

1 **Incidental reinstatement of faces and scenes in medial temporal lobe**
2 **subregions during word recognition**

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14 **Conflict of interest:** The authors declare no conflict of interest.

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16 **Funding:** This work was supported by a grant from the Deutsche Forschungsgemeinschaft
17 (PE-1627/2-1).

18 Abstract

19 During associative retrieval, the brain reinstates neural representations that were present
20 during encoding. The human medial temporal lobe (MTL) with its subregions hippocampus
21 (HC), perirhinal cortex (PRC), and parahippocampal cortex (PHC) plays a central role in neural
22 reinstatement. Previous studies have given compelling evidence for reinstatement in the MTL
23 during explicitly instructed associative retrieval. High-confident recognition may be similarly
24 accompanied by recollection of associated information from the encoding context. It is unclear,
25 however, whether high-confident recognition memory elicits reinstatement in the MTL even in
26 the absence of an explicit instruction to retrieve associated information. Here, we addressed
27 this open question using high-resolution fMRI. Twenty-eight male and female human
28 volunteers engaged in a recognition memory task for words that they had previously encoded
29 together with faces and scenes. Using complementary uni- and multivariate approaches, we
30 show that MTL subregions including the PRC, PHC, and HC differentially reinstate category-
31 specific representations during high-confident word recognition, even though no explicit
32 instruction to retrieve the associated category was given. This constitutes novel evidence that
33 high-confident recognition memory is accompanied by incidental reinstatement of associated
34 category information in MTL subregions, and supports a functional model of the MTL that
35 emphasises content-sensitive representations during both encoding and retrieval.

36 1. Introduction

37 Recognition memory – the ability to distinguish previously encountered from novel
38 items – critically depends on the medial temporal lobe (MTL), including the hippocampus (HC),
39 perirhinal (PRC), parahippocampal (PHC), and entorhinal cortex (EC) (Eichenbaum et al.,
40 2007). The individual functions that these subregions serve in recognition memory remain a
41 subject of some debate (Wixted and Squire, 2011; Bird, 2017). One model that aims to account
42 both for behavioural observations and their underlying neural substrate is the dual-process
43 signal detection model (DPSD): In this view, two complementary processes contribute to
44 recognition: Familiarity is a signal detection process resulting in graded recognition confidence,
45 supported by PRC, whereas recollection is a threshold process resulting in high recognition
46 confidence, and involves retrieval of associated information from the encoding context,
47 supported by HC and PHC (Eichenbaum et al., 2007; Yonelinas et al., 2010).

48 Recent work has integrated such process-based views with more content-based
49 accounts of MTL functioning (Davachi, 2006; Eichenbaum et al., 2007). The latter are based
50 on connectivity studies in non-human primates and rodents (Suzuki and Amaral, 1994a,
51 1994b; Burwell and Amaral, 1998a; Lavenex and Amaral, 2000). Here, the PRC, anatomically
52 connected to the ventral visual stream, processes items, e.g. objects or faces, thereby
53 contributing to familiarity. Meanwhile, the PHC, anatomically connected to the dorsal visual
54 stream, processes spatial context memory, thereby providing the context information
55 underlying recollection. The HC, exchanging information with both streams via anterolateral
56 and posteriomedial subregions of the EC (alEC, pmEC) (Schultz et al., 2015), supports
57 recollection in a content-agnostic manner (Davachi, 2006; Eichenbaum et al., 2007). MTL
58 connectivity in humans is comparable to animals (Zeineh et al., 2012; Maass et al., 2015;
59 Navarro Schröder et al., 2015). Indeed, a number of human functional magnetic resonance
60 imaging (fMRI) studies have demonstrated sensitivity of the PRC to objects, or faces, and of
61 the PHC to spatial or scene information during both perception/encoding (Awipi and Davachi,
62 2008; Litman et al., 2009; Staresina et al., 2011; Schultz et al., 2021) and associative retrieval

63 (Schultz et al., 2012, 2019; Staresina et al., 2012, 2013; Mack and Preston, 2016) (for an
64 overview, see Robin et al., 2019). Similar content-based dissociations have been
65 demonstrated between aIEC and pmEC for faces/objects and scenes/spatial information,
66 respectively (Schultz et al., 2012, 2015; Reagh and Yassa, 2014; Navarro Schröder et al.,
67 2015; Berron et al., 2018).

68 Importantly, content-specific neural representations during retrieval overlap with
69 representations during the original encoding episode (Danker and Anderson, 2010) (but see
70 Favila et al., 2020). This so-called neural reinstatement of the encoding context is thought to
71 underlie the subjective impression of re-experiencing an episode that accompanies
72 recollection, but not familiarity (Eichenbaum et al., 2007; Danker and Anderson, 2010). Indeed,
73 the degree of reinstatement is associated with objective accuracy (Gordon et al., 2014; Liang
74 and Preston, 2017) as well as subjective vividness of the retrieved memory (Kuhl and Chun,
75 2014; St-Laurent et al., 2015; Bone et al., 2020), and interrupting early reinstatement through
76 transcranial magnetic stimulation decreases memory performance (Waldhauser et al., 2016).

77 Content-specificity during memory retrieval has largely been investigated using
78 paradigms that emphasise intentional associative retrieval (Schultz et al., 2012, 2019;
79 Staresina et al., 2012, 2013; Mack and Preston, 2016), e.g. by presenting a cue that was
80 previously paired with an object or scene, and asking participants to retrieve the object or
81 scene from memory (Schultz et al., 2019). Such intentional cued retrieval paradigms are not
82 necessarily comparable to recognition memory. In a recognition paradigm, the task is to judge
83 whether a given item has been previously encountered, and participants are typically asked to
84 qualify their old/new judgments e.g. by rating their confidence (Yonelinas et al., 2010).
85 Importantly, these confidence ratings refer to recognition confidence for the item itself, rather
86 than any associated information that was present during encoding. Since recollection is a
87 threshold-process assumed to selectively lead to high-confidence recognition (Yonelinas et al.,
88 2010), the contributions of recollection and familiarity can be estimated from the asymmetry of
89 the resulting receiver-operating characteristic (ROC) curve (Dunn, 2010; Yonelinas et al.,
90 2010). Recollection is furthermore assumed to involve retrieval of the encoding context,

91 accompanied by neural reinstatement of associated memory content (Eichenbaum et al., 2007;
92 Yonelinas et al., 2010). It follows that items that are recognised with high confidence ought to
93 be accompanied by neural reinstatement of the encoding context, even in the absence of an
94 explicit instruction to retrieve associated information. However, we are not aware of any studies
95 investigating this proposition in subregions of the MTL.

96 Here, we test this open question, using distinct categories (faces, scenes) to track
97 content representations in the MTL during perception and recognition. On the first day of the
98 study, twenty-eight participants underwent fMRI while viewing a total of 120 faces and scenes
99 (ten exemplars per category, six presentations per exemplar). The participants' task was to
100 respond to flickers in the image presentation as quickly as possible to win a small reward
101 (scanned perception phase¹). Next, they learned a list of 260 words, each presented once
102 while paired with one of the faces or scenes, with the task of combining each pair into a single
103 mental image (unscanned encoding phase). The next day, participants returned for a
104 recognition task of the words only, including all 260 target words from the previous day as well
105 as 130 distractor words (scanned recognition phase). For each word, participants rated their
106 confidence that it was old or new. Importantly, there was no instruction to retrieve the
107 associated face or scene. Finally, they solved a source memory task, in which they responded
108 for each word whether it had been paired with a face or a scene the day before (unscanned
109 source phase). For the behavioural analysis, we summarised memory performance for words
110 previously associated with either face or scenes using both model-based (recollection,
111 familiarity) and model-free (corrected recognition, source accuracy) measures. For the fMRI

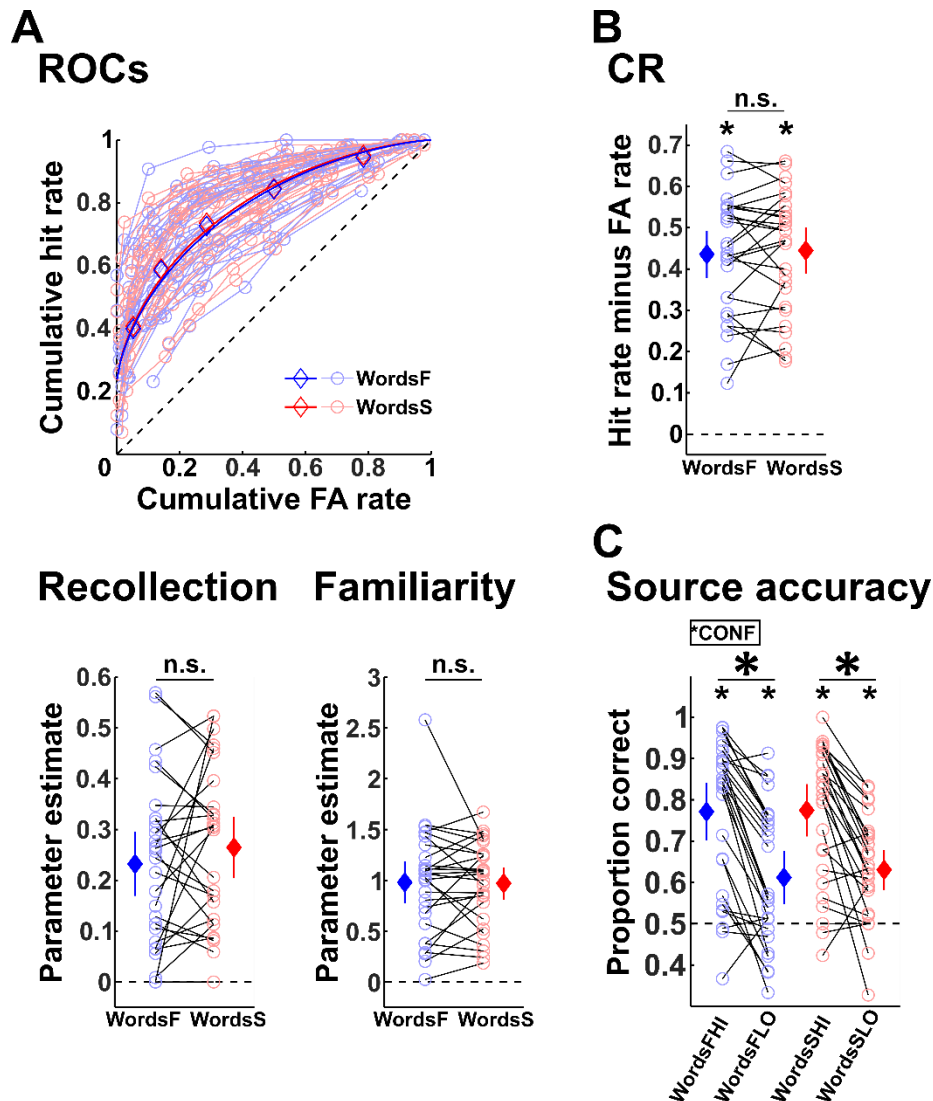
¹ Note that this experiment was originally devised to additionally assess the influence of associated reward on cortical reinstatement. Hence, the perception phase was designed as a reward task. As reward did not have reliable effects on behavioural or neural measures of memory, we here reanalyse the dataset omitting this factor. The brain responses extracted from this phase were modelled at a timepoint in each trial in which no reward information was available.

112 analysis, we tested for i) category sensitivity during face/scene perception, and ii) category
113 reinstatement of the associated faces/scenes during word recognition within participant-
114 specific MTL subregions of interest (ROIs). To this end, we utilised a set of complementary
115 analyses. For the perception phase, we tested for differences in the mean univariate response
116 of each ROI to face and scene perception, and furthermore established multivariate
117 discriminability of faces vs. scenes by training and testing a face/scene classifier on the
118 perception data in a leave-one-run-out fashion. For the recognition phase, we again
119 characterised each region's univariate response profile to words previously associated with
120 faces or scenes that were recognised with high or low confidence. Critically, we tested for
121 neural reinstatement during word recognition by training a multivariate face/scene classifier on
122 the perception phase, and testing it on words that were previously associated with faces or
123 scenes and recognised with high confidence during the recognition phase. As there was no
124 perceptual overlap between the phases, the classifier performance can only be driven by
125 reinstatement of the face/scene encoding context. As recollection is thought to involve the
126 reactivation of context information and lead to high-confident recognition judgments
127 (Eichenbaum et al., 2007; Yonelinas et al., 2010), we expected words that were recognised
128 with high confidence to be accompanied by neural reinstatement of the encoding category.

129 2. Results

130 2.1 Behavioural results

131 Overall, analyses of the behavioural data confirmed i) above chance performance in
132 both the recognition and source phases, and ii) critically, no significant differences between
133 words previously associated with faces (wordsF) and scenes (wordsS) (see Figure 1 for
134 overview of the analysed measures).



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136 **Figure 1.** Behavioural results. Across memory measures, words previously associated with faces
 137 (wordsF) and scenes (wordsS) showed similar performance. **A.** Receiver operating characteristic (ROC)
 138 curves and behavioural modelling. The ROC plot (upper panel) depicts hit rates plotted against false
 139 alarm (FA) rates, cumulative over confidence levels. Note that all participants are above the chance
 140 diagonal. The fitted curves depict the DPSD predictions for wordsF and wordsS, here fitted to the group
 141 averages for illustrative purposes. The lower panel plots the single subject parameter estimates of the
 142 DPSD for recollection and familiarity. **B.** Corrected recognition (CR). **C.** Source accuracy. **Annotation:**
 143 Circles and line plots denote single participants; diamonds denote means across participants; error bars
 144 denote 95% confidence interval; dashed lines denote chance level. *CONF: significant main effect of
 145 recognition confidence. F: previous face association, S: previous scene association, HI: correctly
 146 recognised with high confidence, LO: correctly recognised with low confidence. * $p < .05$. n.s.: not
 147 significant.

148 First, we analysed participants' recognition memory. During the scanned recognition
149 phase, participants rated their recognition confidence for a given word on a scale of 1 ("sure
150 new") to 6 ("sure old"). From the distributions of hits and false alarms at each confidence level,
151 we obtained receiver operating characteristic (ROC) curves, and estimated model parameters
152 for recollection and familiarity (see Figure 1A). As this procedure assumes a lower bound of 0
153 for both parameters, we did not test them against zero (note that all single-subject ROC curves
154 are above the chance diagonal). Recollection did not differ significantly between wordsF and
155 wordsS ($t_{27}=1.124$, $p=.271$), and neither did familiarity ($t_{27}=0.145$, $p=.885$). Additionally, as a
156 model-free measure of recognition performance, we computed corrected recognition (CR, hit
157 rates minus false alarm rates, see Figure 1B). CR exceeded chance for both wordsF
158 ($t_{27}=15.553$, $p<.001$) and wordsS ($t_{27}=16.300$, $p<.001$), and did not differ significantly between
159 wordsF and wordsS ($t_{27}=0.578$, $p=.568$).

160 In the post-scan source phase, for each word, participants gave a forced-choice
161 response whether that word had been paired with a face or a scene the day before. Here, we
162 analysed source accuracy for words that had been recognised with either high (HI) or low (LO)
163 confidence during the recognition phase (i.e. HI: confidence rating = 6, LO: confidence rating
164 = 4-5): wordsFHI, wordsFLO, wordsSHI, wordsSLO (see Figure 1C). A repeated measures
165 ANOVA with the factors category and confidence revealed a highly significant main effect of
166 confidence ($F_{(1,27)}=88.083$, $p<.001$; no other effects, $p\geq.694$) such that high-confident hits
167 yielded higher subsequent source accuracy than low-confident hits. This confidence effect was
168 confirmed using paired t-tests, with source accuracy greater for wordsFHI vs. wordsFLO, and
169 for wordsSHI vs. wordsSLO (both $t_{27}\geq 5.652$, $p<.001$). Finally, source accuracy exceeded
170 chance for wordsFHI, wordsFLO, wordsSHI, and wordsSLO (all $t_{27}\geq 3.578$, $p\leq.001$).

171 **2.2 fMRI results: Strategy**

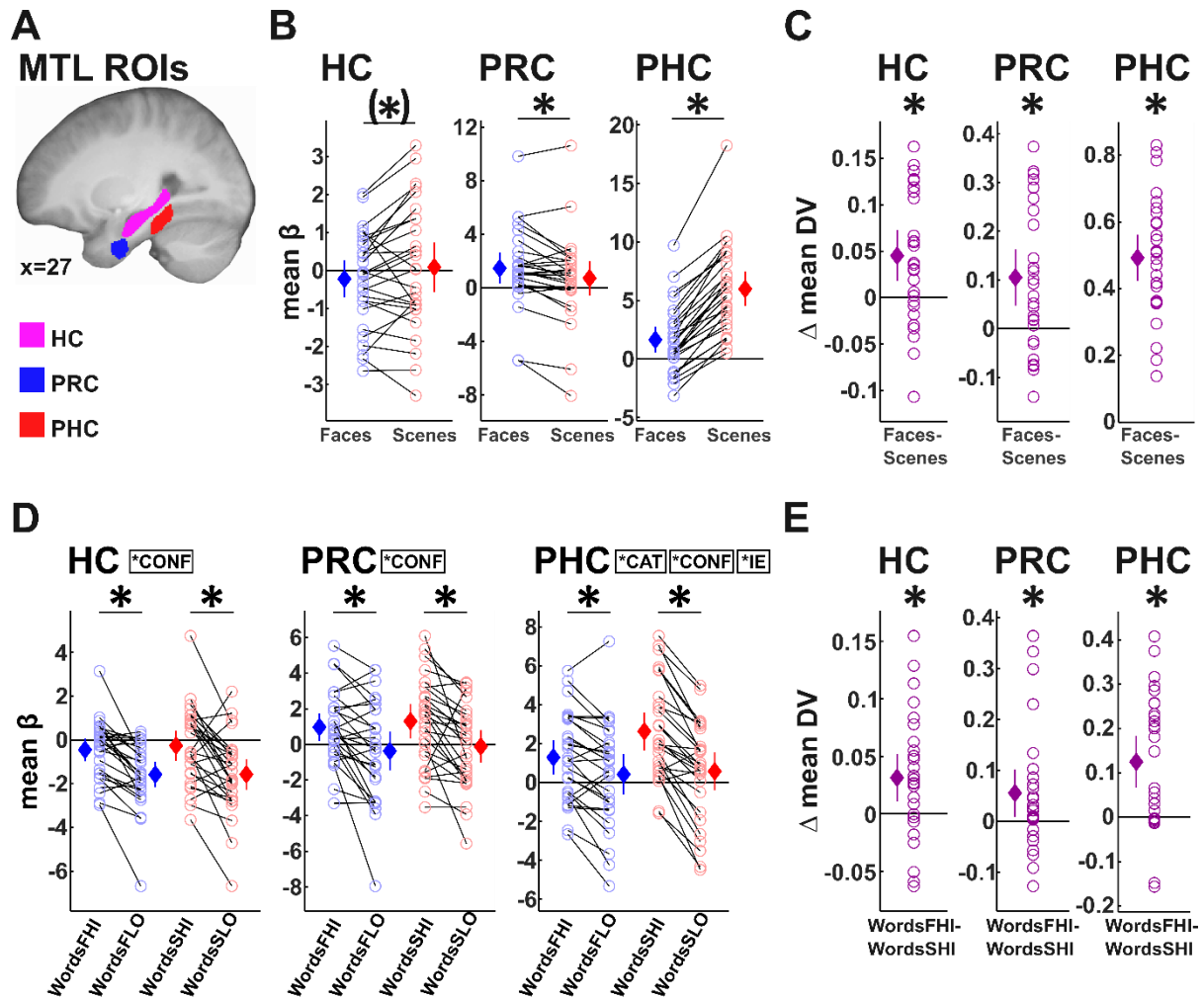
172 fMRI data were analysed within bilateral MTL subregion ROIs (HC, PRC, PHC, aIEC,
173 pmEC) that were manually delineated on the single-subject T1 scans (Insausti et al., 1998;
174 Pruessner et al., 2000, 2002; Maass et al., 2015). First, we sought to establish category

175 sensitivity during the perception phase, using both uni- and multivariate approaches. Then,
176 only those ROIs showing such category sensitivity during perception, i.e. HC, PRC, and PHC
177 (see Figure 2A), were considered for analyses of the recognition phase, as we were primarily
178 interested in reinstatement of the perceptual activity. Here, we again employed both uni- and
179 multivariate approaches.

180 **2.3 Category sensitivity during perception**

181 To establish category sensitivity during perception, we first analysed the MTL ROIs'
182 univariate response profiles by averaging beta estimates for the face and scene regressors
183 from the perception phase within each ROI. A two-way repeated-measures ANOVA with the
184 factors ROI (HC, PHC, PRC, aIEC, pmEC) and category (faces, scenes) revealed a highly
185 significant main effect of ROI ($F_{(2.80,75.57)}=16.341$, $p<.001$) and category ($F_{(1,27)}=39.459$,
186 $p<.001$), as well as an interaction effect ($F_{(2.81,75.96)}=86.399$, $p<.001$). Individual paired t tests
187 within each ROI confirmed category sensitivity in PHC (scenes>faces, $t_{27}=13.593$, $p<.001$) and
188 PRC (faces>scenes, $t_{27}=3.400$, $p=.002$), with a trend-level effect in HC (numerically
189 scenes>faces, $t_{27}=1.878$, $p=.071$) (see Figure 2B). There was no such effect in aIEC or pmEC
190 (both $t_{27}\leq 0.826$, $p\geq .416$). The PHC and PRC effects survived Holm-Bonferroni correction for
191 multiple comparisons (5).

192 A multivariate decoding analysis complemented the univariate results. Multivariate
193 analyses consider voxel patterns consisting of both activations and deactivations, thereby
194 increasing sensitivity (Hebart and Baker, 2018). Face vs. scene classifiers were trained and
195 tested on each ROI's perception data in a leave-one-run-out fashion. We tested the differences
196 between average decision values for face and scene trials (category discriminability) against
197 zero. Category discriminability was above chance in HC, PRC, and PHC (HC: $t_{27}=3.379$,
198 $p=.002$, PRC: $t_{27}=3.739$, $p<.001$, PHC: $t_{27}=14.595$, $p<.001$, see Figure 2C), but not in aIEC or
199 pmEC (both $t_{27}\leq 0.389$, $p\geq .700$). The effects in HC, PRC, and PHC survived Holm-Bonferroni
200 correction for multiple comparisons (5).



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Figure 2. MTL subregions and fMRI results. **A.** For visualisation, single-participant ROIs of HC, PRC, and PHC were normalised, averaged across participants, thresholded at 0.5, and projected onto the mean normalised T1 image. **B.** Averaged beta values from the univariate analysis during face and scene perception. **C.** Differences between averaged decision values during face vs. scene perception from the multivariate decoding analysis. Positive difference values indicate discriminability of faces and scenes. **D.** Averaged beta values from the univariate analysis during high- vs. low confident correct recognition of words previously associated with faces vs. scenes. **E.** Results from the multivariate decoding analysis, with a classifier trained on face vs. scene perception, and tested on highly confidently recognised words previously associated with faces and scenes. Plotted are the differences between average decision values for wordsFHI and wordsSHI. Positive difference values indicate discriminability of wordsFHI and wordsSHI. **Annotation:** Circles and line plots denote single participants; diamonds denote means across participants, and error bars denote 95% confidence interval. *CAT: significant main effect of category; *CONF: significant main effect of recognition confidence; *IE: significant interaction effect of category and recognition confidence. F: previous face association, S: previous scene association, HI:

216 correctly recognised with high confidence, LO: correctly recognised with low confidence. DV: decision
217 value from the multivariate analysis. * $p < .05$, (* $p < .1$).

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219 **2.4 Category sensitivity during word recognition**

220 Having established category sensitivity during perception in HC, PRC, and PHC, we
221 turned to testing the word recognition data from these ROIs for effects of prior association with
222 faces vs. scenes. As recollection-related neural reinstatement is thought to be restricted to
223 high-confidence recognition (Yonelinas et al., 2010), we analysed the univariate response
224 profiles of the MTL ROIs separately for high vs. low confidence hits, and for words previously
225 associated with faces vs. scenes (wordsFHI, wordsFLO, wordsSHI, wordsSLO, see Figure
226 2D). A three-way repeated measures ANOVA with the factors ROI (HC, PRC, PHC),
227 associated category (face, scene), and recognition confidence (high, low) revealed a
228 significant three-way interaction of ROI, category, and confidence ($F_{(1.39,37.59)}=3.998$, $p=.040$).
229 Most other effects were also (marginally) significant (ROI: $F_{(1.74,46.92)}=13.684$, $p<.001$; category:
230 $F_{(1,27)}=6.501$, $p=.017$; confidence: $F_{(1,27)}=59.648$, $p<.001$; ROI x category: $F_{(1.66,44.93)}=5.240$,
231 $p=.013$; category x confidence: $F_{(1,27)}=4.165$, $p=.051$; ROI x confidence: $F_{(1.52,41.05)}=0.292$,
232 $p=.688$). We followed up on the three-way interaction by computing separate two-way ANOVAs
233 (category, confidence) within each ROI. All three ROIs showed highly significant main effects
234 of confidence (all $F_{(1,27)} \geq 20.205$, all $p < .001$). PHC additionally showed a main effect of category
235 ($F_{(1,27)}=11.468$, $p=.002$) and, critically, an interaction of category and confidence, with a larger
236 confidence effect for words previously associated with scenes than with faces ($F_{(1,27)}=17.174$,
237 $p < .001$). There was no such interaction in HC or PRC (all $p \geq .525$). Follow-up paired t -tests
238 between wordsFHI vs. wordsFLO, and wordsSHI vs. wordsSLO were significant in all ROIs (all
239 $t_{27} \geq 3.587$, all $p \leq .0013$), and all tests survived Holm-Bonferroni correction for multiple
240 comparisons (6). In sum, all ROIs showed highly significant univariate activity increases during
241 high-confident compared to low-confident correct word recognition, with the PHC particularly
242 engaged during high-confident recognition of words previously associated with scenes.

243 Finally, we turned to our central analysis of multivariate decoding of the recognition
244 data. The above univariate analysis is limited in that it focuses on overall activity differences
245 between conditions, averaged across each ROI's voxels. Multivariate analyses, in contrast,
246 consider the information that is contained in each ROI's activation pattern (Hebart and Baker,
247 2018). Here, because recollection is thought to involve reinstatement of associated information
248 from the encoding context and lead to high confident hits (Eichenbaum et al., 2007; Yonelinas
249 et al., 2010), we assume that neural activity during high-confident word recognition contains
250 information about the previous face or scene association, reinstating patterns that were
251 present during perception. Hence, a classifier trained to distinguish between faces and scenes
252 during the perception phase and tested on high-confident hits during the recognition phase
253 ought to be able to distinguish between previous face and scene associations. Thus, for each
254 ROI, we tested category discriminability for high confidence words (i.e. the differences between
255 average decision values for wordsFHI and wordsSHI) against zero (see Figure 2E). Category
256 discriminability was above chance in all three ROIs (HC: $t_{27}=3.090$, $p=.005$, PRC: $t_{27}=2.432$,
257 $p=.022$, PHC: $t_{27}=4.361$, $p<.001$), and all three ROI effects survived Holm-Bonferroni correction
258 for multiple comparisons (3).

259 3. Discussion

260 In the present study, we investigated whether high confident recognition of words is
261 accompanied by incidental reinstatement of previously associated faces or scenes in
262 subregions of the medial temporal lobe (MTL). During the recognition phase, participants rated
263 their confidence that a given word was old or new, but, critically, were not asked to intentionally
264 retrieve associated categorical information. Behaviourally, participants successfully
265 recognised words from the encoding phase, and their subsequent source memory for
266 associated categorical information was above chance. Analysis of the fMRI data first confirmed
267 category sensitivity during perception in the MTL. Second, importantly, our data revealed
268 incidental category reinstatement in MTL subregions during word recognition: Hippocampus
269 (HC), perirhinal cortex (PRC), and parahippocampal cortex (PHC) demonstrated multivariate

270 discriminability of previous faces vs. scene associations, using a classifier trained on the
271 perception data. Crucially, the perception and recognition phases did not share any perceptual
272 input, as the perception phase presented faces and scenes, but not words, and the recognition
273 phase presented words, but not faces or scenes. Hence, these multivariate results can only
274 reflect reinstatement of associated face and scene information during word recognition. In
275 addition, the univariate activity profiles of the MTL ROIs during the recognition phase showed
276 robust activity increases for high compared to low confident words.

277 The present study provides novel evidence for incidental reinstatement of faces and
278 scenes in the MTL in a word recognition task. This is in line with the dual process signal
279 detection model (DPSD) of recognition memory, which assumes that some of the queried
280 words – namely, those that are recollected – are accompanied by neural reinstatement of the
281 associated information (Eichenbaum et al., 2007; Yonelinas et al., 2010). Indeed, our data
282 demonstrate that words recognised with high confidence show such reinstatement in the MTL
283 by allowing for multivariate decoding of the previously associated category. This observed
284 category sensitivity within the MTL follows from its anatomical connectivity patterns. To
285 simplify, the PRC vs. PHC serve as relay stations for object-related vs. spatial information,
286 respectively, between the visual system and the HC (Davachi, 2006; Eichenbaum et al., 2007).
287 This account is exemplified in our univariate perception results, with enhanced activity during
288 face perception in the PRC, and enhanced activity during scene perception in the PHC. A
289 number of previous fMRI studies have demonstrated such category dissociations between
290 PRC and PHC during perception and encoding of faces (or objects) vs. spatial stimuli (or
291 scenes) (Awipi and Davachi, 2008; Litman et al., 2009; Staresina et al., 2011; Liang et al.,
292 2013; Berron et al., 2018; Schultz et al., 2019, 2021). Importantly, the bidirectionality of the
293 underlying MTL connectivity might support the reinstatement of representations during
294 memory retrieval (Davachi, 2006; Eichenbaum et al., 2007). Indeed, MTL content sensitivity in
295 the absence of perceptual input, implying cortical reinstatement, has been demonstrated
296 previously (Schultz et al., 2012, 2019; Staresina et al., 2013; Mack and Preston, 2016; Liang
297 and Preston, 2017). Note that these studies investigated intentional retrieval – e.g. Schultz et

298 al. (2019) presented words and asked participants to vividly retrieve a previously associated
299 object vs scene, which was associated with i) elevated category-sensitive univariate retrieval
300 activity in PRC vs. PHC, and ii) increased across-voxel correlation of category-sensitive
301 retrieval and perceptual activity.

302 In contrast, and complementing these earlier results, we investigated reinstatement
303 during recognition. Participants rated their recognition confidence for a given target or
304 distractor word, but were not instructed to retrieve the associated category information. To our
305 knowledge, no previous study has investigated cortical reinstatement in MTL subregions in a
306 recognition memory paradigm without explicit instruction to retrieve associated information.
307 Two studies (Skinner et al., 2014; Bowen and Kensinger, 2017) had participants give
308 recognition judgments for words previously paired with faces and scenes without explicit
309 instruction to retrieve the associated information; however these studies did not focus on
310 subregions of the MTL. Another study (Kuhl et al., 2013) also presented words that had been
311 previously learned with faces and scenes. However, this was not a word recognition task:
312 Participants were asked to explicitly retrieve information about the associated images, either
313 the category of the image (face or scene), or its location (left or right). Here, MTL retrieval
314 representations tracked category regardless of whether participants were focussing on the
315 category or location of the image they were retrieving (however, their ROIs did not distinguish
316 between PRC, PHC, and EC). Note that the absence of an explicit instruction to retrieve
317 associated information in our study does not imply that recollection of these associations was
318 non-conscious, or that the participants actively suppressed these associations. Furthermore,
319 the subsequent behavioural test of source memory indicates that they had retained above-
320 chance explicit memory for the associated category information. Our results demonstrate that
321 cortical reinstatement in the MTL does not require an instruction of intentional, vivid retrieval.

322 Whereas our multivariate results give clear evidence for category reinstatement in the
323 MTL, the univariate data are dominated by category-insensitive confidence effects across MTL
324 subregions. Only in PHC were these effects increased for one category (scenes). The uni- and
325 multivariate approaches differ on a number of dimensions. First, multivariate analyses are

326 generally thought of as more sensitive than univariate analyses (Hebart and Baker, 2018),
327 which may explain why the multivariate analysis yielded evidence for category reinstatement
328 in PRC while the univariate analysis did not. Moreover, while univariate analyses assume that
329 a ROI's involvement in a process will be reflected in elevated mean activity, multivariate
330 analyses assume that both activations and deactivations equally contribute to the information
331 represented in a given ROI (Hebart and Baker, 2018). Here, some caution is warranted
332 regarding the interpretation of our multivariate results: Given the univariate activity differences
333 during the perception phase, a parsimonious explanation would be that, during recognition,
334 PRC represents the retrieved face information, while PHC (and HC) represent the retrieved
335 scene information. This would be in line with earlier functional reports (Schultz et al., 2012,
336 2019; Staresina et al., 2013; Mack and Preston, 2016) as well as the PRC's and PHC's
337 anatomical connectivity to regions of the ventral and dorsal visual stream, respectively (Suzuki
338 and Amaral, 1994a; Eichenbaum et al., 2007). However, in our multivariate analyses, evidence
339 for faces cannot be distinguished from evidence against scenes, and vice versa. This means
340 that each ROI's ability to discriminate between face and scene associations may be driven by
341 that ROI representing face information, or scene information, or both. Hence, our results imply
342 that PRC, PHC, and HC maintain information about previous associations of the words during
343 the recognition phase, but based on the multivariate results alone, we cannot conclude a
344 preference of one category over the other. Indeed, as scenes typically contain objects, to which
345 PRC is sensitive (Robin et al., 2019), it is likely that scene reinstatement also engages PRC to
346 some degree. Finally, as the multivariate analysis classifies recognition trials based on neural
347 patterns from the perception data, it is a direct test of the reinstatement concept, which implies
348 topographical and informational overlap between perception/encoding and retrieval (Danker
349 and Anderson, 2010). Recent approaches, however, have also investigated differences
350 between encoding- and retrieval-related memory representations, emphasising shifts in
351 representational granularity and brain topography (Baldassano et al., 2016; Bainbridge et al.,
352 2020), direction of the information flow (Staresina et al., 2013; Linde-Domingo et al., 2019),
353 and transformation of the memory trace itself (Xiao et al., 2017; Favila et al., 2018).

354 Reinstatement, as investigated here, is therefore only one facet of how the brain represents
355 the content of memory during retrieval.

356 In the univariate data, we observed category-sensitive effects of recognition confidence
357 in PHC, but, unexpectedly, not PRC. This is in contrast to earlier studies showing category-
358 sensitive univariate effects in PRC and PHC during intentional, vivid retrieval (Schultz et al.,
359 2012, 2019; Staresina et al., 2013). Given that all our behavioural measures indicate
360 comparable memory performance for words previously associated with faces and scenes, this
361 effect cannot be attributed to memory performance differences across conditions. However,
362 recent results suggest that scenes could be special memoranda compared to e.g. faces or
363 objects, increasing associative memory by providing a spatial context that binds to items more
364 easily than other material (Robin and Olsen, 2019). Furthermore, although eliciting comparable
365 memory performance, the scenes in our stimulus set had more diverse content (e.g. a
366 mountain side, a coast, a forest) than the face stimuli. These properties could have increased
367 scene reinstatement during the word recognition task. It is important to point out that PRC does
368 not only receive information from the ventral visual stream, but additionally receives a number
369 of inputs from spatial processing regions such as the PHC (Suzuki and Amaral, 1994a; Burwell
370 and Amaral, 1998b). Accordingly, studies have reported evidence for similar processing of
371 object-related and spatial information in the PRC under some circumstances (Berron et al.,
372 2018; Lawrence et al., 2020).

373 Our results show category discriminability in the HC for both the perception and
374 recognition phases, as well as (marginally) elevated mean activity during viewing of scenes
375 compared to faces. Some previous studies, including both functional imaging and lesion
376 studies, imply scene specialisation in the HC (Lee et al., 2005a, 2005b; Graham et al., 2006;
377 Taylor et al., 2007; Zeidman et al., 2015), in line with a prominent role of the HC in spatial
378 processing (Maguire and Mullally, 2013; Maguire et al., 2016; Bellmund et al., 2018). Other
379 studies, however, have shown no evidence for category-level distinctions in the HC (Staresina
380 et al., 2012, 2013; Mack and Preston, 2016; Schultz et al., 2019). Anatomy-based models of
381 MTL function imply a primarily associative or relational role of the HC in episodic memory; in

382 this view, the HC is insensitive to stimulus category (Davachi, 2006; Eichenbaum et al., 2007).
383 However, commonalities between relational, or associative, and spatial hippocampal
384 processing have been noted (Buzsáki and Moser, 2013; Eichenbaum, 2017). Future work may
385 illuminate the circumstances under which HC scene preferences prevail.

386 We note some limitations of the current study. First, recent years have seen rising
387 interest in the role of anterolateral and posteromedial EC subregions (alEC, pmEC) during
388 perception/encoding and retrieval, establishing the notion of category sensitivity in EC
389 subregions during these processes (Schultz et al., 2012, 2015; Reagh and Yassa, 2014;
390 Maass et al., 2015; Navarro Schröder et al., 2015; Berron et al., 2018). Here, we found no
391 evidence for category-sensitive representations in the EC. One methodological challenge in
392 fMRI of the MTL is the signal quality gradient from anterior to posterior MTL, leading to
393 decreased signal-to-noise ratio and increased susceptibility artifacts in the anterior MTL cortex,
394 including the EC (Carr et al., 2010). Hence, our null-results in the EC may be due to signal
395 quality issues. A second potential limitation concerns the recollection vs. familiarity distinction.
396 According to the DPSD, high-confident hits may consist of both recollected and highly familiar
397 items (Yonelinas et al., 2010). While we assume that, based on the underlying model, the
398 observed sensitivity to the associated category during recognition memory was driven by the
399 recollected items rather than the highly familiar items (Eichenbaum et al., 2007; Yonelinas et
400 al., 2010), these processes cannot be disentangled on the item level. Hence, we cannot rule
401 out incidental reinstatement for highly familiar items. Lastly, there has been a discussion
402 whether the MTL is involved in perception at all, or whether all MTL processing is necessarily
403 mnemonic (Suzuki and Baxter, 2009). Our results do not resolve this debate. While we have
404 treated the category-specific MTL processes during the perception phase as perceptual in
405 nature, we cannot rule out that they have a primarily mnemonic function, i.e. memory encoding
406 (Awipi and Davachi, 2008; Staresina et al., 2011).

407 In summary, we show that, in the absence of any differences in perceptual input, the
408 three major subregions of the MTL – HC, PRC, and PHC – nonetheless contain
409 representations of associated category information (faces/scenes) during word recognition.

410 These data support a functional model of episodic memory in the MTL that is informed by
411 anatomical connectivity, and that emphasises the similarity of content representations during
412 perception/encoding and retrieval. Future work may clarify the role of human entorhinal
413 subregions during long-term retrieval of category-sensitive representations, as well as
414 differences in representations involved during perception/encoding vs. retrieval.

415 **4. Materials and Methods**

416 **4.1 Sample**

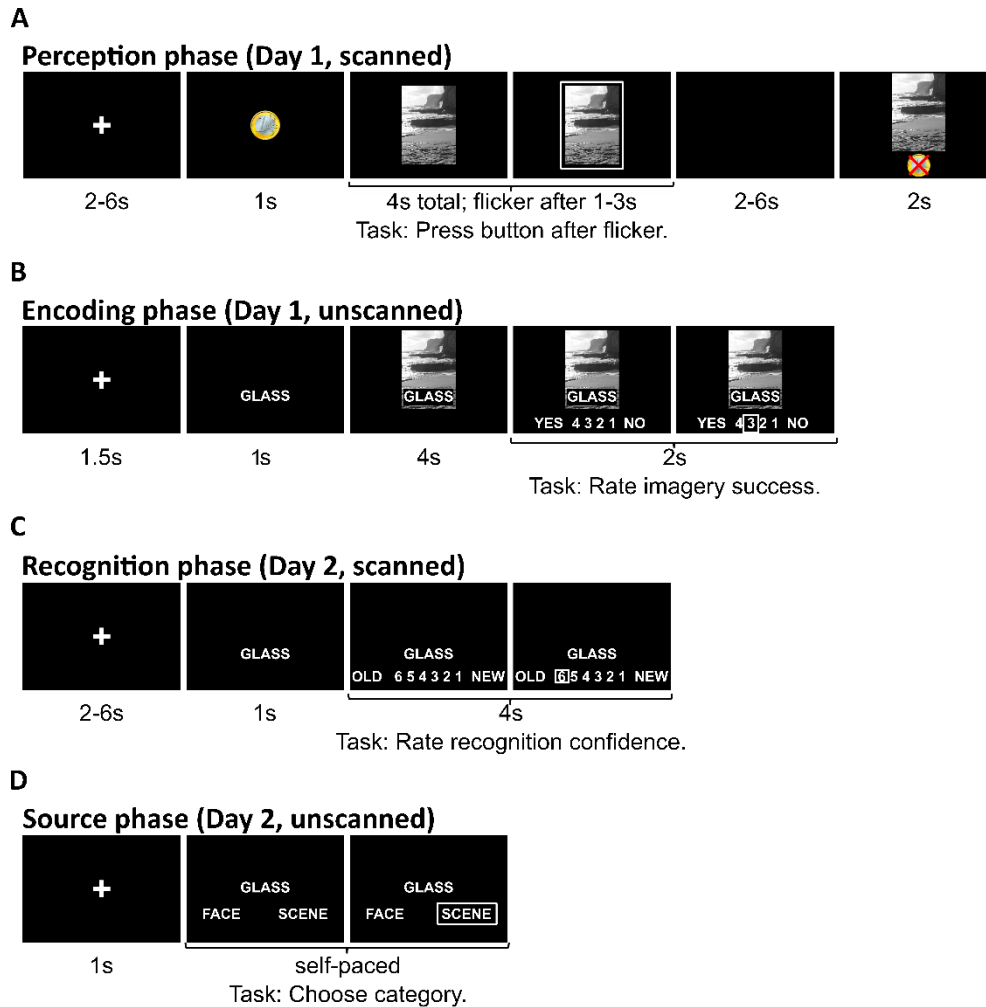
417 We report data from 28 volunteers (8 male, mean age 26.0, range 18-35). Three more
418 were excluded from data analysis (one for excessive head movement, one for falling asleep in
419 the scanner; one dropped out after day one). All volunteers were right-handed, healthy with
420 normal or corrected-to-normal vision, and reported no past neurological or psychiatric
421 diagnoses. They received monetary reimbursement of €10/hour + bonus. Prior to participation,
422 they gave written informed consent. The study procedure was approved by the local ethics
423 committee (Hamburg Board of Physicians).

424 **4.2 General procedure**

425 The experiment was conducted over two consecutive days. Day one comprised the
426 scanned perception (~30min) and unscanned encoding phase (~40min). Day two comprised
427 the scanned recognition (~59min), and unscanned source phase (~25-40min). Mean lag
428 between perception and recognition phase was 19.5h (range: 13.5-24h).

429 **4.3 Stimuli**

430 Stimuli consisted of 10 grayscale neutral faces (Endl et al., 1998) and 10 grayscale
431 natural outdoor scenes (various internet sources) used in a previous study (Schultz et al.,
432 2012), as well as 390 emotionally neutral, concrete German nouns from the Berlin Affective
433 Word List Reloaded (Vö et al., 2009). For each participant, 260 words were randomly selected
434 as encoding items, whereas the remaining 130 served as distractors during the recognition
435 phase.



436

437 **Figure 4.** Example trials for the experimental phases. A: Perception phase. B: Encoding phase. C:

438 Recognition phase. D: Source phase.

439

440 **4.4 Behavioural tasks**

441 The *perception phase* was a modified Monetary Incentive Delay (MID) task (Knutson

442 et al., 2000) (see Figure 4A for details). Each of the 20 faces and scenes appeared 6 times,

443 resulting in 120 trials over 3 runs. Trial order was pseudo-randomised, with no more than 4

444 face or scene trials appearing in a row. Trials started with a 1€ coin followed immediately by a

445 face or scene (initial image presentation). At a random timepoint during image presentation, a

446 flicker (blank screen for 1 frame) prompted participants to press a button as fast as possible to

447 win a reward, using a button box held in their right hand. Finally, the image reappeared with

448 reward feedback. Response time limits adapted to a reward probability of 0.735 over trials,

449 separately for faces and scenes. Participants received a bonus for each earned reward,
450 amounting to ~€3.20 in total.

451 In the *encoding phase* (see Figure 4B for details), participants encoded associations
452 between words and images. Each of the 20 faces and scenes was paired with 13 words,
453 resulting in 260 trials, presented in 5 blocks with self-paced breaks. Trial order was
454 pseudorandomised, with no more than 4 face or scene trials in a row, and identical images
455 separated by at least 10 trials. Per trial, participants were asked to combine a word and image
456 into a single mental image, and rated their imagery success on a scale of 1 to 4. Response
457 layout (1-2-3-4 or 4-3-2-1) was randomly switched between trials.

458 In the *recognition phase* (see Figure 4C for details), all 260 encoded words plus 130
459 distractor words were presented over 5 runs. Trial order was pseudorandomised so that no
460 more than 4 distractors and 4 words associated with either a face or a scene appeared in a
461 row. Per trial, participants were asked to rate their confidence that a given word was new or
462 old, on a scale of 1 to 6. Participants used two button boxes held in their left and right hand,
463 with three buttons mapped on each. Response layout (1-2-3-4-5-6 or 6-5-4-3-2-1) was
464 randomly switched between trials. No instruction was given to retrieve the associated image.

465 In the *source phase* (see Figure 4D for details), all 390 words were presented again,
466 and participants indicated whether a given word had been paired with a face or a scene the
467 day before. Additionally, they indicated whether they associated the word with a reward or not
468 (not pictured; data not included in the present report).

469 All tasks were programmed using Presentation® software (Version 14.9,
470 Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com).

471 **4.5 Behavioural analyses**

472 For the recognition phase, we analysed a model-free outcome measure (corrected
473 recognition, CR) as well as two model-based outcome measures (recollection, familiarity). CR
474 was computed as the difference between hit rate minus false alarm rate (the proportions of

475 confidence ratings ≥ 4 for targets minus distractors, respectively). Recollection and familiarity
476 are parameters in the dual-process model. This model assumes that two processes contribute
477 to recognition memory: An all-or-none threshold process (recollection), and a signal detection
478 process (familiarity) (Yonelinas et al., 2010). Parameter estimates for these processes were
479 obtained from each participant's distribution of recognition confidence ratings, separately for
480 wordsF and wordsS, using maximum likelihood estimation (Dunn, 2010). Finally, for the source
481 phase, we computed source accuracy (proportion of correctly identified source category) for
482 words that, during the recognition phase, had been correctly recognised with high confidence
483 (confidence rating = 6) respectively low confidence (confidence rating = 4-5), separately for
484 wordsF and wordsS.

485 **4.6 MR data acquisition**

486 MR data was acquired on a 3T Siemens TIM TRIO scanner using a 32 channel head
487 coil. The perception and recognition phases were scanned using a high-resolution T2*-
488 weighted EPI sequence (33 descending slices, no gap, 1.5mm isotropic voxels, TR=2.49s,
489 TE=30ms, PAT factor 2) with the field of view aligned to the longitudinal MTL axis. On day 2,
490 an additional T1-weighted MPRAGE structural scan was acquired (240 slices, 1x1x1mm).

491 **4.7 ROI approach**

492 All statistical analyses were conducted in single-subject space within bilateral masks of
493 MTL subregions (HC, PRC, PHC, aIEC, pmEC) that were manually segmented on the T1
494 following existing guidelines (Insausti et al., 1998; Pruessner et al., 2000, 2002; Maass et al.,
495 2015) using MRlcron (Rorden and Brett, 2000). For PRC and PHC, the middle third of the
496 parahippocampal gyrus (i.e. posterior PRC and anterior PHC) was discarded to maximise
497 category sensitivity within these regions (Staresina et al., 2013; Schultz et al., 2019).

498 **4.8 MR data preprocessing**

499 MRI data were analysed in Matlab/SPM12 except where noted. Functional images
500 were corrected for slice acquisition time, head movement, and movement-related distortions.

501 T1 images were coregistered to the functional data using boundary-based registration (FSL
502 `epi_reg`). In order to create Figure 2A, T1 images were segmented into grey matter, white
503 matter, and cerebrospinal fluid, and the resulting flowfields were used to normalise the T1
504 images and single-subject ROIs into MNI (Montreal Neurological Institute) space.

505 **4.9 Univariate analyses**

506 For the univariate analyses, we set up two categorical first-level linear models (GLMs)
507 on the non-normalised, unsmoothed data from the perception and recognition phase,
508 respectively. Runs were concatenated within each phase. Regressors were modelled as stick
509 functions convolved with the canonical hemodynamic response function. For the perception
510 phase, regressors of interest comprised faces vs. scenes during initial image onset, when no
511 reward information was available. Also modelled were the reward feedback onsets, separately
512 for face/reward, face/no reward, scene/reward, and scene/no reward. For the recognition
513 phase, regressors were modelled on the word onset, and regressors of interest comprised
514 words previously associated with faces (F) vs. scenes (S) and correctly recognised with high
515 (HI, confidence rating = 6) vs. low confidence (LO, confidence rating = 4-5) (`wordsFHI`,
516 `wordsFLO`, `wordsSHI`, `wordsSLO`). Also modelled were misses, separately for `wordsF` and
517 `wordsS` (confidence ratings ≤ 3), false alarms and correct rejections for the distractor items,
518 and error trials. Models included a high-pass filter (128s) and autoregressive model (AR(1)) as
519 well as run constants. Beta values from the regressors of interest were averaged within each
520 ROI and submitted to group-level analyses.

521 **4.10 Multivariate analyses**

522 The first-level GLMs underlying the multivariate analyses were set up similarly to the
523 univariate analyses, albeit with a single-trial regressor on each initial image onset as well as
524 reward feedback onset (perception phase, the latter were discarded), and on each word onset
525 (recognition phase). Multivariate decoding was applied to single-trial t -values from each ROI
526 (z-scored within each voxel separately for training and test data), using regularised linear
527 discriminant analysis (LDA) as implemented in the MVPA-light toolbox (Treder, 2020). Two

528 decoding analyses were conducted: First, we tested category discriminability during
529 perception. Here, we trained and tested a classifier on face vs. scene perception in a leave-
530 one-run-out fashion. Second, we tested category reinstatement during the recognition phase.
531 Here, we trained a classifier on face vs. scene perception during the perception phase, and
532 tested it on high-confident hits for words previously associated with faces vs. scenes (wordsFHI
533 vs. wordsSHI) from the recognition phase. These analyses resulted in decision values for each
534 testing trial and ROI, with increasing values indicating face evidence, and decreasing values
535 indicating scene evidence. As the zero point in these analyses is arbitrary (representing the
536 midpoint of all trials in the testing set), we computed group level analyses on the differences
537 between decision values for face minus scene trials (perception phase) and wordsFHI minus
538 wordsSHI (recognition phase), with positive difference values indicating face vs. scene
539 discriminability.

540 5. Acknowledgments

541 We thank Matthias Treder for helpful discussions of the multivariate analysis approach.

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