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Delay-dependent contributions of medial temporal lobe regions to episodic memory retrieval

Maureen Ritchey¹, Maria E. Montchal¹, Andrew P. Yonelinas² & Charan Ranganath^{1,2}

¹Center for Neuroscience, University of California, Davis
²Department of Psychology, University of California Davis

Corresponding author:
Maureen Ritchey
Center for Neuroscience
1544 Newton Ct., Davis, CA 95618
Phone: 530-757-8865
meritchey@ucdavis.edu

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Abstract

The medial temporal lobes play an important role in episodic memory, but over time, hippocampal contributions to retrieval may be diminished. However, it is unclear whether such changes are related to the ability to retrieve contextual information, and whether they are common across all medial temporal regions. Here, we used functional neuroimaging to compare neural responses during immediate and delayed recognition. Results showed that recollection-related activity in the posterior hippocampus declined after a one-day delay. In contrast, activity was relatively stable in the anterior hippocampus and in neocortical areas. Multi-voxel pattern similarity analyses also revealed that anterior hippocampal patterns contained information about context during item recognition, and after a delay, context coding in this region was related to successful retention of context information. Together, these findings suggest that the anterior and posterior hippocampus have different contributions to memory over time and that neurobiological models of memory must account for these differences.

Key words: fMRI, multi-voxel pattern analysis, representational similarity analysis, recognition memory, consolidation

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51 The medial temporal lobes (MTL) are known to play a key role in the formation of
52 lasting memories, but there has been considerable debate about whether their involvement in
53 memory retrieval is stable over time. Some models have suggested that the hippocampal
54 formation (HF) is critical for supporting new memories, but that, over time, memories can be
55 supported by neocortical areas alone. In one account, the shift from hippocampal to cortical
56 representation reflects a transfer of the memory trace through a time-dependent process known
57 as systems consolidation [1, 2]. This type of transfer is thought to preserve the quality and
58 contents of the memory, although older memories may generally be weaker. Other accounts,
59 however, have argued that changes in hippocampal versus cortical involvement are accompanied
60 by the transformation of episodic memories, which require the HF, into semantic memories,
61 which lack episodic context information and can be supported by cortex alone [3, 4].

62

63 Changes in the neural bases of memory have typically been described as unfolding over
64 very long timescales, but some studies have documented changes even across relatively short
65 delays. For instance, some functional magnetic resonance imaging (fMRI) studies have shown
66 that, when both encoding and retrieval are controlled in the laboratory, retrieval-related activity
67 in the HF declines from immediate to delayed test with even a one-day delay [5-7, but see 8].
68 These findings are echoed by work demonstrating that a night of sleep, or even a brief nap, can
69 alter the neural bases of memory [6, 9, 10] and have long-term consequences for memory [11].
70 Although these findings are often interpreted as reflecting the early stages of memory systems
71 consolidation, it has remained a challenge to separate changes in neural representation from
72 concomitant changes in episodic quality or content. For instance, one study found that
73 differences in HF activity for recent versus remote autobiographical retrieval could be explained
74 by differences in memory vividness [12]. One way to control for these differences is to limit
75 analysis to memories endorsed with high confidence or recollection [5, 6, 13, 14]. However,
76 even this approach could be insensitive to differences in the kinds of details that accompany
77 recollection, such as information related to episodic context. The HF is especially involved in
78 tasks that require retrieval of contextual details [15-18], so differences between HF and cortical
79 contributions to memory over time could be due to changes in contextual retrieval.

80

81 Another challenge to understanding changes in the neural bases of memory is that current
82 models have not accounted for heterogeneity of function within the MTL. In particular, the

81 perirhinal cortex (PRC) and parahippocampal cortex (PHC) are critically involved in episodic
82 memory, yet they affiliate with different large-scale cortical networks [19-21] and are widely
83 believed to be functionally distinct from each other and from the HF [15-18, 22]. Nonetheless,
84 current models have been vague with respect to their predictions for the PRC and PHC, either
85 grouping them alongside the HF [1, 3, 23] or ignoring them altogether [4]. The PRC and PHC
86 also functionally interact with different pathways along the longitudinal axis of the HF [19, 24,
87 25], suggesting additional heterogeneity within the HF. For instance, the anterior and posterior
88 HF are thought to play different roles in memory for spatial context [26-28], with coarse context
89 coding in the anterior HF and specific place coding in the posterior HF [28, 29]. Because
90 memories can lose contextual specificity over time [30, 31], differences in the scale of context
91 processing in the MTL might be associated with differences in MTL contributions to memory
92 over time. Despite this heterogeneity, prior imaging studies have not systematically investigated
93 time-dependent differences in recruitment of the anterior and posterior HF, PRC, and PHC
94 during retrieval. Thus, an important next step is to clarify the roles of the anterior and posterior
95 HF and parahippocampal areas in supporting memory over time.

96 The goal of the present study was to use fMRI to examine changes in MTL activity
97 during immediate and delayed item recollection. Across two days, participants encoded
98 sentences, each of which described an association between an item and a room in a house, such
99 that each item was associated with one of eight contexts (Figure 1A). Immediately after the
100 second encoding session, participants were scanned while completing an item recognition test.
101 To evaluate responses related to item recollection and context memory, we first compared the
102 overall magnitude of recollection-related activity for each delay, which allowed us to determine
103 whether changes in MTL involvement are observed even when controlling for subjective
104 recollection. Next, we leveraged a novel multi-voxel pattern similarity analysis approach [32]
105 that measured the sensitivity of voxel patterns in MTL subregions to information about shared
106 study context [c.f., 33, 34], thereby providing an objective measure of context reactivation. This
107 analysis allowed us to determine whether a region's continued involvement in recollection is
108 related to its representation of context information in memory. Moreover, we used a region-of-
109 interest (ROI) approach to separately examine the properties of the anterior and posterior HF,
110 PRC, and PHC (Figure 1B), thus shedding new light on the regional specificity of memory
111 changes within the MTL.

Results

Behavioral results

Behavioral data are presented in Table 1. Item memory was evaluated by comparing discriminability for old versus new items in the item recognition test. Item memory was above chance for both immediate, $t(27)=22.16$, $p<.001$, and delayed test, $t(27)=18.85$, $p<.001$, and, not surprisingly, accuracy was higher for items tested immediately than after a delay, $t(27)=8.54$, $p<.001$. This difference was observed for both recollection, $t(27)=9.51$, $p<.001$, and familiarity, $t(27)=5.06$, $p<.001$, contributions to item recognition. Context memory was evaluated by comparing discriminability of intact and recombined sentences in the associative recognition test. Participants successfully discriminated between intact and recombined sentences for both immediate, $t(26)=8.22$, $p<.001$, and delayed test, $t(26)=8.17$, $p<.001$, and again, associative recognition accuracy was higher for sentences tested immediately than after a delay, $t(26)=5.13$, $p<.001$. Consistent with the idea that item recollection might involve the reactivation of associative information, associative recognition accuracy was higher for recognized items that were associated with a “remember” response than for recognized items that were not, $F(1,26)=14.20$, $p<.001$. The difference in source accuracy did not interact with delay, $F(1,26)=.27$, $p=.61$.

During the item recognition test, participants were faster to correctly recognize items from the immediate list than from the delayed list, $F(1,26)=13.87$, $p=.001$. Importantly, this difference did not interact with memory status, $F(1,26)=.06$, $p=.80$: that is, the delay effect was observed both for recognized items accompanied by a “remember” response (immediate: $1.35 \pm .23$ s; delayed: $1.40 \pm .24$ s) and for those that were not (immediate: $1.64 \pm .35$ s; delayed: $1.70 \pm .29$ s). The lack of interaction suggests that response time differences cannot account for delay-dependent activation changes that are specific to recollection. During the associative recognition test, participants were also faster to correctly recognize intact sentences from the immediate list ($2.01 + .37$ s) than from the delayed list ($2.24 + .51$ s), $t(26) = 3.59$, $p=.001$.

Recollection-related activity during immediate and delayed recognition

We first tested for delay-dependent differences in recollection-related activity during item recognition. Mean activity estimates were extracted from anatomical ROI masks of the anterior HF, posterior HF, PRC, and PHC (Figure 1B), then compared with a memory (recollection,

142 familiarity) x delay (immediate, delayed) repeated-measures ANOVA. Within each of these
143 ROIs, activity was greater for recollection than familiarity trials (all $F_s > 4.6$, all $p_s < .046$;
144 Figure 2). This recollection effect was stable over time in bilateral PRC, PHC, and anterior HF
145 (all interaction $F_s < 1.67$, $p_s > .21$). However, in the posterior HF, the recollection effect
146 interacted with delay (left: $F(1,18)=5.68$, $p=.028$; right: $F(1,18)=3.93$, $p=.063$), such that the
147 posterior HF was more active for immediate than delayed recollection trials (left: $F(18)=5.61$,
148 $p=.029$; right: $F(18)=5.75$, $p=.028$), with no concomitant change in familiarity trials, $F_s < 1.26$,
149 $p_s > .27$. No region showed delay-dependent changes in familiarity estimates (Supplementary
150 File 1). The apparent difference in delay effects between the anterior and posterior HF was borne
151 out as an ROI by delay interaction, $F(1,18)=5.80$, $p=.027$, indicating that these areas are
152 dissociable on the basis of their contributions in recollection over time.

153 Because recognition accuracy was higher for items tested immediately than after a delay,
154 findings of delay-dependent differences might be confounded by differences in the numbers of
155 recollection and familiarity trials contributing to the analysis. To control for this potential
156 confound, all comparisons were re-analyzed using a model in which trials were randomly
157 sampled to match numbers of recollection and familiarity across delays. These analyses
158 replicated the MTL ROI findings described above (Figure 2 – supplement 2).

159 Many studies have shown that recollection is also associated with enhanced activation
160 within an extended neocortical network outside of the MTL [20, 35, 36], sometimes referred to
161 as the “core recollection network” [37]. To test whether recollection-related activity in this
162 network was modulated by delay, we conducted ROI analyses for the retrosplenial cortex,
163 posterior cingulate, precuneus, angular gyrus, and medial prefrontal cortex. In the left
164 hemisphere, all of these regions showed a main effect of memory, all $F_s > 9.5$, $p_s < .007$, with no
165 significant interactions with delay, $F_s < 2.21$, $p_s > .15$ (Figure 3A). In the right hemisphere,
166 recollection-related activity in the right precuneus and posterior cingulate declined across the
167 delay (Figure 3 – supplement 1). However, recollection effects in these regions were weaker in
168 general, consistent with previous findings that cortical activity associated with recollection of
169 verbal materials tends to be strongest in the left hemisphere [38]. Exploratory whole-brain,
170 voxel-wise comparisons revealed that both immediate and delayed recollection were associated
171 with activity in the recollection network (corrected $p < .05$; Figure 3B), with no significant delay-
172 dependent differences in recollection-related activity (corrected $p < .05$). To better define where

173 recollection-related activity was insensitive to delay, we identified regions that were conjointly
174 involved in immediate and delayed recollection (corrected joint $p < .05$) while excluding voxels
175 showing even small delay differences (liberally defined at $p < .05$ uncorrected). All neocortical
176 regions within the recollection network contained clusters that survived this approach (Figure 3 –
177 supplement 2). These results suggest that, for the most part, recollection-related responses in the
178 neocortical recollection network were maintained across the delay.

179 Results from these univariate analyses indicate that differences in brain activity
180 associated with immediate and delayed recollection varied across MTL subregions. The anterior
181 HF and cortical MTL areas maintained their contributions to recollection over time, whereas
182 posterior HF effects were sensitive to delay. Thus, even when memories at both delays were
183 endorsed with recollection, there were changes in posterior HF involvement in memory
184 recognition.

185 **Context similarity during immediate and delayed recognition**

186 Our next analyses tested whether MTL activity patterns during item recognition carried
187 information about the context (i.e., room) that had been associated with the item at encoding. As
188 depicted in Figure 4A, multi-voxel patterns within each ROI were estimated for every
189 recollection trial, and pairs of trials were compared by calculating the similarity between their
190 associated voxel patterns. Similarity values were then summarized according to whether the
191 items had shared context information during encoding (same room from the same study list: e.g.,
192 “the apple is in the *bedroom*” and “the pencil is in the *bedroom*”) or had not shared information
193 (different rooms from the same study list: e.g., “the apple is in the *bedroom*” and “the chair is in
194 the *kitchen*”). Because there was no context information present during the item recognition
195 phase, any pattern similarity differences between these pair types must be ascribed to the
196 reactivation of context information from memory. Thus, context similarity was defined as the
197 difference in pattern similarity between same-room and different-room pairs, evaluated
198 separately for each ROI. Note that because the locations were typical rooms in a house, this form
199 of context retrieval may reflect a mixture of both spatial and semantic context information (i.e.,
200 remembering the general location or semantic features of the room associated with the item).

201 Because only a few studies [33, 34, 39] have shown that MTL multi-voxel patterns carry
202 information about previously learned context information, even at immediate recall, our first
203 analyses sought to establish the presence of pattern information related to context similarity

204 during immediate recollection, when context memory was strongest. In the left anterior HF,
205 pattern similarity was significantly greater among same-room pairs than different-room pairs,
206 $t(18)=2.34, p=.015$ (Figure 4B), and a similar trend was observed in the left PRC, $t(18)=1.73,$
207 $p=.051$. There were no significant effects for any of the other MTL regions, $ts<1, ps>.18$ (Figure
208 4 – supplement 1). Context similarity effects were also absent from cortical regions outside of
209 the MTL, either immediately or after a delay, $ts<1.8, ps>.05$, suggesting that these effects were
210 selective to the left anterior MTL. The MTL findings were verified with a randomization test
211 showing that pattern similarity for same-room pairs exceeded what would be expected by chance
212 if context information were randomly assigned (Figure 4 – supplement 2). Additionally, when
213 the same analysis was run with familiarity trials instead of recollection trials, no differences were
214 observed between same and different context trial pairs, $ts<1, ps>.2$ (Figure 4 – supplement 3).
215 This distinction is consistent with the claim that pattern similarity differences were related to the
216 reactivation of shared context information, which should be more evident during memory
217 recollection.

218 After determining that left anterior MTL regions showed evidence for context similarity
219 at the immediate test, we next tested whether context similarity effects in these regions changed
220 over time. The left PRC showed a significant main effect of context similarity across both
221 delays, $F(1,18)=5.78, p=.027$, and context similarity did not interact with delay, $F(1,18)=.54,$
222 $p=.47$. In fact, the PRC showed a marginal context similarity effect for the delayed list as well,
223 $t(18)=1.54, p=.07$, suggesting that the sensitivity of this region to context information was stable
224 over time. The anterior HF, on the other hand, showed neither a significant main effect,
225 $F(1,18)=2.99, p=.10$, nor interaction, $F(1,18)=1.13, p=.30$. The absence of a clear main effect or
226 interaction may be due, in part, to substantial variability in context similarity effects during
227 delayed recollection. One possibility is that this variability is related to individual differences in
228 retention of context information in memory. To test this hypothesis, we correlated individual
229 subjects' context similarity estimates (i.e., the voxel pattern differences between same- and
230 different-context trial pairs) with their performance on the subsequent associative recognition
231 test, based on the idea that the associative recognition test relied on the same kind of room
232 information measured by the pattern similarity analysis. Indeed, participants who performed best
233 on the associative recognition test also showed the largest context similarity effect in the left
234 anterior HF during delayed recollection, $r=.53, t(16)=2.53, p=.022$ (Figure 4C). This relationship

235 was significant even after controlling for individual differences in the number of recollection
236 trials, $t(15)=2.81$, $p=.013$. For the PRC, the correlation was in the same direction but not
237 significant, $r=.25$, $t(16)=1.02$, $p=.32$. Finally, there was no significant relationship between
238 anterior HF context similarity and associative recognition for the immediate list, $r=-.17$,
239 $t(16)=.71$, $p=.49$; however, there was little variability in the similarity estimates for these trials.
240 These findings provide strong evidence that, after a delay, the context similarity analysis was
241 picking up on meaningful associative information during the item recollection period. Moreover,
242 they are consistent with the memory transformation account, in that anterior HF involvement in
243 context coding over time was contingent on the retention of context information in memory.

244

Discussion

245 The current study provided novel evidence that HF and parahippocampal areas play
246 different roles in supporting memory over time. During item recollection, the involvement of
247 cortical MTL areas was stable over time. Within the HF, however, there were different effects
248 for anterior and posterior regions. Whereas posterior HF showed reduced recollection-related
249 activity after a one-day delay, recollection-related activity in anterior HF remained relatively
250 stable. Furthermore, anterior HF activity patterns carried information about contexts associated
251 with the items at study, and this pattern information was maintained over time in participants
252 who successfully retained context associations. Below, we relate these findings to extant
253 neurobiological models of memory and discuss the specific contributions of individual MTL
254 regions. We conclude that models of memory must account for variability among MTL
255 subregions with respect to their involvement in memory retrieval over time.

256 Differences in recollection-related activity along the longitudinal axis of the HF

257 Both the standard consolidation model and memory transformation accounts predict that
258 HF activity during retrieval should decline with increasing retention intervals, although they
259 assign different explanations to this decline. To our knowledge, neither account makes explicit
260 predictions about variability along the longitudinal axis of the HF. In the present study, the
261 anterior and posterior HF had dissociable responses during immediate and delayed retrieval.
262 Whereas recollection-related activity in the posterior HF decreased over time, activity in the
263 anterior HF was relatively stable across the one-day delay. In previous fMRI studies that used
264 paradigms comparable to the one used here, HF results have been somewhat mixed: some studies

265 have shown that HF activity was greater for early than delayed retrieval [5, 6, 13, 14, 40, 41], but
266 others have reported no change [8, 42, 43] or even the opposite effect [9, 44]. Some of these
267 differences may be related to the sensitivity of the fMRI analysis to specific memory processes:
268 some studies reporting no change used simple comparisons of targets and foils [8] or recognized
269 and forgotten trials [42], whereas studies that isolated activity for high-confidence, recollection-
270 based or associative hits have often reported delay-dependence [5, 6, 13, 14, 40, 41, but see 43].
271 Although some delay effects have been localized to the anterior HF [6, 14], differences in the
272 posterior HF have been commonly observed for studies using associative memory tasks [5, 40,
273 41]. By investigating delay effects within anatomically restricted regions, the current approach
274 might have improved our ability to detect differences in localization that might not have been
275 readily apparent in a group analysis applying voxel-wise thresholds. Thus, the finding that
276 changes in recollection-related activity were circumscribed to the posterior HF is consistent with
277 the available literature, but would not have been predicted by extant models.

278 Studies of autobiographical memory have examined differences between recent and
279 remote memories across a more extended timescale [45], and some of these studies have
280 compared the role of the anterior and posterior HF. For example, one study reported that the
281 anterior HF showed a larger delay-dependent difference than the posterior HF during
282 autobiographical memory retrieval [12]. Another study used multi-voxel pattern analysis to
283 decode information about autobiographical events. This study reported that patterns in the
284 posterior HF could be used to decode remote but not recent autobiographical memories during
285 repeated retrieval events, whereas patterns in the anterior HF could be used to decode both recent
286 and remote memories [46, 47]. At face value, these findings might seem to contradict the present
287 results, but there are numerous differences between autobiographical memory tasks and
288 paradigms that focus on laboratory-controlled events. In particular, the use of repeated retrieval
289 events and long retention delays could complicate the interpretation of fMRI studies of
290 autobiographical memory retrieval. During remote autobiographical retrieval, hippocampal
291 activity could be related to the construction of a new memory for an old event, or to the retrieval
292 of the original memory or its more recent reconstructions. Another issue is that differences
293 between recent and remote autobiographical memories can be confounded by differences in
294 vividness and context specificity. Indeed, in the study by Gilboa et al. (2004), there were no
295 significant delay-dependent differences in the HF after controlling for vividness. Although

296 laboratory-controlled studies are not immune to this possible confound, the issue was mitigated
297 in the present study by limiting analyses to memory retrieval accompanied by recollection and by
298 identifying neural patterns associated with studied context information.

299 An important question for future research is how changes in neural representation over a
300 one-day interval relate to the changes over longer intervals that are the focus of memory
301 consolidation and transformation accounts. There is considerable evidence suggesting that early
302 stages of systems consolidation can be initiated during the first night of sleep after learning [48],
303 but little is known about how initial changes in hippocampal representation are related to longer-
304 lasting changes. It is possible that the changes in activation magnitude and pattern similarity
305 observed here reflect forgetting of certain aspects of context information, and that qualitatively
306 different kinds of changes—particularly in cortical representation—might be apparent over a
307 longer interval.

308 **Contributions of the anterior HF to context memory**

309 The relative stability of recollection-related activity in the anterior HF may be related to
310 its continued involvement in supporting context memory over time. Because recollection can be
311 triggered by different kinds of associative details, including information about encoding context,
312 we separately examined the sensitivity of the multi-voxel patterns to context information learned
313 during encoding. Multi-voxel patterns in the left anterior HF were sensitive to context similarity
314 during immediate recollection, and after a delay this effect was strongest for participants who
315 could accurately retrieve context associations. According to one view of HF function, the
316 anterior HF may be especially involved in representing episodic context at a global level [28]. In
317 support of this view, the anterior HF contains cells with larger place fields than the posterior HF
318 [49], and it is involved in coding information about the coarse location of objects [29], the global
319 position of landmarks [50, 51], and the gist of memories [52, 53]. Taking this view into
320 consideration, it may be that pattern similarity effects in the anterior HF reflect the activation of
321 generalized context information (e.g., general features of the room associated with the item at
322 study) that was shared across many encoding events. As discussed below, the posterior HF might
323 support more specific representations of context (e.g., remembering the exact location in which a
324 specific item was imagined in the bedroom) in a more time-limited way. Regardless of the scale
325 of anterior HF representations, it is noteworthy that recollection-related activity in the anterior
326 HF was relatively stable over the delay, and that the anterior HF continued to show evidence for

327 context coding in participants who retained context information in memory, suggesting that the
328 type of information carried by the anterior HF can be long lasting. These findings are compatible
329 with the memory transformation account, which models posit that the HF should be involved in
330 retrieval so long as its preferred form of mnemonic information is maintained.

331 Irrespective of delay, an important finding of the present study was that multi-voxel
332 patterns carried information about incidentally reactivated context associations during item
333 recollection. A few previous studies have shown that neural patterns present during encoding are
334 reactivated during item recognition [54, 55] and cued recall [39, 56], and that patterns within the
335 MTL carry information related to study context [33, 34]. For instance, during cued recall,
336 patterns in the anterior HF, PRC, and PHC were shown to carry information about the study
337 context [33]. However, there has been little evidence that item recollection involves the
338 spontaneous reactivation of context-related patterns even without an overt source decision,
339 despite the assumption that recollection typically involves contextual retrieval. In one study,
340 Johnson and colleagues [54] showed that a classifier trained to discriminate among study
341 contexts was sensitive to context information that was incidentally reactivated during
342 recognition, and that for the posterior cingulate, context reactivation was especially apparent for
343 items accompanied by recollection. However, this study did not report context reactivation
344 effects within the HF. The present work expands on these findings to demonstrate that, during
345 recollection, left anterior HF patterns carried information about the context associated with an
346 item during encoding, even when context was not explicitly cued or re-presented. The context
347 similarity effect in the HF was relatively small, perhaps because HF patterns are more sensitive
348 to similarities in object-context associations than to context alone [34, 57]. The finding that
349 context-related pattern similarity was predictive of associative recognition performance,
350 however, provides converging evidence that hippocampal voxel patterns carry behaviorally
351 relevant context information. Nevertheless, future work will be necessary to determine the
352 sensitivity of hippocampal voxel pattern information to other kinds of context manipulations.

353 **Similarities between the anterior HF and PRC**

354 The PRC had a similar response profile to the anterior HF, in that it was stable in its
355 recollection-related activity over time. It also tended to show context similarity effects that
356 persisted across the delay. The anterior HF is strongly connected with the PRC, which is part of
357 an anterior temporal system thought to be important for processing, remembering, and assigning

358 value to items [20]. These two regions may work together to support memory for item or item-
359 context associations, and context similarity effects in the anterior HF may reflect the retrieval of
360 contextual information in response to an item cue. The PRC, on the other hand, has been linked
361 to item recognition [e.g., 58, 59], recollection of item associations [60], and semantic processing
362 [e.g., 61, 62]. Thus, the prior literature is most consistent with a role for the PRC in item
363 processing, and the finding of a context similarity effect in the PRC was unexpected. However,
364 there is some evidence that the PRC may additionally carry some information about context,
365 such as the locations of items in space [63]. PRC lesions have also been shown to disrupt some
366 forms of context memory, including object-context associations [64], positional changes in
367 object arrays [65], and contextual fear [66]—although these impairments have typically been
368 more circumscribed than those observed following PHC damage [64, 65]. Based on this
369 literature and the present data, we cannot rule out the possibility that like the anterior HF, the
370 PRC is involved in the long-term storage of the association between an object and the general
371 context in which it was encountered. Alternatively, it could be that the anterior HF and PRC are
372 both sensitive to shared context information, but for different reasons: whereas the anterior HF
373 might carry general representations of context, pattern similarity effects in the PRC might reflect
374 the recollection of items associated with each room, through episodic associations learned during
375 encoding or through existing semantic associations.

376 **The time-limited role of posterior HF in recollection**

377 In contrast to the anterior HF and PRC, the posterior HF was neither stable in its
378 contributions to recollection over time nor did it show enhanced pattern similarity during
379 retrieval of objects that shared the same contextual associations. As noted above, it is possible
380 that the posterior HF encodes highly specific contextual details [28], such as precise locations
381 within a spatial context [29, 49] or positions within a sequence [34], which might be useful for
382 disambiguating among related contexts. For instance, in one study, hemodynamic responses in
383 the posterior HF were greater during the retrieval of precise rather than coarse location
384 information associated with an object [29]. It is possible that, here, the reduction in posterior HF
385 activity across the delay reflects the forgetting of trial-specific context information. Prior work in
386 rodents has shown that memories may lose their contextual specificity over time [30, 31], and
387 that the loss of specificity is associated with diminished dependence on the dorsal HF (which
388 may be homologous to the posterior HF in humans) during retrieval [67]. In addition, if the

389 posterior HF codes only specific context information, this could explain the absence of a context
390 similarity effect in this region. By definition, the multi-voxel pattern similarity analysis used here
391 depended on similarities among trials that had been associated with the same “room,” and was
392 therefore insensitive to trial-specific information. Some previous studies have used approaches
393 that have enabled them to identify event- or scene-specific patterns, and these studies have
394 shown that this kind of specific information can be decoded from multi-voxel patterns in the HF
395 [34, 68, 69], and that the specificity of HF patterns is positively related to memory performance
396 [70]. In this study, we were unable to directly measure trial-specific information in the posterior
397 HF, but future studies could incorporate graded levels of context specificity in order to test its
398 relation to response changes over time.

399 **Neocortical contributions to recollection**

400 The role of the MTL in memory has often been contrasted against the role of neocortical
401 areas in memory, which are thought to increase or remain stable in their support of memory over
402 time [1, 3, 4]. However, most models have excluded the PRC and PHC from their discussion of
403 cortical function [1, 3, 4, but see 71] and previous studies have not typically included these
404 regions as ROIs [but see 8]. Here, we provide novel evidence that the roles of the HF and
405 parahippocampal areas are dissociable in terms of their involvement in recognition memory over
406 time. Whereas recollection-related activity in the posterior HF declined from immediate to
407 delayed retrieval, activity in the PRC and PHC remained stable. One interesting point of
408 divergence is between the posterior HF and PHC, which are strongly interconnected [20]. Like
409 the posterior HF, the PHC has been implicated in memory for specific context information [15-
410 17], and the PHC has also been shown to carry information about scene-specific associations
411 [e.g., 39]. Here, patterns in both regions were insensitive to shared context information, yet the
412 PHC was involved in memory recollection after a one-day delay, whereas the posterior HF was
413 not. Future work should address whether PHC representations simply remain more stable over
414 time, as compared with those in the posterior HF, or whether there are other differences that
415 might explain their different activation profiles.

416 Beyond the MTL, across both delays, recollection-related activity was also observed in a
417 network of regions including the retrosplenial cortex, posterior cingulate, precuneus, angular
418 gyrus, and medial prefrontal cortex. This network is thought to be important for context memory
419 and recollection [20, 36, 72]. Importantly, these findings suggest that most areas involved in

420 recollection, whether they are within the MTL or not, maintain their involvement across a one-
421 day delay. Altogether, these findings clearly demonstrate that neurobiological models of memory
422 must go beyond simple dichotomies between the MTL and neocortex to address the role of
423 specific HF and parahippocampal areas.

424 **Future directions and conclusions**

425 The present results raise several questions to be addressed in future studies. One question
426 involves the role of the PRC and PHC in immediate and delayed recollection. Here, we found
427 that both regions supported recollection immediately and after a one-day delay, but that patterns
428 in the PRC but not the PHC were sensitive to shared context information. Future work should
429 address whether the PRC and PHC are similarly involved in memory tested after longer intervals
430 and with measures that are more sensitive to the specificity of information retained in memory.
431 Additionally, because memory was tested after a one-day delay, we cannot disentangle changes
432 attributable to active sleep-dependent processes [73] from more passive time-dependent changes.
433 Finally, an important next step would be to compare the item-location associations used here
434 with associations that may be less dependent on HF function, such as unitized associations [74,
435 75] or emotional associations (Yonelinas & Ritchey, in revision). In particular, emotional
436 memories are forgotten more slowly than neutral memories [e.g., 76], and some evidence
437 suggests that the persistence of emotional recollection is related to the function of anterior MTL
438 structures [77].

439 In summary, this study provided novel evidence that regions within the MTL play
440 different roles in supporting item recollection over time. The results highlight the need to revise
441 existing models to incorporate differences between MTL areas. In particular, it will be important
442 for models to distinguish between the anterior and posterior HF, which may show different
443 changes in their contributions to memory over time.

444 **Methods**

445 **Participants**

446 Data were acquired from 30 young adults (15 female; ages 18-31 years). Data from one
447 participant was excluded due to button box issues during the scan, and data from another
448 participant was excluded due to head motion and poor performance. Of the remaining 28

449 participants, 9 were excluded from fMRI data analyses due to insufficient variability in memory
450 performance (i.e., fewer than 9 recollection or familiarity trials). Thus, the fMRI analyses
451 included 19 participants (9 female). Due to technical problems, one of these participants
452 completed the item recognition but not associative recognition task. Participants reported that
453 they were native English speakers, free of neurological and psychiatric disorders, and eligible for
454 MRI. Participants reported sleeping, on average, 7.42 hours (range: 5 to 12 hours) between the
455 first and second session.

456 **Stimuli**

457 Stimuli consisted of 252 nouns that referred to objects. For each participant, these words
458 were randomly assigned to one of 3 lists (N=84 each): the Day 1 encoding list (delayed list), the
459 Day 2 encoding list (immediate list), or the lure list for item recognition. During encoding, items
460 were placed into sentences describing the location of the object, which could be in one of 8
461 rooms in a house: bathroom, bedroom, den, dining room, kitchen, living room, office, and patio
462 area. For example, on one trial, a possible sentence might read, “The apple is in the bedroom.”
463 Thus, the room associated with each item constituted its encoding context, which might include a
464 mixture of spatial and semantic information about the room. The 8 contexts were randomly
465 assigned to either the immediate or delayed encoding list, such that only 4 contexts were
466 presented on either day.

467 **Experimental Design**

468 There were two experimental sessions that occurred on consecutive days (Figure 1A). On
469 Day 1, participants completed an encoding task. On Day 2, participants completed another
470 encoding task, an item recognition task, and an associative recognition task. Both encoding tasks
471 took place in the same laboratory testing rooms. The recognition tasks took place in the scanner,
472 with the item recognition task beginning as soon as the participant was positioned within the
473 scanner, approximately 20 minutes after the end of the Day 2 encoding task. All fMRI analyses
474 focus on the item recognition task.

475 During the two encoding tasks, participants studied sentences in which trial-unique object
476 nouns were paired with one of 8 contexts (Figure 1A). The set of items and contexts was
477 different on each day. Different contexts were assigned to each day in order to avoid confounds

478 related to contextual interference across days. During each encoding task, 84 sentences appeared
479 on-screen for 5 s each, separated by jittered fixation intervals (mean = 4 s, range = 2—10 s).
480 Participants were instructed to rate on a continuum how well they were able to imagine the
481 pairing on a 6-point scale, with 1=*not well* and 6=*very well*. Trial order was randomly
482 determined for each participant. Immediately after each encoding task, participants were cued to
483 group the 4 previously-studied rooms into two houses, based on random assignment. This
484 grouping manipulation did not alter memory performance and will not be considered further.

485 The item recognition task was designed to assess memory for the items studied during
486 encoding. During this task, participants were presented with words from both encoding lists and
487 the lure list (Figure 1a). Words were presented for 2s each, separated by jittered fixation intervals
488 (mean = 4s, range = 2—10 s). Participants were asked to determine whether the word was old
489 (studied either day) or new (unstudied) using a modified 6-point remember-know scale,
490 including responses for *definitely new*, *probably new*, *not sure*, *probably old*, *definitely old*, and
491 *remember*. For half of the participants, the scale was presented in reverse order. Participants
492 were instructed that they should use the “remember” response any time they could recall any
493 kind of specific detail from when they initially studied that item, whereas the other memory
494 responses reflected graded levels of memory confidence in the absence of a specific detail. We
495 did not explicitly instruct the participants to remember the associated room during the item
496 recognition phase; rather we emphasized that any type of detail would qualify for a “remember”
497 response. This was because we did not want participants to engage in a strategy in which they
498 called to mind the rooms on every trial, which would have interfered with our ability to detect
499 room information arising from memory. Trials from each list were evenly divided across 3
500 functional imaging runs, such that each run contained the same number of trials associated with
501 each studied location. A unique sequence of trials and jittered fixation intervals was randomly
502 determined for each participant.

503 The associative recognition task was designed to assess memory for the item-context
504 associations made during encoding. During this task, participants were presented with sentences
505 that were either identical to sentences that they had studied during either encoding session
506 (“intact”) or sentences that were recombinations of items and contexts that were both previously
507 studied but not as part of the same sentence (“recombined”). Of the 84 sentences studied on each
508 day, 28 were presented as intact and 56 were presented as recombined. The items and contexts in

509 the recombined sentences were always drawn from the same day list. Sentences were presented
510 for 3s each, separated by jittered fixation intervals (mean = 4s, range = 2—10 s). Participants
511 were asked to rate whether the sentence was intact or recombined on a 6-point scale, including
512 response for *definitely recombined*, *probably recombined*, *guess recombined*, *guess intact*,
513 *probably intact*, and *definitely intact*. For half of the participants, the scale was presented in
514 reverse order. Trials from each list were evenly divided across 3 functional imaging runs, and
515 trial order was randomly determined for each participant.

516 **Behavioral Analysis**

517 Behavioral analyses were based on the full available sample for each task. Item
518 recognition performance was measured as the discriminability (d') between old items (from the
519 immediate or delayed list) and new items. Item recognition was further broken down into
520 estimates of recollection and familiarity according to the dual-process model of recognition
521 memory. Recollection was defined as $(R_{old} - R_{new}) / (1 - R_{new})$, where R_{old} is the rate of “R”
522 responses to old items, and R_{new} is the rate of “R” responses to new items. Familiarity was
523 defined as $(F_{old} / (1 - R_{old})) - (F_{new} / (1 - R_{new}))$, where F_{old} is the rate of “definitely old” and “probably
524 old” responses to old items, and F_{new} is the rate of “definitely old” and “probably old” responses
525 to new items. Note that these process estimates were computed to allow comparison to previous
526 studies. The primary findings of the study, however, do not depend on assumptions specific to
527 the dual process model. Associative recognition performance was measured as the
528 discriminability (d') between intact and recombined sentences, separately for the immediate or
529 delayed encoding list. To determine the relation between item recognition and associative
530 recognition, the proportion of correct associative recognition responses was calculated for items
531 previously marked as recollected, familiar, or forgotten. All statistical comparisons on the
532 behavioral data were conducted in R version 3.1.1 (<http://www.R-project.org>).

533 **Image Acquisition & Pre-Processing**

534 Scanning was performed on a Siemens Skyra 3T scanner system with a 32-channel head
535 coil. High-resolution T1-weighted structural images were acquired using a magnetization
536 prepared rapid acquisition gradient echo (MPRAGE) pulse sequence (field of view = 25.6 cm,
537 image matrix = 256 x 256, 208 axial slices with 1.0 mm thickness). Functional images were
538 acquired using a multi-band gradient echo planar imaging (EPI) sequence (TR = 1220 ms; TE =

539 24 ms; FOV = 19.2 cm; image matrix = 64 x 64; flip angle = 67; multi-band factor = 2; 38 axial
540 slices; voxel size = 3.0 x 3.0 x 3.0 mm).

541 SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) was used to pre-process the
542 images, including realignment, normalization, and smoothing. The high-resolution T1 image was
543 skull-stripped via segmentation. Functional images were realigned, correcting for motion, and
544 resliced. Resliced, native-space images served as the basis for the anatomical ROI analyses, in
545 which manually segmented ROIs (see *ROI Definition*) were co-registered to the mean functional.
546 For group voxel-wise analyses, the mean functional was co-registered to the skull-stripped
547 anatomical image, moving all of the functional images in register with the anatomical image. At
548 this point, the anatomical and functional images were warped to a group-derived template
549 generated using diffeomorphic registration (DARTEL) and normalized to MNI space. Functional
550 images were smoothed with a 6-mm Gaussian kernel. Skull-stripped anatomical images were
551 also warped and smoothed for use as an explicit mask for subsequent functional analyses.
552 Quality assurance included the identification of “suspect” time-points via the Artifact Detection
553 Tools (ART; http://www.nitrc.org/projects/artifact_detect), defined as time-points marked by
554 greater than .3 mm in movement or 1.3% global mean signal change. One participant was
555 excluded from analysis due to excess motion (> 3 mm) within the functional runs.

556 **ROI Definition**

557 The anterior HF (HC head), posterior HF (HC body and tail), PRC, and PHC were
558 manually segmented on the MPRAGE coronal plane according to previously published
559 guidelines [78, 79]. In brief, the most posterior slice of the anterior HF was defined as the last
560 slice containing the gyrus intralimbicus; the posterior HF immediately followed. The anterior
561 extent of the PRC was defined as 2 mm anterior to the limen insula or the most anterior slice in
562 which the collateral sulcus was visible, whichever was more anterior. The most posterior slice of
563 the PRC was defined as 4 mm posterior to the anterior/posterior HF transition. The PHC
564 immediately followed the PRC, and the posterior extent was defined as 2 mm posterior to the
565 appearance of the posterior crus of the fornix. The PRC segmentation included the entire lateral
566 bank and dorsal half of the medial bank of the collateral sulcus. The PHC segmentation included
567 the medial bank of the collateral sulcus, extending to the most medial aspect of the
568 parahippocampal gyrus. Some analyses also included a set of regions outside of the medial

569 temporal lobes, including the retrosplenial cortex, posterior cingulate, precuneus, angular gyrus,
570 and medial prefrontal cortex. These ROIs were labeled with FreeSurfer cortical parcellation tools
571 (<http://surfer.nmr.mgh.harvard.edu/>) using the Destrieux atlas [80] for the following labels:
572 G_cingul-Post-ventral, G_cingul-Post-dorsal, G_precuneus, G_pariet_inf-Angular, and
573 S_suborbital. Segmented brains were co-registered to the mean functional image and split into
574 masks for each ROI (see Figure 1B for an example set of MTL ROIs). Masks were filtered to
575 exclude voxels with low signal, defined as having mean temporal SNR (calculated across all
576 functional runs) more than 1 standard deviation below the ROI mean. For visualization in
577 standard space, ROI masks were warped to MNI space and combined across subjects into
578 probabilistic maps.

579 **Data Analysis**

580 For ROI analyses, models were run on unsmoothed functional images in native space.
581 ROI summary statistics, including pattern similarity estimates, were extracted with in-house
582 scripts (Source Code 1) in MATLAB 2009b (The MathWorks, Inc., Natick, MA), and statistical
583 comparisons were conducted in R version 3.1.1 (<http://www.R-project.org>). For voxel-wise
584 analyses, models were run on smoothed functional images in standard MNI space, and statistical
585 comparisons were conducted in SPM8.

586 **Univariate activation analyses.** Event-related stick-function regressors were used to
587 model trials corresponding to one of 9 conditions: immediate recollection, immediate familiarity,
588 immediate forgotten, delayed recollection, delayed familiarity, delayed forgotten, correct
589 rejections, false alarms, and no-response trials. “Recollection” trials were defined as old items
590 that were correctly recognized and endorsed with recollection (i.e., *R* response). “Familiarity”
591 trials were defined as old items that were correctly recognized but not endorsed with recollection
592 (i.e., *probably old* or *definitely old* responses). Six motion parameter regressors were included in
593 the model. Spike regressors were also included to model time-points identified as ART suspects.
594 Whole-brain fixed-effects contrasts were evaluated to obtain estimates of activity in response to
595 each trial type relative to implicit baseline. Contrast maps for “recollection-related activity” were
596 created by computing the activation difference between recollection and familiarity trials,
597 separately for each delay. The difference in recollection-related activity contrast images between
598 immediate and delayed trials was then used to estimate delay-dependent changes in recollection-

599 related activity.

600 For ROI random-effects analyses, contrast estimates were averaged within ROI masks of
601 the left and right anterior HF, posterior HF, PRC, and PHC. Contrast means were compared with
602 repeated-measures ANOVAs with factors for memory status (recollection, familiarity) and delay
603 (immediate, delayed). For comparison of effects across ROIs, estimates of recollection-related
604 activity were compared with repeated-measures ANOVAs with factors for ROI, hemisphere, and
605 delay. For completeness, activity estimates for familiarity and miss trials were also compared,
606 but recollection-related activity was the *a priori* focus of the experiment. For voxel-wise
607 random-effects analyses, contrast maps were evaluated with one-sample t-tests. Clusters were
608 considered significant (cluster-corrected $p < .05$) if they contained at least 36 voxels within a
609 mask of the entire brain, based on simulations with the 3dClustSim tool in AFNI
610 (<http://afni.nimh.nih.gov>). Delay-insensitive effects were identified as clusters that showed
611 recollection-related activity for both immediate and delayed lists, each thresholded at $p < .032$ for
612 a joint voxel-wise threshold of $p < .001$, exclusively masking for any significant effect of delay
613 (liberally defined at $p < .05$).

614 **Pattern similarity analysis.** Pattern similarity analyses [32] were conducted on
615 unsmoothed functional images in native space. Single trial models were generated to estimate the
616 response to each individual trial (N=252 per participant), resulting in a beta image for every trial.
617 Similar to the procedure described by Mumford and colleagues [81], a separate general linear
618 model was run for each individual trial, with the first regressor containing a stick function
619 mapped to the onset of the individual trial and the second regressor containing stick functions
620 modeling all of the other trials, with additional motion and nuisance regressors as described
621 above. For each participant, the voxel-wise pattern of hemodynamic activity within each ROI
622 was extracted from each of the 252 single-trial beta images.

623 Separately for each ROI, trial patterns were correlated with each other using Pearson's r .
624 Correlations were limited to pairs of trials from the same encoding list and memory status: that
625 is, immediate recollection trials were correlated only with other immediate recollection trials
626 (and likewise for delayed trials). Pattern similarity values were aggregated according to whether
627 or not the items had shared context information during encoding, i.e., same-room versus
628 different-room similarity. For instance, as depicted in Figure 3A, the item pair “apple” and

629 “pencil” share information because they were encoded in sentences pairing them with the same
630 room (“bedroom”), whereas the item pair “apple” and “chair” do not share information because
631 they had been paired with different rooms. Different-room pairs excluded pairs of rooms that had
632 been experimentally grouped after encoding (see *Experimental Design*). Thus, for any given
633 item, its same-room pairs included all other items encoded with the same room, and its different-
634 room pairs included items encoded with one of two other rooms on the same day. To control for
635 differences in pattern similarity between runs, same-room and different-room similarity were
636 first averaged within each run, and then similarity values from the three runs were averaged
637 together. To control for similarities among adjacent trials, only pairs at least two trials apart were
638 included in the analysis; however, because trial sequences were randomly determined for each
639 participant, temporal autocorrelation was unlikely to produce spurious pattern similarity effects
640 at the group level [82]. Pairs containing trials with outlying global signal values were also
641 excluded, based on the global average of absolute standardized values calculated for each within-
642 brain voxel. Pattern similarity values were Fisher-transformed for statistical comparison.

643 Because room information was not present during the item recognition phase and must be
644 attributed to memory processes, the difference between same-room and different-room similarity
645 was taken as evidence for context similarity. This difference was tested with one-sample *t*-tests
646 based on our directional hypothesis that same-room similarity should be greater than different-
647 room similarity. For regions showing evidence for context similarity in the immediate condition,
648 when context memory was strongest, we additionally tested the influence of delay on context
649 similarity was tested with repeated-measures ANOVAs with factors for pair type (same-room,
650 different-room) and delay (immediate, delayed). Finally, Pearson’s correlation was used to test
651 the relationship between context similarity and subsequent associative recognition performance
652 for the delayed list, and multiple linear regression was used to verify that the observed
653 relationship was not explained by differences in the number of item recollection trials. One
654 participant was excluded from the regression analyses due to below-chance associative
655 recognition performance.

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864 **Figure Captions**

865 **Figure 1. Task design and regions of interest.** **A)** Overview of the experimental design. Here, all fMRI
866 analyses are conducted on data from the item recognition phase. **B)** ROIs included in the main analyses,
867 including the anterior hippocampus (ant. HF), posterior hippocampus (post. HF), perirhinal cortex (PRC),
868 and parahippocampal cortex (PHC). Coronal MRI slices show manually-traced ROIs from a
869 representative subject, resliced to functional resolution and warped into MNI space for display on a
870 template brain.

871
872 **Figure 2. Recollection-related activity in the MTL.** Univariate estimates of recollection-related activity
873 (i.e., the difference in activation for recollection and familiarity trials) for left hemisphere MTL ROIs
874 (similar results hold for right hemisphere ROIs; see Figure 2 – supplement 1). Asterisk (*) denotes a
875 significant interaction between delay (immediate, delayed) and memory status (recollection, familiarity),
876 $p < .05$. Error bars denote the standard error of the mean. See Figure 2 – supplement 2 for results from a
877 model in which the number of recollection and familiarity trials were matched between delays. Summary
878 statistics for individual subjects are contained in Figure 2 – Source Data 1, and group-averaged activity
879 estimates for all conditions can be found in Supplementary File 1.

880
881 **Figure 3. Recollection-related activity in the cortical recollection network.** **A)** Univariate estimates of
882 recollection-related activity, i.e., the difference in activation for recollection and familiarity trials, for
883 cortical ROIs in the recollection network. Results for left-hemisphere ROIs are shown (see Figure 3 –
884 supplement 1 for right-hemisphere ROIs). Error bars denote the standard error of the mean. Note that
885 although the precuneus appears to show a reduction in recollection-related activity over time, the
886 interaction was not significant. Summary statistics for individual subjects are contained in Figure 3 –
887 Source Data 1. **B)** Voxel-wise maps of recollection-related activity, i.e., the difference between
888 recollection and familiarity trial activity, thresholded to display significant clusters (voxel-wise $p < .001$,
889 cluster-corrected $p < .05$). Maps are displayed separately for immediate and delayed recollection. Surface
890 images were rendered in Caret using the PALS atlas (left hemisphere shown; see Figure 3 – supplement 1
891 for right hemisphere). Peaks are reported in Supplementary File 2. The conjunction of immediate and
892 delayed recollection-related activity is shown in Figure 3 – supplement 2.

893
894 **Figure 4. Context similarity in anterior MTL during recollection.** **A)** Schematic of the pattern
895 similarity analysis procedure. **B)** Estimates of pattern similarity (Pearson's r) for same-room and
896 different-room pairs are plotted for the left anterior HF and left PRC (see Figure 4 – supplement 1 for

897 other regions). Asterisk (*) denotes a significant effect of context similarity, i.e., the difference in
898 similarity for same- and different-room pairs, $p < .05$. Error bars denote the standard error of the mean. The
899 cross (+) denotes a marginally significant effect, $p < .08$. Summary statistics for individual subjects are
900 contained in Figure 4 – Source Data 1. A non-parametric randomization test confirmed that same-room
901 similarity was greater than what was likely to be observed by chance (Figure 4 – supplement 2).
902 Furthermore, these effects were observed only for recollection trials, not familiarity trials (Figure 4 –
903 supplement 3). C) The relationship between associative recognition accuracy (d') and context similarity
904 in the left anterior HF.

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909 **Table 1: Behavioral results**

910

Item Recognition	“R” rate	“4” or “5” rate	d’	Recollection	Familiarity
immediate	.46 ± .22	.40 ± .22	1.79 ± .43	.44 ± .22	.46 ± .18
delayed	.25 ± .19	.43 ± .17	1.14 ± .32	.22 ± .18	.32 ± .13
novel	.04 ± .05	.23 ± .09	-	-	-
Associative Recognition	“intact” rate	d’	% correct for “R” responses	% correct for “4” or “5” responses	
immediate intact	.78 ± .13	1.34 ± .59	73.5 ± 16.6	68.6 ± 14.8	
delayed intact	.64 ± .17	.59 ± .38	65.1 ± 18.4	57.7 ± 11.4	
immediate recombined	.34 ± .14	-	-	-	
delayed recombined	.43 ± .13	-	-	-	

911 Note: Summary statistics for individual subjects are contained in Table 1 – Source Data 1.

912

913

914 **List of figure supplements**

915 **Figure 2 – supplement 1.** Recollection-related activity in right-hemisphere MTL ROIs.

916 **Figure 2 – supplement 2.** Recollection-related activity in a model controlling for the number of trials
917 between delays.

918 **Figure 3 – supplement 1.** Recollection-related activity in the right hemisphere of the cortical recollection
919 network.

920 **Figure 3 – supplement 2.** Conjunction of immediate and delayed recollection-related activity.

921 **Figure 4 – supplement 1.** Context similarity effects in all MTL ROIs.

922 **Figure 4 – supplement 2.** Randomization test confirming context similarity effects in the anterior MTL.

923 **Figure 4 – supplement 3.** Context similarity in the anterior MTL during familiarity.

924

925 **List of source data**

926

927 **Table 1 – Source Data 1.** Behavioral data.

928 **Figure 2 – Source Data 1.** Activation estimates for MTL ROIs.

929 **Figure 3 – Source Data 1.** Activation estimates for cortical recollection network ROIs.

930 **Figure 4 – Source Data 1.** Pattern similarity estimates.

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933 **Other supplementary files**

934

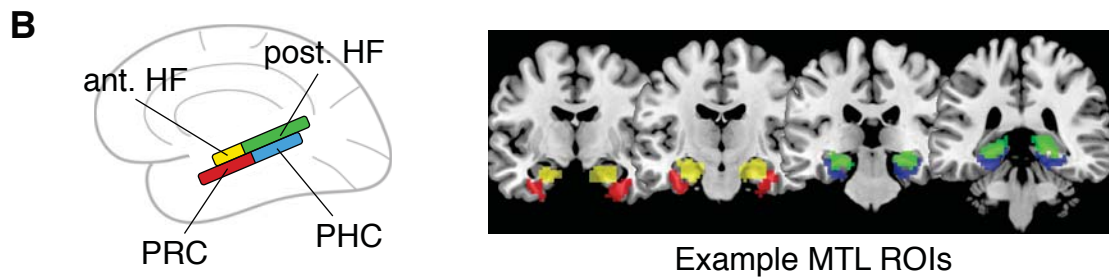
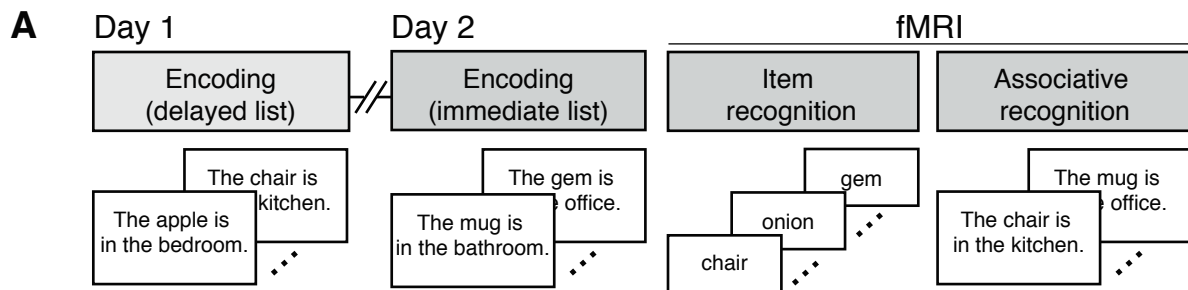
935 **Supplementary File 1.** MTL activity estimates for all conditions (related to Figure 2).

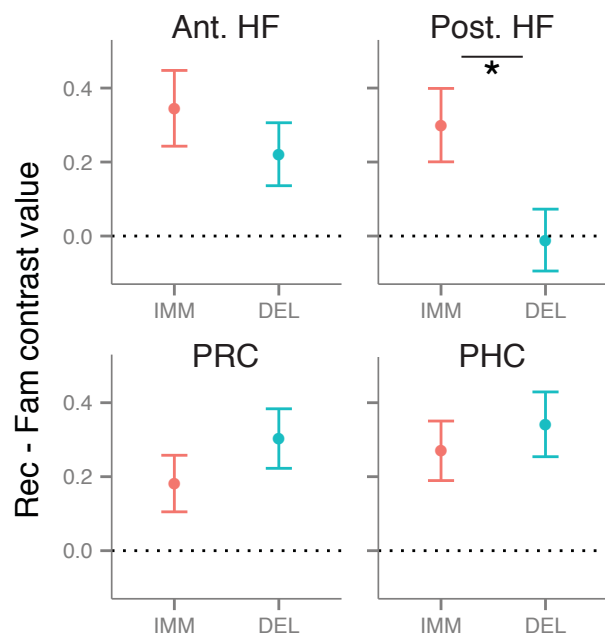
936 **Supplementary File 2.** Table of peak coordinates from the voxel-wise comparison of recollection and
937 familiarity trial activity (related to Figure 3).

938 **Source Code 1.** Custom Matlab code for the pattern similarity analysis.

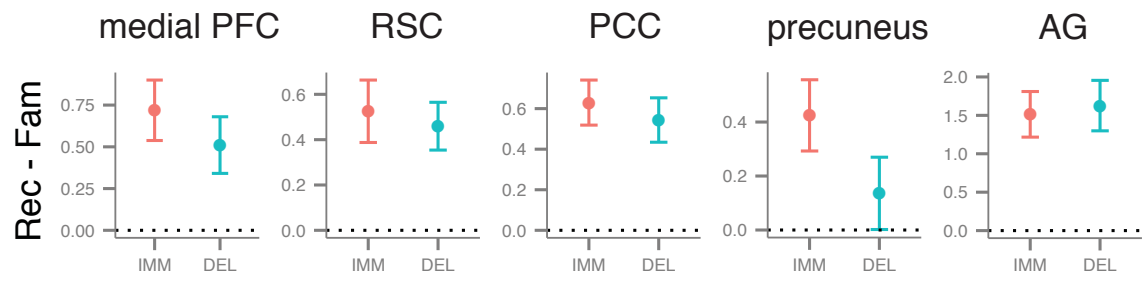
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