

1 **Category-specific item encoding in the medial temporal lobe and beyond: The**
2 **role of reward.**

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4 **Authors:** Heidrun Schultz^{1,2,3*}, Jungsun Yoo^{1,2,4}, Dar Meshi^{1,2,5}, Hauke R. Heekeren^{1,2}

5 ¹Department of Education and Psychology, Freie Universität Berlin, Germany

6 ²Center for Cognitive Neuroscience Berlin, Freie Universität Berlin, Germany

7 ³Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

8 ⁴Department of Cognitive Sciences at University of California, Irvine, USA

9 ⁵Department of Advertising and Public Relations, Michigan State University, East Lansing, Michigan,

10 USA

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12 ***Corresponding author:** Heidrun Schultz, Max Planck Institute for Human Cognitive and Brain
13 Sciences, Stephanstr. 1A, 04103 Leipzig, Germany. Email address: heidrun.schultz@cbs.mpg.de

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16 **Abstract**

17 Forming new memories is a fundamental part of human life, and the medial temporal lobe (MTL) is
18 central to memory formation. Recent research suggests that within MTL, the perirhinal and
19 parahippocampal cortices (PRC, PHC) process object and scene memory, respectively, whereas the
20 hippocampus (HC) is agnostic to stimulus category. It is unclear, however, whether MTL category
21 specificity extends to item encoding. Furthermore, MTL does not act in isolation: Reward-related
22 memories are formed in interplay with the dopaminergic midbrain (substantia nigra/ventral
23 tegmental area, SNVTA) and amygdala (AMY), but it is unclear whether reward modulates neural item
24 encoding in a category-specific way. To address these questions, we had 39 healthy volunteers (27 for
25 all memory-based analyses) undergo functional magnetic resonance imaging while they solved an
26 incidental encoding task, which paired objects or scenes with high or low reward, followed by a next-
27 day surprise recognition test. Behaviourally, high reward preferably enhanced object memory.
28 Importantly, neural activity in PRC and PHC reflected item encoding of objects and scenes,
29 respectively. Moreover, AMY encoding effects were selective for high-reward objects, with a similar
30 pattern in PRC. SNVTA and HC showed no clear evidence of item encoding. The behavioural and neural
31 asymmetry of reward-related encoding effects may be conveyed through an anterior-temporal
32 memory system, including AMY and PRC, potentially in interplay with the ventromedial prefrontal
33 cortex (vmPFC).

34 **1 Introduction**

35 The ability to turn experiences into new episodic memories is a central part of life. Beginning with the
36 famous patient H.M. in the 1950s (Scoville and Milner, 1957), a large body of research indicates a
37 critical role for the medial temporal lobe (MTL) in the encoding and retrieval of episodic memories
38 (Zola-Morgan and Squire, 1990; Eichenbaum et al., 2007; Squire and Zola-Morgan, 2011). The MTL is not
39 homogeneous, however, but consists of several subregions including the hippocampus (HC), perirhinal
40 cortex (PRC), and parahippocampal cortex (PHC), which differ in their cytoarchitecture as well as
41 anatomical connectivity with the rest of the brain (Burwell, 2000, 2001; Eichenbaum et al., 2007; van
42 Strien et al., 2009; Ding et al., 2016; Berron et al., 2017). What, then, are the individual contributions
43 of these subregions to episodic memory? A powerful predictor of MTL subregion function is
44 anatomical connectivity (Davachi, 2006; Eichenbaum et al., 2007). Data from non-human primates and
45 rodents indicate differential connectivity of the MTL input/output regions, PRC and PHC, to the ventral
46 and dorsal visual stream, respectively (Suzuki and Amaral, 1994a; Burwell and Amaral, 1998a).
47 Therefore, these regions are thought to process information in a category-specific way, with object-
48 related processing in the PRC, and spatial processing in the PHC (Eichenbaum et al., 2007; Robin et al.,
49 2018). This information is then relayed, both directly and via the entorhinal cortex (EC), to the HC,
50 where these streams converge (Witter and Amaral, 1991; Suzuki and Amaral, 1994b; Tamamaki and
51 Nojyo, 1995; Burwell and Amaral, 1998b; Lavenex and Amaral, 2000; Doan et al., 2019). HC's role in
52 memory is therefore thought to be associative and agnostic to stimulus categories (Davachi, 2006;
53 Eichenbaum et al., 2007). In humans, functional connectivity of MTL subregions resembles these
54 anatomical findings in animals (Kahn et al., 2008; Libby et al., 2012; Maass et al., 2015; Navarro
55 Schröder et al., 2015). Indeed, human patient studies support the notion of a category-specific
56 organisation of MTL subregions (Lee et al., 2005a, 2005b; Taylor et al., 2007; Mundy et al., 2013).
57 Functional imaging studies have localised object-related and spatial processing to PRC and PHC,
58 respectively, during a range of tasks including perception (Litman et al., 2009; Liang et al., 2013; Berron
59 et al., 2018), associative encoding (Awipi and Davachi, 2008; Staresina et al., 2011), associative

60 retrieval (Staresina et al., 2012, 2013; Mack and Preston, 2016; Schultz et al., 2019), working memory
61 (Libby et al., 2014), short-term memory reactivation (Schultz et al., 2012), and recognition memory
62 (Martin et al., 2013; Kafkas et al., 2017). It is unclear, however, whether this object-related vs. spatial
63 distinction in PRC vs. PHC generalises to item encoding. There are numerous reports of PRC
64 involvement in item encoding (Davachi et al., 2003; Ranganath et al., 2004; Staresina and Davachi,
65 2008; Wang et al., 2013). However these studies did not contrast categories; hence it is unclear
66 whether these PRC item encoding effects are category-specific. On the other hand, PHC and the larger
67 parahippocampal place area (PPA) have been implicated in category-specific item encoding for scenes
68 compared to faces in studies that either did not report effects in PRC (Prince et al., 2009), or showed
69 category-independent item-encoding effects in PRC for both faces and scenes (Preston et al., 2010).
70 Given the reports outlined above that PRC and PHC respond to the viewing of object-related and
71 spatial stimuli, and are differentially involved in their *associative* encoding, there are strong reasons
72 to expect a similar dissociation of MTL cortices *for item encoding* of objects and scenes.

73 A mostly separate line of research has investigated how memories are formed in the first place,
74 regardless of category. The dopaminergic reward system, to which the MTL is densely connected
75 (Haber and Knutson, 2010; Shohamy and Adcock, 2010; Miendlarzewska et al., 2016), plays a key role.
76 In a seminal article, Lisman and Grace (2005) have described a mechanism in which the HC and
77 dopaminergic system interact to encode new long-term memories. Here, hippocampal novelty signals
78 are relayed via the ventral striatum (VS) to the dopaminergic midbrain, where they trigger a dopamine
79 response that in turn promotes long-term potentiation in HC (Lisman and Grace, 2005). In humans,
80 reward and reward motivation enhance memory formation, accompanied by functional modulations
81 of the HC and dopaminergic midbrain (substantia nigra/ventral tegmental area, SNVTA) (Wittmann et
82 al., 2005, 2008; Adcock et al., 2006; Wolosin et al., 2012; Miendlarzewska et al., 2016). Importantly,
83 not only the HC, but also the MTL cortex and adjacent amygdala (AMY) are innervated by the SNVTA
84 (Beckstead et al., 1979; Scatton et al., 1980; Insausti et al., 1987; Oades and Halliday, 1987) and
85 connected to other regions of the reward network including the ventromedial prefrontal cortex

86 (vmPFC) (Russchen and Price, 1984; Amaral and Insausti, 1992; Carmichael and Price, 1995; McIntyre
87 et al., 1996; Kondo et al., 2005; Price, 2007; Kondo and Witter, 2014).

88 However, these two lines of research – category specificity and reward enhancement of memory –
89 have never been jointly investigated. It is therefore unclear whether reward enhances memory
90 formation for objects and scenes in similar ways. Given the connectivity outlined above, memory
91 formation for objects and scenes could be enhanced in a category-independent way through
92 hippocampal mechanisms, and/or in a category-specific way through modulation of MTL cortex. The
93 PRC and AMY may play a unique role in reward-enhanced item encoding. PRC may link object features
94 to reward information (Miyashita, 2019), and PRC and AMY are both parts of a hypothesised “anterior
95 temporal system” (AT) that is thought to represent the (motivational) salience of unitised entities such
96 as objects (Ranganath and Ritchey, 2012; Ritchey et al., 2015). Indeed, it has been shown that another
97 strong behavioural motivator – emotion – selectively enhances item encoding in PRC and AMY, but
98 not context encoding in PHC and HC (Ritchey et al., 2019). Findings of item vs. context dissociations in
99 MTL, in turn, may be tied to object-related vs. spatial processing (Davachi, 2006). It follows that reward
100 modulation of neural item encoding effects may be at least in part category-specific.

101 Hence, we have identified two open questions. One, does category specificity in the MTL cortex extend
102 to item encoding? Moreover, two, does reward modulate item encoding in a category-specific
103 manner? To close these gaps in the literature, we investigated the neural effects of successful item
104 encoding for two categories (objects and scenes), fully crossed with two reward magnitudes (high and
105 low). Thirty-nine participants (27 for all memory-based analyses) underwent functional magnetic
106 resonance imaging (fMRI) while they solved an incidental encoding task in which novel objects and
107 scenes predicted high or low reward. One day later, they returned to the lab for a surprise recognition
108 memory test. Behaviourally, we expected high reward to improve recognition memory for both
109 objects and scenes. We furthermore expected activity in MTL, AMY, and SNVTA to reflect this

110 enhanced encoding in a category-independent (HC, SNVTA) and category-specific manner (PRC/AMY
111 for objects, PHC for scenes).

112 **2 Materials and Methods**

113 2.1 Participants

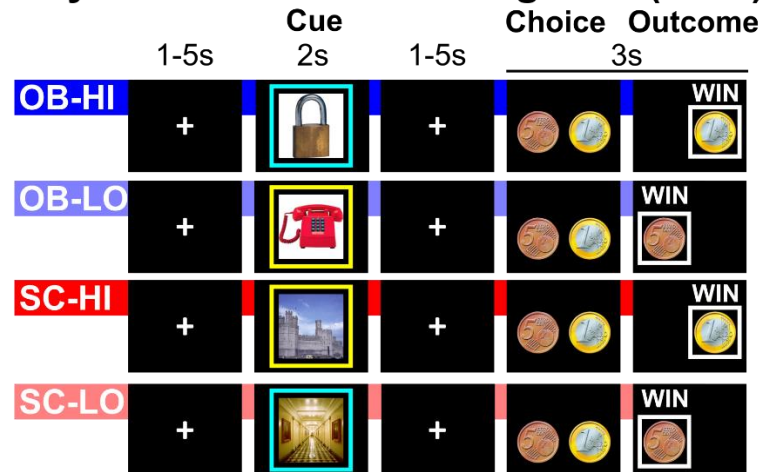
114 A total of 39 participants (“full sample”, 25 female, mean age 24.2 years, range 18-32) took part in the
115 fMRI study. All were right-handed, had normal or corrected-to-normal vision, and were native
116 speakers of German. A subsample of 27 participants (“memory sample”, 19 female, mean age 24.6
117 years, range 19-32) was selected for memory-based analyses (model 1) based on their memory
118 performance (corrected recognition [CR] > 0.083 in each of the four conditions, see below; this
119 threshold was chosen as a compromise between memory performance in the subsample and
120 experimental power). Additional non-memory based analyses (model 2) were carried out in the full
121 sample. All participants gave written informed consent in a manner approved by the local ethics
122 committee. They received monetary reimbursement for their participation (€8/hour plus up to €5
123 reward during the incidental encoding task). Thirty-three fMRI datasets were complete, contributing
124 240 trials each, 6 suffered partial data loss due to equipment malfunction, contributing 200-238 trials
125 each.

126 2.2 Stimuli and Procedure

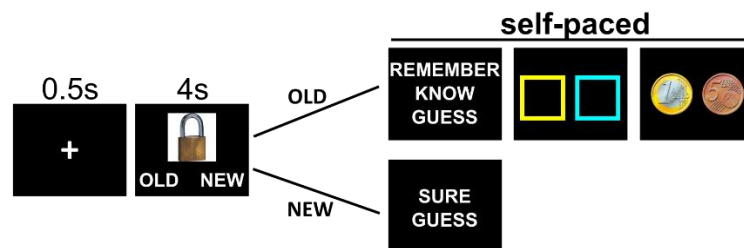
127 A total of 360 colour photographs of objects and scenes (180 each) were obtained from established
128 databases (Brady et al., 2008; Konkle et al., 2010a, 2010b) and an internet search. Of these, 240 (120
129 objects, 120 scenes) were used as targets in the incidental encoding task (Figure 1A), the others served
130 as distractors in the surprise recognition task (Figure 1B). Assignment of images to targets and
131 distractors was randomised for each participant. An additional 8 photographs (4 objects, 4 scenes),
132 not included in the 360 experimental stimuli, were obtained from the same sources and used during
133 training before the incidental encoding task (see below). Each image was sized 256x256 pixels. All
134 tasks were programmed using Presentation® software (Version 18.2, Neurobehavioral Systems, Inc.,

135 Berkeley, CA, www.neurobs.com). The fMRI task was projected onto a mirror mounted on the head
 136 coil, and responses were collected using an MRI-compatible button box. The behavioural recognition
 137 task was presented on a laptop.

A Day 1. Incidental encoding task (fMRI)



B Day 2. Recognition task (behavioural)



138

139 **Figure 1.** Experimental paradigm. A. Day 1 Incidental encoding task. B. Day 2 Recognition task. Note that text
 140 options (e.g. Remember – Know – Guess) were arranged horizontally in the experiment. See main text for details.
 141 Abbreviations: OB: objects, SC: scenes, HI: high reward, LO: low reward.

142 *Day 1: Incidental Encoding Task (fMRI).* The incidental encoding task was designed to fully cross
 143 stimulus category (objects, scenes) and anticipated reward magnitude (high, low). This resulted in the
 144 following experimental conditions: object-high (OB-HI), object-low (OB-LO), scene-high (SC-HI), scene-
 145 low (SC-LO). The task was presented in 6 runs of 40 trials each (240 trials total), with a short break
 146 between runs. Trials were pseudo-randomised so that each run contained equal trial numbers of each
 147 condition. Additionally, no more than 3 trials belonging to the same level of each factor (category,
 148 reward) appeared in a row. Each trial consisted of a cue, choice, and outcome phase (see Figure 1A

149 for example trials for each condition). During the *cue phase* (2s), an image (object or scene) was
150 presented surrounded by a yellow or blue frame. Importantly, the combination of image category and
151 frame colour coded reward magnitude: In a given run, an object with a yellow frame or a scene with
152 a blue frame indicated high reward, while an object with a blue frame or a scene with a yellow frame
153 indicated low reward. Category-frame combinations alternated over runs, with the run order
154 counterbalanced over participants. The combinations were explicitly instructed at the beginning of
155 each run (note that this is not a reward learning task). The cue phase was followed by a variable
156 fixation (1-5s), whose duration was drawn randomly from a uniform distribution. During the following
157 *choice phase*, two coins were presented, respectively, on the left and right side of the screen and
158 participants were asked to indicate whether they anticipated a high (1€) or low (5C) reward in this
159 trial. Response sides were assigned randomly. Upon button press, the chosen coin was outlined by a
160 white frame for 0.5 s or until 2s after choice onset, whichever was shorter. In the *outcome phase*, only
161 the chosen coin (1€ or 5C) remained on the screen, together with the word GEWINN (“Win”) if the
162 participant had indicated the correct reward magnitude during the choice phase. For incorrect
163 choices, the coin would be crossed out, and the word NICHTS (“nothing”) appeared on the screen. If
164 the participant failed to press the button, the coin would also be crossed out, and the words ZU
165 LANGSAM (“too slow”) appeared on the screen. The outcome phase lasted 1s or until 3s after choice
166 onset, whichever was longer. Trials were offset by a variable fixation interval of 1-5s, drawn randomly
167 from a uniform distribution.

168 Note that we varied the magnitude of reward (high vs. low), rather than presence vs. absence of
169 reward. Hence, the task was designed to produce ceiling performance to ensure that participants
170 would receive the high or low reward in the majority of trials. Trials in which participants did not gain
171 the high or low reward were excluded from further analysis. Additionally, we presented the image and
172 frame simultaneously to cue reward magnitude, rather than using a pre-stimulus reward cue. Reward
173 probability was 100%, provided that participants correctly identified the reward magnitude during the
174 choice phase of the trial. These last two measures were taken to ensure that participants paid

175 attention to the image, and to shift the assumed dopamine response from the reward outcome to the
176 reward cue presentation (image plus frame) (Shohamy and Adcock, 2010). Additionally, a fraction of
177 the winnings (up to €5, with high reward items 20x more valuable than low reward items) was paid
178 out directly after the fMRI session on day 1. This was done to ensure that participants would not
179 discount reward magnitude due to delayed gratification (Peters and Büchel, 2011).

180 *Day 2: Surprise Recognition Task (behavioural)*. On the following day, participants returned to the lab
181 to complete a surprise recognition memory test. All 120 objects and 120 scenes from the fMRI task
182 (targets) were presented again without the coloured frames, together with 60 objects and 60 scenes
183 that served as distractors. Stimuli were presented in 6 blocks with short resting breaks between
184 blocks. Stimuli order was pseudo-randomised such that each block contained equal trial numbers of
185 each condition, and no more than 3 stimuli belonging to the same level of each factor (category,
186 reward), and no more than 3 distractors appeared in a row. For each image, participants indicated
187 whether the image was ALT (“old”, presented during the fMRI task) or NEU (“new”). “Old” judgments
188 were followed up by a choice between ERINNERT (“remember”), BEKANNT (“know”) or GERATEN
189 (“guess”). This is an established procedure to distinguish between two processes thought to
190 contribute to recognition memory: Recollection and familiarity (Tulving, 1985; Yonelinas et al., 2010).
191 Participants were carefully instructed to only indicate “remember” if they had a vivid recollection of
192 the image, including recall of contextual information. This was followed by two source memory tasks,
193 consisting of forced-choice screens for the frame colour and for the reward magnitude. On the other
194 hand, “new” judgments were followed up by a choice between SICHER (“sure”) and GERATEN
195 (“guess”), without the frame and reward screens. All judgments were self-paced except the initial
196 “old”/“new” judgment (4s).

197 *Conditions of interest*. In the encoding task, we manipulated item category (OB, object; SC, scene), and
198 reward (HI, high; LO; low), resulting in 4 combinations: OB-HI, OB-LO, SC-HI, SC-LO. The “old”/“new”
199 choices from the day 2 recognition phase were then used to back-sort the trials from the day 1

200 encoding phase into the following conditions of interest: OB-HI-H (object – high reward – hit), OB-HI-
201 M (object – high reward – miss), OB-LO-H (object – low reward – hit), OB-LO-M (object – low reward
202 – miss), SC-HI-H (scene – high reward – hit), SC-HI-M (scene – high reward – miss), SC-LO-H (scene –
203 low reward – hit), and SC-LO-M (scene – low reward – miss).

204 2.3 Behavioural analyses

205 For the encoding task, we analysed the proportion of trials in which participants correctly identified
206 the reward magnitude, calculated separately for each encoding condition (OB-HI, OB-LO, SC-HI, SC-
207 LO). These proportions were then submitted to a two-way repeated measures ANOVA with the factors
208 category and reward. For the recognition task, we calculated corrected recognition (CR) as the hit rate
209 (proportion of “old” responses for targets) minus the false alarm rate (proportion of “old” responses
210 to distractors, calculated separately for object and scene distractors). Additionally, from the
211 distributions of “remember” and “know” responses, we calculated estimates for recollection and
212 familiarity using the formula described in (Yonelinas and Jacoby, 1995). CR, recollection, and
213 familiarity were calculated separately for each encoding condition (OB-HI, OB-LO, SC-HI, SC-LO) and
214 submitted to two-way repeated measures ANOVAs with the factors category and reward. Similar
215 analyses were conducted on the source memory responses for frame colour ($source_{frame}$) and reward
216 magnitude ($source_{reward}$). As source memory involves retrieval of contextual detail, which is usually
217 associated with recollection (Eichenbaum et al., 2007), we conducted source memory analyses only
218 for recollected (“remember”) trials.

219 2.4 MRI acquisition

220 The study was scanned on a Siemens Tim Trio 3T MRI scanner using a 32-channel head coil. First, a
221 high-resolution T1-weighted structural image was scanned (MPRAGE, 1mm isotropic voxels). Then, six
222 functional runs were acquired using a T2*-weighted gradient-echo, echo-planar pulse sequence (40
223 interleaved slices, 1.5x1.5mm in-plane resolution, 2mm slice thickness with 20% distance factor,
224 TR=1800ms, TE=30ms, multiband factor=2, PAT factor (GRAPPA)=2, 260 volumes per run). Slices were

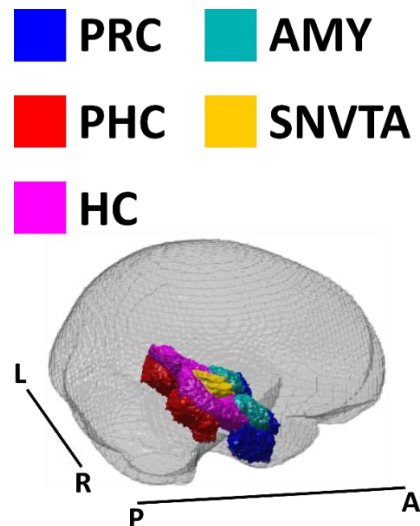
225 oriented in parallel to the AC-PC line and adjusted to optimise PFC coverage, with the field of view
226 covering nearly the whole brain excepting very superior frontal and parietal cortex. The first 5 images
227 of each functional run were discarded to allow for magnetic field stabilisation. Additionally, a 3D
228 magnetisation transfer (MT) FLASH structural image was acquired (1mm isotropic voxels) after the
229 functional runs.

230 2.5 fMRI preprocessing and analysis

231 *Strategy.* To account for the interindividual variability of MTL anatomy (Pruessner et al., 2002), our
232 main analyses were carried out in individual space within bilateral regions of interest (ROIs). These
233 encompassed the MTL subregions HC, PRC, and PHC, and additionally AMY and SNVTA (see Figure 2).
234 The MTL and AMY ROIs were manually segmented on each participant's T1 image using established
235 landmarks (Insausti et al., 1998; Pruessner et al., 2000, 2002). Given previous findings that object and
236 scene selectivity changes gradually along the MTL cortex axis (Litman et al., 2009; Liang et al., 2013),
237 to optimise category selectivity we discarded the putative transition zone (posterior PRC and anterior
238 PHC) in line with previous studies (Staresina et al., 2011, 2012, 2013; Schultz et al., 2019). The SNVTA
239 ROI was manually segmented on each participant's MT image as described in (Bunzeck and Düzel,
240 2006). In addition to the ROI analyses, control analyses were carried out on a voxel-wise level in
241 Montreal Neurological Institute (MNI) space.

242 *fMRI analysis pipeline.* Functional runs were first corrected for differences in slice acquisition time,
243 then realigned and unwrapped to correct for movement and movement-related distortions using
244 algorithms implemented in SPM12 (Wellcome Trust Centre for Neuroimaging, London, UK;
245 <http://www.fil.ion.ucl.ac.uk/spm/>). The structural T1 image was coregistered to the mean functional
246 volume using SPM12, and alignment was further improved using boundary-based registration as
247 implemented in FSL `epi_reg`. The MT image was then coregistered to the T1 using SPM12. First-level
248 statistical analyses (see below for details) were carried out on the non-normalised, unsmoothed data.
249 For the ROI analyses, the ROIs were resampled to functional space, and first-level beta values were

250 averaged across all voxels of each ROI. For the additional voxel-wise analyses, the T1 images were
251 segmented into grey matter, white matter, and cerebrospinal fluid using SPM12. Deformation fields
252 from this step were then used for MNI normalisation of the first-level beta images, and the normalised
253 beta images were resampled to a 1mm isotropic voxel size, and smoothed with a Gaussian kernel
254 (6mm full width at half maximum).



255
256 **Figure 2. ROIs.** Single-participant regions of interest were MNI-normalised, averaged over the full sample (n=39),
257 and thresholded at 0.5. Here they are visualised within the standard SPM12 brain mask (mask_ICV.nii).
258 Abbreviations: PRC: perirhinal cortex, PHC: parahippocampal cortex, HC: hippocampus, AMY: amygdala, SNVTA:
259 substantia nigra/ventral tegmental area, A: anterior, P: posterior, R: right, L: left.

260 *fMRI statistics.* First-level general linear models were set up in SPM12. The six functional runs were
261 concatenated. To account for this, the high-pass filter (128s) and autoregressive model AR(1) were
262 adapted, and session constants included in the model. For our main analyses (model 1), the following
263 conditions of interest were modelled: OB-HI-H, OB-HI-M, OB-LO-H, OB-LO-M, SC-HI-H, SC-HI-M, SC-
264 LO-H, SC-LO-M. Conditions were modelled as impulse regressors using a canonical hemodynamic
265 response function (HRF). Each trial phase (cue, choice, outcome) was modelled separately, and
266 subsequent analyses were focused on the cue phase only. Additional regressors of no interest were
267 included to model error trials, separately for object and scene trials. Error trials were defined as
268 incorrect or no response during the Incidental Encoding Task, and/or no response during the old/new

269 choice of the Recognition Task. Model 2 was set up identically, with the exception that the conditions
270 of interest did not include the memory factor (hence, OB-HI, OB-LO, SC-HI, SC-LO). For the ROI analyses
271 (model 1), the resulting beta images for each condition of interest were averaged across voxels of each
272 participant's ROIs, before being submitted to a group-level four-way repeated-measures ANOVA with
273 the factors region, category, reward, and subsequent memory. Where appropriate, Greenhouse-
274 Geisser correction was applied. Follow-up analyses were then carried out within each ROI. For the
275 voxel-wise analyses (model 2), normalised, smoothed beta maps were submitted to a second-level
276 random effects analysis (flexible factorial as implemented in SPM12) that included the factors
277 category and reward as well as a subject factor. The resulting brain activation maps were corrected
278 for multiple comparisons using peak-level family-wise error correction within a study-specific MNI
279 brain mask consisting of the following: (i) the manually delineated masks of HC and SNVTA, normalized
280 to MNI space and averaged over the full sample ($n=39$), thresholded at 0.5, and (ii) an existing mask
281 from the Rangel Neuroeconomics Laboratory (www.rnl.caltech.edu/resources/index.html), which
282 contains brain regions consistently implicated in reward processing including vmPFC, VS, and posterior
283 cingulate cortex (PCC) (Bartra et al., 2013; Clithero and Rangel, 2014).

284 **3 Results**

285 3.1 Behavioural results

286 *Incidental encoding task.* As expected, accuracy in the incidental encoding task was near ceiling (mean
287 [SEM] % accuracy: OB-HI: 98.5 [0.4], OB-LO: 98.4 [0.4], SC-HI: 97.0 [0.7], SC-LO: 97.8 [0.5]). A repeated
288 measures ANOVA with the factors category and reward showed a significant effect of category (higher
289 accuracy for object trials, $F_{(1,26)}=5.111$, $p=.032$), but no effect of reward or interaction of category and
290 reward ($p \geq .212$). Importantly, only trials with accurate responses in the encoding task were
291 considered in the behavioural analyses of recognition memory as well as the fMRI analyses.

292 *Recognition task.* For the recognition task, we expected improved subsequent memory for high-
293 reward compared to low-reward items for both objects and scenes (see Table 1 for overview). We

294 analysed corrected recognition (CR, hit rate minus false alarm rate) for each condition. A repeated
295 measures ANOVA yielded a main effect of reward (high > low, $F_{(1,26)}=18.297$, $p<.001$) and,
296 unexpectedly, a main effect of category (objects > scenes, $F_{(1,26)}=7.404$, $p=.011$) as well as an
297 interaction effect of category and reward ($F_{(1,26)}=9.961$, $p=.004$). Follow-up paired t-tests indicated that
298 high-reward objects were remembered better than low-reward objects (OB-HI>OB-LO, $t_{(26)}=5.568$,
299 $p<.001$), while high-reward scenes were remembered better than low-reward scenes on a trend level
300 only (SC-HI>SC-LO, $t_{(26)}=1.759$, $p=.090$). Hence, the observed interaction effect indicates a greater
301 reward enhancement of object memory compared to scene memory. We also explored whether these
302 results reflected a general difference between objects and scenes, e.g. due to systematic differences
303 in visibility or memorability between the two categories. Such a difference should be apparent in both
304 the high-reward and low-reward condition. However, the difference between objects and scenes was
305 only significant in the high-reward (OB-HI vs. SC-HI, $t_{(26)}=3.590$, $p=.001$), but not in the low-reward
306 condition (OB-LO vs. SC-LO, $t_{(26)}=0.596$, $p=.556$), indicating that the observed main effect of category
307 was driven by the interaction effect.

308 Additional analyses were conducted to explore whether the observed memory effects were specific
309 to a memory process (recollection or familiarity, see Materials and Methods) or sample (memory
310 subsample as in the analyses above, $n=27$, or full sample, $n=39$). Importantly, all memory measures
311 (CR, recollection, familiarity) at both sample sizes showed the observed interaction between category
312 and reward in the same direction, with greater reward enhancement of object memory than scene
313 memory (memory subsample: $F_{(1,26)}\geq 9.961$, $p\leq .004$; full sample: $F_{(1,38)}\geq 6.372$, $p\leq .018$, see Table 1).

Outcome	OB-HI	OB-LO	SC-HI	SC-LO	Effect of category	Effect of reward	Interaction
CR ¹	0.382 (0.023)	0.295 (0.017)	0.317 (0.020)	0.287 (0.018)	$F_{(1,26)}=7.404,$ $p=0.011$	$F_{(1,26)}=18.297,$ $p<0.001$	$F_{(1,26)}=9.961,$ $p=0.004$
CR ²	0.330 (0.022)	0.222 (0.023)	0.254 (0.023)	0.231 (0.020)	$F_{(1,38)}=4.386,$ $p=0.043$	$F_{(1,38)}=29.980,$ $p<0.001$	$F_{(1,38)}=26.278,$ $p<0.001$
Recollection ¹	0.194 (0.021)	0.124 (0.015)	0.138 (0.021)	0.117 (0.018)	$F_{(1,26)}=3.209,$ $p=0.085$	$F_{(1,26)}=18.711,$ $p<0.001$	$F_{(1,26)}=10.018,$ $p=0.004$
Recollection ²	0.173 (0.017)	0.103 (0.012)	0.118 (0.016)	0.106 (0.014)	$F_{(1,38)}=3.903,$ $p=0.055$	$F_{(1,38)}=19.582,$ $p<0.001$	$F_{(1,38)}=13.536,$ $p<0.001$
Familiarity ¹	1.016 (0.092)	0.800 (0.075)	0.836 (0.077)	0.777 (0.072)	$F_{(1,26)}=1.949,$ $p=0.175$	$F_{(1,26)}=9.482,$ $p=0.005$	$F_{(1,26)}=6.372,$ $p=0.018$
Familiarity ²	0.868 (0.078)	0.598 (0.077)	0.663 (0.074)	0.584 (0.071)	$F_{(1,38)}=3.376,$ $p=0.074$	$F_{(1,38)}=19.642,$ $p<0.001$	$F_{(1,38)}=14.603,$ $p<0.001$

314 **Table 1.** Overview over recognition memory results, demonstrating consistent effects of our experimental
315 manipulations across all outcome measures at both sample sizes. The table contains mean (SEM) values for all
316 four conditions as well as F and p values from two-way repeated measures ANOVAs with the factors category
317 and reward.¹Memory sample ($n=27$), ²full sample ($n=39$).

318 *Source memory.* Finally, we analysed the responses to the source memory tasks, in which participants
319 indicated which frame colour ($source_{frame}$) and reward magnitude ($source_{reward}$) had been associated
320 with each image. Note that source memory analyses were conducted for “remember” trials only,
321 which reduced the memory sample to 19 participants with at least four “remember” responses per
322 condition, or fewer than half of the original sample size. For $source_{frame}$, we analysed the proportion
323 of correct responses (mean [SEM] $source_{frame}$: OB-HI: 0.587 [0.031], OB-LO: 0.474 [0.026], SC-HI: 0.578
324 [0.044], SC-LO: 0.494 [0.044]). $source_{frame}$ exceeded chance performance for OB-HI ($t_{(18)}=2.774,$
325 $p=.013$) and, on a trend level, for SC-HI ($t_{(18)}=1.766, p=.094$), but not for OB-LO or SC-LO (all $p\geq 0.340$).
326 A repeated measures ANOVA with the factors category and reward yielded a main effect of reward
327 (high > low, $F_{(1,18)}=11.497, p=.003$, all other $p\geq 0.675$). Paired t-tests revealed a significant difference

328 between OB-HI and OB-LO ($t_{(18)}=3.307$, $p=.004$), but not between SC-HI and SC-LO ($p=.137$). For
329 source_{reward}, we analysed the proportion of trials in which participants indicated that an image had
330 been paired with high reward (mean [SEM] source_{reward}: OB-HI: 0.765 [0.041], OB-LO: 0.689 [0.052],
331 SC-HI: 0.737 [0.040], SC-LO: 0.633 [0.056]). Note that, as high memory confidence may in itself be
332 rewarding (Schwarze et al., 2013), these trials are biased towards “high reward” source responses in
333 all conditions, and chance level is therefore meaningless. A repeated measures ANOVA with the
334 factors category and reward yielded a main effect of reward (high > low, $F_{(1,18)}=10.962$, $p=.004$, all
335 other $p \geq 0.234$) such that participants were more likely to indicate “high reward” to high-reward than
336 to low-reward items. Paired t-tests indicate that this was the case for both OB-HI vs. OB-LO ($t_{(18)}=2.432$,
337 $p=.026$) and SC-HI vs. SC-LO ($t_{(18)}=2.110$, $p=.049$).

338 3.2 fMRI: ROI results – Category, subsequent memory, and the role of reward

339 *Overall analysis.* First, we analysed whether reward modulated memory encoding for objects and
340 scenes in our ROIs (model 1, memory subsample). Beta values from our conditions of interest (OB-HI-
341 H, OB-HI-M, OB-LO-H, OB-LO-M, SC-HI-H, SC-HI-M, SC-LO-H, SC-LO-M; with H: hit, M: miss in the
342 subsequent recognition phase) were averaged across all voxels of each ROI (HC, PRC, PHC, AMY,
343 SNVTA) and submitted to a four-way repeated-measures ANOVA with the factors ROI, category,
344 reward, and subsequent memory. We report interactions of the ROI factor with any experimental
345 factors. This analysis revealed significant two-way interactions of ROI with category
346 ($F_{(1.75,45.50)}=133.036$, $p<.001$) and memory ($F_{(2.85,74.02)}=9.819$, $p<.001$), a three-way interaction of ROI
347 with category and memory ($F_{(2.26,58.75)}=6.493$, $p<.001$), and a four-way interaction of ROI with category,
348 reward, and memory ($F_{(2.26,58.75)}=3.228$, $p=.020$). The interaction of ROI with reward was marginally
349 significant ($F_{(2.26,58.75)}=2.880$, $p=.051$). There was no other interaction effects involving the ROI factor
350 (all $p \geq .511$).

351 Given the significant four-way interaction of ROI, category, reward, and memory, we computed
352 individual three-way ANOVAs within each ROI as well as follow-up tests where appropriate. A
353 summary of results for each ROI is given in Figure 3A.

354 *HC*. The HC showed a significant main effect of category (scenes > objects, $F_{(1,26)}=70.192$, $p<.001$). No
355 other main effect or interaction was significant (all $p\geq.207$).

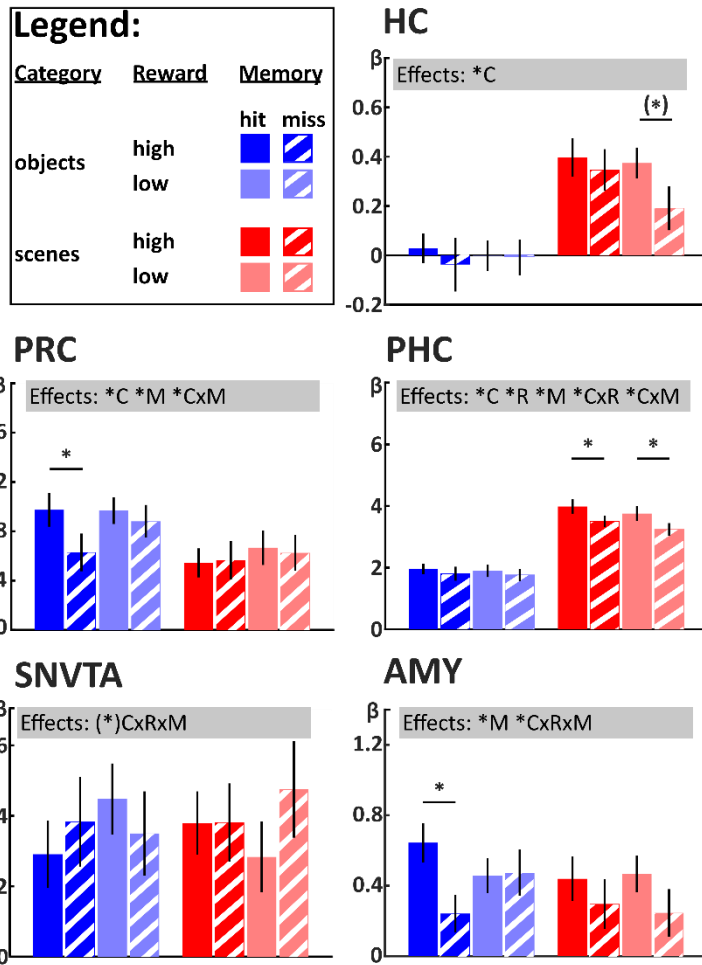
356 *PRC*. The PRC showed significant main effects of category (objects > scenes, $F_{(1,26)}=10.557$, $p=.003$) and
357 subsequent memory (hits > misses, $F_{(1,26)}=5.840$, $p=.023$). Importantly, the interaction of category and
358 subsequent memory was also significant ($F_{(1,26)}=6.558$, $p=.017$), indicating that subsequent memory
359 effects were stronger for objects than scenes. No other main or interaction effect was significant (all
360 $p\geq.118$). To explore which conditions showed subsequent memory effects, we additionally computed
361 paired t-tests between subsequent hits and misses for OB-HI, OB-LO, SC-HI, and SC-LO. Notably, only
362 the subsequent memory effect for OB-HI was significant ($t_{(26)}=3.036$, $p=.005$, all other $p\geq.412$).

363 *PHC*. The PHC showed significant main effects of category (scenes > objects, $F_{(1,26)}=153.697$, $p<.001$)
364 and subsequent memory (hits > misses, $F_{(1,26)}=29.407$, $p<.001$). Importantly, the interaction of
365 category and subsequent memory was also significant ($F_{(1,26)}=6.372$, $p=.018$), indicating that
366 subsequent memory effects were stronger for scenes than objects. Additionally, we observed a
367 significant main effect of reward (high > low, $F_{(1,26)}=10.391$, $p=.003$), as well as a significant interaction
368 effect of category and reward (greater reward effect for scenes than objects, $F_{(1,26)}=4.658$, $p=.040$) –
369 note however the lack of a significant interaction of these effects with the ROI factor in the overall
370 analysis above. Again, we explored which conditions showed subsequent memory effects using
371 pairwise t-tests between subsequent hits and misses. We observed significant effects of subsequent
372 memory for both SC-HI and SC-LO ($t_{(26)}=[3.788\ 3.998]$, $p<.001$), but not for either OB-HI or OB-LO (all
373 $p\geq.181$).

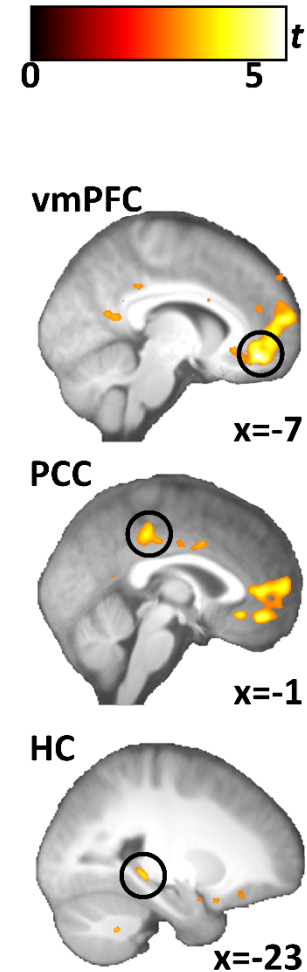
374 AMY. The AMY showed a significant main effect of subsequent memory (hits > misses, $F_{(1,26)}=7.040$,
375 $p=.013$) as well as a significant three-way interaction of category, reward, and subsequent memory
376 ($F_{(1,26)}=4.369$, $p=.047$). To identify the constituents of this three-way interaction, we computed
377 separate two-way ANOVAs (reward, memory) for objects and scenes, respectively, assessing the
378 interaction effects only. AMY showed a significant interaction effect of reward and subsequent
379 memory for objects ($F_{(1,26)}=7.183$, $p=.013$) but not scenes ($p=.651$). Again, we explored which
380 conditions showed subsequent memory effects using pairwise t-tests between subsequent hits and
381 misses. Notably, only the subsequent memory effect for OB-HI was significant ($t_{(26)}=3.385$, $p=.002$, all
382 other $p \geq .101$).

383 SNVTA. Contrary to our expectations, the SNVTA showed no significant main effects or interactions,
384 save for a trend-level three-way interaction of category, reward, and subsequent memory
385 ($F_{(1,26)}=2.957$, $p=.097$, all other $p \geq .315$). In particular, neither the main effect of reward nor the
386 interaction of reward and subsequent memory were significant (all $p \geq .651$).

A ROI results (model 1)



B high > low (model 2)



387

388 **Figure 3.** Overview over fMRI results. A. Average beta values for each condition of model 1 (memory sample,
 389 n=27) in each of the 5 ROIs. Grey boxes indicate results from individual three-way repeated measures ANOVA
 390 with the factors category (C), reward (R), and subsequent memory (M). * $p < .05$, (*) $p < .1$. Error bars indicate SEM.
 391 B. Voxel-wise activity for the high > low reward contrast in model 2 (full sample, n=39). Display threshold $p < .001$,
 392 $k \geq 5$ voxels. Statistical maps are projected onto the normalised, averaged T1.

393 3.3 fMRI: Voxel-wise effects of reward (model 2)

394 The previous sections demonstrated clear effects of our reward manipulation on behavioural
 395 measures of memory, for objects more so than scenes. The neural effects of reward on memory
 396 formation showed a similar asymmetry. Specifically, subsequent memory effects for objects in PRC
 397 and AMY were only significant for high-reward objects, while subsequent memory effects for scenes

398 in PHC were significant for both high-reward and low-reward scenes. Against our expectations,
399 however, we did not observe main effects of reward, or interaction effects of reward with subsequent
400 memory that were independent of category, in either HC or SNVTA. Therefore, as a control analysis,
401 we tested whether our task succeeded in engaging the reward network, and whether these effects
402 differed between objects and scenes. We used a reduced model with two factors (category, reward)
403 and tested for main effects of reward as well as interaction effects of reward and category. By
404 disregarding the memory factor, we made use of the increased experimental power of the full sample
405 ($n=39$). Additionally, we used a voxel-wise approach in MNI-normalised data to be able to identify
406 small clusters of activity, which may not be picked up in an ROI analysis. Effects are reported for, and
407 corrected for multiple comparisons within, a brain mask comprising vmPFC, VS, PCC, HC, and SNVTA
408 (see Materials and Methods for details).

409 Table 2 gives an overview of the observed voxel-wise effects located inside the mask. The high > low
410 reward contrast revealed clusters of activity with peaks in vmPFC (MNI [x y z]: [-7 42 -12], $t_{(38)} = 5.74$,
411 $p_{FWE} < .001$), PCC ([-1 -32 42], $t_{(38)} = 4.4$, $p_{FWE} = .024$), and left posterior HC ([-23 -34 -5], $t_{(38)} = 4.40$,
412 $p_{FWE} = .037$). Additional clusters in bilateral HC, VS, and vmPFC emerged at an uncorrected threshold of
413 $p < .001$. Notably, there was no activity in the SNVTA, even at a relaxed uncorrected threshold of $p < .01$.
414 The objects x reward interaction ([OB-HI>OB-LO]>[SC-HI>SC-LO]) yielded clusters in vmPFC only at an
415 uncorrected threshold of $p < .001$ (all $p_{FWE} \geq .199$). For the scene x reward interaction ([SC-HI>SC-
416 LO]>[OB-HI>OB-LO]), a cluster in right HC was marginally significant ([30 -32 -2], $t_{(38)} = 4.11$, $p_{FWE} = .061$).
417 Additionally, clusters in right HC and SNVTA emerged at an uncorrected threshold of $p < .001$ (see Table
418 2).

419 Lastly, as main effects in a factorial design may be driven by interaction effects, we identified brain
420 regions in which both the OB-HI > OB-LO and SC-HI > SC-LO contrast exceeded a threshold of $p < .001$
421 uncorrected (inclusive masking approach). This analysis yielded clusters located in the vmPFC (see
422 Table 2).

Contrast	Region	# voxels	x	y	z	t	p_{FWE}
Main effect: High > low	vmPFC	5063	-7	42	-12	5.74	<.001*
		8	-25	28	-17	3.65	.232
	PCC	416	-1	-32	42	4.40	.024*
		189	-23	-34	-5	4.27	.037*
	L HC	79	-33	-27	-16	3.75	.178
		16	-32	-13	-19	3.61	.257
		16	-17	-15	-26	3.59	.271
	R HC	109	20	-29	-13	3.90	.116
		66	26	-18	-21	3.84	.141
		23	32	-16	-15	3.43	.383
VS	1	5	10	-1	3.70	.204	
		2	12	-1	3.27	.525	
Interaction: (OB-HI > OB-LO) > (SC-HI > SC-LO)	vmPFC	47	-5	25	-14	3.71	.199
		5	-6	26	-11	3.54	.304
		28	0	38	-12	3.45	.369
		1	-2	32	-23	3.19	.598
Interaction: (SC-HI > SC-LO) > (OB-HI > OB-LO)	R HC	54	30	-32	-2	4.11	.061(*)
		28	35	-22	-14	3.54	.304
Inclusive masking ¹ : OB-HI>OB-LO and SC-HI>SC-LO	vmPFC	8	-7 (-7)	46 (47)	-15 (-15)	4.27 (3.29)	.038 (.509)
		48	-8 (-8)	50 (50)	-5 (-3)	3.97 (3.42)	.095 (.395)
		24	-7 (-7)	41 (41)	-6 (-4)	3.75 (3.39)	.181 (.419)
		26	-1 (0)	44 (43)	4 (4)	3.73 (3.60)	.187 (.264)
		1	-2 (-2)	52 (52)	6 (6)	3.47 (3.17)	.353 (.620)
	4	-4 (-6)	54 (54)	4 (4)	3.44 (3.22)	.376 (.570)	

423 **Table 2.** Overview of significant clusters from the voxel-wise analysis within a brain mask comprising vmPFC, VS,
424 PCC, HC, and SNVTA (see Materials and Methods). Uncorrected threshold $p < .001$, cluster threshold: 5 voxels
425 total including voxels outside mask. # voxels refers to the number of voxels within the mask. p_{FWE} refers to the
426 p value of the peak voxel after family-wise error correction within the brain mask. ¹For the inclusive masking
427 analysis, we report coordinates and statistical values for OB-HI>OB-LO inclusively masked with SC-HI>SC-LO
428 (outside brackets), and vice versa (inside brackets). * $p_{FWE} < .05$, (*) $p_{FWE} < .1$.

429 **4 Discussion**

430 *Summary.* The present study's goals were twofold: One, to investigate whether the documented
431 dichotomy between PRC and PHC for object and scene memory extends to item encoding, and two,
432 to investigate whether reward modulates item encoding of objects and scenes. Behaviourally, high
433 reward predominantly enhanced subsequent memory for objects in both model-free (CR) and model-
434 based (recollection, familiarity) outcome measures. Evidence for reward enhancement of memory for
435 scenes, on the other hand, was modest. Importantly, neural activity in PRC and PHC predicted
436 subsequent item memory for objects and scenes, respectively. Furthermore, neural encoding activity
437 exhibited an asymmetry that mirrored our behavioural findings: Encoding activity in AMY was selective
438 for high-reward objects, with a similar (albeit non-significant) pattern in PRC, while encoding activity
439 in PHC did not differ between high- and low-reward scenes. Finally, reward-related brain activity,
440 regardless of stimulus category, was centred on the vmPFC.

441 *Category-specific incidental item encoding in the MTL cortex.* We observed opposite patterns of
442 category-specific incidental item encoding in PRC and PHC, with object encoding in PRC and scene
443 encoding in PHC. Category specificity as an organising principle for the functional architecture of the
444 MTL has been shown in a number of imaging studies for processes including perception (Litman et al.,
445 2009; Liang et al., 2013; Berron et al., 2018), associative encoding (Awipi and Davachi, 2008; Staresina
446 et al., 2011), associative retrieval (Staresina et al., 2012, 2013; Mack and Preston, 2016; Schultz et al.,
447 2019), working memory (Libby et al., 2014), short-term memory reactivation (Schultz et al., 2012), and
448 recognition memory (Martin et al., 2013; Kafkas et al., 2017). However, to our knowledge, our study
449 is the first to demonstrate a double dissociation between PRC and PHC for category-specific item
450 encoding, thereby filling an important gap in the literature and supporting a model of MTL function
451 that draws on anatomical connectivity to predict functional specialisation (Davachi, 2006; Eichenbaum
452 et al., 2007).

453 While scene-specific item encoding has been previously observed in PHC and the larger
454 parahippocampal place area (Prince et al., 2009; Preston et al., 2010), the same cannot be said for
455 object-specific item encoding in PRC. In their 2010 paper, Preston and colleagues investigated
456 incidental encoding of faces and scenes during a target detection task, observing subsequent memory
457 effects for scenes in PHC, and subsequent memory effects for both faces and scenes in PRC (note that
458 restricting the analysis to face-selective voxels in PRC yielded a response pattern consistent with face-
459 specific encoding, however, the interaction between category and memory was not significant). In
460 contrast, PRC in our study did not show a subsequent memory effect for scenes at all. Preston and
461 colleagues' study design differs from ours in a number of ways. They assessed recognition memory
462 immediately after the encoding task rather than after a one-day delay, and their participants were
463 aware that they would be tested on their recognition memory as the study included two encoding-
464 recognition cycles. Potentially, intentional encoding leads to increased elaboration of the encoding
465 stimuli and therefore to additional recruitment of PRC during scene encoding (however, memory
466 performance [CR, hits minus false alarms] is roughly matched between the two studies). Additionally,
467 we note that on a descriptive level, our object encoding effect in PRC appears to be specific to high-
468 reward objects. It is possible that while incidental encoding does not engage PRC in a category-specific
469 fashion, adding a motivational factor such as reward does. We will return to this line of thought later
470 in the discussion.

471 We observed category specificity in the MTL cortex during item encoding. Previous work has
472 demonstrated such effects for associative encoding (Awipi and Davachi, 2008; Staresina et al., 2011).
473 It has been argued (Davachi, 2006; Eichenbaum et al., 2007) that item memory is a distinct process
474 from associative, relational, or context memory. In this view, item memory stems from object-related
475 processing in the anterior MTL cortex (PRC), and is associated with the subjective sensation of
476 familiarity, whereas associative memory is related to spatial and multi-modal processing in the
477 posterior MTL cortex (PHC) and HC, and associated with the subjective sensation of recollection.
478 Nevertheless, we observed scene-specific item memory in the PHC. Notably, the present results as

479 well as prior work (Awipi and Davachi, 2008; Staresina et al., 2011, 2012, 2013; Martin et al., 2013;
480 Schultz et al., 2019) suggest that category specificity in the MTL cortex emerges even if memory
481 processes are held constant. Thus, category specificity is an essential commonality between different
482 memory processes, even if object and spatial processing may map preferentially onto item and
483 associative/ recollective memory, respectively (Davachi, 2006; Eichenbaum et al., 2007). However,
484 PRC and PHC also distinguish between item and context recall even when the stimulus material is
485 being held constant (Wang et al., 2013), and studies have shown dissociable effects of experimental
486 manipulations on different memory processes (Wittmann et al., 2005, 2011; Bisby and Burgess, 2013;
487 McCullough et al., 2015; Madan et al., 2017; Ritchey et al., 2019). This implies that process
488 dissociations may have additional predictive value for MTL function that go beyond a distinction based
489 on stimulus categories. Future research may determine how exactly category specificity maps onto
490 process dissociations.

491 *Asymmetric effects of reward on behavioural and neural measures of memory.* We observed a
492 preferential enhancement of object memory by reward, accompanied by a similar asymmetry in the
493 neural data: Subsequent memory effects in AMY were selective for high-reward objects, with a similar,
494 albeit non-significant, pattern in PRC, while PHC showed subsequent memory effects for both high-
495 and low-reward scenes. (Note that this effect is unlikely to reflect a general difference between object
496 and scene encoding, for example due to differences in salience or luminance between the categories,
497 since memory for low-reward objects did not differ from memory for low-reward scenes.) The clear
498 behavioural bias for high-reward objects in the present study is surprising, given that previous studies
499 have shown motivational effects on encoding when only scenes were used (Adcock et al., 2006;
500 Bunzeck et al., 2012; Spaniol et al., 2014; Rouhani et al., 2018) but see e.g. (Steiger and Bunzeck, 2017).
501 One potential reason for this could be memory performance. The incidental encoding task in the
502 present study yielded a comparably low memory performance that was based mainly on familiarity
503 rather than recollection, while reward effects on memory have been associated with recollection or

504 high-confidence hits (Wittmann et al., 2005, 2011; Adcock et al., 2006). It is therefore possible that a
505 more robust reward effect on scenes would have emerged with higher proportions of recollection.

506 More intriguingly, the observed behavioural and neural asymmetry may be explained within an
507 existing framework of memory, the PMAT framework (Ranganath and Ritchey, 2012; Ritchey et al.,
508 2015). This theory poses that two large-scale brain networks underlie memory, with an anterior-
509 temporal (AT) system, including PRC and AMY, representing objects and their motivational
510 significance, and a posterior-medial (PM) system, including PHC, representing (spatial) context.
511 Indeed, PRC and AMY have been associated with acquiring stimulus-reward associations (Liu and
512 Richmond, 2000; Liu et al., 2000; Rudebeck et al., 2017). In this view, the HC may play a role both in
513 sharpening and integrating information received from these systems (Ranganath and Ritchey, 2012;
514 Ritchey et al., 2015). Previously, the HC, in interplay with SNVTA, has also been implicated in reward
515 enhancement of episodic encoding of highly confident or recollected items (Wittmann et al., 2005;
516 Adcock et al., 2006). Here, in a task that yielded low memory performance based mainly on familiarity,
517 we observed a behavioural advantage of high-reward object encoding and subsequent-memory
518 effects for high-reward objects in two putative AT regions, AMY and PRC, but not in HC or SNVTA. It is
519 possible that the AT system is sufficient for supporting reward enhancement of low-confident object
520 memory. But if HC integrates information from both streams, then perhaps item memory for scenes,
521 processed preferably along regions of the PM system, is less likely to receive an advantage from
522 motivational factors unless it reaches HC's recollection threshold. Indeed, we are not aware of studies
523 showing motivational enhancement of low-confident scene memory, and it is worth pointing out that
524 our source memory effects, computed for recollected trials only, appear more balanced between
525 objects and scenes. These considerations are somewhat speculative and require further research. One
526 prediction would be that the observed asymmetry between reward enhancement of objects and
527 scenes decreases at higher rates of highly confident memory responses.

528 In a recent study, Ritchey and colleagues (2019) found that PRC and AMY supported encoding of
529 emotional over neutral items, whereas the PHC and HC supported context encoding for both
530 emotional and neutral items, but were not engaged in item encoding. Behavioural data showed a
531 similar asymmetry: Emotion enhanced item memory but did not affect context memory. Item and
532 context processing in the MTL cortices have been previously linked to their putative roles in object-
533 related and spatial processing (Davachi 2006, Eichenbaum 2007), facilitating parallels between Ritchey
534 et al.'s results and ours. Modulation of item encoding by motivational factors such as emotion or, in
535 our case, reward, may not require the HC, but instead be carried by PRC and AMY (note, however,
536 that in this study, the items consisted of scene images, and the context consisted of tasks solved during
537 encoding).

538 *Category specificity and category independence in the HC.* The HC showed a robust effect of scene
539 viewing compared to object viewing. While some accounts of MTL see the HC's role in memory as
540 category-independent (Davachi, 2006; Eichenbaum et al., 2007), others emphasise the role of HC in
541 spatial (Moser et al., 2008; Hartley et al., 2014) and scene processing (Maguire and Mullally, 2013).
542 Moreover, while we observed a pronounced scene effect in HC in the present dataset, an earlier study
543 - using a similar stimulus set, albeit a different (intentional, associative) encoding task - did not (Schultz
544 et al., 2019). Recent work indicates that different subfields of HC may be differentially sensitive to
545 both task and stimuli (Dalton et al., 2018). Targeted high-resolution investigations of HC subfields may
546 further specify the circumstances in which HC responses are category-specific or category-
547 independent. We also did not observe overall effects of subsequent memory in HC. HC has been
548 implicated in recollective, or highly confident recognition memory (Wittmann et al., 2005; Adcock et
549 al., 2006; Eichenbaum et al., 2007). Memory performance in the present study was overall low, which
550 may explain why neural encoding processes were mainly observed in the MTL cortex, thought to
551 support familiarity (Eichenbaum et al., 2007; Martin et al., 2013), rather than HC.

552 *Reward-related processing in the MTL and beyond.* Against our hypotheses, we did not observe reward
553 responses in the SNVTA and only limited evidence for reward processing in the HC and VS. Activity in
554 the SNVTA and VS, a major target region of the SNVTA's dopaminergic projections (Haber and Knutson,
555 2010), has been shown to vary with prediction error (Schultz, 1998; O'Doherty et al., 2003; Pessiglione
556 et al., 2006; D'Ardenne et al., 2008; Rolls et al., 2008). Hence, the task developed for the present study
557 aimed to shift the prediction error and therefore the putative dopaminergic response to the
558 presentation of the encoding cue (see Materials and Methods). It is, however, not a learning task, as
559 the reward contingencies were explicitly conveyed to the participants prior to each run. Diederer and
560 colleagues (Diederer et al., 2016) argued that SNVTA's role in adaptive prediction error coding may
561 be particularly pronounced in tasks that require learning of reward contingencies. While previous
562 studies have shown SNVTA engagement during encoding of stimuli in tasks that did not require such
563 learning (Wittmann et al., 2005; Adcock et al., 2006), future work may show whether SNVTA/VS
564 prediction error signalling in a reinforcement learning task covaries with successful episodic memory
565 encoding. So far, it has been demonstrated that encoding of *irrelevant* objects during cue presentation
566 actually interferes with striatal learning (Wimmer et al., 2014), but it is unclear whether the same
567 holds true for episodic encoding of the reward-predicting cues.

568 On the other hand, we observed robust reward signals in the vmPFC. The vmPFC is a major part of the
569 brain's reward system (Haber and Knutson, 2010), and thought to code a range of processes, including
570 subjective value (Kable and Glimcher, 2009; Hebscher and Gilboa, 2016). Intriguingly, it is also thought
571 to play a role in memory, namely the acquisition and utilisation of abstract knowledge structures, so-
572 called schemas (Hebscher and Gilboa, 2016). In our encoding task, participants had to match a
573 stimulus (e.g. an image of a coffee cup surrounded by a blue frame) to an existing abstract knowledge
574 structure (e.g. "objects surrounded by a blue frame signal high reward"). Memory schemas predicting
575 high reward may be encoded more deeply than schemas predicting low reward, leading to elevated
576 vmPFC engagement. Indeed, recent work implies that vmPFC is necessary for processing configural
577 objects in which a combination of features, but not one feature alone, signals their value (Pelletier

578 and Fellows, 2019). Similarly, in the present task, neither stimulus category nor frame colour, but only
579 their combination, signalled reward magnitude. Effects of high reward were observed in vmPFC for
580 both object and scene trials. While the vmPFC has been suggested as a convergence zone of the AT
581 and PM systems (Ranganath and Ritchey, 2012; Ritchey et al., 2015), anatomical connectivity between
582 that region and the MTL cortex varies along the anterior-posterior MTL axis (Kondo et al., 2005; Price,
583 2007; Kondo and Witter, 2014) and may be particularly pronounced for anterior MTL cortex (PRC,
584 entorhinal cortex) (Eichenbaum, 2017). However, anatomical labelling may not be directly comparable
585 between species (Price, 2007; Haber and Knutson, 2010), and resting-state connectivity in humans has
586 indicated preferential functional connectivity of the vmPFC with PHC rather than PRC (Kahn et al.,
587 2008). Therefore, a query for future work is whether vmPFC engagement during a reward task could
588 bias reward-related object encoding by modulating one MTL pathway over the other.

589 *Future directions.* The fate of a memory trace is not solely determined by neural processing during
590 encoding. For example, reward during encoding may enhance post-encoding consolidation processes,
591 by biasing recently-encoded memories for offline replay (Kumaran et al., 2016). Similarly, reward
592 associations acquired during encoding modulate brain activity during retrieval (Wolosin et al., 2012;
593 Elward et al., 2015). In sum, the observed behavioural effects of reward on object memory may have
594 been driven in part by neural processing outside the time window observed in the present study,
595 which may be addressed in future work.

596 *Conclusions.* In sum, we present novel evidence for a double dissociation between anterior and
597 posterior MTL cortex for incidental item encoding of objects and scenes, respectively. Additionally,
598 reward preferably modulated object rather than scene encoding, evident in behavioural measures and
599 anterior temporal lobe signalling. A potential limitation of our study lies in the comparatively low
600 memory performance, which was mainly based on familiarity rather than recollection. Future work
601 may further elucidate the neural mechanisms underlying the distinct effects of reward on the
602 encoding of different stimulus categories.

603

604 **5 References**

605 Adcock RA, Thangavel A, Whitfield-Gabrieli S, Knutson B, Gabrieli JDE (2006) Reward-motivated
606 learning: mesolimbic activation precedes memory formation. *Neuron* 50:507–517.

607 Amaral DG, Insausti R (1992) Retrograde transport of D-[3H]-aspartate injected into the monkey
608 amygdaloid complex. *Exp Brain Res* 88:375–388.

609 Awipi T, Davachi L (2008) Content-specific source encoding in the human medial temporal lobe. *J Exp*
610 *Psychol Learn Mem Cogn* 34:769–779.

611 Bartra O, McGuire JT, Kable JW (2013) The valuation system: a coordinate-based meta-analysis of
612 BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage* 76:412–
613 427.

614 Beckstead RM, Domesick VB, Nauta WJ (1979) Efferent connections of the substantia nigra and ventral
615 tegmental area in the rat. *Brain Res* 175:191–217.

616 Berron D, Neumann K, Maass A, Schütze H, Fließbach K, Kiven V, Jessen F, Sauvage M, Kumaran D,
617 Düzel E (2018) Age-related functional changes in domain-specific medial temporal lobe
618 pathways. *Neurobiol Aging* 65:86–97.

619 Berron D, Vieweg P, Hochkeppeler A, Pluta JB, Ding S-L, Maass A, Luther A, Xie L, Das SR, Wolk DA,
620 Wolbers T, Yushkevich PA, Düzel E, Wisse LEM (2017) A protocol for manual segmentation of
621 medial temporal lobe subregions in 7 Tesla MRI. *NeuroImage Clin* 15:466–482.

622 Bisby JA, Burgess N (2013) Negative affect impairs associative memory but not item memory. *Learn*
623 *Mem Cold Spring Harb N* 21:21–27.

624 Brady TF, Konkle T, Alvarez GA, Oliva A (2008) Visual long-term memory has a massive storage capacity
625 for object details. *Proc Natl Acad Sci U S A* 105:14325–14329.

626 Bunzeck N, Doeller CF, Dolan RJ, Düzel E (2012) Contextual interaction between novelty and reward
627 processing within the mesolimbic system. *Hum Brain Mapp* 33:1309–1324.

628 Bunzeck N, Düzel E (2006) Absolute coding of stimulus novelty in the human substantia nigra/VTA.
629 *Neuron* 51:369–379.

630 Burwell RD (2000) The parahippocampal region: corticocortical connectivity. *Ann N Y Acad Sci* 911:25–
631 42.

632 Burwell RD (2001) Borders and cytoarchitecture of the perirhinal and postrhinal cortices in the rat. *J*
633 *Comp Neurol* 437:17–41.

634 Burwell RD, Amaral DG (1998a) Cortical afferents of the perirhinal, postrhinal, and entorhinal cortices
635 of the rat. *J Comp Neurol* 398:179–205.

636 Burwell RD, Amaral DG (1998b) Perirhinal and postrhinal cortices of the rat: interconnectivity and
637 connections with the entorhinal cortex. *J Comp Neurol* 391:293–321.

- 638 Carmichael ST, Price JL (1995) Limbic connections of the orbital and medial prefrontal cortex in
639 macaque monkeys. *J Comp Neurol* 363:615–641.
- 640 Clithero JA, Rangel A (2014) Informatic parcellation of the network involved in the computation of
641 subjective value. *Soc Cogn Affect Neurosci* 9:1289–1302.
- 642 Dalton MA, Zeidman P, McCormick C, Maguire EA (2018) Differentiable Processing of Objects,
643 Associations, and Scenes within the Hippocampus. *J Neurosci Off J Soc Neurosci* 38:8146–
644 8159.
- 645 D’Ardenne K, McClure SM, Nystrom LE, Cohen JD (2008) BOLD responses reflecting dopaminergic
646 signals in the human ventral tegmental area. *Science* 319:1264–1267.
- 647 Davachi L (2006) Item, context and relational episodic encoding in humans. *Curr Opin Neurobiol*
648 16:693–700.
- 649 Davachi L, Mitchell JP, Wagner AD (2003) Multiple routes to memory: distinct medial temporal lobe
650 processes build item and source memories. *Proc Natl Acad Sci U S A* 100:2157–2162.
- 651 Diederer K, Spencer T, Vestergaard MD, Fletcher PC, Schultz W (2016) Adaptive Prediction Error
652 Coding in the Human Midbrain and Striatum Facilitates Behavioral Adaptation and Learning
653 Efficiency. *Neuron* 90:1127–1138.
- 654 Ding S-L et al. (2016) Comprehensive cellular-resolution atlas of the adult human brain. *J Comp Neurol*
655 524:3127–3481.
- 656 Doan TP, Lagartos-Donate MJ, Nilssen ES, Ohara S, Witter MP (2019) Convergent Projections from
657 Perirhinal and Postrhinal Cortices Suggest a Multisensory Nature of Lateral, but Not Medial,
658 Entorhinal Cortex. *Cell Rep* 29:617-627.e7.
- 659 Eichenbaum H (2017) Prefrontal-hippocampal interactions in episodic memory. *Nat Rev Neurosci*
660 18:547–558.
- 661 Eichenbaum H, Yonelinas AP, Ranganath C (2007) The medial temporal lobe and recognition memory.
662 *Annu Rev Neurosci* 30:123–152.
- 663 Elward RL, Vilberg KL, Rugg MD (2015) Motivated Memories: Effects of Reward and Recollection in the
664 Core Recollection Network and Beyond. *Cereb Cortex N Y N 1991* 25:3159–3166.
- 665 Haber SN, Knutson B (2010) The reward circuit: linking primate anatomy and human imaging.
666 *Neuropsychopharmacol Off Publ Am Coll Neuropsychopharmacol* 35:4–26.
- 667 Hartley T, Lever C, Burgess N, O’Keefe J (2014) Space in the brain: how the hippocampal formation
668 supports spatial cognition. *Philos Trans R Soc Lond B Biol Sci* 369:20120510.
- 669 Hebscher M, Gilboa A (2016) A boost of confidence: The role of the ventromedial prefrontal cortex in
670 memory, decision-making, and schemas. *Neuropsychologia* 90:46–58.
- 671 Insausti R, Amaral DG, Cowan WM (1987) The entorhinal cortex of the monkey: III. Subcortical
672 afferents. *J Comp Neurol* 264:396–408.

- 673 Insausti R, Juottonen K, Soininen H, Insausti AM, Partanen K, Vainio P, Laakso MP, Pitkänen A (1998)
674 MR volumetric analysis of the human entorhinal, perirhinal, and temporopolar cortices. *AJNR*
675 *Am J Neuroradiol* 19:659–671.
- 676 Kable JW, Glimcher PW (2009) The neurobiology of decision: consensus and controversy. *Neuron*
677 63:733–745.
- 678 Kafkas A, Migo EM, Morris RG, Kopelman MD, Montaldi D, Mayes AR (2017) Material Specificity Drives
679 Medial Temporal Lobe Familiarity But Not Hippocampal Recollection. *Hippocampus* 27:194–
680 209.
- 681 Kahn I, Andrews-Hanna JR, Vincent JL, Snyder AZ, Buckner RL (2008) Distinct cortical anatomy linked
682 to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. *J*
683 *Neurophysiol* 100:129–139.
- 684 Kondo H, Saleem KS, Price JL (2005) Differential connections of the perirhinal and parahippocampal
685 cortex with the orbital and medial prefrontal networks in macaque monkeys. *J Comp Neurol*
686 493:479–509.
- 687 Kondo H, Witter MP (2014) Topographic organization of orbitofrontal projections to the
688 parahippocampal region in rats. *J Comp Neurol* 522:772–793.
- 689 Konkle T, Brady TF, Alvarez GA, Oliva A (2010a) Conceptual distinctiveness supports detailed visual
690 long-term memory for real-world objects. *J Exp Psychol Gen* 139:558–578.
- 691 Konkle T, Brady TF, Alvarez GA, Oliva A (2010b) Scene memory is more detailed than you think: the
692 role of categories in visual long-term memory. *Psychol Sci* 21:1551–1556.
- 693 Kumaran D, Hassabis D, McClelland JL (2016) What Learning Systems do Intelligent Agents Need?
694 Complementary Learning Systems Theory Updated. *Trends Cogn Sci* 20:512–534.
- 695 Lavenex P, Amaral DG (2000) Hippocampal-neocortical interaction: a hierarchy of associativity.
696 *Hippocampus* 10:420–430.
- 697 Lee ACH, Buckley MJ, Pegman SJ, Spiers H, Scahill VL, Gaffan D, Bussey TJ, Davies RR, Kapur N, Hodges
698 JR, Graham KS (2005a) Specialization in the medial temporal lobe for processing of objects
699 and scenes. *Hippocampus* 15:782–797.
- 700 Lee ACH, Bussey TJ, Murray EA, Saksida LM, Epstein RA, Kapur N, Hodges JR, Graham KS (2005b)
701 Perceptual deficits in amnesia: challenging the medial temporal lobe “mnemonic” view.
702 *Neuropsychologia* 43:1–11.
- 703 Liang JC, Wagner AD, Preston AR (2013) Content representation in the human medial temporal lobe.
704 *Cereb Cortex N Y N* 1991 23:80–96.
- 705 Libby LA, Ekstrom AD, Ragland JD, Ranganath C (2012) Differential connectivity of perirhinal and
706 parahippocampal cortices within human hippocampal subregions revealed by high-resolution
707 functional imaging. *J Neurosci Off J Soc Neurosci* 32:6550–6560.
- 708 Libby LA, Hannula DE, Ranganath C (2014) Medial temporal lobe coding of item and spatial information
709 during relational binding in working memory. *J Neurosci Off J Soc Neurosci* 34:14233–14242.

- 710 Lisman JE, Grace AA (2005) The hippocampal-VTA loop: controlling the entry of information into long-
711 term memory. *Neuron* 46:703–713.
- 712 Litman L, Awipi T, Davachi L (2009) Category-specificity in the human medial temporal lobe cortex.
713 *Hippocampus* 19:308–319.
- 714 Liu Z, Murray EA, Richmond BJ (2000) Learning motivational significance of visual cues for reward
715 schedules requires rhinal cortex. *Nat Neurosci* 3:1307–1315.
- 716 Liu Z, Richmond BJ (2000) Response differences in monkey TE and perirhinal cortex: stimulus
717 association related to reward schedules. *J Neurophysiol* 83:1677–1692.
- 718 Maass A, Berron D, Libby LA, Ranganath C, Düzel E (2015) Functional subregions of the human
719 entorhinal cortex. *eLife* 4.
- 720 Mack ML, Preston AR (2016) Decisions about the past are guided by reinstatement of specific
721 memories in the hippocampus and perirhinal cortex. *NeuroImage* 127:144–157.
- 722 Madan CR, Fujiwara E, Caplan JB, Sommer T (2017) Emotional arousal impairs association-memory:
723 Roles of amygdala and hippocampus. *NeuroImage* 156:14–28.
- 724 Maguire EA, Mullally SL (2013) The hippocampus: a manifesto for change. *J Exp Psychol Gen* 142:1180–
725 1189.
- 726 Martin CB, McLean DA, O’Neil EB, Köhler S (2013) Distinct familiarity-based response patterns for faces
727 and buildings in perirhinal and parahippocampal cortex. *J Neurosci Off J Soc Neurosci*
728 33:10915–10923.
- 729 McCullough AM, Ritchey M, Ranganath C, Yonelinas A (2015) Differential effects of stress-induced
730 cortisol responses on recollection and familiarity-based recognition memory. *Neurobiol Learn*
731 123:1–10.
- 732 McIntyre DC, Kelly ME, Staines WA (1996) Efferent projections of the anterior perirhinal cortex in the
733 rat. *J Comp Neurol* 369:302–318.
- 734 Miendlarzewska EA, Bavelier D, Schwartz S (2016) Influence of reward motivation on human
735 declarative memory. *Neurosci Biobehav Rev* 61:156–176.
- 736 Miyashita Y (2019) Perirhinal circuits for memory processing. *Nat Rev Neurosci* 20:577–592.
- 737 Moser EI, Kropff E, Moser M-B (2008) Place cells, grid cells, and the brain’s spatial representation
738 system. *Annu Rev Neurosci* 31:69–89.
- 739 Mundy ME, Downing PE, Dwyer DM, Honey RC, Graham KS (2013) A critical role for the hippocampus
740 and perirhinal cortex in perceptual learning of scenes and faces: complementary findings from
741 amnesia and fMRI. *J Neurosci Off J Soc Neurosci* 33:10490–10502.
- 742 Navarro Schröder T, Haak KV, Zaragoza Jimenez NI, Beckmann CF, Doeller CF (2015) Functional
743 topography of the human entorhinal cortex. *eLife* 4.
- 744 Oades RD, Halliday GM (1987) Ventral tegmental (A10) system: neurobiology. 1. Anatomy and
745 connectivity. *Brain Res* 434:117–165.

- 746 O'Doherty JP, Dayan P, Friston K, Critchley H, Dolan RJ (2003) Temporal difference models and reward-
747 related learning in the human brain. *Neuron* 38:329–337.
- 748 Pelletier G, Fellows LK (2019) A Critical Role for Human Ventromedial Frontal Lobe in Value
749 Comparison of Complex Objects Based on Attribute Configuration. *J Neurosci Off J Soc*
750 *Neurosci* 39:4124–4132.
- 751 Pessiglione M, Seymour B, Flandin G, Dolan RJ, Frith CD (2006) Dopamine-dependent prediction errors
752 underpin reward-seeking behaviour in humans. *Nature* 442:1042–1045.
- 753 Peters J, Büchel C (2011) The neural mechanisms of inter-temporal decision-making: understanding
754 variability. *Trends Cogn Sci* 15:227–239.
- 755 Preston AR, Bornstein AM, Hutchinson JB, Gaare ME, Glover GH, Wagner AD (2010) High-resolution
756 fMRI of content-sensitive subsequent memory responses in human medial temporal lobe. *J*
757 *Cogn Neurosci* 22:156–173.
- 758 Price JL (2007) Definition of the Orbital Cortex in Relation to Specific Connections with Limbic and
759 Visceral Structures and Other Cortical Regions. *Ann N Y Acad Sci* 1121:54–71.
- 760 Prince SE, Dennis NA, Cabeza R (2009) Encoding and retrieving faces and places: distinguishing
761 process- and stimulus-specific differences in brain activity. *Neuropsychologia* 47:2282–2289.
- 762 Pruessner JC, Köhler S, Crane J, Pruessner M, Lord C, Byrne A, Kabani N, Collins DL, Evans AC (2002)
763 Volumetry of temporopolar, perirhinal, entorhinal and parahippocampal cortex from high-
764 resolution MR images: considering the variability of the collateral sulcus. *Cereb Cortex N Y N*
765 *1991* 12:1342–1353.
- 766 Pruessner JC, Li LM, Serles W, Pruessner M, Collins DL, Kabani N, Lupien S, Evans AC (2000) Volumetry
767 of hippocampus and amygdala with high-resolution MRI and three-dimensional analysis
768 software: minimizing the discrepancies between laboratories. *Cereb Cortex N Y N* 1991
769 10:433–442.
- 770 Ranganath C, Ritchey M (2012) Two cortical systems for memory-guided behaviour. *Nat Rev Neurosci*
771 13:713–726.
- 772 Ranganath C, Yonelinas AP, Cohen MX, Dy CJ, Tom SM, D'Esposito M (2004) Dissociable correlates of
773 recollection and familiarity within the medial temporal lobes. *Neuropsychologia* 42:2–13.
- 774 Ritchey M, Libby LA, Ranganath C (2015) Cortico-hippocampal systems involved in memory and
775 cognition: the PMAT framework. *Prog Brain Res* 219:45–64.
- 776 Ritchey M, Wang S-F, Yonelinas AP, Ranganath C (2019) Dissociable medial temporal pathways for
777 encoding emotional item and context information. *Neuropsychologia* 124:66–78.
- 778 Robin J, Rai Y, Valli M, Olsen RK (2018) Category specificity in the medial temporal lobe: A systematic
779 review. *Hippocampus*.
- 780 Rolls ET, McCabe C, Redoute J (2008) Expected value, reward outcome, and temporal difference error
781 representations in a probabilistic decision task. *Cereb Cortex N Y N* 1991 18:652–663.
- 782 Rouhani N, Norman KA, Niv Y (2018) Dissociable effects of surprising rewards on learning and memory.
783 *J Exp Psychol Learn Mem Cogn* 44:1430–1443.

- 784 Rudebeck PH, Ripple JA, Mitz AR, Averbeck BB, Murray EA (2017) Amygdala Contributions to Stimulus-
785 Reward Encoding in the Macaque Medial and Orbital Frontal Cortex during Learning. *J*
786 *Neurosci Off J Soc Neurosci* 37:2186–2202.
- 787 Russchen FT, Price JL (1984) Amygdalostriatal projections in the rat. Topographical organization and
788 fiber morphology shown using the lectin PHA-L as an anterograde tracer. *Neurosci Lett* 47:15–
789 22.
- 790 Scatton B, Simon H, Le Moal M, Bischoff S (1980) Origin of dopaminergic innervation of the rat
791 hippocampal formation. *Neurosci Lett* 18:125–131.
- 792 Schultz H, Sommer T, Peters J (2012) Direct evidence for domain-sensitive functional subregions in
793 human entorhinal cortex. *J Neurosci Off J Soc Neurosci* 32:4716–4723.
- 794 Schultz H, Tibon R, LaRocque KF, Gagnon SA, Wagner AD, Staresina BP (2019) Content tuning in the
795 medial temporal lobe cortex: Voxels that perceive, retrieve. *eNeuro*.
- 796 Schultz W (1998) Predictive reward signal of dopamine neurons. *J Neurophysiol* 80:1–27.
- 797 Schwarze U, Bingel U, Badre D, Sommer T (2013) Ventral striatal activity correlates with memory
798 confidence for old- and new-responses in a difficult recognition test. *PLoS One* 8:e54324.
- 799 Scoville WB, Milner B (1957) Loss of recent memory after bilateral hippocampal lesions. *J Neurol*
800 *Neurosurg Psychiatry* 20:11–21.
- 801 Shohamy D, Adcock RA (2010) Dopamine and adaptive memory. *Trends Cogn Sci* 14:464–472.
- 802 Spaniol J, Schain C, Bowen HJ (2014) Reward-enhanced memory in younger and older adults. *J*
803 *Gerontol B Psychol Sci Soc Sci* 69:730–740.
- 804 Squire LR, Zola-Morgan M (1991) The cognitive neuroscience of human memory since H.M. *Annu Rev*
805 *Neurosci* 34:259–288.
- 806 Staresina BP, Cooper E, Henson RN (2013) Reversible information flow across the medial temporal
807 lobe: the hippocampus links cortical modules during memory retrieval. *J Neurosci Off J Soc*
808 *Neurosci* 33:14184–14192.
- 809 Staresina BP, Davachi L (2008) Selective and shared contributions of the hippocampus and perirhinal
810 cortex to episodic item and associative encoding. *J Cogn Neurosci* 20:1478–1489.
- 811 Staresina BP, Duncan KD, Davachi L (2011) Perirhinal and parahippocampal cortices differentially
812 contribute to later recollection of object- and scene-related event details. *J Neurosci Off J Soc*
813 *Neurosci* 31:8739–8747.
- 814 Staresina BP, Henson RNA, Kriegeskorte N, Alink A (2012) Episodic reinstatement in the medial
815 temporal lobe. *J Neurosci Off J Soc Neurosci* 32:18150–18156.
- 816 Steiger TK, Bunzeck N (2017) Reward Dependent Invigoration Relates to Theta Oscillations and Is
817 Predicted by Dopaminergic Midbrain Integrity in Healthy Elderly. *Front Aging Neurosci* 9:1.
- 818 Suzuki WA, Amaral DG (1994a) Perirhinal and parahippocampal cortices of the macaque monkey:
819 cortical afferents. *J Comp Neurol* 350:497–533.

- 820 Suzuki WA, Amaral DG (1994b) Topographic organization of the reciprocal connections between the
821 monkey entorhinal cortex and the perirhinal and parahippocampal cortices. *J Neurosci Off J*
822 *Soc Neurosci* 14:1856–1877.
- 823 Tamamaki N, Nojyo Y (1995) Preservation of topography in the connections between the subiculum,
824 field CA1, and the entorhinal cortex in rats. *J Comp Neurol* 353:379–390.
- 825 Taylor KJ, Henson RNA, Graham KS (2007) Recognition memory for faces and scenes in amnesia:
826 dissociable roles of medial temporal lobe structures. *Neuropsychologia* 45:2428–2438.
- 827 Tulving E (1985) Memory and consciousness. *Can Psychol Can* 26:1–12.
- 828 van Strien NM, Cappaert NLM, Witter MP (2009) The anatomy of memory: an interactive overview of
829 the parahippocampal-hippocampal network. *Nat Rev Neurosci* 10:272–282.
- 830 Wang W-C, Yonelinas AP, Ranganath C (2013) Dissociable neural correlates of item and context
831 retrieval in the medial temporal lobes. *Behav Brain Res* 254:102–107.
- 832 Wimmer GE, Braun EK, Daw ND, Shohamy D (2014) Episodic memory encoding interferes with reward
833 learning and decreases striatal prediction errors. *J Neurosci Off J Soc Neurosci* 34:14901–
834 14912.
- 835 Witter MP, Amaral DG (1991) Entorhinal cortex of the monkey: V. Projections to the dentate gyrus,
836 hippocampus, and subicular complex. *J Comp Neurol* 307:437–459.
- 837 Wittmann BC, Dolan RJ, Düzel E (2011) Behavioral specifications of reward-associated long-term
838 memory enhancement in humans. *Learn Mem Cold Spring Harb N* 18:296–300.
- 839 Wittmann BC, Schiltz K, Boehler CN, Düzel E (2008) Mesolimbic interaction of emotional valence and
840 reward improves memory formation. *Neuropsychologia* 46:1000–1008.
- 841 Wittmann BC, Schott BH, Guderian S, Frey JU, Heinze H-J, Düzel E (2005) Reward-related FMRI
842 activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent
843 long-term memory formation. *Neuron* 45:459–467.
- 844 Wolosin SM, Zeithamova D, Preston AR (2012) Reward modulation of hippocampal subfield activation
845 during successful associative encoding and retrieval. *J Cogn Neurosci* 24:1532–1547.
- 846 Yonelinas AP, Aly M, Wang W-C, Koen JD (2010) Recollection and familiarity: examining controversial
847 assumptions and new directions. *Hippocampus* 20:1178–1194.
- 848 Yonelinas AP, Jacoby LL (1995) The Relation between Remembering and Knowing as Bases for
849 Recognition: Effects of Size Congruency. *J Mem Lang* 34:622–643.
- 850 Zola-Morgan S, Squire LR (1990) The neuropsychology of memory. Parallel findings in humans and
851 nonhuman primates. *Ann N Y Acad Sci* 608:434–450; discussion 450-456.
- 852