Content tuning in the medial temporal lobe cortex: Voxels that perceive, retrieve

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Abstract

How do we recall vivid details from our past based only on sparse cues? Research suggests that the phenomenological reinstatement of past experiences is accompanied by neural reinstatement of the original percept. This process critically depends on the medial temporal lobe (MTL). Within the MTL, perirhinal cortex (PRC) and parahippocampal cortex (PHC) are thought to support encoding and recall of objects and scenes, respectively, with the hippocampus (HC) serving as a content-independent hub. If the fidelity of recall indeed arises from neural reinstatement of perceptual activity, then successful recall should preferentially draw upon those neural populations within content-sensitive MTL cortex that are tuned to the same content during perception. We tested this hypothesis by having eighteen human participants undergo functional magnetic resonance imaging (fMRI) while they encoded and recalled objects and scenes paired with words. Critically, recall was cued with the words only. While HC distinguished successful from unsuccessful recall of both objects and scenes, PRC and PHC were preferentially engaged during successful vs. unsuccessful object and scene recall, respectively. Importantly, within PRC and PHC, this content-sensitive recall was predicted by content tuning during perception: Across PRC voxels, we observed a positive relationship between object tuning during perception and successful object recall, while across PHC voxels, we observed a positive relationship between scene tuning during perception and successful scene recall. Our results thus highlight content-based roles of MTL cortical regions for episodic memory and reveal a direct mapping between content-specific tuning during perception and successful recall.

Significance Statement

Episodic memory, our ability to encode and later recall experiences, involves neural overlap between perceptual and recall activity. Research has shown that this phenomenon depends on the medial temporal lobe (MTL). Within MTL, perirhinal (PRC) and parahippocampal cortex (PHC) are engaged during encoding and recall of objects and scenes, respectively, linked by content-independent

49 hippocampus (HC). Here, we find that within MTL cortex, content tuning during perception predicts

50 successful recall of that content: We observe a positive relationship between object tuning and

51 object recall across PRC voxels, and between scene tuning and scene recall across PHC voxels. These

52 results highlight the role of stimulus content for understanding MTL, and demonstrate a clear

53 mapping between content tuning and content recall.

1 Introduction

One of the most intriguing features of the human brain is its ability to recall vivid episodes from long-term memory in response to sparse cues. For example, the word 'breakfast' may elicit recall of visual information including spatial (e.g. a bright kitchen) and object details (e.g. a croissant). This phenomenological reinstatement of past experiences is mirrored in cortical reinstatement – a neural reactivation of the original perceptual trace (Danker and Anderson, 2010). The medial temporal lobe (MTL) and its subregions play a key role in recall (Zola-Morgan and Squire, 1990; Eichenbaum et al., 2007). Anatomically, the MTL's input/output regions, perirhinal cortex (PRC) and parahippocampal cortex (PHC), have differentially weighted reciprocal connections to the ventral and dorsal visual stream, respectively (Suzuki and Amaral, 1994a; Lavenex and Amaral, 2000; van Strien et al., 2009). They are therefore well-suited to relay content-sensitive signals from sensory areas to the hippocampus (HC) during perception and encoding and vice versa during retrieval. Indeed, these parallel information streams converge in the HC, enabling it to support memory in a content-independent manner (Davachi, 2006; Eichenbaum et al., 2007; Danker and Anderson, 2010). In support of this view, human functional imaging studies have linked object-related vs. spatial processing to PRC vs. PHC for a range of tasks, including perception (Litman et al., 2009), context encoding (Awipi and Davachi, 2008; Staresina et al., 2011), reactivation after interrupted rehearsal (Schultz et al., 2012), and associative retrieval of object-scene pairs (Staresina et al., 2013b). Conversely, the HC, instead of representing perceptual content, is thought to store indices linking distributed cortical memory traces (Teyler and DiScenna, 1986; Teyler and Rudy, 2007), thereby well-suited to coordinate pattern completion from partial cues (Marr, 1971; Norman and O'Reilly, 2003; Staresina et al., 2012; Horner et al., 2015).

The reciprocity of MTL connectivity implies overlapping activity profiles between perception and retrieval in content-sensitive pathways, and is thought to underlie cortical reinstatement (Eichenbaum et al., 2007; Danker and Anderson, 2010). Indeed, there is evidence that neural activity

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79   that was present during the original encoding of a memory is reinstated during retrieval, as

80   demonstrated using univariate analyses of encoding-retrieval overlap (Nyberg et al., 2000; Wheeler

81   et al., 2000; Kahn et al., 2004), correlative encoding-retrieval similarity measures (Staresina et al.,

82   2012; Ritchey et al., 2013), and multivariate decoding approaches (Polyn et al., 2005; Johnson et al.,

83   2009; Mack and Preston, 2016; Liang and Preston, 2017). Moreover, cortical reinstatement scales

84   with the reported fidelity of recall (Kuhl et al., 2011; Kuhl and Chun, 2014). Content-sensitive

85   retrieval representations in higher-order visual cortex/MTL, as investigated here, may differ from

86   frontoparietal representations in that they may be closer to the perceptual trace (Favila et al., 2018).

87   The precise topographical mapping of content-sensitivity at perception to cortical reinstatement at

88   retrieval, however, is unclear. If cortical reinstatement reflects a restoration of a distinct neural state

89   during the original encoding experience, then successful recall of content should predominantly

90   draw on neural populations that distinguished the content from others during perception. That is,

91   the more content-tuned neural populations are during perception, the more diagnostic they should

92   be of successful recall of their preferred content.

93   Here, we investigated content-sensitivity of MTL subregions during episodic memory recall, and how

94   it maps to content tuning during perception. To this end, we had participants undergo fMRI while

95   they encoded and retrieved adjectives paired with an object or scene image. During retrieval, they

96   only saw the adjective cue and tried to recall the associated object or scene. If HC contributes to

97   recall in a content-independent fashion (as predicted by MTL connectivity), we would expect similar

98   involvement during cued recall of both objects and scenes. Conversely, since MTL anatomy predicts

99   content-sensitivity in PRC and PHC, we expect a preference for object recall in PRC and for scene

100 recall in PHC. Critically, within PRC, we expect a positive correlation such that voxels exhibiting

101 stronger object tuning during perception should be recruited more strongly for successful object

102 recall. In contrast within PHC, we expect a positive correlation such that voxels exhibiting stronger

103 scene tuning during perception should be recruited more strongly for successful scene recall.

2 Materials and Methods

2.1 Participants

A total of 34 volunteers (all right-handed, native English speakers, normal or corrected-to-normal vision) participated in the fMRI experiment. Sixteen participants were excluded from data analysis. Of those, one was excluded due to excessive movement, and one due to non-compliance. Fourteen datasets suffered data loss due to scanner malfunction. The results of the remaining n=18 participants (11 female; mean age 22.7 yrs, range 18-33 yrs) are reported here. We note that the final sample size is within range, albeit on the lower end, of recent fMRI studies investigating content specificity in MTL cortex (e.g. Liang & Preston, 2017: n=15; Mack & Preston, 2016: n=24; Reagh & Yassa, 2014: n=18, Staresina et al., 2012: n=20). All participants gave written informed consent in a manner approved by the local ethics committee, and were paid for their participation.

2.2 Stimuli and Procedure

Stimuli consisted of 60 images of objects and 60 images of scenes (Konkle et al., 2010a, 2010b) as well as 120 English adjectives (Staresina et al., 2011). An additional 5 objects, 5 scenes, and 10 adjectives were used for practice. Per stimulus subcategory (e.g. desk, garden, etc.), only one image was used. Adjective-image pairs were randomized for each participant.

During fMRI, participants viewed stimuli via projection to a mirror mounted on the head coil, and responded using an MR compatible button box. The fMRI task (Figure 1A) used a slow event-related design, consisting of four runs (two object runs, two scene runs). Object and scene runs were presented in an alternating order that was counterbalanced across participants. Each run included an encoding and a retrieval phase (30 trials each), as well as pre- and post-encoding resting phases (3 minutes each). In each trial of the encoding phase, participants saw an object or scene image (400 x 400 pixels) presented in the center of the screen together with an adjective. Participants were asked to press the left or right button on a right-hand button box if they thought the adjective and

128   image matched or did not match, respectively ("decide whether the adjective could be used to

129   describe the image"). Adjective-image pairs were presented for 5s, followed by 10s of an arrows task

130   (active baseline task) (Stark and Squire, 2001) during which participants indicated the direction of

131   left- or right-pointing arrows by pressing the left or right button. In the retrieval phase, the

132   adjectives from the encoding phase were presented again in randomized order. Adjectives were

133   presented for 5s, and participants were asked to press the left button if they successfully recalled

134   the associated image, and the right button if they did not. Each retrieval trial was again followed by

135   10s of the arrows task. Before and after encoding, participants additionally engaged in an odd-even

136   numbers task for 180s (offline resting phase), separated from the task phases by a transition screen

137   (10s each). In the odd-even task, participants were presented with random numbers between 1 and

138   99 and pressed the left button for even numbers and the right button for odd numbers. Altogether,

139   each run lasted 22 min.
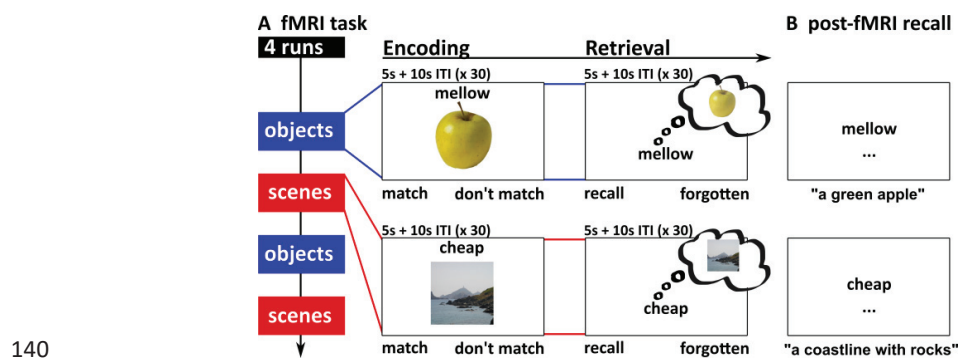
141   **Figure 1. Experimental paradigm. A**. The fMRI task consisted of two object and two scene runs, each

142   comprising an encoding and a retrieval phase. During encoding, participants saw adjective-object or adjective-

143   scene pairs. During retrieval, only the adjective was presented and participants tried to recall the associated

144   object or scene from memory. Not shown: Each fMRI trial was followed by 10s of an active baseline task (ITI,

145   arrows task), and the encoding phase was preceded and followed by a resting phase (odd-even numbers task,

146   180s) (see main text for details). **B**. In the post-fMRI recall task, participants typed in descriptions of the

147   associated object and scene for each adjective.

148 Since memory responses given during the fMRI task were subjective, two measures were taken to

149 ensure that the scanned retrieval portion accurately captured brain activity related to success vs.

150 failure to recall. First, prior to the fMRI task, participants were explicitly instructed only to press

151 'recall' if they could vividly recall details of the associated image and to press 'forgotten' otherwise.

152 Second, we additionally employed a post-fMRI recall task (Figure 1B) in order to obtain an objective

153 memory measure. Again, participants were presented with each adjective, in the same order as

154 during the fMRI retrieval phase. The task was to type a brief description of the associated image or a

155 '?' in case the target image was not recalled.

156 Critically, only trials with matching subjective and objective memory responses entered fMRI

157 analyses (i.e. subjective 'recall' response during the fMRI task plus successful recall in the post-test,

158 or subjective 'forgotten' response during the fMRI task plus unsuccessful recall in the post-test). This

159 resulted in the following conditions of interest: object-recalled (OR), object-forgotten (OF), scene-

160 recalled (SR), scene-forgotten (SF).

161 **2.3 fMRI acquisition**

162 Brain data were acquired using a GE Discovery MR750 3T system (GE Medical Systems) and a 32-

163 channel head coil. For the functional runs, we used a gradient-echo, echo-planar pulse sequence (48

164 slices, 2.5mm isotropic voxels, TR=1000ms, TE=30ms, ascending acquisition order, multiband factor

165 3, 1300 volumes per run). The slice stack was oriented in parallel to the longitudinal MTL axis and

166 covered nearly the whole brain (in some participants with larger brains, superior frontal cortex was

167 not covered). The first 10 images of each run were discarded prior to analysis to allow for

168 stabilization of the magnetic field. Additionally, a high-resolution whole-brain T1-weighted structural

169 image (1x1x1mm, TR=7.9ms, TE=3.06ms) was acquired for each participant.

170 **2.4 fMRI preprocessing and analysis**

171 *Regions of interest (ROI) strategy*. Considering the high anatomical variability of the MTL (Pruessner

172 et al., 2002), all analyses were carried out in unsmoothed, single-participant space within anatomical

173 ROIs of the MTL (HC, PRC, PHC). These were hand-drawn on each participant's T1 images using

174 existing guidelines (Insausti et al., 1998; Pruessner et al., 2000, 2002), and resampled to functional

175 space. To maximize object vs. scene sensitivity in the MTL cortex ROIs, considering gradual changes

176 in content sensitivity along the parahippocampal gyrus (Litman et al., 2009; Liang et al., 2013), the

177 posterior third of PRC and the anterior third of PHC were excluded from analysis (Staresina et al.,

178 2011, 2012, 2013b). Across participants, the average number of voxels per bilateral ROI, in functional

179 space and accounting for signal dropout, was 649.89 voxels (SEM: 15.07 voxels) for HC, 146.83

180 (11.68) for PRC, and 345.22 (10.92) for PHC. Signal dropout was defined through the implicit masking

181 procedure in the SPM first-level GLM estimation, using a liberal masking threshold of 0.2.

182 *Preprocessing*. All analyses were carried out using Matlab and SPM12. Functional images were first

183 corrected for differences in acquisition time (slice time correction), then corrected for head

184 movement and movement-related magnetic field distortions using the 'realign and unwarp'

185 algorithm implemented in SPM12. Structural images were then coregistered to the mean functional

186 image before being segmented into grey matter, white matter, and CSF. Deformation fields from the

187 segmentation procedure were used for MNI normalization (used for visualization only, see Figure 2A

188 – all analyses were done in native space).

189 *Univariate analyses*. For the first-level general linear model, all runs were concatenated and the

190 high-pass filter (128s) and autoregressive model AR(1) + w were adapted to account for run

191 concatenation. Regressors for our conditions of interest (OR, OF, SR, and SF for the encoding and

192 retrieval phase, respectively) were modeled using a canonical hemodynamic response function (HRF)

193 with a variable duration of each trial's RT, assuming that memory-related processing of the stimulus

194 is concluded at the time of the response. These regressors only included trials with matching

195 memory responses during the fMRI task and post-fMRI recall. Non-matching trials (e.g. 'recall'

196 response during the scan, but failed explicit recall during the post-scan) entered separate regressors

197 of no interest. Additionally, the first-level model included non-convolved nuisance regressors for

198   each volume of the transition and resting periods, and run constants. The resulting beta estimates

199   from the retrieval phase were averaged across each participant's ROIs before entering a group-level

200   repeated-measures ANOVA with the factors region, content, and recall success. In case of sphericity

201   violations, the degrees of freedom were adjusted using Greenhouse-Geisser correction.

202   *Perception-retrieval overlap (PRO)*. We asked whether, within each MTL cortex ROI (PRC, PHC),

203   successful recall of a particular content is predicted, across voxels, by content tuning during

204   perception. In that case, within PRC, there should be a positive correlation such that voxels that

205   show stronger tuning to objects compared to scenes during perception should also be more engaged

206   during successful compared to unsuccessful object recall. Similarly, within PHC, there should be a

207   positive correlation such that voxels that show stronger tuning to scenes compared to objects during

208   perception should be more engaged during successful compared to unsuccessful scene recall. This

209   should be reflected in an across-voxel correlation of the effect sizes of the respective perception and

210   recall contrasts, which we tested in the following way: We computed, for each participant, four *t*

211   contrast images: (i-ii) the between-content perception contrasts from the encoding phase (objects >

212   scenes [O > S], computed as (OR + OF) > (SR + SF), and scenes > objects (S > O), computed as (SR +

213   SF) > (OR + OF)), irrespective of subsequent memory outcome); (iii) the within-content recall

214   contrast for objects from the retrieval phase (OR > OF); (iv), the within-content recall contrast for

215   scenes from the retrieval phase (SR > SF). *T* values across voxels were then vectorized for each

216   participant and ROI. The perception-retrieval overlap for objects (PRO-O) was defined as the Pearson

217   correlation coefficient between the object perception contrast *t* values (O > S) and the object recall

218   contrast *t* values (OR > OF). Likewise, the perception-retrieval overlap for scenes (PRO-S) was

219   defined as the Pearson correlation coefficient between the scenes perception contrast (S > O) and

220   the scene recall contrast (SR > SF). Note that we only included voxels with positive values in the

221   perception contrast (O > S for PRO-O, S > O for PRO-S) in this analysis to ensure that correlations are

222   carried by voxels tuned to objects rather than scenes for PRO-O, and to scenes rather than objects

223   for PRO-S. To ensure that these correlations would capture local rather than cross-hemispheric

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224   topographical relationships, the correlation coefficients were computed in left and right ROIs

225   separately, then *Fisher z*-transformed and averaged. The resulting values were submitted to a two-

226   way repeated measures ANOVA with the factors region (PRC, PHC) and correlation type (PRO-O,

227   PRO-S), and followed up with two-sample and one-sample *t*-tests.

228   One possible concern is that PRO might be biased by temporal autocorrelations, which are greater

229   within a run than between runs. Note though that the task consists of four functional runs, with two

230   object- and two scene-only runs in alternating order. Each run contains an encoding and retrieval

231   phase. Thus, in PRO, we correlate a contrast containing data from all four runs (O vs. S from all

232   encoding phases) with contrasts containing data from only two runs (PRO-O: OR > OF; PRO-S: SR >

233   SF). Consequently, both PRO-O and PRO-S correlate a contrast spanning all four runs with a contrast

234   spanning two runs, making the overall temporal distance between contrasts equal. Moreover,

235   whereas any bias arising from temporal autocorrelation would have similar impact across brain

236   regions, we expect opposing patterns of PRO-O and PRO-S in PRC and PHC.

237   *Control analysis 1: Specificity*. In the above analysis, we correlate, across voxels of each ROI, the

238   object perception contrast with the object recall contrast for PRO-O, and the scene perception

239   contrast with the scene recall contrast for PRO-S. Importantly, we use only voxels with positive

240   values in the perception contrast, i.e. object-selective voxels for PRO-O and scene-selective voxels

241   for PRO-S. We expect positive values for PRO-O but not PRO-S in PRC, and for PRO-S but not PRO-O

242   in PHC. However, one might argue that such results lack specificity: The object perception contrast in

243   PRC may not only correlate with object recall (PRO-O), but also with scene recall. Similarly, the scene

244   perception contrast in PHC may not only correlate with scene recall (PRO-S), but also object recall.

245   This would indicate a non-specific relationship between perception and recall such that stronger

246   content tuning during perception would predict stronger recall effects for either content. To control

247   for this, we additionally computed the correlation between the object perception contrast (O > S,

248   positive voxels only) and the scene recall contrast (SR > SF) for PRC, and the correlation between the

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249   scene perception contrast (S > O, positive voxels only) and the object recall contrast (OR > OF) for

250   PHC.

251   *Control analysis 2: Signal-to-noise ratio*. Another possible concern might arise regarding the possible

252   impact of differences in signal-to-noise ratio across voxels. Since the analysis is based on *t* contrasts

253   between conditions, rather than estimates of activation in single conditions, we consider it unlikely

254   that SNR gradients across voxels bias these results. Nevertheless, we additionally computed PRO as

255   described above, but using partial Pearson correlations that included the temporal SNR of each voxel

256   as a control variable. Temporal SNR was computed as the mean value of the preprocessed,

257   unfiltered functional time series, divided by its standard deviation (separately per run, then

258   averaged across runs).

259   **3 Results**

260   **3.1 Behavioral results**

261   We queried successful recall of objects and scenes at two time-points: During the fMRI task,

262   participants merely responded 'recall' or 'forgotten' in response to each word cue (*subjective recall*).

263   During a post-scan explicit word-cued recall task, participants typed in descriptions of the associated

264   image, which were then scored by the authors (*objective recall*). Subjective responses during the

265   fMRI task did not significantly differ by content ($t_{(17)}$=0.685, *p*=.502), with nearly 50% 'recall' and

266   'forgotten' responses for both objects and scenes (mean [SEM] % subjective 'recall' responses:

267   objects: 51.2 [1.8], scenes 52.6 [2.6]). Likewise, objective recall rates during the post-test did not

268   significantly differ by content ($t_{(17)}$=0.043, *p*=.966, mean [SEM] % objective recall: objects: 38.2 [2.8],

269   scenes: 38.3 [3.1]). To test whether subjective 'recall' responses in the scanner were more likely to

270   be followed by objective recall during the post-test, we calculated the proportions of successful

271   objective recall separately for subjective 'recall' and 'forgotten' responses, and submitted these to a

272   two-way repeated measures ANOVA with the factors content (objects, scenes) and subjective

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273 response ('recall', 'forgotten'). This analysis yielded a significant effect of subjective response

274 ($F_{(1,17)}$=280.661, p<.001; no effect of content or interaction, ps≥.682); compared to subjective

275 'forgotten' responses, subjective 'recall' responses in the scanner were more likely to be followed by

276 objective recall during the post-test for both objects (mean [SEM] % objective recall: 67.1 [4.3] after

277 subjective 'recall' vs. 9.0 [1.6] after subjective 'forgotten') and scenes (66.5 [4.8] vs. 8.2 [2.2]). Note

278 that only trials with consistent subjective and objective memory responses entered fMRI analysis

279 (i.e. in the fMRI analysis, 'R' ('recalled') corresponds to a subjective 'recall' response during the fMRI

280 task as well as accurate objective recall during the post-test; 'F' ('forgotten') corresponds to a

281 subjective 'forgotten' response during the fMRI task as well as failed objective recall during the post-

282 test). A repeated-measures ANOVA on the numbers of trials that entered fMRI analysis with the

283 factors content (objects, scenes) and trial type (R, F) showed a significant effect of trial type

284 ($F_{(1,17)}$=6.473, p=.021), with more 'F' than 'R' trials (mean [SEM] number of trials: OR: 19.8 [1.5]. OF:

285 25.9 [1.3], SR: 20.1 [1.7], SF: 25.2 [1.6]; no effect of content or interaction, ps≥.668). All participants

286 in the final sample contributed at least 8 trials per regressor of interest (OR, OF, SR, SF).

287 **3.2 Content-independent vs. content-sensitive retrieval processing in MTL**

288 **subregions**

289 Univariate analyses were carried out within bilateral single-participant ROIs of HC, PRC, and PHC

290 (Figure 2A). To characterize each MTL ROI with regard to its overall content-independent or content-

291 sensitive response profile during retrieval, single-participant beta values for the regressors of

292 interest (OR, OF, SR, SF) from the retrieval phase were averaged across all voxels for each

293 individual's ROI. ROI averages were then submitted to a repeated-measures three-way ANOVA with

294 the factors region (HC, PRC, PHC), content (objects, scenes), and recall success (recalled, forgotten).

295 This yielded a significant three-way interaction of region, content, and recall success

296 ($F_{(1.46,24.80)}$=10.014, p=.002), as well as significant two-way interactions of region with content

297 ($F_{(1.42,24.10)}$=13.544, p<.001) and region with recall success ($F_{(1.81,30.79)}$=6.305, p=.006).

298   Subsequent analyses were carried out separately for each ROI, using two-way repeated-measures

299   ANOVAs (including the factors content and recall success; Figure 2B-D). We expected content-

300   independent recall in the HC, reflected in a main effect of successful recall. Conversely, we expected

301   content-sensitive recall in the PRC and PHC, reflected in interaction effects of content and recall,

302   with a preference for object recall in the PRC and scene recall in the PHC.
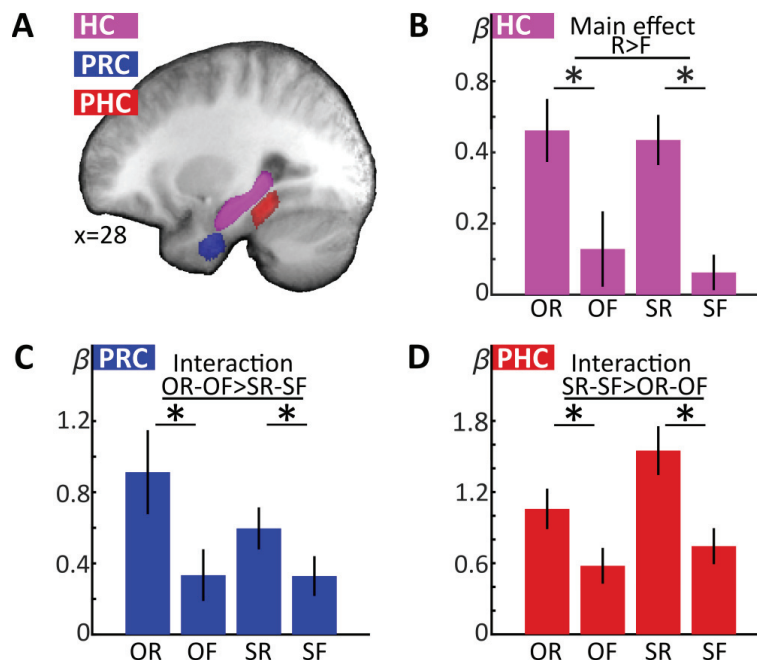
304   **Figure 2. MTL ROIs and univariate retrieval results**. **A**. To illustrate ROI localization, manually delineated ROIs

305   for each participant's HC, PRC, and PHC were MNI-normalized, averaged across participants and projected on

306   the mean normalized T1 (averaged ROI threshold > 0.5). **B-D**. Retrieval-phase beta values were averaged

307   within each participant's individual ROIs and submitted to group analyses. HC (**B**) showed a main effect of

308   successful recall, while PRC (**C**) and PHC (**D**) additionally showed interaction effects, indicating preference for

309   object recall (PRC) and scene recall (PHC), respectively. O: object, S: scene, R: recalled, F: forgotten. Error bars

310   denote SEM. *p<.05 (two-tailed) for pairwise t-tests.

311 HC showed a significant main effect of successful recall ($F_{(1,17)}$=24.509, p<.001), but no effect of

312 content nor a recall success x content interaction (p≥.496). By contrast, PRC showed a significant

313 main effect of successful recall ($F_{(1,17)}$=18.137, p=.001), as well as a recall x content interaction

314 ($F_{(1,17)}$=4.579, p=.047) due to a stronger recall effect for objects relative to scenes. There was no main

315 effect of content in PRC (p=.173). Finally, PHC showed a significant main effect of content

316 ($F_{(1,17)}$=16.804, p=.001), recall success ($F_{(1,17)}$=27.329, p<.001), and a significant recall success x

317 content interaction ($F_{(1,17)}$=7.723, p=.013) due to a stronger recall effect for scenes relative to

318 objects. To further characterize each ROI's response profile, we computed post-hoc paired t-tests to

319 assess object recall effects (OR vs. OF) and scene recall effects (SR vs. SF) in each ROI. All single

320 comparisons were significant ($ts_{(17)}$≥2.667, ps≤.016). Critically, however, as indicated by the above

321 interaction effects, the object recall effect was greater than the scene recall effect in PRC, and vice

322 versa in PHC. Taken together, the ROI results show content-independent recall-related activity in HC

323 versus a preference for object recall activity in PRC and for scene recall activity in PHC.

324 **3.3 Perception-retrieval overlap (PRO)**

325 The preceding analysis established a preference for object recall in PRC and a preference for scene

326 recall in PHC. Next, we assessed whether successful recall in these ROIs preferentially recruited

327 voxels that were also diagnostic of object vs. scene perception during encoding. Note that this

328 approach goes beyond a simple overlap of contrasts (as in a conjunction analysis): Rather than

329 asking whether two contrasts exceed threshold in the same voxels, we ask whether there is a

330 positive relationship between two contrasts such that voxels with a greater effect size in one

331 contrast tend to show a greater effect size in the other (see Figure 3A for illustrative participant-level

332 data). To this end, for each participant and ROI, we computed PRO-O (the correlation between the

333 object perception contrast [O > S] from the encoding phase and the object recall contrast [OR > OF]

334 from the retrieval phase), and PRO-S (the correlation between the scene perception contrast [S > O]

335 from the encoding phase and the scene recall contrast [SR > SF] from the retrieval phase; see

336   Methods for details). Note that PRO-O and PRO-S only included voxels tuned to either objects or

337   scenes, as only voxels with positive values in the perception contrasts entered the correlation. We

338   expected that PRC would show evidence for PRO-O: Voxels that are more tuned to objects over

339   scenes during perception would be preferentially recruited during successful compared to

340   unsuccessful object recall. In PHC, we expected evidence for PRO-S: Voxels that are more tuned to

341   scenes over objects during perception would be preferentially recruited during successful compared

342   to unsuccessful scene recall. We did not expect evidence for PRO-S in PRC or evidence for PRO-O in

343   PHC.

344   Before assessing the correlation between perception and retrieval contrasts, we confirmed PRC and

345   PHC showed overall content tuning during perception. First, we tested whether the perception

346   contrast yielded significant differences between objects and scenes when averaged across all voxels

347   of each ROI. Second, we tested whether a majority of voxels in each ROI would show content tuning.

348   Averaged across voxels, activation during object perception differed significantly from scene

349   perception for both PRC (objects > scenes, t_{17}=7.367, p<.001) and PHC (scenes > objects, t_{17}=7.640,

350   p<.001). As expected, HC showed no significant content tuning (t_{17}=1.470, p=.160, numerically

351   scenes > objects). Furthermore, the majority of PRC voxels showed object tuning, i.e. positive values

352   in the O > S perception contrast (mean proportion: 63.70% [SEM: 1.60%]; one-sample t-test against

353   50%: t_{17}=8.59, p<.001), whereas the majority of PHC voxels showed scene tuning, i.e. positive values

354   in the S > O perception contrast (69.93% [2.04%], t_{17}=9.78, p<.001). In the HC, the numerical majority

355   of voxels were positive in the S > O contrast (S>O: 51.20% [1.16%]; t_{17}=1.03, p=.315).

356   Results from the PRO analysis are summarized in Figure 3B. First, to confirm differences between

357   PRC and PHC, we submitted the Fisher z-transformed correlation coefficients to a two-way repeated-

358   measures ANOVA with the factors region (PRC, PHC) and content (PRO-O, PRO-S). This confirmed a

359   significant interaction between region and content ($F_{1,17}$=21.866, p<.001).

16

In PRC, correlation coefficients between the object perception contrast at encoding and the object recall contrast were significantly above zero (PRO-O, $t_{17}=4.910$, $p<.001$), while correlation coefficients between the scene perception contrast at encoding and the scene recall contrast were not (PRO-S, $t_{17}=0.500$, $p=.623$). Furthermore, PRO-O trended to be greater than PRO-S ($t_{17}=2.073$, $p=.054$). In contrast, in PHC, correlation coefficients between the scene perception contrast at encoding and the scene recall contrast were significantly above zero (PRO-S, $t_{17}=6.832$, $p<.001$), while correlation coefficients between the object perception contrast at encoding and the object recall contrast were not (PRO-O, $t_{17}=0.008$, $p=.994$). PRO-S was significantly greater than PRO-O ($t_{17}=5.124$, $p<.001$).
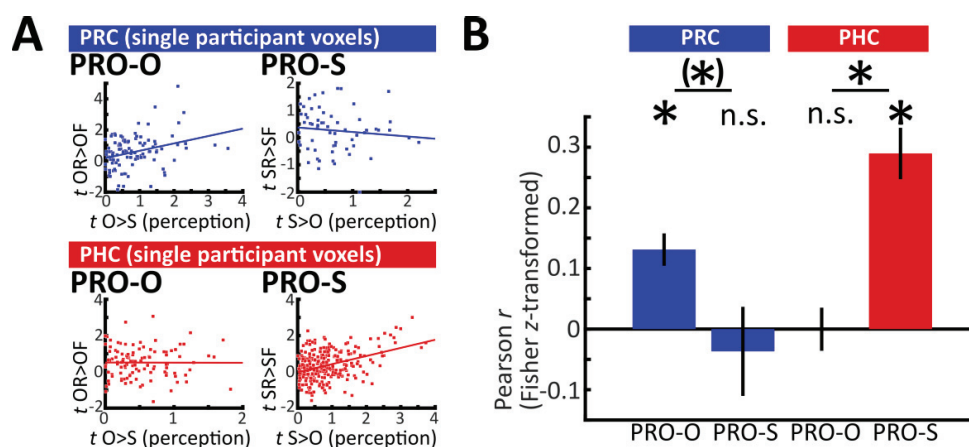
Figure 3. Perception-retrieval overlap (PRO). A. Illustrative data from two single participants' ROIs. *T* values from the objects > scenes perception contrast (x axes, positive voxels only) are plotted against *t* values from the object recall contrast (PRO-O, left column), while *t* values from the scenes > objects perception contrast (positive voxels only) are plotted against the scene recall contrast (PRO-S, right column). Data points indicate single voxels. In these example data, PRC voxels with greater effect sizes for object perception tended to show greater effect sizes for successful object recall (upper left scatterplot). Similarly, PHC voxels with greater effect sizes for scene perception tended to show greater effect sizes for successful scene recall (lower right scatterplot). Note that these within-participant scatterplots are for visualization only. **B**. Group averages of *Fisher z*-transformed correlation coefficients for PRO-O and PRO-S for PRC and PHC. Across PRC voxels, object

379   tuning predicted object recall (PRO-O), but scene tuning did not predict scene recall (PRO-S). Across PHC

380   voxels, scene tuning predicted scene recall, but object tuning did not predict object recall. * $p<.05$, (*) p<.1

381   (two-tailed) for one-sample and paired t-tests, n.s.: not significant. Error bars denote SEM.

382   To test whether these findings are restricted to MTL cortical regions, we repeated the above analysis

383   in HC. PRO-S, but not PRO-O, differed significantly from 0 (mean [SEM] PRO-O: 0.017 [0.030], $t_{17}=$

384   0.565, $p=.580$, PRO-S: 0.059 [0.025], $t_{17}=2.330$, $p=.032$). Furthermore, PRO-O and PRO-S did not

385   differ from each other ($t_{17}=0.823$, $p=.422$).

386   Our findings of PRO-O in PRC and PRO-S in PHC show that content tuning during perception in these

387   ROIs predicts successful recall of that same content. To test the specificity of these findings, we

388   repeated the analysis, this time testing whether content tuning would additionally predict recall of

389   the non-preferred content. This would imply a non-specific relationship between content tuning

390   during perception and recall. Hence, in PRC, we correlated the object perception contrast (O > S,

391   positive voxels only) with the scene recall contrast. Correlation coefficients did not differ significantly

392   from 0 (mean [SEM]: 0.031 [0.031], $t_{17}=1.011$, $p=.323$), and were significantly smaller than PRO-O

393   ($t_{17}=3.536$, $p=.003$). In PHC, we correlated the scene perception contrast (S > O, positive voxels only)

394   with the object recall contrast. Correlation coefficients were significantly greater than 0 (mean

395   [SEM]: 0.120 [0.043], $t_{17}=2.789$, $p=.013$). Importantly, they were also significantly smaller than PRO-S

396   ($t_{17}=5.007$, $p<.001$). In sum, across PRC voxels, object tuning during perception predicted object

397   recall (PRO-O) but not scene recall, and there was no relationship between scene tuning and scene

398   recall. In contrast, across PHC voxels, scene tuning during perception predicted scene recall (PRO-S)

399   to a greater extent than object recall, and there was no relationship between object tuning and

400   object recall.

401   As a second control analysis, we computed PRO-O and PRO-S for PRC and PHC using partial Pearson

402   correlations with each voxel's temporal SNR as a control variable (see Methods). The statistical

403 pattern was nearly identical for both the ANOVA and follow-up *t* tests, with the exception of the

404 paired *t* test between PRO-O and PRO-S in PRC, which was now significant (t_{17}=2.486, *p*=.024).

3.4 Multiple comparisons correction

406 Throughout our univariate (3.2) and PRO analyses (3.3), a number of paired and one-sample t-tests

407 were used to further characterize the result patterns. Applying Holm-Bonferroni correction to all

408 groups of *t*-tests in our main analyses, the following results emerge: For the univariate analysis, all

409 paired *t*-tests remain significant (n=6 tests [OR vs. OF and SR vs. SF in all three ROIs], see Figure 2 B-D

410 and Results 3.2). For PRO, the significance pattern of the one-sample *t*-tests against 0 remains

411 identical (n=4 tests [PRO-S and PRO-O in PRC and PHC], Figure 3B and Results 3.3). Similarly, for PRO,

412 the significance pattern of the paired *t*-tests remains identical (n=2 tests [PRO-O vs. PRO-S in PRC

413 and PHC], Figure 3B and Text 3.3), with a significant difference between PRO-O and PRO-S in PHC,

414 and a trend difference in PRC.

4 Discussion

416 Investigating cued recall of objects and scenes in the human MTL, we observed a triple dissociation

417 across MTL subregions: While HC was engaged during successful recall of both content types, PRC

418 preferentially tracked successful object recall and PHC preferentially tracked successful scene recall.

419 Moreover, we demonstrate an across-voxel mapping of content-sensitive recall effects in PRC and

420 PHC to content-tuning during the preceding encoding phase, suggesting that successful recall tends

421 to draw on the same voxels that represent percepts with high specificity.

422 Before proceeding with the discussion, some notes on terminology: We refer to the object vs. scene

423 contrasts as "tuning" responses to emphasize the fact that PRO is based on differential responses

424 (one category over the other). As our stimuli are categorical, we do not mean this to imply that these

425 voxels respond in a graded fashion to a more or less optimal value of a continuous variable (e.g.)

426 (Priebe, 2016). Furthermore, our results are agnostic to the debate whether MTL processing

427   contributes to perception, or whether it necessarily serves a mnemonic function (Bussey and

428   Saksida, 2007; Baxter, 2009; Suzuki, 2009, 2010; Graham et al., 2010; Squire and Wixted, 2011). We

429   refer to the observed content tuning in the MTL cortex as perception as it results from sensory

430   processing of objects and scenes, but we note that it may ultimately serve to encode

431   representations into memory. In fact, as our perceptual contrast comes from the encoding phase of

432   the experiment (albeit averaging successful and unsuccessful memory encoding), it may contain

433   domain-specific encoding activity (Staresina et al., 2011) in addition to perceptual activity. In future

434   work, an objects/scenes contrast from an independent localizer may reduce the amount of

435   concurrent encoding activity, however it does not resolve the aforementioned question whether

436   MTL processing can be purely perceptual.

437   The present study provides strong evidence for an MTL memory model emphasizing an interplay of

438   both content-sensitive and -independent modules: According to this view, PRC and PHC show

439   differential involvement in object and scene processing, respectively, based on their anatomical

440   connectivity profiles with the ventral and dorsal visual streams. HC links both circuits through direct

441   and indirect (via entorhinal cortex) connections to PRC and PHC, implying a content-independent

442   role of HC in memory (Suzuki and Amaral, 1994a, 1994b; Lavenex and Amaral, 2000; Davachi, 2006;

443   Eichenbaum et al., 2007; van Strien et al., 2009; Wixted and Squire, 2011; Ranganath and Ritchey,

444   2012). Our findings of content-independent recall effects in HC, accompanied by preferential object

445   recall in PRC and preferential scene recall in PHC, are in line with this view. Importantly, these

446   connections are bidirectional (Suzuki and Amaral, 1994a, 1994b; Lavenex and Amaral, 2000;

447   Eichenbaum et al., 2007), enabling information transfer from visual cortex via PRC/PHC to HC during

448   perception and encoding, and vice versa during retrieval (Staresina et al., 2013b). This parallelism of

449   MTL connectivity may underlie the phenomenon of cortical reinstatement - the reactivation of the

450   same sensory cortical regions during recall that were already active during perception (Eichenbaum

451   et al., 2007; Danker and Anderson, 2010). Our findings extend this concept: Even within content-

452   sensitive cortical regions, voxels that are particularly tuned to one content type over the other

453   during perception tend to be differentially reactivated when that content is successfully recalled.

454   Importantly, such cortical reinstatement may underlie the psychological phenomenon of 're-living'

455   episodic memories during vivid recall (Eichenbaum et al., 2007; Danker and Anderson, 2010; Kuhl et

456   al., 2011; Kuhl and Chun, 2014).

457   Our results constitute an important update to an existing body of work investigating content-

458   sensitive recall. Previous studies have investigated cortical reinstatement by comparing cued

459   retrieval of object-related and spatial information. However, most did not focus on differences

460   between MTL cortices (Khader et al., 2005, 2007; Kuhl et al., 2011; Gordon et al., 2014; Kuhl and

461   Chun, 2014; Morcom, 2014; Skinner et al., 2014; Bowen and Kensinger, 2017; Lee et al., 2018).

462   Those that did demonstrate that recall success is accompanied by domain-specific activity in MTL,

463   largely in line with our present findings. Staresina et al. (2012) showed that PHC reinstates scene

464   information, while PRC reinstates low-level visual information (color) during successful, but not

465   unsuccessful recall. Similarly, Staresina et al. (2013b) demonstrated content-sensitive recall

466   responses in PHC and PRC during successful, but not unsuccessful retrieval of object-scene

467   associations, driven by content-independent HC signals. One study presented evidence that, during

468   object-cued recall of famous faces and places, PRC and PHC reinstate perceptual activity from an

469   independent localizer task in a category-specific manner, with face reinstatement in PRC, and place

470   reinstatement in PHC (Mack and Preston, 2016). While that study only included correct memory

471   trials, making it difficult to directly link the observed category reinstatement in PRC and PHC to

472   successful vs. unsuccessful recall, the authors could demonstrate that item-specific reinstatement in

473   PRC and HC (not PHC) predicted variations in subsequent response times for correct responses to a

474   memory probe. Finally, one study showed a dissociation between PRC vs. PHC for the reinstatement

475   of an imagery task (person vs. place/object) during successful but not unsuccessful source memory,

476   but that study did not involve perceptual processing during the imagery task (Liang and Preston,

477   2017). Importantly, the present study is the first to demonstrate a clear double dissociation between

478   PRC and PHC during successful vs. unsuccessful object and scene recall triggered by a content-

479   neutral cue, and to tie it to perceptual content tuning in a direct, voxel-wise manner.

480   Importantly, we observed preferential, but not exclusive, processing of objects and scenes in PRC

481   and PHC, respectively. Both regions also show significant recall effects for their less-preferred

482   content. Furthermore, in PHC, voxels that were tuned to scenes over objects during perception were

483   also more active during successful object recall, albeit significantly less so than during scene recall.

484   Previous studies have shown such overlap in content sensitivity in the MTL, with some object

485   processing in PHC and some scene processing in PRC (Buffalo et al., 2006; Preston et al., 2010;

486   Hannula et al., 2013; Liang et al., 2013; Martin et al., 2013; Staresina et al., 2013b; Martin et al.,

487   2018). In particular, content sensitivity in the MTL cortex may not be abruptly demarcated, but

488   follow a gradient (Litman et al., 2009; Liang et al., 2013). We sought to minimize this overlap by

489   restricting analyses to the anterior two thirds of PRC and posterior two thirds of PHC, excluding the

490   transition zone of the parahippocampal gyrus (Staresina et al., 2011, 2012, 2013b). Nevertheless,

491   these two MTL subregions are not anatomically segregated, but show considerable interconnections

492   (Suzuki and Amaral, 1994a; Lavenex and Amaral, 2000), facilitating cooperation. Furthermore,

493   naturalistic scene images typically contain discernible objects, and many objects have a

494   spatial/configurational component. A cardboard box, for example, may have the same general shape

495   as a building, which has been shown to engage PHC (Epstein and Kanwisher, 1998). Similarly, object

496   size modulates PHC activity (Cate et al., 2011; Konkle and Oliva, 2012). Thus, the significant (albeit

497   weaker) responses of PRC and PHC during recall of their less-preferred content could stem from

498   functional overlap in objects and scene processing, or from ambiguity in the stimuli themselves.

499   Future studies could elucidate this ambiguity by controlling object and spatial features in these

500   stimuli, albeit perhaps at the expense of decreasing natural validity.

501   It is important to note that our perception-retrieval overlap (PRO) differs from existing approaches

502   that test for pattern similarity between encoding and retrieval (pattern reinstatement). For instance,

503   'encoding-retrieval similarity' (ERS) has shown that, relative to forgotten trials, successfully

504   remembered trials are more similar to their respective encoding trials (Staresina et al., 2012; Ritchey

505   et al., 2013). Similarly, in multivariate pattern analysis (MVPA), a classifier may be trained on

506   encoding trials to distinguish between voxel patterns associated with different content or tasks, and

507   then tested on retrieval trials (e.g. Polyn et al., 2005; Johnson et al., 2009; Mack and Preston, 2016;

508   Liang and Preston, 2017). PRO, on the other hand, relies on across-voxel correlations of contrasts,

509   rather than single conditions or trials. Hence, voxels with low values in the perception contrast may

510   still be highly activated relative to baseline. Previously, Haxby and colleagues used contrast

511   correlations (Haxby et al., 2001) to demonstrate that content tuning during perception is stable

512   between runs. Here, we test contrast correlations between tasks; specifically, whether content

513   tuning – i.e. the difference between object and scene responses – can predict activity associated

514   with successful recall of objects (PRO-O) and scenes (PRO-S) across voxels. It is important to note

515   that, unlike ERS and MVPA, PRO does not reflect pattern reinstatement in the strictest sense, as all

516   correlations contain a contrast between both content types, whereas reinstatement assumes the

517   reactivation of only one content type. Thus, PRO could be considered a more constrained form of a

518   conjunction, or inclusive masking, analysis. These methods test whether two or more contrasts

519   exceed some threshold in the same voxels - implying topographical overlap of the constituting

520   contrasts, but, critically, not a positive correlation across voxels. While our results likely reflect an

521   influence of cortical reinstatement, they illuminate a distinct aspect of it compared to pattern

522   similarity in the sense of ERS and MVPA: The latter methods demonstrate that distributed patterns

523   of activity associated with a certain content are reinstated during recall, while our results link

524   content-sensitive recall effects to voxels that are highly tuned to that content over another. A similar

525   link has been demonstrated between content tuning and recognition memory for PRC activity

526   (Martin et al., 2016): In that study, distributed voxel patterns in PRC that were diagnostic of face

527   recognition also showed face-sensitive perceptual tuning. However, that study did not establish a

528   positive across-voxel relationship between the magnitudes of the two effects.

529 Content-sensitive recall effects have been demonstrated in (not predominantly perceptual) brain

530 regions outside MTL (e.g.) (Kahn et al., 2004; Johnson et al., 2009; Kuhl et al., 2013; Ritchey et al.,

531 2013; Kuhl and Chun, 2014; Long et al., 2016; Xiao et al., 2017; Favila et al., 2018). What

532 distinguishes these representations from those observed in MTL? Recent findings indicate that

533 frontoparietal reinstatement effects may not only be stronger (Long et al., 2016), but represent a

534 transformed version of the original trace (Xiao et al., 2017) that is less perceptual in nature (Favila et

535 al., 2018) and more modulated by retrieval goals (Kuhl et al., 2013). In contrast, reinstatement in

536 ventral/medial temporal lobe has been shown to be more incidental in nature (Kuhl et al., 2013).

537 These findings underline that multiple systems are involved during successful recall, and while

538 perception-retrieval overlap appears to be an important pillar of recollection, not all content-

539 sensitive recall effects involve reinstatement of the exact perceptual trace.

540 Links can also be drawn between our PRO findings to other forms of memory, such as recognition

541 memory and repetition suppression. In these studies, the stimuli themselves, rather than associative

542 cues, are presented during retrieval, leading to concurrent perceptual and retrieval processes.

543 Litman et al. (Litman et al., 2009) showed similar gradients along the anterior-posterior MTL cortex

544 axis (i) for processing of novel objects and scenes, and (ii) for repetition suppression effects for

545 objects and scenes (although there appears to be some overlap between object and scene repetition

546 suppression effects, Berron et al., 2016). Prince et al. (Prince et al., 2009) demonstrated differential

547 effects of successful face and place recognition within clusters that responded preferentially to faces

548 and places in general. Finally, Martin et al. (2016) demonstrated a link between face recognition and

549 face tuning in PRC voxels.

550 Taken together, our results support an MTL model of episodic memory based on anatomical

551 connectivity and demonstrate a direct topographical mapping between content-sensitive perception

552 and recall in the MTL cortex. One remaining question is how mnemonic content is conveyed and

553 transformed from content-sensitive MTL cortex to content-independent HC. Much of the

554   information exchange between PRC/PHC and HC is relayed via the entorhinal cortex and its

555   anterolateral and posteriormedial subregions (Suzuki and Amaral, 1994b; Maass et al., 2015;

556   Navarro Schröder et al., 2015), which have similarly been shown to support content-sensitive

557   processing (Schultz et al., 2012; Reagh and Yassa, 2014; Navarro Schröder et al., 2015; Berron et al.,

558   2018), albeit potentially in a more integrated fashion (Schultz et al., 2015). How entorhinal retrieval

559   processing relates to content tuning is unclear, though there is evidence for reinstatement of

560   encoding representations in the entorhinal cortex (Staresina et al., 2013a). Future research may

561   investigate the relationship between encoding and retrieval in the entorhinal cortex by making use

562   of advanced high-resolution and ultra-high field approaches, thereby enhancing our understanding

563   of the human MTL in its entirety.

564

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