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Concurrent representations of reinstated and transformed memories and their modulation by reward

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24 **Abstract**

25 An integral part of episodic retrieval is the reinstatement of neural activity that was present in the
26 medial temporal lobe during encoding. However, neural memory representations do not remain static.
27 Consolidation promotes the transformation of representations that are specific to individual episodes
28 towards more generalized representations that reflect commonalities across episodes. Moreover,
29 reward has been shown to augment episodic memory by enhancing consolidation, and it may accelerate
30 the transformation of neural memory representations. We investigated this account with n=40 human
31 participants using fMRI and an associative memory task. They encoded pictures of objects, each with
32 one of four recurring scenes. Two scenes led to high reward, two led to low reward. The next day,
33 participants encountered the objects again and retrieved the scenes from memory. Using
34 representational similarity analysis, we demonstrate that retrieval is concurrently accompanied by the
35 reinstatement of original neural representations and the activation of transformed, more generalized
36 memories. Specifically, the parahippocampal cortex reinstates scene-specific patterns from the
37 encoding phase during successful retrieval. In contrast, activity patterns in the medial prefrontal cortex
38 and anterior hippocampus reflect transformed memories: They become more similar to each other for
39 memories sharing the same scene, independent of memory success. Importantly, high reward enhances
40 memory transformation in the anterior hippocampus. The brain thus maintains complementary memory
41 representations: An episodic representation that resembles the original encoding pattern, and a
42 generalized representation that summarizes commonalities across memories - in part for particularly
43 valuable information.

44 *Keywords:* reinstatement, memory transformation, memory generalization, medial prefrontal cortex,
45 medial temporal lobe

46 **Introduction**

47 The human ability to retain memories is remarkable: Seemingly effortlessly, we can recall the
48 picnic we had yesterday in rich detail. At the same time, we also know how picnics generally work,
49 allowing us to easily plan for an upcoming event that may take place on the next weekend. This is
50 because, over time, the commonalities across similar episodes are extracted and the memories are thus
51 transformed into more generalized knowledge. Such knowledge can take the form of, for example,
52 mental schemas, scripts, or categories (Ghosh & Gilboa, 2014; Gilboa & Marlatte, 2017).

53 Distinct forms of memories are reflected in distinct neural patterns. On the one hand, episodic
54 recall is accompanied by reinstatement of the original encoding activity. This has especially been shown
55 in content-sensitive regions of the medial temporal lobe (MTL), including the parahippocampal cortex
56 (PHC) (Schultz et al., 2019; Schultz, Sommer, et al., 2022; Staresina et al., 2012) and the (posterior)
57 hippocampus (HC) (Bone & Buchsbaum, 2021).

58 On the other hand, neural patterns associated with generalized memories do not reflect the
59 encoding activity of any individual episode. Over time, memories that share common features undergo a
60 transformation so that their neural representations become more similar. This has been shown in the
61 medial prefrontal cortex (mPFC) and HC (Audrain & McAndrews, 2022; Tomparly & Davachi, 2017).

62 The mPFC may thus represent transformed memories in the form of generalized knowledge
63 structures (Ghosh & Gilboa, 2014; Gilboa & Marlatte, 2017; Milivojevic et al., 2015; Paulus et al., 2021),
64 whereas the hippocampus may contain both types of memory representations. Notably, there is some
65 evidence for a functional specialization within the hippocampus – with more general memories, such as
66 an episode’s gist, being supported by the anterior HC, and more detailed episodic memories being more
67 reliant on the posterior HC (Collin et al., 2015; Gilboa & Moscovitch, 2021; Guo & Yang, 2020; Poppenk
68 et al., 2013; Sekeres et al., 2018).

69 Tomparry and Davachi (2017) recently investigated memory transformation through multivariate
70 pattern analysis of fMRI data. They had participants encode pairs of unique objects with one of four
71 recurring scenes. Either immediately following encoding or one week later, participants were cued with
72 the objects to retrieve the scenes from memory. In both the mPFC and MTL, neural patterns during
73 retrieval were more similar to each other for objects that had shared the same scene (retrieval-retrieval
74 similarity). Critically, this was only the case during the delayed memory test, indicating that the
75 memories underwent a transformation over time. The authors concluded that consolidation promotes
76 representational convergence of memories that share overlapping features, which may be an important
77 building block for memory generalization.

78 We here seek to build on this work to address three questions. First, the reported increase in
79 retrieval-retrieval similarity for objects sharing the same scene (Tomparry & Davachi, 2017) may not
80 necessarily reflect memory generalization. Instead, it may be a byproduct of scene reinstatement, i.e.
81 the reactivation of the same scene-specific encoding pattern during retrieval (Mack & Preston, 2016;
82 Wing et al., 2015): If the same scene encoding pattern is reinstated in two retrieval trials, these trials
83 may then be more similar to each other, thus potentially driving retrieval-retrieval similarity. Such an
84 effect could even increase over time, given the mPFC's time-dependent role in memory retrieval (Barry
85 et al., 2018; Bonnici et al., 2012; Bonnici & Maguire, 2018; Sekeres et al., 2018; Sommer, 2017). Here,
86 we address this issue by also examining scene reinstatement as a potential alternative account for the
87 effect reflected in retrieval-retrieval similarity.

88 Second, we investigate whether generalized memory representations can be expressed even in
89 the absence of successful retrieval of individual episodes. Given that generalization entails loss of
90 episodic detail (Sekeres et al., 2018), we suggest that such generalized representations may be activated
91 by an episodic retrieval cue, even if these representations do not provide sufficient detail to drive
92 successful episodic retrieval.

93 Third, previous work has been agnostic with regards to the drivers of memory generalization.
94 We here suggest that memory transformation is promoted by reward. Neural replay during
95 consolidation appears to be critical to generalization (Kumaran et al., 2016; Liu et al., 2019), and
96 rewarded memoranda are preferably replayed post encoding (Gruber et al., 2016; Sterpenich et al.,
97 2021). In general, we thus suggest that reward may facilitate memory generalization.

98 Specifically, the mPFC has been implicated not only in representing generalized knowledge
99 structures (Gilboa & Marlatte, 2017) but also in reward processing (Haber & Knutson, 2010). Indeed
100 there is evidence that mPFC representations may be shaped by value (Baram et al., 2021; Moneta et al.,
101 2023; Paulus et al., 2021). Similarly, the anterior HC may not only be particularly involved in
102 representations of broad, general memories, but may also process motivationally relevant aspects of a
103 memory - such as reward (Poppenk et al., 2013). We thus hypothesize that reward facilitates the
104 representational convergence of memories that share overlapping features.

105 To address these questions, we conducted a two-day fMRI study with n=40 participants. On day
106 one, participants engaged in an incidental encoding task (adapted from Gruber et al., 2016), in which
107 they associated a series of single objects with one of four recurring scenes. Two of the scenes led to high
108 reward, and the two other scenes to low reward. The next day, participants returned for a surprise
109 scene recall task (adapted from Tomparry & Davachi, 2017). Here, participants were cued with each
110 object to recall the associated scene.

111 First, we tested the hypothesis that scene-specific reinstatement is present in the PHC and
112 posterior HC, but not the mPFC. Successful retrieval should thus be associated with greater encoding-
113 retrieval similarity for trials that share the same scenes, compared to those that share different scenes.

114 Second, we tested the hypothesis that the mPFC and anterior HC, but not the PHC, represent
115 transformed memories. This would be reflected in increased retrieval-retrieval similarity for objects that

116 had shared the same encoding scene. Third, we expected this effect to be greater for overlapping
117 memories that had been highly rewarded.

118

119 **Method**

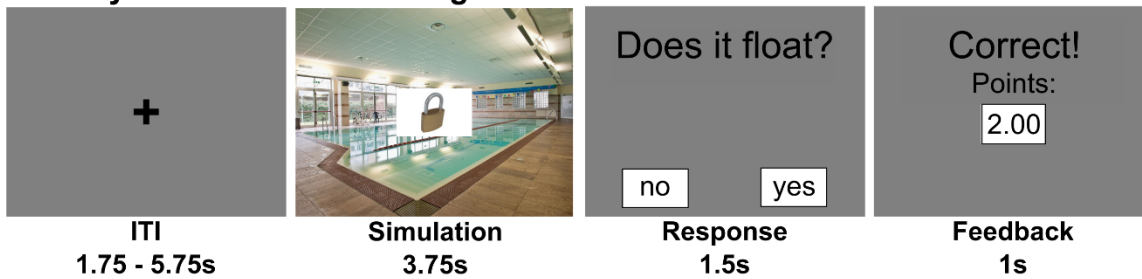
120 **Sample**

121 A total of n=42 volunteers took part in the study. Of these, two were excluded from data
122 analysis (one due to equipment failure, one did not return for the second day). We thus report data
123 from n=40 participants (mean age: 26.25 years, age range: 19-35 years, 28 women, 12 men). They were
124 native German speakers with normal or corrected-to normal vision and without a history of psychiatric
125 or neurological disorder. The study protocol was approved by the ethics committee of the medical
126 faculty of the University of Leipzig (171/19-ek), and all participants provided written informed consent
127 prior to participating. They received 9€/hour and an additional bonus of up to 15€, depending on their
128 performance during the encoding task.

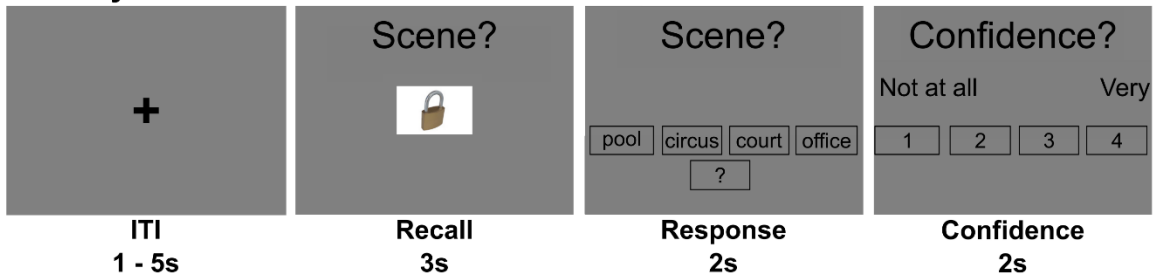
129 **Procedure and tasks**

130 Participants took part in two fMRI sessions on consecutive days (mean delay between fMRI
131 sessions: 22h 35min, range: 19h 30min – 26h 0min). On day one, they engaged in the incidental
132 encoding task; on day two, they returned for the surprise scene recall task.

A Day 1: Incidental Encoding Task

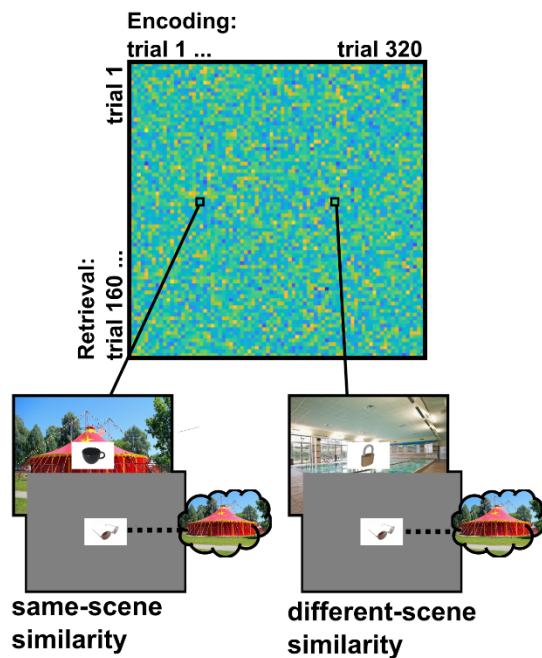


B Day 2: Scene Recall Task

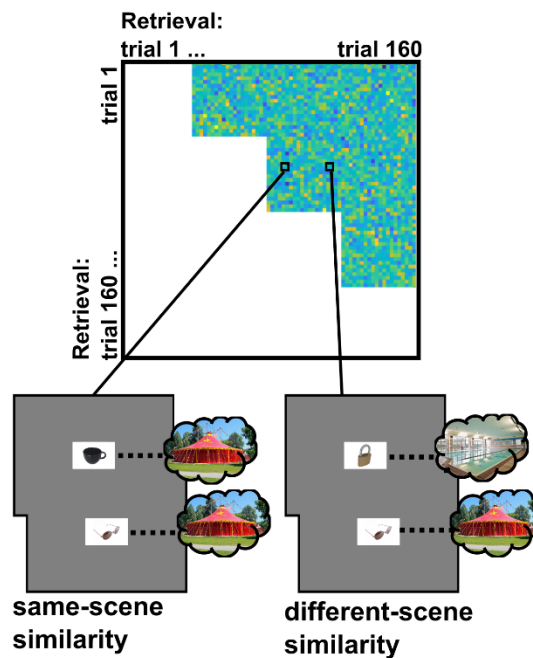


C Representational similarity analysis

Encoding-retrieval similarity



Retrieval-retrieval similarity



133

134 **Figure 1. A.** Example trial for the incidental encoding task. After a variable inter-trial interval of 1.75 – 5.75s,

135 participants viewed one of 160 objects on top of one of four scenes, and mentally engaged in a scene-specific

136 simulation task (here: “Would the object float on the water?”) for 3.75s. They had 1.5s to respond “yes” or “no”,

137 and received reward feedback (high: 2.00 points, low: 0.02 points) for 1s for each correct response. **B.** Example

138 trial for the scene recall task. After a variable ITI, participants viewed one of the objects from the encoding phase
139 for 3s and tried to retrieve the scene from memory. They then had 2s to respond by choosing a label presented on
140 the screen (e.g. “swimming pool”). If they chose a scene label, they then had 2s to rate the confidence of their
141 choice on a scale of one (“not at all confident”) to four (“very confident”). **C. Representational similarity analysis.**
142 We used two measures to assess similarity between trials that either shared a scene (same-scene similarity) or did
143 not (different-scene similarity). To test reinstatement of scene-specific activity from the encoding phase, we
144 assessed encoding-retrieval similarity. That is, we correlated pairs of retrieval trials with encoding trials that shared
145 the same scene or not. To test for memory generalization based on overlapping features (i.e. the same scene), we
146 assessed retrieval-retrieval similarity. That is, we correlated pairs of trials from the retrieval phase that had either
147 shared a scene (same-scene similarity) or had not (different-scene similarity). For copyright reasons, we here
148 display photographs that are similar to the actual experimental stimuli (scene images from <http://pixabay.com>;
149 object images by the investigators).

150

151 ***Day 1: Incidental encoding task***

152 The incidental encoding task (Figure 1A) was adapted from Gruber et al. (2016) (see also Schultz
153 et al., 2023). In each trial, participants viewed one of 160 objects paired with one of four recurring
154 scenes: A circus, a basketball court, an office, and a swimming pool. Participants were asked to mentally
155 simulate a scene-specific action and respond to a corresponding question (e.g. “Would the object float
156 on water?” for the swimming pool scene). Correct responses yielded a high or low reward. Importantly,
157 two of the scenes were always paired with high reward (2 points), while the other two scenes were
158 always paired with low reward (0.02 points). Points were later converted to monetary reward.
159 Allocation of scenes to reward magnitudes were instructed prior to scanning, and counterbalanced
160 across participants. Each object-scene pair was presented twice, with the repetition occurring within the
161 same run. This yielded a total of 320 trials over four runs.

162 ***Day 2: Scene recall task***

163 The scene recall task (Figure 2A) was adapted from Tompary and Davachi (2017) (see also
164 Schultz et al., 2023). In each trial, one of the objects from the encoding task was presented, and
165 participants were asked to recall the scene that it had been paired with. They responded with one of five
166 choices (verbal labels for the four scenes plus a “don’t know” option). If they responded with a scene,
167 they were also asked to rate the confidence of their choice on a scale from one (not at all) to four (very).
168 Each object was presented once, yielding a total of 160 trials across four runs.

169 Day two also included an unscanned recall task for the reward magnitude (Schultz et al., 2023),
170 as well as questionnaires. These are not part of the present report.

171 **Implementation**

172 Tasks were implemented in Octave (RRID:SCR_014398) and the Psychophysics Toolbox
173 (RRID:SCR_002881). We note that, due to a bug in the code, object images in both the incidental
174 encoding task and scene recall task were stretched to an approximately 4:3 format.

175 **Behavioral analysis**

176 For the incidental encoding task, we computed proportions of correct responses as well as
177 median response times for correct responses, separately for high and low reward trials. For the scene
178 recall task, we computed proportions of correct scene recall, separately for high and low reward trials.
179 All further analyses included only trials for which the encoding task had been answered correctly on
180 both repetitions. We tested for effects of reward using paired *t*-tests on all three behavioral measures.
181 Statistical analyses were conducted in R (RRID:SCR_001905) and RStudio (RRID:SCR_000432).

182 **MRI acquisition**

183 MRI data were acquired on a Siemens Prisma 3T system. Functional data were scanned using a
184 whole-brain T2*-weighted gradient-echo, echo-planar pulse sequence (2mm isotropic voxels, 72
185 interleaved slices, TR=2000ms, TE=25ms, multiband acceleration factor=3). On each day, five functional
186 runs were acquired: One run of 120 volumes of rest followed by either four runs of 526 volumes (task

187 plus rest, day one) or 206 volumes (task, day 2). Gradient-echo fieldmaps were acquired at the
188 beginning of each session. On day one, we also acquired a T1-weighted structural image (MPRAGE, 1mm
189 isotropic voxels). Additional structural scans (DWI, MP2RAGE) were acquired that were not analyzed for
190 the present report.

191 **MRI preprocessing and first-level statistics**

192 The MRI data were first converted to the Brain Imaging Data Structure (BIDS) (Gorgolewski et
193 al., 2016). Preprocessing was performed using fMRIPrep 21.0.2 (Esteban et al., 2019; Esteban,
194 Markiewicz, Goncalves, et al., 2022) (RRID:SCR_016216) based on Nipype 1.6.1 (Esteban, Markiewicz,
195 Burns, et al., 2022; Gorgolewski et al., 2011) (RRID:SCR_002502).

196 The T1-weighted image (T1w) was corrected for intensity non-uniformity, skull-stripped, and
197 segmented into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF). It was then
198 normalized to standard space (MNI152NLin2009cAsym). From the functional data, first, a reference
199 image was estimated for use in the motion correction and co-registration steps. The functional data
200 were slice-time corrected to the middle temporal slice, motion-corrected, and corrected for
201 susceptibility distortions using the fieldmap acquired at the start of each session. Functional data were
202 then co-registered to the T1w using boundary-based registration (Greve & Fischl, 2009) with six degrees
203 of freedom (for further preprocessing details, see <https://fmriprep.org/en/21.0.2/>).

204 We conducted the further processing in MATLAB (RRID:SCR_001622) and SPM12
205 (RRID:SCR_007037). Specifically, we set up two sets of first-level general linear models (GLMs) on the
206 unsmoothed, non-normalized data: one set for the encoding and one for the retrieval data. Each trial
207 was estimated in a separate GLM (Mumford et al., 2012), with a single regressor on the simulation onset
208 respectively recall onset. Each model also contained categorical regressors for all other onsets,
209 separately for each of the conditions (HR: high reward/remembered, HF: high reward/forgotten, LR: low
210 reward/remembered, LF: low-reward/forgotten) as well as a categorical regressor encompassing all

211 button presses. All of these regressors were convolved with the hemodynamic response function (HRF).
212 Additionally, each model included a set of seven non-convolved noise regressors extracted during
213 preprocessing, i.e. the six rigid motion regressors (three translations, three rotations) as well as
214 framewise displacement. Functional runs were concatenated, and session constants were included in
215 the models. The resulting beta maps for each trial of the encoding and retrieval sessions were converted
216 to t maps. Finally, the t maps were minimally smoothed with a Gaussian kernel of 2mm full width at half
217 maximum (Dimsdale-Zucker & Ranganath, 2018).

218 **Regions of interest**

219 We employed bilateral anatomical masks of the PHC, the whole HC as well as its anterior and
220 posterior subdivisions, and mPFC. For the PHC, anterior HC, and posterior HC masks, we automatically
221 segmented each participant's T1w using ASHS (Yushkevich et al., 2015) and the Penn Memory Center 3T
222 ASHS Atlas for T1-weighted MRI (Xie et al., 2016). We reviewed each individual segmentations and
223 found that the automated process led to a successful outcome for our participant population.

224 The PHC masks were then manually adjusted according to guidelines suggested by (Pruessner et
225 al., 2002). The anterior and posterior HC masks were also combined into a single HC mask. All masks
226 were then resampled to each participant's functional space. For visualization (Figure 3, 4A-B), the masks
227 were warped into standard space using the transformation matrix from the T1w normalization, and
228 averaged across participants.

229 For the mPFC mask, we used the Brainnetome atlas (Fan et al., 2016) and combined left and
230 right medial area 11, 13, and 14 as well as left and right subgenual area 32. This mask was warped from
231 standard space into each participant's single subject space using the inverse transformation from the
232 T1w normalization and the functional reference image (see above).

233 **Representational similarity analysis**

234 From the minimally smoothed single-trial t maps, we extracted and vectorized t values from
235 each ROI for each trial. Similarity was operationalized as the average Fisher-z-transformed Pearson
236 correlation coefficient between pairs of trials. Our approach is illustrated in Figure 1C. For the MTL ROIs
237 (PHC, HC), similarity values were calculated separately for the left and right hemisphere and then
238 averaged.

239 First, to test for episodic reinstatement of scene-specific information, we computed *encoding-*
240 *retrieval-similarity*. Here, we computed the average similarity between pairs consisting of an encoding
241 and a retrieval trial, separately for the following conditions: High-reward remembered trial pairs sharing
242 the same scene (HR-same) or different scene (HR-diff), and similarly for high-reward forgotten trial pairs
243 (HF-same, HF-diff), low-reward remembered trial pairs (LR-same, LR-diff), and low-reward forgotten trial
244 pairs (LF-same, LF-diff). We excluded trial pairs containing the same object as well as trials with incorrect
245 encoding responses.

246 Second, to test for memory generalization, we computed *retrieval-retrieval similarity*. Here, we
247 computed the average similarity between pairs of retrieval trials, separately for the following conditions:
248 High-reward remembered trial pairs sharing either the same scene (HR-same) or different scenes (HR-
249 diff), and similarly for high-reward forgotten trials (HF-same, HF-diff), low-reward remembered trials
250 (LR-same, LR-diff), and low-reward forgotten trials (LF-same, LF-diff). We excluded trial pairs from the
251 same fMRI run as well as trials with incorrect encoding responses.

252 Statistical analyses of the similarity values were conducted in R. To test for effects of our
253 experimental manipulations on encoding-retrieval similarity and retrieval-retrieval similarity in each ROI,
254 we submitted the mean similarity scores for each participant and condition to repeated-measures
255 ANOVAs (R: `afex::aov_ez`) (Singmann et al., 2021) with the factors reward (high, low), memory
256 (remembered, forgotten), and similarity (same scene, different scene). We conducted follow-up paired
257 comparisons as necessary.

258 **Representational similarity analysis – complementary searchlight analyses**

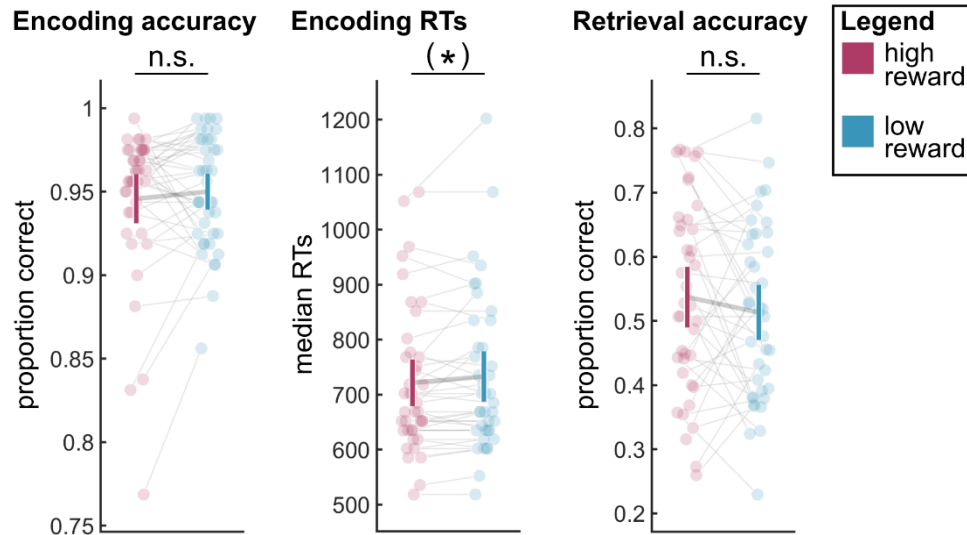
259 We complemented the above ROI analyses of encoding-retrieval similarity and retrieval-retrieval
260 similarity with a searchlight analysis. To this end, we repeated the above analysis within a moving
261 searchlight (3 voxel radius) centered on every voxel inside each participant's brain mask. For each
262 condition (i.e. HR-same, HR-diff, HF-same, HF-diff, LR-same, LR-diff, LF-same, LF-diff), the resulting
263 fisher-z transformed correlation coefficients were written out as a statistical image. For each participant,
264 we then combined these statistical images into first level contrast images: Following up on the ROI
265 results, for encoding-retrieval similarity, we computed the interaction effect of memory and similarity
266 ($[1 -1 -1 1 1 -1 -1 1]$). For retrieval-retrieval similarity, we computed the main effect of similarity ($[1 -1 1 -$
267 $1 1 -1 1 -1]$). These contrast images were normalized to standard space using the transformation matrix
268 from the T1w normalization, and smoothed with a Gaussian kernel of 6mm full width at half maximum
269 (SPM12). The resulting maps were then submitted to a second-level one-sample *t*-test in SPM12.
270 Multiple comparisons correction was achieved through peak-level family-wise error correction (FWE)
271 within the anatomical masks of the HC and PHC (encoding-retrieval similarity) and the mPFC mask
272 (retrieval-retrieval similarity). Finally, to explore effects outside our ROIs, we also applied FWE
273 correction across the whole brain.

274 **Results**

275 **Behavioral results**

276 Accuracy on the incidental encoding task was, as intended, near ceiling (Figure 2), and did not
277 differ for high versus low reward trials ($t_{(39)}=0.766$, $p=.449$). There was a trend for correct responses to
278 be faster in the high than the low reward condition ($t_{(39)}=1.755$, $p=.087$, Figure 2).

279 Participants correctly recalled around half of the scenes. While accuracy was numerically higher
280 for high-reward trials (high reward: 53.7%, low reward: 51.3%, Figure 2), the difference was not
281 significant ($t_{(39)}=1.147$, $p=.258$).



282

283 **Figure 2. Behavioral results.** Left panel: Accuracy during the incidental encoding task. Middle panel: Median
284 response times (RTs) for correct responses during the incidental encoding task. Right panel: Accuracy during the
285 scene recall task. Error bars indicate 95% confidence interval. Abbreviations: n.s., not significant; (*) $.05 < p < .1$.

286

287 **Encoding-retrieval similarity: The PHC reinstates scene-specific patterns during retrieval**

288 We tested whether, during retrieval, the three ROIs would reinstate scene-specific patterns
289 from the encoding phase. To this end, we calculated the average similarities between pairs of retrieval
290 trials and encoding trials that either shared the same scene or not (same-scene versus different-scene
291 similarity). Reinstatement would be reflected in greater same-scene than different-scene similarity. We
292 expected this similarity effect for remembered trials, particularly in the PHC and HC, with the mPFC
293 serving as control.

294 **ROI analyses**

295 In each of the three ROIs (mPFC, PHC, and HC), we computed a three-way repeated-measures
296 ANOVA with the factors reward (high, low), memory (remembered, forgotten), and similarity (same
297 scene, different scene). We report main effects of similarity as well as interactions that include the

298 similarity factor, as other effects (such as e.g. a main effect of memory) do not reflect reinstatement of
299 the specific scene.

300 The mPFC (Figure 3, left panel) did not show an effect involving the similarity factor (all
301 $F_{(1,39)} \leq 0.482$, all $p \geq .492$).

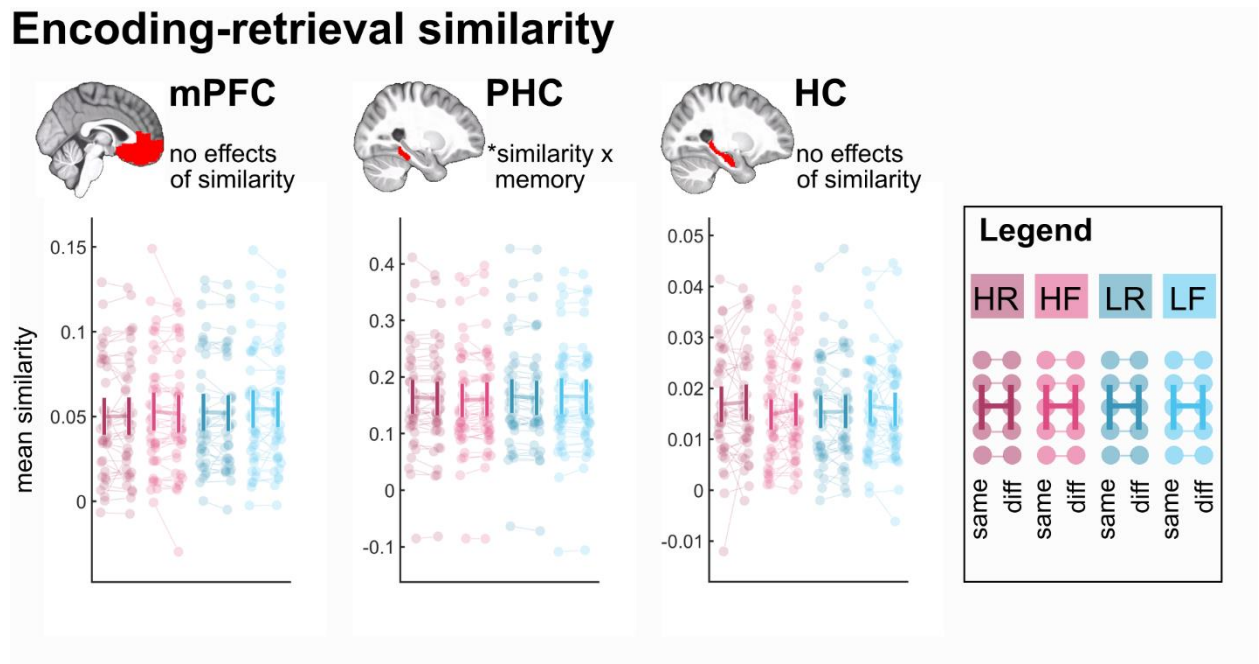
302 The PHC (Figure 3, middle panel) showed an interaction of similarity and memory ($F_{(1,39)} = 5.370$,
303 $p = .026$), reflecting a greater similarity effect for remembered than forgotten trials. No other effects
304 involving the similarity factor were significant (all $F_{(1,39)} \leq 2.079$, all $p \geq .157$). To follow up on this
305 interaction, we averaged over the reward factor, and compared same- vs. different scene similarity
306 separately for remembered and forgotten trials. Same-scene similarity was significantly greater than
307 different-scene similarity for remembered ($t_{(39)} = 2.796$, $p = .008$) but not forgotten trials ($t_{(39)} = 0.617$,
308 $p = .541$). This pattern is consistent with reinstatement of scene-specific encoding activity during
309 successful memory retrieval.

310 Overall, the HC (Figure 3, right panel) did not show any effects involving the similarity factor (all
311 $F_{(1,39)} \leq 1.235$, all $p \geq .273$). However, previous research suggests that the posterior HC may be particularly
312 involved in representing episodic detail (Poppenk et al., 2013). We therefore repeated the above
313 analysis separately for the anterior and posterior HC. The anterior HC did not show any effects involving
314 the similarity factor (all $F_{(1,39)} \leq 0.367$, all $p \geq .548$), while the posterior HC only showed a trend-level
315 interaction of reward and similarity ($F_{(1,39)} = 3.534$, $p = .068$, all other $F_{(1,39)} \leq 0.891$, all $p \geq .351$, numerically
316 greater similarity effect for low-reward than high-reward trials).

317 ***Complementary searchlight analysis***

318 To follow up on our findings of scene-specific reinstatement during remembered trials in the
319 PHC, we repeated the same analysis using a searchlight approach. The contrast for the interaction effect
320 of memory and similarity (i.e. [1 -1 -1 1 1 -1 -1 1]) on the conditions HR-same, HR-diff, HF-same, HF-diff,
321 LR-same, LR-diff, LF-same, LF-diff) was computed on the single-subject level and submitted to a one-

322 sample t test on the group level. However, at $p < .001$ uncorrected, this analysis yielded no significant
323 voxels within a combined mask of the PHC and HC. Furthermore, no voxels survived FWE correction
324 across the whole brain. We note that, due to the high interindividual variability in MTL anatomy
325 (Pruessner et al., 2002), analyses in group space are typically less sensitive than analyses within
326 individual MTL ROIs.
327



328
329 **Figure 3. Encoding-retrieval similarity.** Average encoding-retrieval similarity values in the three a-priori
330 ROIs: mPFC, PHC, and HC. Notes refer to effects from three-way repeated-measures ANOVAs with the factors
331 reward, memory, and similarity (see main text for details). Error bars indicate 95% confidence interval.
332 Abbreviations: HR: high-reward/remembered; HF: high-reward/forgotten; LR: low-reward/remembered, LF: low-
333 reward/forgotten; same: same-scene similarity, diff: different-scene similarity; * $p < .05$.

334

335 Retrieval-retrieval similarity: The mPFC and anterior HC represent transformed memories

336 Next, we tested whether memory representations with overlapping features (i.e. the same
337 scene) showed evidence for generalization. To this end, we calculated the average similarities between

338 pairs of retrieval trials that either shared the same scene (same-scene similarity) or not (different-scene
339 similarity). Memory generalization would be reflected in greater same-scene than different-scene
340 similarity. We expect this similarity effect predominantly in the mPFC and HC, with the PHC serving as
341 control.

342 **ROI analyses**

343 As with the encoding-retrieval similarity analysis above, we computed, for each of the ROIs, a
344 three-way repeated-measures ANOVA with the factors reward (high, low), memory (remembered,
345 forgotten), and similarity (same scene, different scene). We report main effects of similarity as well as
346 interactions that include the similarity factor, as other effects (such as a main effect of memory) do not
347 reflect generalization.

348 The mPFC (see Figure 4A) showed a significant main effect of similarity (same-scene similarity >
349 different-scene similarity, $F_{(1,39)}=13.455$, $p<.001$). This is consistent with the emergence of generalized
350 memory representations for episodes that share overlapping features. No other effect involving the
351 similarity factor was significant (all $F_{(1,39)}\leq 1.932$, all $p\geq .172$).

352 The PHC (see Figure 4A) did not yield an effect involving the similarity factor (all $F_{(1,39)}\leq 0.774$, all
353 $p\geq .384$).

354 Overall, for the HC (see Figure 4A), we observed a trend-level main effect of similarity (same-
355 scene similarity > different-scene similarity, $F_{(1,39)}=3.670$, $p=.063$), qualified by a trend-level interaction of
356 reward and similarity ($F_{(1,39)}=2.891$, $p=.097$). This pattern reflected a larger similarity effect for high-
357 reward than low-reward trials. Given that the anterior portion of the HC may be particularly involved in
358 processing generalized information as well as reward (Guo & Yang, 2020; Poppenk et al., 2013), we
359 repeated the above analyses in anterior vs. posterior portions of the HC (Figure 4B).

360 The anterior HC showed a significant interaction of reward and similarity ($F_{(1,39)}=9.743$, $p=.003$).
361 This is consistent with reward-enhanced generalization of overlapping memories. No other effect that

362 included the similarity factor was significant (all $F_{(1,39)} \leq 1.213$, all $p \geq .278$). To follow up on this interaction,
363 we averaged over the memory factor, and compared same-scene vs. different scene similarity,
364 separately for high-reward and low-reward trials. Same-scene similarity was significantly greater than
365 different-scene similarity for high-reward trials ($t_{(39)} = 2.686$, $p = .011$), but not for low-reward trials
366 ($t_{(39)} = 1.624$, $p = .112$). The anterior HC thus showed a result pattern that was more pronounced than the
367 result pattern in the whole HC ROI.

368 The posterior hippocampus, on the other hand, showed a trend-level main effect of similarity
369 (same-scene similarity > different-scene similarity, $F_{(1,39)} = 3.880$, $p = .056$). No other effect including the
370 similarity factor was significant ((all $F_{(1,39)} \leq 1.652$, all $p \geq .206$).

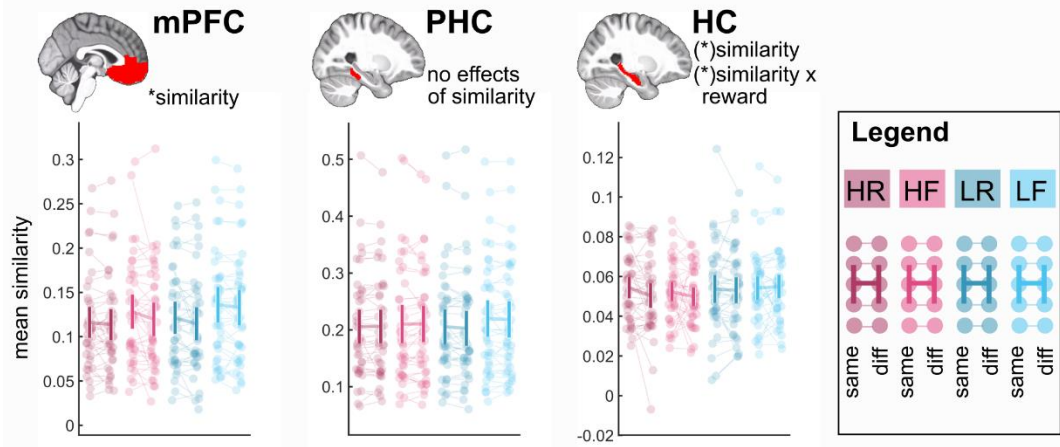
371 ***Complementary searchlight analysis***

372 To corroborate our main findings of overall memory generalization in the mPFC, we conducted
373 the same analysis using a searchlight approach. The contrast for the main effect of similarity (i.e. [1 -1 1 -
374 1 1 -1 1 -1] on the conditions HR-same, HR-diff, HF-same, HF-diff, LR-same, LR-diff, LF-same, LF-diff) was
375 computed on the single-subject level and submitted to a one-sample t-test on the group level. We
376 applied small-volume correction across the anatomical mPFC mask. This analysis yielded a significant
377 peak within the mPFC (MNI coordinates: [6 54 -6], $t_{(39)} = 5.212$, $p_{SVC} = .003$, Figure 4C). We visualized this
378 effect by extracting the mean similarity values across the entire cluster (thresholded at $p < .001$) for each
379 condition and subject. The result pattern resembles the one reported for the anatomical mPFC ROI (see
380 above). In addition, two further peaks survived FWE-correction across the whole brain: The left
381 postcentral gyrus ([-44 -22 54], $t_{(39)} = 8.890$, $p_{FWE} \leq .001$), and the bilateral occipital cortex ([0 -88 2],
382 $t_{(39)} = 8.325$, $p_{FWE} \leq .001$).

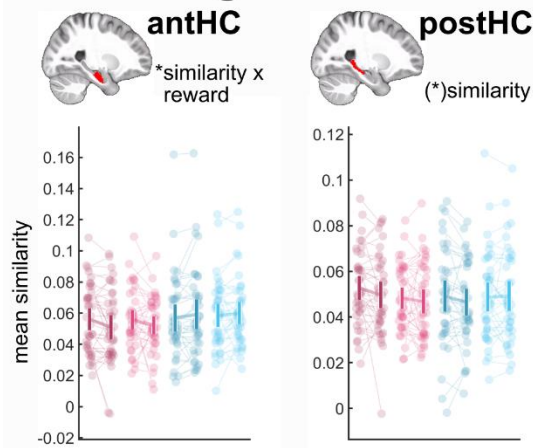
383

Retrieval-retrieval similarity

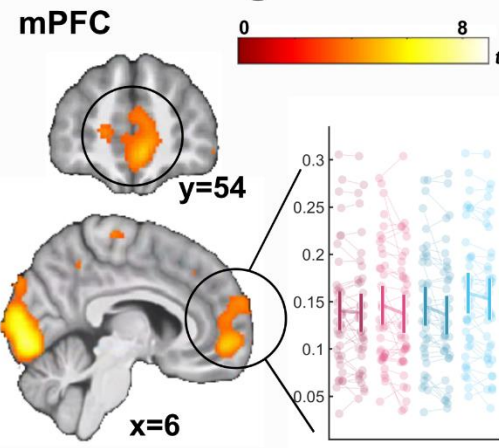
A Regions of interest



B HC long axis



C Searchlight



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Figure 4. Retrieval-retrieval similarity. A. Average retrieval-retrieval similarity values in the three a-priori ROIs: mPFC, PHC, and HC. B. Average retrieval-retrieval similarity in the anterior vs. posterior portion of the HC. C. Results of whole-brain searchlight analysis for the main effect of similarity (same-scene similarity > different-scene similarity across levels of reward and memory). Average retrieval-retrieval similarity was extracted for visualization. Display threshold $p < .001$ unc., $k = 5$ voxels. Notes refer to effects from three-way repeated-measures ANOVAs with the factors reward, memory, and similarity (see main text for details). Error bars indicate 95% confidence interval. Abbreviations: HR: high-reward/remembered; HF: high-reward/forgotten; LR: low-

392 reward/remembered, LF: low-reward/forgotten; same: same-scene similarity, diff: different-scene similarity;
393 * $p < .05$, (*) $.05 < p < .1$.

394 Discussion

395 With the present fMRI study, we set out to examine whether the brain concurrently represents
396 episodic memory representations as well as more generalized memory representations that encode
397 commonalities across episodes.

398 First, we examined the reinstatement of scene patterns from the encoding experience, thought
399 to reflect episodic memory. We observed evidence for memory reinstatement in the PHC, but not the
400 mPFC or HC. Second, we tested for memory transformation – i.e. the representational convergence of
401 neural retrieval patterns for memories that share overlapping features. This is thought to reflect the
402 shift from individual episodes into generalized memory. We found evidence for such memory
403 transformation in the mPFC and HC, but not the PHC. Intriguingly, memory transformation in the mPFC
404 affected all memories, regardless of reward magnitude or retrieval success. In contrast, memory
405 transformation in the anterior HC was enhanced by reward. We note, however, that unlike previous
406 studies (e.g.) (Gruber et al., 2016; Schultz, Yoo, et al., 2022; Wittmann et al., 2005) we did not observe a
407 reward effect on behavioral retrieval accuracy, and only a marginal effect on response times during
408 encoding (see also Schultz et al., 2023).

409 Our results thus extend our knowledge derived from studies that had tested retrieval after a
410 consolidation period of three days (Audrain & McAndrews, 2022) and one week (Tomparry & Davachi,
411 2017). Here, we demonstrate (i) that memory transformation has already taken place after one day, (ii)
412 that it is partly enhanced by reward, and (iii) that generalized memory representations can be activated
413 even in absence of successful retrieval of a particular episodic memory.

414 Importantly, did our analysis of retrieval-retrieval similarity truly reflect transformed memories?
415 Transformation implies two things: That a representation has changed over time, and that it is dissimilar

416 to the original encoding pattern. Previous studies have focused on the first implication and
417 demonstrated that memories sharing the same scene become more similar to each other over time
418 (Audrain & McAndrews, 2022; Tomparly & Davachi, 2017). The second implication is equally critical. This
419 is because retrieval-retrieval similarity could also be a consequence of common scene reinstatement: If
420 the same-scene-specific encoding pattern is reinstated in two retrieval trials, these would also be similar
421 to each other. Such an effect would not reflect a transformation away from the original encoding
422 pattern.

423 To address this, we analyzed concurrent scene reinstatement (i.e. scene-specific encoding-
424 retrieval similarity). Our results imply that retrieval-retrieval similarity was not merely driven by scene
425 reinstatement: First, there was little topographical overlap between the two effects, with scene
426 reinstatement predominantly in the PHC, and retrieval-retrieval similarity predominantly in the mPFC
427 and (anterior) HC. Second, scene reinstatement was modulated by memory success whereas retrieval-
428 retrieval similarity was not. This pattern indicates that our findings in the mPFC and anterior HC truly
429 reflect a transformed memory representation rather than a reinstatement of a shared encoding pattern.

430 Memory transformation – in the sense of representational convergence of overlapping
431 memories - has previously been observed for the mPFC (Audrain & McAndrews, 2022; Tomparly &
432 Davachi, 2017). These findings are consistent with a role of the mPFC in representing generalized
433 knowledge structures (Ghosh & Gilboa, 2014; Gilboa & Marlatte, 2017; Paulus et al., 2021).

434 Generalization may be driven by replay of episodic memories during consolidation. This process
435 would allow the cortex to extract commonalities across similar memories and to store these as more
436 generalized representations (Kumaran et al., 2016; Liu et al., 2019; Sekeres et al., 2018). Here, we show
437 that such effects do not require three (Audrain & McAndrews, 2022) or seven days (Tomparly & Davachi,
438 2017) to emerge. Instead, they are already present a single day after encoding.

439 Notably, in the mPFC, the activation of transformed memory representations was independent
440 of memory success. This is somewhat at odds with previous studies that reported memory
441 transformation for correctly recalled trials only (Audrain & McAndrews, 2022; Tomparý & Davachi,
442 2017). However, both of these studies included control analyses for trials without overt scene recall
443 (recognition trials, Tomparý & Davachi, 2017; forgotten trials, Audrain & McAndrews, 2022). In both
444 cases, the mPFC patterns were numerically consistent with representational convergence, though they
445 were statistically inconclusive. If the mPFC encodes representations that generalize across episodes that
446 share common content (Audrain & McAndrews, 2022; Gilboa & Marlatte, 2017; Sekeres et al., 2018),
447 these would get activated whenever one of these episodes is being probed. However, given that these
448 representations abstract away from unique features that are specific to individual episodes, they would
449 not contain sufficient episodic detail to drive episodic recall.

450 Contrary to our hypothesis, reward did not foster memory transformation in the mPFC, but only
451 in the anterior HC. Reward has been shown to increase neural replay (Gruber et al., 2016; Sterpenich et
452 al., 2021) and promote consolidation (Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011;
453 Spaniol et al., 2014; Wittmann et al., 2005). Therefore, we had hypothesized that reward would
454 facilitate representational convergence. The reason for this dissociation between the mPFC and anterior
455 HC is unclear. The mPFC has been previously demonstrated to encode value-shaped representations of
456 knowledge (Baram et al., 2021; Moneta et al., 2023; Paulus et al., 2021). Furthermore, both the mPFC
457 and HC are linked to the brain's reward circuit (Haber & Knutson, 2010), and the anterior portion of the
458 HC is particularly connected to the mPFC (Adnan et al., 2016; Barnett et al., 2021; Poppenk et al., 2013).
459 Specifically, post-encoding functional connectivity between the mPFC and anterior HC predicts
460 subsequent memory transformation, both behaviorally (Audrain & McAndrews, 2022) and neurally
461 (Tomparý & Davachi, 2017). The anterior HC may also be particularly involved in motivational aspects of

462 memory (Murty et al., 2017; Poppenk et al., 2013). Hence, one may have expected similar effects of
463 reward on memory transformation in the anterior HC and mPFC.

464 However, consolidation is not complete after one night. Given that memory transformation may
465 last for years, accompanied by a neural shift from HC to neocortex (Sekeres et al., 2018), it is possible
466 that such reward effects on neural similarity emerge first in the HC and then shift to the mPFC at a later
467 time point. Indeed, the HC may constitute a quick learning system that rapidly acquires not only episodic
468 memory traces, but also regularities from similar events (Kumaran & McClelland, 2012; Schapiro et al.,
469 2017). Through reward-biased replay, it may then coordinate the acquisition of generalized memory
470 representations in the slower neocortical system (Kumaran et al., 2016). This may be one reason why,
471 after a comparatively short time window of one day, we only observed reward effects on memory
472 transformation in the anterior HC. Whether the differences between the mPFC and HC indeed reflect
473 different time-courses of reward-enhanced memory transformation could be tested in future work using
474 repeated retrieval sessions.

475 The hippocampus has been suggested to be functionally differentiated along its longitudinal
476 axis, with more gist-like, schematic representations in the anterior HC, and more fine-grained, episodic
477 representations in the posterior HC (Audrain & McAndrews, 2022; Guo & Yang, 2020; Poppenk et al.,
478 2013). In particular, the (posterior) HC has been implicated in the reinstatement of low-level visual
479 features (Bone & Buchsbaum, 2021), but also of events (Tomparry & Davachi, 2017) and categories
480 (Schultz, Sommer, et al., 2022). Our results only partially support this distinction. We indeed observed
481 distinct result patterns along the longitudinal axis of the HC: The anterior HC showed increased memory
482 transformation for high-reward retrieval trials. The posterior HC, on the other hand, did not yield
483 evidence for episodic scene reinstatement.

484 Instead, we only observed scene reinstatement in the PHC. When participants correctly recalled
485 a scene, the activation pattern in the PHC was more similar to the activation pattern during encoding of

486 that scene. This is in line with previous research showing scene-specific pattern reinstatement in the
487 PHC (Meyer & Benoit, 2022; Schultz et al., 2019; Schultz, Sommer, et al., 2022; Staresina et al., 2012)
488 and scene-specific memory processing in general (Liang & Preston, 2017; Schultz et al., 2012; Schultz,
489 Yoo, et al., 2022; Staresina et al., 2013). Anatomically, the PHC is a connecting hub between the dorsal
490 visual stream and downstream regions in the MTL, including the entorhinal cortex and HC (Lavenex &
491 Amaral, 2000; Suzuki & Amaral, 1994b, 1994a), and thus well-positioned to support spatial, scene-
492 specific, or contextual memory (Eichenbaum et al., 2007).

493 The concurrent presence of original and transformed memory representations is consistent with
494 accounts that the same memories exist in multiple forms at different levels of abstraction, with their
495 relative strength of activation dependent on e.g. task demands (Gilboa & Moscovitch, 2021; Sekeres et
496 al., 2018). Here, we observed that the same retrieval trials elicited both reinstated and transformed
497 memory representations. These were present in the MTL and mPFC, respectively. Does this suggest that
498 the two are independent of each other? Previous work has demonstrated that, during autobiographical
499 retrieval, mPFC activity precedes and drives HC activity (McCormick et al., 2020, but see Campbell et al.,
500 2018). Furthermore, a higher integrity of the anatomical connection between the HC and mPFC is
501 associated with richer autobiographical memories (Williams et al., 2020). It is possible that the memory
502 representations in the mPFC are instantiated earlier, but are by themselves insufficient to elicit
503 successful episodic retrieval. However, if these are passed on through top-down modulation of the MTL
504 (McCormick et al., 2020; Nawa & Ando, 2019; St Jacques et al., 2011), they may guide episodic retrieval
505 and thus aid in recovering the details of a memory trace. Other methods with a higher temporal
506 resolution, such as electrophysiological measures, may further elucidate these potential interactions
507 between the complementary memory representations in the mPFC and MTL.

508 In summary, we have provided evidence for the concurrent activation of two types of memory
509 representations – in the PHC of the original activity pattern that was present during encoding and in the

510 mPFC and anterior HC of activity patterns that resemble transformed, generalized memories. Reward
511 enhances neural memory transformation in the anterior HC, though it does not reliably promote
512 episodic memory. Our results thus broaden our knowledge of the processes that lead to memory
513 generalization, while motivating new questions about how reward shapes the structure of memory.

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519 **Data and code availability**

520 All data necessary to reproduce the reported results, i.e. behavioral data, ROI similarity values,
521 and *t*-maps for the whole-brain searchlight analyses, are shared on OSF along with an R markdown file
522 (<https://osf.io/yracl/>).

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