M =$
 229 8.41). Thus, there were between 7 and 10 repetitions of each stimulus across all
 230 perception trials and 7 to 10 repetitions of each stimulus across all memory trials. All
 231 stimuli were displayed on a projector at the back of the scanner bore, which subjects
 232 viewed through a mirror attached to the head coil. Subjects made responses for both tasks
 233 on an MR-compatible button box.

234 *Experiment 2.* As in Experiment 1, Experiment 2 began with a behavioral session, during
 235 which subjects learned 32 unique word-image associations to 100% criterion. A scan
 236 session immediately followed. During the scan, subjects participated in both perception
 237 and memory runs. In contrast to Experiment 1, subjects performed one of two goal-

238 dependent memory tasks during memory runs: 1) color memory, where they selectively
 239 recalled the color feature of the associated image from the word cue; 2) object memory,
 240 where they selectively recalled the object feature of the associated image from the word
 241 cue (Fig. 2A, B). Note that subjects were introduced to the goal-dependent color and
 242 object retrieval tasks immediately prior to the scan, and did not perform these tasks during
 243 the associative learning session. Details of each phase of the experiment, in relation to
 244 Experiment 1, are described below.

245 Subjects learned 32 word-image associations following the same procedure as in
 246 Experiment 1. Once in the scanner, subjects participated in three types of runs: perception,
 247 color memory, and object memory. Procedures were the same as in Experiment 1 unless
 248 noted. During perception runs, subjects viewed the images one at a time while performing
 249 a cover task of detecting black crosses that infrequently appeared on images. On a given
 250 perception trial, the object image was overlaid with a central white fixation cross and
 251 presented centrally on a gray background for .75 s. The central white fixation cross was
 252 then presented alone on a gray background for either 1.25, 3.25, 5.25, 7.25, or 9.25 s
 253 (25%, 37.5%, 18.75%, 12.5%, 6.25% of trials per run, respectively) before the start of the
 254 next trial. These interstimulus intervals were randomly assigned to trials. Subjects
 255 performed the detection task as in Experiment 1. Each perception run consisted of 64
 256 perception trials (2 trials per stimulus) in random order, with lead in and lead out time as in
 257 Experiment 1.

258 During color and object memory runs, subjects were presented with the word cues one at
 259 a time, recalled only the color feature or only the object feature of the associated images,
 260 and evaluated the vividness of their recollections. We chose not to have subjects explicitly
 261 report information about the relevant feature during these runs in order to avoid conflating
 262 memory representations with decision- or motor-related information. On each memory trial,
 263 the word cue was presented centrally in white characters on a gray background for .3 s.
 264 This was followed by a 2.2 s recall period where the screen was blank. Subjects were
 265 instructed to use this period to recall only the relevant feature of the associated image from
 266 memory and to hold it in mind as vividly as possible for the entire duration of the blank
 267 screen. At the end of the recall period, a white fixation cross was presented centrally on a
 268 gray background for either 1.5, 3.5, 5.5, 7.5, or 9.5 s (37.5%, 25%, 18.75%, 12.5%, 6.25%

269 of trials per run, respectively), prompting subjects to make one of three memory vividness
 270 decisions via button box as in Experiment 1. The interstimulus intervals were randomly
 271 assigned to trials. Color and object memory runs consisted of 64 memory trials (2 trials per
 272 stimulus) presented in random order, with lead in and lead out time as in Experiment 1.

273 All subjects completed 4 perception runs, 4 color memory runs, and 4 object memory runs,
 274 with each stimulus presented twice in every run. Thus, there were 8 repetitions of each
 275 stimulus for each run type. Runs were presented in four sequential triplets, with each triplet
 276 composed of one perception run followed by color and object memory runs in random
 277 order. As in Experiment 1, stimuli were displayed on a projector at the back of the scanner
 278 bore, which subjects viewed through a mirror attached to the head coil. Subjects made
 279 responses for all three tasks on an MR-compatible button box.

280 **MRI acquisition**

281 *Experiment 1.* Images were acquired on a 3T Siemens Allegra head-only MRI system at
 282 the Center for Brain Imaging at New York University. Functional data were acquired with a
 283 T2*-weighted echo-planar imaging (EPI) sequence with partial coverage (repetition time =
 284 2 s, echo time = 30 ms, flip angle = 82°, 34 slices, 2.5 x 2.5 x 2.5 mm voxels) and an 8
 285 channel occipital surface coil. Slightly oblique coronal slices were aligned approximately
 286 120° with respect to the calcarine sulcus at the occipital pole and extended anteriorly
 287 covering the occipital lobe, ventral temporal cortex and posterior parietal cortex. A whole-
 288 brain T1-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) 3D
 289 anatomical volume (1 x 1 x 1 mm voxels) was also collected.

290 *Experiment 2.* Images were acquired on a 3T Siemens Skyra MRI system at the Robert
 291 and Beverly Lewis Center for NeuroImaging at the University of Oregon. Functional data
 292 were acquired using a T2*-weighted multiband EPI sequence with whole-brain coverage
 293 (repetition time = 2 s, echo time = 25 ms, flip angle = 90°, multiband acceleration factor =
 294 3, inplane acceleration factor = 2, 72 slices, 2 x 2 x 2 mm voxels) and a 32 channel head
 295 coil. Oblique axial slices were aligned parallel to the plane defined by the anterior and
 296 posterior commissures. A whole-brain T1-weighted MPRAGE 3D anatomical volume (1 x 1
 297 x 1 mm voxels) was also collected.

298 **fMRI processing**

299 FSL v5.0 (Smith et al., 2004) was used for functional image preprocessing. The first four
 300 volumes of each functional run were discarded to allow for T1 stabilization. To correct for
 301 head motion, each run's timeseries was realigned to its middle volume. Each timeseries
 302 was spatially smoothed using a 4 mm full width at half maximum Gaussian kernel and
 303 high-pass filtered using Gaussian-weighted least squares straight line fitting with $\sigma = 64.0$
 304 s. Volumes with motion relative to the previous volume greater than 1.25 mm in
 305 Experiment 1 (half the width of a voxel) or greater than .5 mm in Experiment 2 were
 306 excluded from subsequent analyses. A lower threshold was chosen for Experiment 2 due
 307 to high motion artifact susceptibility in multiband sequences. Freesurfer v5.3 (Fischl, 2012)
 308 was used to perform segmentation and cortical surface reconstruction on each subject's
 309 anatomical volume. Boundary-based registration was used to compute the alignment
 310 between each subject's functional data and their anatomical volume.

311 All fMRI processing was performed in individual subject space. To estimate the neural
 312 pattern of activity evoked by the perception and memory of every stimulus, we conducted
 313 separate voxelwise general linear model (GLM) analyses of each subject's smoothed
 314 timeseries data from the perception and memory runs in each experiment. Perception
 315 models included 32 regressors of interest corresponding to the presentation of each
 316 stimulus. Events within these regressors were constructed as boxcars with stimulus
 317 presentation duration convolved with a canonical double-gamma hemodynamic response
 318 function. Six realignment parameters were included as nuisance regressors to control for
 319 motion confounds. First-level models were estimated for each run using Gaussian least
 320 squares with local autocorrelation correction ("prewhitening"). Parameter estimates and
 321 variances for each regressor were then registered into the space of the first run and
 322 entered into a second-level fixed effects model. This produced *t*-maps representing the
 323 activation elicited by by viewing each stimulus for each subject. No normalization to a
 324 group template was performed. Memory models were estimated using the same
 325 procedure, with a regressor of interest corresponding to the recollection of each of the 32
 326 stimuli. For the purposes of this model, the retrieval goal manipulation in Experiment 2 was
 327 ignored. All retrieval events were constructed as boxcars with a combined cue plus recall
 328 duration before convolution. This produced *t*-maps representing the activation elicited by

329 remembering each stimulus relative to baseline for each subject. The previously described
 330 perception and memory GLMs were run two ways: 1) by splitting the perception and
 331 memory runs into two halves (odd vs even runs) and running two independent GLMs per
 332 run type; 2) by using all perception and memory runs in each GLM. The split-half models
 333 were only used for stimulus-level analyses conducted within run type, while models run on
 334 all of the data were used for feature-level analyses conducted within run type and for
 335 reinstatement analyses conducted across run type. Finally, for Experiment 2, two
 336 additional memory models were estimated. These models included only color memory
 337 trials or only object memory trials, which allowed us to estimate and compare patterns
 338 evoked during the two goal-dependent retrieval tasks.

339 **Region of interest definition**

340 ROIs (Fig. 3A) were produced for each subject in native subject space using multiple
 341 group-defined atlases. Our choice of group atlas for each broader cortical region of interest
 342 was based on our assessment of the best validated method for parcellating regions in that
 343 area. For retinotopic regions in OTC, we relied on a probabilistic atlas published by Wang
 344 et al. (2014). We combined bilateral V1v and V1d regions from this atlas to produce a V1
 345 ROI and bilateral LO1 and LO2 regions to produce an LO ROI. For high-level OTC, we
 346 used the output of Freesurfer segmentation routines to combine bilateral fusiform gyrus,
 347 collateral sulcus, and lateral occipitotemporal sulcus cortical labels to create a ventral
 348 temporal cortex (VTC) ROI. To subdivide LPC, we first selected the lateral parietal nodes
 349 of networks 5, 12, 13, 15, 16, and 17 of the 17 network resting state atlas published by
 350 Yeo et al. (2011). We refer to parietal nodes from Network 12 and 13 (subcomponents of
 351 the frontoparietal control network) as dorsal lateral intraparietal sulcus (dLatIPS) and
 352 ventral lateral intraparietal sulcus (vLatIPS), respectively. We altered the parietal node of
 353 Network 5 (dorsal attention network) by eliminating vertices in lateral occipital cortex and
 354 by subdividing it along the intraparietal sulcus into a dorsal region we refer to as posterior
 355 intraparietal sulcus (pIPS) and an ventral region we call ventral IPS (vIPS), following
 356 Sestieri et al. (2017). The ventral region also corresponds closely to what others have
 357 called PGp (Caspers et al., 2012; Glasser et al., 2016). Finally, due to their small size, we
 358 combined the parietal nodes of Networks 15, 16, and 17 (subcomponents of the default
 359 mode network) into a region we collectively refer to as angular gyrus (AnG). All regions

360 were first defined on Freesurfer's average cortical surface (shown in Fig. 3A) and then
 361 reverse-normalized to each subject's native anatomical surface. They were then projected
 362 into the volume at the resolution of the functional data to produce binary masks.

363 **Experimental design and statistical analysis**

364 Our experimental design for Experiment 1 included two types of cognitive tasks, which
 365 subjects performed in different fMRI runs—perception of visual stimuli, and retrieval of the
 366 same stimuli from long-term memory. Each of the 32 stimuli had one of four color features
 367 and one of eight object features. Experiment 2 was performed on an independent sample
 368 of subjects, and had a similar design to Experiment 1, except that subjects in Experiment 2
 369 performed two goal-dependent versions of the memory retrieval task: color memory and
 370 object memory (see Tasks and Procedure). Our sample size for each experiment was
 371 consistent with similar fMRI studies in the field and was determined before data collection.
 372 Our dependent variables of interest for both experiments were stimulus-evoked BOLD
 373 activity patterns. In each experiment, separate *t*-maps were obtained for each stimulus
 374 from the perception and memory runs (see fMRI processing and Fig. 3B). Experiment 2
 375 memory *t*-maps were derived from a single model that collapsed across the two goal-
 376 dependent memory tasks except when testing for goal-related effects. When testing for
 377 goal-related effects, we used *t*-maps that were separately estimated from the color and
 378 object memory tasks. We intersected all *t*-maps with binary ROI masks to produce
 379 stimulus-evoked voxel patterns for each ROI. Our ROIs included early and high-level
 380 visual areas in OTC that we believed would be responsive to the features of our stimuli, as
 381 well as regions spanning all of LPC (see Regions of interest definition). Analyses focused
 382 on cortical regions at multiple levels of spatial granularity. In order to evaluate whether
 383 perceptually-based and memory-based processing differed between LPC and OTC, we
 384 grouped data from individual ROIs according to this distinction and evaluated effects of
 385 ROI group (OTC, LPC). Given prior work implicating dorsal parietal cortex in top-down
 386 attention (Corbetta and Shulman, 2002), we also tested for differences in goal-modulated
 387 memory processing between dorsal and ventral LPC regions. To do this, we grouped
 388 individual LPC ROIs according to their position relative to the intraparietal sulcus and
 389 evaluated effects of LPC subregion (dorsal, ventral). We report follow-up statistical tests
 390 performed on data from individual ROIs in Tables 1-3. All statistical tests performed on

391 BOLD activity patterns (described below) were implemented in R v3.4. All *t*-tests were two-
 392 tailed. With the exception of tests performed at the individual ROI level, all tests were
 393 assessed at $\alpha = 0.05$. Tests in the 8 individual ROIs are reported in Tables, where
 394 uncorrected *p*-values are reported with significance after correcting for multiple
 395 comparisons indicated. Here, a conservative Bonferroni-corrected *p*-value of $0.05/8 =$
 396 0.00625 was used to indicate significance.

397 We first tested whether perception and memory activity patterns contained stimulus-level
 398 information. To do this, we computed the Fisher *z*-transformed Pearson correlation
 399 between *t*-maps estimated from independent split-half GLM models, separately for
 400 perception and memory tasks. These correlations were computed separately for each
 401 subject and ROI. We then averaged values corresponding to correlations between the
 402 same stimulus (within-stimulus correlations; e.g., blue insect - blue insect) and values
 403 corresponding to stimuli that shared neither color nor object category (across-both
 404 correlations; e.g., red insect - yellow backpack). The average across-both correlation
 405 functioned as a baseline and was subtracted from the average within-stimulus correlation
 406 to produce a measure of stimulus information. This baseline was chosen to facilitate
 407 comparisons between stimulus and feature information metrics (see below). Stimulus
 408 information was computed for each subject, ROI, and run type (perception, memory). We
 409 used mixed effects ANOVAs to test whether stimulus information varied as a function of
 410 region (within-subject factor), run type (within-subject factor), and/or experiment (across-
 411 subject factor).

412 We next tested whether perception and memory activity patterns contained information
 413 about stimulus features (color, object). We computed the Fisher *z*-transformed Pearson
 414 correlation between every pair of *t*-maps from a given subject and ROI, separately for
 415 perception and memory. Within-stimulus identity correlations were excluded because the
 416 correlation coefficient was 1.0. We then averaged correlation values across stimulus pairs
 417 that shared a color feature (within-color correlations; e.g., blue bird - blue insect), stimulus
 418 pairs that shared an object category feature (within-object correlations; e.g., blue insect -
 419 red insect), and stimulus pairs that shared neither color nor object category (across-both
 420 correlations; e.g., red insect - yellow backpack). The average across-both correlation
 421 functioned as a baseline and was subtracted (a) from the average within-color correlation

422 to produce a measure of color information, and (b) from the average within-object
 423 correlation to produce a measure of object information. Thus, positive values for these
 424 measures reflected the presence of stimulus feature information. Because the perception
 425 and memory tasks did not require subjects to report the features of the stimuli (in either
 426 Experiment 1 or 2), feature information values could not be explained in terms of planned
 427 motor responses. Color and object feature information measures were computed for each
 428 subject, ROI, and run type (perception, memory). We used mixed effects ANOVAs to test
 429 whether feature information varied as a function of region (within-subject factor), run type
 430 (within-subject factor), feature dimension (within-subject factor), and/or experiment
 431 (across-subject factor). We also performed one sample *t*-tests to assess whether feature
 432 information was above chance (zero) during perception and memory.

433 We then tested whether feature-level information and stimulus-level information were
 434 preserved from perception to memory (reinstated). We computed the Fisher *z*-transformed
 435 Pearson correlation between perception and memory patterns for every pair of stimuli,
 436 separately for each subject and ROI. Excluding within-stimulus correlations, we then
 437 averaged correlation values across stimulus pairs that shared a color feature (within-color
 438 correlations; e.g., blue insect - blue bird), stimulus pairs that shared an object category
 439 feature (within-object correlations; e.g., blue insect - red insect), and stimulus pairs that
 440 shared neither color nor object category (across-both correlations; e.g., blue insect - yellow
 441 backpack). The average across-both correlation functioned as a baseline and was
 442 subtracted (a) from the average within-color correlation to produce a measure of color
 443 reinstatement, and (b) from the average within-object correlation to produce a measure of
 444 object reinstatement. Note that these metrics are equivalent to those described in the prior
 445 analysis, but with correlations computed across perception and memory rather than within
 446 perception and memory. Thus, positive values for these measures reflected the
 447 preservation of feature information across perception and memory, or feature
 448 reinstatement. We used mixed effects ANOVAs to test whether feature reinstatement
 449 varied as a function of region (within-subject factor), feature dimension (within-subject
 450 factor), and/or experiment (across-subject factor). We also performed one sample *t*-tests to
 451 assess whether feature reinstatement was above chance (zero). To produce a measure of
 452 stimulus reinstatement that was comparable to our measures of feature reinstatement, we

453 averaged within-stimulus correlation values (e.g., blue insect - blue insect) and then
 454 subtracted the same baseline (the average of across-both correlations). We evaluated
 455 whether stimulus reinstatement could be accounted for by color and object feature
 456 reinstatement or whether it exceeded what would be expected by additive color and object
 457 feature reinstatement. To do this we compared stimulus reinstatement to summed color
 458 and object feature reinstatement. We used mixed effects ANOVAs to test whether
 459 reinstatement varied as a function of region (within-subject factor), reinstatement level
 460 (stimulus, summed features; within-subject factor), and/or experiment (across-subject
 461 factor).

462 To test whether task goals influenced feature information during memory, we recomputed
 463 color and object feature information separately using *t*-maps estimated from the color and
 464 object memory tasks in Experiment 2. We averaged these feature information values into
 465 two conditions: goal-relevant (color information for the color memory task; object
 466 information for the object memory task) and goal-irrelevant (color information during the
 467 object memory task; object information during the color memory task). We used repeated
 468 measures ANOVAs to test whether feature information varied as function of region and
 469 goal-relevance (within-subject factors). We also performed one sample *t*-tests to assess
 470 whether goal-relevant feature information and goal-irrelevant feature information were
 471 above chance (zero) during memory.

472 **Results**

473 **Behavior**

474 Subjects in both experiments completed a minimum of 6 test blocks during the associative
 475 learning session prior to scanning (Exp 1: $M = 6.65$, $SD = 0.79$; Exp 2: $M = 6.91$, $SD =$
 476 0.69). During fMRI perception runs, subjects performed the target detection task with high
 477 accuracy (Exp 1: $M = 89.0\%$, $SD = 6.8\%$; Exp 2: $M = 91.6\%$, $SD = 2.7\%$). In Experiment 1,
 478 subjects reported that they experienced vivid memory on a mean of 86.4% of fMRI
 479 memory trials ($SD = 8.4\%$), weak memory on 10.4% of trials ($SD = 7.1\%$), no memory on
 480 1.3% of trials ($SD = 1.8\%$), and did not respond on the remaining 1.8% of trials ($SD =$
 481 2.3%). In Experiment 2, the mean percentage of vivid, weak, no memory, and no response

482 trials was 86.1% (SD = 9.0%), 5.2% (SD = 6.1%), 3.4% (SD = 5.2%), and 5.4% (SD =
 483 6.2%), respectively. The percentage of vivid memory responses did not significantly differ
 484 between Experiment 1 and Experiment 2 ($t_{32} = 0.13$, $p = 0.897$, independent samples t -
 485 test). Within each experiment, there were no differences in the percentage of vivid memory
 486 responses across stimuli with different color features (Exp 1: $F_{3,48} = 1.19$, $p = 0.323$; Exp 2:
 487 $F_{3,48} = 0.48$, $p = 0.697$; repeated measures ANOVAs) or different object features (Exp 1:
 488 $F_{7,112} = 1.68$, $p = 0.121$; Exp 2: $F_{7,112} = 1.28$, $p = 0.266$).

489 **Stimulus information during perception versus memory** 490 **retrieval**

491 As a first step, we sought to replicate recent work from Xiao and colleagues (2017) that
 492 compared the strength of stimulus-level representations during perception and memory
 493 retrieval. Xiao et al. observed that ventral visual cortex contained stronger stimulus-level
 494 representations during perception than memory retrieval, while frontoparietal cortex
 495 showed the opposite pattern. To test for this pattern in our data, we quantified the strength
 496 of stimulus-level information in OTC and LPC, combining data across experiments (see
 497 Materials and Methods). We did this separately for patterns evoked during perception and
 498 memory retrieval. We then entered stimulus information values into an ANOVA with factors
 499 of ROI group (OTC, LPC), run type (perception, memory), and experiment (Exp 1, Exp 2).
 500 Consistent with Xiao et al., we observed a highly significant interaction between ROI group
 501 and run type ($F_{1,32} = 113.6$, $p < 0.001$; Fig. 4A,C). In LPC, stimulus information was greater
 502 during memory than during perception (main effect of run type: $F_{1,32} = 40.8$, $p < 0.001$),
 503 while in OTC stimulus information was greater during perception than memory (main effect
 504 of run type: $F_{1,32} = 28.0$, $p < 0.001$). These findings support the idea that stimulus-level
 505 information in LPC and OTC is differentially expressed depending on whether the stimulus
 506 is internally generated from memory or externally presented. This result motivates more
 507 targeted questions about the representation of stimulus features in OTC and LPC across
 508 perception and memory.

509 Feature information during perception versus memory retrieval

510 To assess feature information, we took advantage of the fact that our stimuli were
 511 designed to vary along two visual feature dimensions—color and object category. In both
 512 experiments, we quantified the strength of color and object feature information during
 513 perception and memory (see Materials and Methods). Of critical interest was whether the
 514 relative strength of perceptual and mnemonic feature information differed across LPC and
 515 OTC. We entered feature information values from all ROIs into an ANOVA with factors of
 516 ROI group (OTC, LPC), run type (perception, memory), feature dimension (color, object),
 517 and experiment (Exp 1, Exp 2). Critically, the relative strength of perception and memory-
 518 based feature information differed across LPC and OTC, as reflected by a highly
 519 significant interaction between ROI group and run type ($F_{1,32} = 29.27$, $p < 0.001$; Fig. 4B).
 520 This effect did not differ across experiments (ROI group x run type x experiment
 521 interaction: $F_{1,32} = 0.55$, $p = 0.462$; Fig. 4B).

522 In LPC, feature information was reliably stronger during memory than during perception
 523 (main effect of run type: $F_{1,32} = 11.65$, $p = 0.002$; Fig. 4B), with no difference in this effect
 524 across individual LPC ROIs (run type x ROI interaction $F_{4,128} = 1.55$, $p = 0.192$; Fig. 4D).
 525 Averaging across the color and object dimensions and also across experiments, feature
 526 information was above chance during memory ($t_{33} = 4.79$, $p < 0.001$; one sample t -test),
 527 but not during perception ($t_{33} = 0.14$, $p = 0.892$). In Table 1 we report the results of t -tests
 528 assessing feature information separately for each LPC ROI. Unrelated to our main
 529 hypotheses, there was a marginally significant main effect of feature dimension in LPC
 530 ($F_{1,32} = 3.95$, $p = 0.056$), with somewhat stronger object information than color information.
 531 This effect of feature dimension did not interact with run type ($F_{1,32} = 0.004$, $p = 0.952$).

532 In OTC, we observed a pattern opposite to LPC: feature information was marginally
 533 stronger during perception than during memory (main effect of run type: $F_{1,32} = 3.93$, $p =$
 534 0.056 ; Fig. 4B). Again, this effect did not differ across individual OTC ROIs (run type x ROI
 535 interaction: $F_{2,64} = 1.72$, $p = 0.187$; Fig. 4D). Averaging across the color and object
 536 dimensions and across experiments, feature information was above chance both during
 537 perception ($t_{33} = 4.68$, $p < 0.001$) and during memory ($t_{33} = 3.01$, $p = 0.005$). Table 1
 538 includes assessments of feature information for each OTC ROI separately. As in LPC,

there was a significant main effect of feature dimension in OTC ($F_{1,32} = 18.59$, $p < 0.001$), with stronger object information than color information. This effect of feature dimension interacted with run type ($F_{1,32} = 4.90$, $p = 0.034$), reflecting a relatively stronger difference between color and object information during perception than during memory. All together, these results establish that feature-level information was differentially expressed in OTC and LPC depending on whether stimuli were perceived or remembered.

Reinstatement during memory retrieval

We next quantified stimulus and feature reinstatement during memory retrieval. Whereas the prior analyses examined stimulus and feature information during perception and memory retrieval separately, here we examined whether stimulus-specific and feature-specific activity patterns were preserved from perception to memory retrieval (see Materials and Methods). Because perception and memory trials had no overlapping visual elements, any information preserved across stages must reflect memory retrieval.

To test whether feature information was preserved across perception and memory, we entered feature reinstatement values from all ROIs into an ANOVA with factors of ROI group (OTC, LPC), feature dimension (color, object), and experiment (Exp 1, Exp 2). There was no reliable difference in the strength of feature reinstatement between OTC and LPC (main effect of ROI group: $F_{1,32} = 0.90$, $p = 0.350$). There was a marginal main effect of experiment on feature reinstatement ($F_{1,32} = 3.10$, $p = 0.088$; Fig. 5A), with numerically lower feature reinstatement in Experiment 2 (where subjects recalled only one stimulus feature) than in Experiment 1 (where subjects recalled the entire stimulus). When collapsing across color and object dimensions, feature reinstatement in OTC was above chance in both Experiment 1 ($t_{16} = 2.37$, $p = 0.031$; one sample t -test) and Experiment 2 ($t_{16} = 2.33$, $p = 0.033$). In LPC, feature reinstatement was above chance in Experiment 1 ($t_{16} = 2.58$, $p = 0.020$), but not in Experiment 2 ($t_{16} = -0.007$, $p = 0.995$). Thus, the task demands in Experiment 2 may have had a particular influence on LPC feature representations—a point we examine in the next section. In Table 2 we assess feature reinstatement in individual OTC and LPC ROIs (see also Fig. 5B).

567 To test whether color and object feature reinstatement fully accounted for stimulus
 568 reinstatement, we compared summed color and object reinstatement values to stimulus
 569 reinstatement values. Reinstatement values from all ROIs were entered into an ANOVA
 570 with factors of ROI group (OTC, LPC), reinstatement level (stimulus, summed features),
 571 and experiment (Exp 1, Exp 2). There was a significant main effect of reinstatement level
 572 ($F_{1,32} = 4.31$, $p = 0.046$), with stimulus reinstatement larger than summed feature
 573 reinstatement (Fig. 5A). There was a marginally significant difference in the magnitude of
 574 this effect between OTC and LPC (reinstatement level interaction x ROI group: $F_{1,32} =$
 575 3.59 , $p = 0.067$). In LPC, stimulus reinstatement reliably exceeded summed feature
 576 reinstatement (main effect of reinstatement level: $F_{1,32} = 5.46$, $p = 0.026$; Fig. 5A). This
 577 effect did not differ across experiments (reinstatement level x experiment interaction: $F_{1,32}$
 578 $= 0.81$, $p = 0.375$; Fig. 5A) or across LPC ROIs (reinstatement level x ROI interaction:
 579 $F_{4,128} = 0.95$, $p = 0.438$; Fig. 5B). In Table 2 we assess the difference between stimulus
 580 reinstatement and summed feature reinstatement for each LPC ROI. In OTC, stimulus
 581 reinstatement did not significantly differ from summed feature reinstatement (main effect of
 582 reinstatement level: $F_{1,32} = 0.35$, $p = 0.560$; Fig. 5A), with no difference across experiments
 583 (reinstatement level x experiment interaction: $F_{1,32} = 0.30$, $p = 0.590$) and a marginal
 584 difference across ROIs (reinstatement level x ROI interaction: $F_{2,64} = 2.58$, $p = 0.084$).
 585 Tests in individual OTC ROIs (Table 2) showed that stimulus reinstatement significantly
 586 exceeded summed feature reinstatement in VTC only. These results replicate prior
 587 evidence of stimulus-level reinstatement in LPC (Kuhl and Chun, 2014; Lee and Kuhl,
 588 2016; Xiao et al., 2017) and VTC (Lee et al., 2012), but provide unique insight into the
 589 relative strength of feature- vs. stimulus-level reinstatement in these regions.

590 **Goal-dependence of feature information during memory** 591 **retrieval**

592 In a final set of analyses, we tested whether retrieval goals influenced feature information
 593 expressed in LPC during memory retrieval. Using data from Experiment 2 only, we
 594 recomputed color and object feature information separately for trials where the goal was
 595 recalling the color feature of the stimulus and trials where the goal was recalling the object
 596 feature of the stimulus (see Materials and Methods). Of interest was the comparison

597 between goal-relevant feature information (e.g., color information on color memory trials)
 598 and goal-irrelevant feature information (e.g., color information on object memory trials; Fig.
 599 6B). Because there is a strong body of evidence suggesting that dorsal and ventral parietal
 600 regions are differentially sensitive to top-down vs. bottom-up visual attention (Corbetta and
 601 Shulman, 2002), we specifically tested whether sensitivity to retrieval goals varied across
 602 dorsal and ventral LPC subregions (Fig. 6A).

603 To test whether goal sensitivity varied between dorsal and ventral LPC subregions, we
 604 entered memory-based feature information values from LPC ROIs into an ANOVA with
 605 factors of LPC subregion (dorsal LPC, ventral LPC) and goal-relevance (relevant,
 606 irrelevant). In line with our hypothesis, there was a robust interaction between LPC
 607 subregion and goal-relevance ($F_{1,16} = 9.05$, $p = 0.008$; Fig. 6C). Namely, there was reliably
 608 stronger goal-relevant than goal-irrelevant feature information in dorsal LPC (main effect of
 609 goal-relevance: $F_{1,16} = 5.30$, $p = 0.035$; Fig. 6C). This effect did not differ across individual
 610 dorsal LPC ROIs (goal-relevance x ROI interaction: $F_{1,16} = 1.01$, $p = 0.330$; Fig. 6E). In
 611 dorsal LPC, goal-relevant feature information marginally exceeded chance (goal-relevant:
 612 $t_{16} = 1.93$, $p = 0.072$; one sample t -test) whereas goal-irrelevant feature information did not
 613 differ from chance ($t_{16} = -0.49$, $p = 0.628$). In contrast to the pattern observed in dorsal
 614 LPC, feature information was not influenced by goals in ventral LPC (main effect of goal-
 615 relevance: $F_{1,16} = 0.61$, $p = 0.447$; Fig. 6C), nor did this effect vary across ventral LPC
 616 ROIs (goal-relevance x ROI interaction: $F_{2,32} = 0.16$, $p = 0.855$; Fig. 6E). In fact, both goal-
 617 relevant and goal-irrelevant information were significantly above chance in ventral LPC
 618 (goal-relevant: $t_{16} = 2.48$, $p = 0.025$; goal-irrelevant: $t_{16} = 2.64$, $p = 0.018$; Fig. 6C). The
 619 interaction between dorsal vs. ventral LPC and goal-relevance was driven primarily by a
 620 difference in the strength of goal-irrelevant feature information. Goal-irrelevant feature
 621 information was significantly stronger in ventral LPC than in dorsal LPC ($t_{16} = 3.15$, $p =$
 622 0.006 ; paired sample t -test), whereas the strength of goal-relevant feature information did
 623 not significantly differ across ventral and dorsal LPC ($t_{16} = -0.19$, $p = 0.850$). In Table 3 we
 624 assess the goal-relevant and goal-irrelevant feature information in individual ROIs (see
 625 also Fig. 6D). Collectively, these findings provide novel evidence for a functional distinction
 626 between memory representations in dorsal and ventral LPC, with top-down memory goals
 627 biasing feature representations toward relevant information in dorsal LPC, but not ventral

LPC. Because there was no evidence for preferential representation of goal-relevant feature information during memory retrieval in OTC ($F_{1,16} = 1.51$, $p = 0.237$; Fig. 6D), the bias observed in dorsal LPC was not inherited from earlier visual regions.

Discussion

Here, across two fMRI experiments, we showed that OTC and LPC were differentially biased to represent stimulus features during either perception or memory retrieval. In OTC, color and object feature information were stronger during perception than during memory retrieval, whereas in LPC, feature information was stronger during memory retrieval than during perception. Despite these biases, we observed that stimulus-specific patterns evoked in LPC during perception were reinstated during memory retrieval. Finally, in Experiment 2 we found that retrieval goals biased dorsal LPC representations toward relevant stimulus features in memory, whereas ventral LPC represented both relevant and irrelevant features regardless of the goal.

Transformation of representations from OTC to LPC

Traditionally, cortical memory reactivation has been studied in sensory regions. Empirical studies focusing on these regions have provided ample evidence for the hypothesis that memory retrieval elicits a weak copy of earlier perceptual activity (O'Craven and Kanwisher, 2000; Wheeler et al., 2000; Slotnick et al., 2005; Pearson et al., 2015). While this idea accounts for our results in OTC, it does not explain our results in LPC, where both stimulus-level information and feature-level information were stronger during memory retrieval than perception. What accounts for this reversal in LPC? Given that our memory task was likely more attentionally demanding than our perception task, one possibility is that LPC is less sensitive to the source of a stimulus (perception vs. memory) than to the amount of attention that a stimulus is afforded. While this would still point to an important dissociation between OTC and LPC, there are several reasons why we think that attentional demands do not fully explain the memory bias we observed in LPC, particularly in ventral LPC.

655 First, although top-down attention has been consistently associated with dorsal but not
 656 ventral LPC (Corbetta and Shulman, 2002), we observed a bias toward memory
 657 representations in both dorsal and ventral LPC. Moreover, in Experiment 2—where we
 658 specifically manipulated subjects' feature-based attention during memory retrieval—we
 659 found that feature information in ventral LPC was remarkably insensitive to task demands.
 660 In fact, irrelevant feature information was significantly represented in ventral LPC and did
 661 not differ in strength from relevant feature information. Second, there is evidence that
 662 univariate BOLD responses in ventral LPC are higher during successful memory retrieval
 663 than during perception (Daselaar, 2009; Kim et al., 2010), paralleling our pattern-based
 664 findings. Third, there is direct evidence that primate ventral LPC receives strong
 665 anatomical (Cavada and Goldman-Rakic, 1989; Clower et al., 2001) and functional
 666 (Vincent et al., 2006; Kahn et al., 2008) drive from the medial temporal lobe regions that
 667 are critical for recollection. Finally, recent evidence from rodents indicates that parietal
 668 cortex (though not necessarily a homologue of human ventral LPC) is biased towards
 669 memory-based representations (Akrami et al., 2018). Namely, neurons in rat posterior
 670 parietal cortex were shown to carry more information about sensory stimuli from prior trials
 671 than from the current trial. Strikingly, this bias toward memory-based information was
 672 observed even though information from prior trials was not task-relevant. Thus, there is
 673 strong converging evidence that at least some regions of LPC are intrinsically biased
 674 toward memory-based representations and that this bias cannot be explained in terms of
 675 attention. That said, we do not think attention and memory are unrelated. An alternative
 676 way of conceptualizing the present results with regards to attention is that perception and
 677 memory exist along an external vs. internal axis of attention (Chun and Johnson, 2011). By
 678 this account, LPC—and ventral LPC, in particular—is biased toward representing
 679 internally-generated information whereas OTC is biased toward representing external
 680 information (see also Honey, Newman, & Schapiro, 2017).

681 Another factor that potentially influenced our pattern of results is stimulus repetition.
 682 Namely, all stimuli and associations in our study were highly practiced and retrieval was
 683 relatively automatic by the time subjects entered the scanner. While the use of overtrained
 684 associations was intended to reduce the probability of failed retrieval trials, it is possible
 685 that repeated retrieval 'fast-tracked' memory consolidation (Antony et al., 2017), thereby

strengthening cortical representation of memories (Tompary and Davachi, 2017). While a rapid consolidation account does not directly predict that memory-based representations would be stronger in LPC than OTC, future work should aim to test whether the bias toward memory-based representations in LPC increases as memories are consolidated. To be clear, however, we do not think that overtraining is *necessary* to observe a memory bias in LPC, as several prior studies have found complementary results with limited stimulus exposure (Long, Lee, and Kuhl, 2016; Akrami et al., 2018).

More broadly, our findings demonstrate a situation where the idea of memory reactivation fails to capture the relationship between neural activity patterns evoked during perception and memory retrieval. Instead, our findings are consistent with a model of memory in which stimulus representations are at least partially transformed from sensory regions to higher-order regions including LPC (Xiao et al, 2017). Future experimental work will be necessary to establish how stimulus, task, and cognitive factors influence this transformation of information across regions.

Pattern reinstatement within regions

Consistent with prior studies, we observed stimulus-specific reinstatement of perceptual patterns during memory retrieval in LPC (Buchsbaum et al., 2012; Kuhl and Chun, 2014; Ester et al., 2015; Chen et al., 2016; Lee and Kuhl, 2016; Xiao et al., 2017) and VTC (Lee et al., 2012). Interestingly, we observed reinstatement in LPC and VTC despite the fact that these regions each had a bias toward either mnemonic (LPC) or perceptual (VTC) information. While these findings may seem contradictory, it is important to emphasize that the biases we observed were not absolute. Rather, there was significant feature information in OTC during memory retrieval, and though we did not observe significant feature information in LPC during perception, other studies have reported LPC representations of visual stimuli (Bracci et al., 2017; Lee et al., 2017). Thus, we think it is likely that the reinstatement effects that we and others have observed co-occur with a large but incomplete transfer of stimulus representation from OTC during perception to LPC during retrieval.

Notably, the stimulus reinstatement effects that we observed in LPC could not be explained by additive reinstatement of color and object information. Because we tested

716 subjects on lure images during the associative learning task, subjects were required to
 717 learn more than just color-object feature conjunctions in our experiments. Thus, LPC
 718 representations, like subjects' memories, likely reflected the conjunction of more than just
 719 color and object information. This proposal is consistent with theoretical arguments and
 720 empirical evidence suggesting that parietal cortex – and, in particular, angular gyrus –
 721 serves as a multimodal hub that integrates event features in memory (Shimamura, 2011;
 722 Wagner et al., 2015; Bonnici et al., 2016; Yazar et al., 2017). Given that ventral LPC is
 723 frequently implicated in semantic processing (Binder and Desai, 2011), stimulus-specific
 724 representations in ventral LPC may reflect a combination of perceptual and semantic
 725 information. In contrast, stimulus-specific representations in dorsal LPC and VTC, which
 726 are components of two major visual pathways, are more likely to reflect combinations of
 727 high-level but fundamentally perceptual features.

728 **Influence of retrieval goals on LPC representations**

729 Substantial evidence from electrophysiological (Toth and Assad, 2002; Freedman and
 730 Assad, 2006; Ibos and Freedman, 2014) and BOLD (Liu et al., 2011; Erez and Duncan,
 731 2015; Bracci et al., 2017; Vaziri-Pashkam and Xu, 2017; Long and Kuhl, 2018)
 732 measurements indicates that LPC representations of perceptual events are influenced by
 733 top-down goals. Our results provide novel evidence that, in dorsal LPC, specific features of
 734 a remembered stimulus are dynamically strengthened or weakened according to the
 735 current goal. This finding provides a critical bridge between perception-based studies that
 736 have emphasized the role of LPC in goal-modulated stimulus coding and memory-based
 737 studies that have found representations of remembered stimuli in LPC. Importantly,
 738 because we did not require subjects to behaviorally report any remembered feature
 739 information, the mnemonic representations we observed cannot be explained in terms of
 740 action planning (Andersen and Cui, 2009). The fact that we observed goal-modulated
 741 feature coding in dorsal, but not ventral, LPC is consistent with theoretical accounts
 742 arguing that dorsal LPC is more involved in top-down attention whereas ventral LPC is
 743 more involved in bottom-up attention (Corbetta and Shulman, 2002). Cabeza et al. (2008)
 744 has argued that LPC's role in memory can similarly be explained in terms of top-down and
 745 bottom-up attentional processes segregated across dorsal and ventral LPC. However,
 746 from this account, LPC is not thought to actively represent mnemonic content. Thus, while

our findings support the idea that dorsal and ventral LPC are differentially involved in top-down vs. bottom-up memory processes, they provide critical evidence that these processes involve active representation of stimulus features.

Interestingly, although we observed no difference between goal-relevant and goal-irrelevant feature information in ventral LPC, both were represented above chance. This is consistent with the idea that ventral LPC represents information received from the medial temporal lobe, perhaps functioning as an initial mnemonic buffer (Baddeley, 2000; Vilberg and Rugg, 2008; Kuhl and Chun, 2014; Sestieri et al., 2017). Ventral LPC representations may then be selectively gated according to current behavioral goals, with goal-relevant information propagating to dorsal LPC. This proposal is largely consistent with a recent theoretical argument made by Sestieri et al. (2017). However, it differs in the specific assignment of functions to LPC subregions. Whereas Sestieri et al. (2017) argue that dorsal LPC is contributing to goal-directed processing of perceptual information only, our results indicate that dorsal LPC also represents mnemonic information according to current goals. Given the paucity of experiments examining the influence of goals on mnemonic representations in LPC (c.f. Kuhl et al., 2013), additional work is needed. However, our findings provide important evidence, motivated by existing theoretical accounts, that retrieval goals differentially influence mnemonic feature representations across LPC subregions.

Conclusions

In summary, we showed that LPC not only actively represented features of remembered stimuli, but that these LPC feature representations were stronger during memory retrieval than perception. Moreover, whereas ventral LPC automatically represented remembered stimulus features irrespective of goals, dorsal LPC feature representations were flexibly and dynamically influenced to match top-down goals. Collectively, these findings provide novel insight into the functional significance of memory representations in LPC.

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902 Legends

903 **Figure 1.** Stimuli. In both experiments, stimuli were images of 32 common objects. Each
 904 object was a unique conjunction of one of four color features and one of eight object
 905 features. Color features were blue, green, red, and yellow. Object features were
 906 backpacks, cups, fish, flowers, hats, insects, shoes, fruit (Experiment 1 only), and birds
 907 (Experiment 2 only). See also Materials and Methods.

908 **Figure 2.** Experimental design and task structure. **A**, In both experiments, human subjects
 909 learned word-image paired associates prior to scanning. In the scanner, subjects viewed
 910 and recalled the image stimuli in alternate perception and memory runs. In Experiment 2,
 911 subjects performed two different goal-dependent memory tasks, during which they
 912 selectively recalled only the color feature or only the object feature of the associated
 913 image. **B**, Subjects learned 32 word-image pairs to a 100% criterion in the behavioral
 914 training session. During scanned perception trials, subjects were briefly presented with a
 915 stimulus. Subjects judged whether a small infrequent visual target was present or absent
 916 on the stimulus. During scanned memory trials, subjects were presented with a previously
 917 studied word cue, and recalled the associated stimulus (Experiment 1) or only the color or
 918 object feature of the associated stimulus (Experiment 2). After a brief recall period,
 919 subjects made a vividness judgment about the quality of their recollection (vivid, weak, no
 920 memory). See also Materials and Methods.

921 **Figure 3.** Regions of interest and pattern similarity analyses. **A**, Anatomical ROIs
 922 visualized on the Freesurfer average cortical surface. OTC ROIs included V1 and LO,
 923 defined using a group atlas of retinotopic regions (Wang et al., 2014), and VTC, defined
 924 using Freesurfer segmentation protocols. LPC ROIs included 5 ROIs that spanned dorsal
 925 and ventral LPC: pIPS, dLatIPS, vLatIPS, AnG, and vIPS. LPC ROIs were based on a
 926 group atlas of cortical regions estimated from spontaneous activity (Yeo et al., 2011). All
 927 ROIs were transformed to subjects' native anatomical surfaces and then into functional
 928 volume space prior to analysis. **B**, For each ROI, we estimated the multivoxel pattern of
 929 activity evoked by each stimulus during perception and memory. Patterns for stimuli that
 930 shared color or object features were compared. Analyses quantified feature information

931 within perception trials, within memory trials, and across perception and memory trials
 932 (reinstatement). See also Materials and Methods.

933 **Figure 4.** Stimulus-level and feature-level information during perception versus memory.
 934 **A**, The relative strength of perceptual vs. mnemonic stimulus information differed between
 935 OTC and LPC ($F_{1,32} = 113.6$, $p < 0.001$). Across both experiments, OTC contained
 936 stronger stimulus information during perception than during memory ($F_{1,32} = 28.0$, $p <$
 937 0.001), while LPC contained stronger stimulus information during memory than during
 938 perception ($F_{1,32} = 40.8$, $p < 0.001$). **B**, Across both experiments, the relative strength of
 939 perceptual vs. mnemonic feature information also differed between OTC and LPC ($F_{1,32} =$
 940 29.27 , $p < 0.001$). OTC contained marginally stronger feature information during
 941 perception than during memory ($F_{1,32} = 3.93$, $p = 0.056$), while LPC contained stronger
 942 feature information during memory than during perception ($F_{1,32} = 11.65$, $p = 0.002$).
 943 Legend is the same as in A. Bars in A and B represent mean \pm SEM across 17 subjects.
 944 **C**, Stimulus information during perception and memory plotted separately for each ROI,
 945 collapsed across experiment. **D**, Color and object feature information during perception
 946 and memory plotted separately for each ROI, collapsed across experiment. Points in C
 947 and D represent mean \pm SEM across 34 subjects. See Table 1 for results of *t*-tests
 948 assessing perceptual and mnemonic feature information for each ROI separately.

949 **Figure 5.** Feature and stimulus reinstatement effects. **A**, Feature and stimulus
 950 reinstatement plotted separately for OTC and LPC and for each experiment. Across both
 951 experiments, stimulus reinstatement reliably exceeded summed levels of color and object
 952 feature reinstatement in LPC ($F_{1,32} = 5.46$, $p = 0.026$). This effect was marginally greater
 953 than the effect observed in OTC ($F_{1,32} = 3.59$, $p = 0.067$), where stimulus reinstatement
 954 was well-accounted for by summed color and object feature reinstatement ($F_{1,32} = 0.35$, p
 955 $= 0.560$). Bars represent mean \pm SEM across 17 subjects. **B**, Color reinstatement, object
 956 reinstatement, and stimulus reinstatement plotted separately for each ROI, collapsed
 957 across experiment. Points represent mean \pm SEM across 34 subjects. See Table 2 for
 958 results of *t*-tests assessing feature and stimulus reinstatement for each ROI separately.

959 **Figure 6.** Feature information during memory retrieval as a function of goal-relevance. **A**,
 960 ROIs from Figure 3A grouped according to a dorsal/ventral division along the intraparietal

961 sulcus (see Materials and Methods). **B**, Color and object features were coded as either
 962 goal-relevant or goal-irrelevant according to the current retrieval goal. **C**, The effect of
 963 goal-relevance on mnemonic feature information differed significantly between dorsal and
 964 ventral LPC subregions ($F_{1,16} = 9.05$, $p = 0.008$). In dorsal LPC, goal-relevant feature
 965 information was stronger than goal-irrelevant feature information ($F_{1,16} = 5.30$, $p = 0.035$).
 966 In ventral LPC, there was no effect of goal-relevance on feature information ($F_{1,16} = 0.61$, p
 967 $= 0.447$), and both goal-relevant ($t_{16} = 2.48$, $p = 0.025$) and goal-irrelevant ($t_{16} = 2.64$, $p =$
 968 0.018) feature information were represented above chance. **D**, The difference between
 969 goal-relevant and goal-irrelevant feature information plotted separately for each ROI. **E**,
 970 Color and object feature information plotted separately for color and object memory tasks
 971 and for each dorsal and ventral LPC ROI. Bars and points represent mean \pm SEM across
 972 17 subjects. See Table 3 for results of t -tests assessing mnemonic feature information
 973 according to goal-relevance for each ROI separately.

974 **Table 1.** One sample t -tests comparing perceptual and mnemonic feature information to
 975 chance (zero) and paired t -tests comparing perceptual and mnemonic feature information
 976 for each feature dimension and ROI.

977 * = $p < 0.00625$ following multiple comparisons correction for 8 ROIs

978 **Table 2.** One sample t -tests comparing color and object feature reinstatement to chance
 979 (zero) and paired sample t -tests comparing stimulus reinstatement to summed feature
 980 reinstatement for each ROI.

981 * = $p < 0.00625$ following multiple comparisons correction for 8 ROIs

982 **Table 3.** One sample t -tests comparing goal-relevant and goal-irrelevant feature
 983 information during memory retrieval to chance (zero) and paired sample t -tests comparing
 984 goal-relevant to goal-irrelevant feature information for each ROI.

985 * = $p < 0.00625$ following multiple comparisons correction for 8 ROIs

986

987 **Tables**988 **Table 1.** Feature information during perception and memory in individual ROIs

ROI	Perception				Memory				Perception > Memory			
	Color		Object		Color		Object		Color		Object	
	t_{33}	p	t_{33}	p	t_{33}	p	t_{33}	p	t_{33}	p	t_{33}	p
V1	2.32	0.027	3.29	0.002*	2.55	0.015	1.18	0.246	0.42	0.677	1.66	0.106
LO	0.83	0.410	5.04	<0.001*	-0.41	0.687	3.58	0.001*	0.92	0.364	2.28	0.029
VTC	-0.97	0.338	5.00	<0.001*	0.87	0.390	2.54	0.016	-1.76	0.088	1.92	0.064
pIPS	-2.24	0.032	0.18	0.858	1.82	0.078	2.72	0.010	-3.05	0.005*	-1.99	0.054
dLatIPS	-2.81	0.008	0.18	0.855	0.64	0.528	2.39	0.023	-2.06	0.048	-1.52	0.139
vLatIPS	-1.81	0.080	0.66	0.513	1.76	0.087	3.15	0.003*	-2.69	0.011	-1.47	0.151
AnG	0.10	0.919	0.36	0.718	3.48	0.001*	3.48	0.001*	-2.87	0.007	-2.31	0.027
vIPS	0.31	0.761	2.82	0.008	2.18	0.036	3.48	0.001*	-1.55	0.130	-0.39	0.699

989

990

991 Table 2. Feature and stimulus reinstatement in individual ROIs

ROI	Color		Object		Stimulus > Color + Object	
	t_{33}	p	t_{33}	p	t_{33}	p
V1	0.56	0.582	1.16	0.253	0.42	0.674
LO	3.11	0.004*	2.27	0.030	-0.87	0.389
VTC	0.53	0.597	2.10	0.044	2.30	0.028
pIPS	1.29	0.207	0.60	0.556	2.47	0.019
dLatIPS	2.10	0.043	-0.64	0.524	1.61	0.118
vLatIPS	2.04	0.050	-0.59	0.560	1.92	0.063
AnG	1.94	0.062	0.75	0.461	0.65	0.519
vIPS	1.20	0.239	0.91	0.368	3.12	0.004*

992

993

994 Table 3. Feature information during memory by goal-relevance in individual ROIs

ROI	Relevant		Irrelevant		Relevant > Irrelevant	
	t_{16}	p	t_{16}	p	t_{16}	p
V1	-1.11	0.285	2.24	0.040	-2.10	0.052
LO	-0.28	0.780	0.53	0.602	-0.58	0.568
VTC	0.54	0.595	0.99	0.336	-0.31	0.759
pIPS	1.85	0.084	-0.06	0.953	1.79	0.092
dLatIPS	1.80	0.092	-0.76	0.458	2.38	0.030
vLatIPS	3.53	0.003*	1.87	0.081	0.87	0.397
AnG	2.23	0.040	3.39	0.004*	0.30	0.765
vIPS	1.33	0.204	1.06	0.304	0.54	0.600

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