1	Re-expression of CA1 and entorhinal activity patterns preserves		
2	temporal context memory at long timescales		
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18 ABSTRACT

19 Converging, cross-species evidence indicates that memory for time is supported by hippocampal 20 area CA1 and entorhinal cortex. However, limited evidence characterizes how these regions preserve temporal memories over long timescales (e.g., months). At long timescales, memoranda 21 22 may be encountered in multiple temporal contexts, potentially creating interference. Here, using 7T fMRI, we measured CA1 and entorhinal activity patterns as human participants viewed 23 24 thousands of natural scene images distributed, and repeated, across many months. We show that 25 memory for an image's original temporal context was predicted by the degree to which 26 CA1/entorhinal activity patterns from the first encounter with an image were re-expressed during 27 re-encounters occurring minutes to months later. Critically, temporal memory signals were 28 dissociable from predictors of recognition confidence, which were carried by distinct medial 29 temporal lobe expressions. These findings suggest that CA1 and entorhinal cortex preserve 30 temporal memories across long timescales by coding for and reinstating temporal context 31 information.

32 INTRODUCTION

- 33 Episodic memory fundamentally involves the ability to remember not only *what* happened in the
- 34 past, but *when* it happened¹. Indeed, placing memories in time critically enables experiences to
- 35 be organized into personal narratives that span weeks, months, and years². Yet, the majority of
- 36 cognitive neuroscience studies of human memory only consider memory across relatively short
- 37 timescales (overwhelmingly, within a single experimental session/day). At longer timescales,
- 38 one of the particular challenges to retaining precise temporal memories is that previously-
- 39 encoded information is likely to be 're-encountered' in new temporal contexts³. For example,
- 40 remembering precisely when you *first saw* a particular movie may be complicated by re-
- 41 watching that movie at a later date. Understanding how memories of specific temporal contexts
- 42 are preserved when experiences are repeated over long timescales (days, weeks, months) requires
- 43 identifying not only the neural structures that are involved, but the mechanistic contributions that
- 44 these structures support.
- 45 Broadly, the medial temporal lobe (MTL) system is known to critically support episodic
- 46 memory^{4–6}. However, within the MTL system, hippocampal subfield CA1 and entorhinal cortex
- 47 (ERC) have emerged as being particularly important for processing and remembering temporal
- 48 information^{7–11}. For example, so-called "time cells" in CA1 and ERC have been shown to code
- 49 for elapsed time in rodents^{12–15}, with similar effects recently observed in the human hippocampus
- 50 and ERC^{16,17}. Putatively, time cells in CA1 and ERC provide the basis for *temporal context*
- 51 *representations* that allow individual memories to be 'placed' in time¹⁸. While human fMRI
- 52 studies have provided important evidence that activation levels in the hippocampus and ERC are
- 53 associated with the precision of temporal memory^{19,20}, measures of activation, alone, are not well
- 54 suited to measuring temporal context representations. Rather, temporal context is thought to be
- 55 reflected in distributed patterns of activity or ensemble representations 21,22 .
- 56 Importantly, to the extent that CA1 and ERC do code for the temporal context in which events
- 57 occur, there are multiple—and mechanistically distinct—ways in which these representations
- 58 might preserve temporal memories. On the one hand, when a given stimulus is re-encountered in
- 59 a new temporal context, CA1 and/or ERC may encode the new temporal context as *distinct* from
- 60 the original context²³. Forming distinct temporal context representations across repeated
- 61 encounters is potentially beneficial to temporal memory by improving discriminability of these
- 62 contexts²⁴. On the other hand, when a stimulus is re-encountered in a new temporal context, this
- 63 potentially creates an opportunity to *reinstate* a prior temporal context 25,26 . For example, when a
- 64 familiar movie is on television, this might trigger recall of the original temporal context in which
- 65 the movie was encountered. Reinstatement of the original temporal context may strengthen that
- 66 context representation and thereby preserve memory for when the movie was first encountered.

- 67 Critically—and in contrast to a context distinctiveness account—a context reinstatement account
- makes the prediction that, when a stimulus is re-encountered, memory for the original temporal
- 69 context will be preserved to the extent that activity patterns in CA1 and/or ERC are *similar* to (or
- reinstate) the activity patterns expressed when the stimulus was first encountered.

71 Here we sought to characterize the neural mechanisms that preserve temporal context memory

- 72 when events are re-encountered across long timescales (days to months). To address this, we
- 73 describe a massive human fMRI experiment in which participants encountered thousands of
- natural scene images repeatedly during 30-40 scan sessions distributed over an 8-10 month
- 75 window²⁷. After all scans were completed, participants performed a temporal memory task in
- 76 which a subset of images were presented and participants were asked to estimate when each
- image was *first encountered* (on a scale that ranged from days to months in the past). The focus
- 78 of our analyses was to test whether temporal memory precision was predicted by the degree to
- 79 which patterns of neural activity expressed when images were first encountered were re-
- 80 expressed when these images were re-encountered (a potential marker of context reinstatement).
- 81 By leveraging the ultra-high field strength (7T) and high spatial resolution (1.8-mm) of our
- 82 imaging protocol, we interrogated subregions of the hippocampus (including CA1) and
- 83 surrounding MTL structures (including ERC). This experimental design yielded an
- 84 unprecedented ability to understand how temporally-precise memories are preserved over long
- 85 timescales that are critical for real-world memories.

86 **RESULTS**

87 Precise temporal memory persists across months

88 Eight participants completed two experimental phases (Fig. 1a). The first phase consisted of a

- 89 continuous recognition task conducted during fMRI scanning. The second phase consisted of a
- 90 final memory test conducted outside of the scanner. During the continuous recognition phase,
- 91 participants viewed 9,209-10,000 natural scene images across 30-40 fMRI sessions and indicated
- 92 whether or not each image had previously been encountered at any point in the experiment (Fig.
- 93 1b). Each image was presented up to three times with these exposures pseudo-randomly
- 94 distributed across the entire experiment (Fig. 1d). At least two days after completion of the last
- 95 session of the continuous recognition phase, participants completed a final memory test on a
- 96 subset of images (Fig. 1c). Each trial of the final memory test began with a recognition memory
- 97 judgment on a 1-6 confidence scale (1: 'high confidence new', 6: 'high confidence old'). For
- 98 images judged to be 'old', participants were also prompted to make frequency and temporal
- 99 memory judgments. For the frequency judgment, participants were asked how many times they
- 100 had seen the image during the continuous recognition phase (1, 2, 3, or 4 or more). For the
- 101 temporal memory judgment, which is the primary focus of the present study, participants were

- 102 instructed to position a marker along a continuous timeline when in the experiment each image
- 103 was first encountered.

104



106 Figure 1. Experimental design. (a) Overview of experimental procedures: participants completed two 107 experimental phases. The continuous recognition phase consisted of 30-40 separate fMRI scan sessions 108 distributed across 8-10 months. Across these sessions, thousands of natural scene images were pseudo-109 randomly presented up to three times. After all of the scan sessions were completed, participants 110 performed a final memory test on a subset of images outside of the scanner on a separate day (2-7 days 111 later). (b) Continuous recognition test. While maintaining central fixation, participants viewed sequences 112 of natural scenes and reported whether each image had been seen at any previous point in the experiment. 113 (c) Final memory test. Each trial of the final memory test began with a recognition memory judgment in 114 which participants made a recognition decision together with a confidence rating from 1-6 (1: 'high 115 confidence new', 6: 'high confidence old'). For each image judged as 'old', a frequency test followed in 116 which participants were asked how many times they had seen the image before (1, 2, 3, or 4 or more). 117 Following that, participants were asked to indicate on a continuous timeline when the image in question 118 was *first encountered* (temporal memory test; see Methods for more information). (d) Timeline of an 119 example image. Each old image used in the final memory test was presented three times during the 120 continuous recognition phase and associated with four temporal lags. The first fMRI scan session of the 121 continuous recognition phase for each participant corresponds to Day 0. All temporal lags were quantified 122 in seconds and transformed with the natural logarithm for further analyses. (e) Behavioral measure of

123 temporal memory. Item-wise temporal memory error was quantified as the difference between the ranked 124 actual and ranked estimated temporal positions.

125

- 126 All participants performed above chance on the recognition memory test (Fig. 2a; hit rate greater
- 127 than false alarm rate: $t_7 = 8.24$, p < 0.001, two-tailed paired-sample *t*-test). Separating the data
- 128 across three confidence levels (low, medium, and high) revealed that recognition memory
- 129 accuracy (d') increased with levels of subjective confidence (Fig. 2b; $F_{2,14} = 16.66$, p < 0.001,
- 130 one-way repeated-measures ANOVA). Results for the frequency test are reported in
- 131 Supplementary Fig. 1.

132 Of critical interest was the accuracy of temporal memory judgments, which required participants

- to recall the first time each scene was encountered over the course of the up to 10-month
- 134 experiment. To reduce the effects of non-linearity in temporal memory judgments (e.g., response
- bias towards the center of the timeline, see Methods and Supplementary Fig. 2), we converted
- 136 both the actual (objective) and the estimated (subjective) temporal positions to ranked positions
- 137 for further analyses. Based on the ranks, we quantified item-wise temporal memory error by
- 138 comparing the distance between the actual and estimated ranked positions (Fig. 1e). To
- 139 determine temporal accuracy across participants, we ran a mixed-effects linear regression model
- 140 for estimated against actual temporal position with participants as a random effect. Results from
- 141 this analysis indicated that participants were able to place images in their correct temporal
- 142 contexts with above-chance accuracy (Fig. 2c; group-level $\beta = 0.302$, p < 0.001). We further
- 143 evaluated temporal memory accuracy for each participant using a permutation test (see
- 144 Methods). This analysis revealed that temporal memory performance was above chance for
- seven out of the eight participants (Fig. 2d; ps < 0.01; one participant: p = 0.083). The relatively
- 146 high accuracy of the temporal memory judgments is notable when considering that participants
- 147 were not informed that they would be tested on temporal memory until after all of the continuous
- 148 recognition sessions.



150

151 Figure 2. Behavioral results. (a) Recognition performance for each participant quantified by hit rate and 152 false alarm (FA) rate. Hit rates were reliably above FA rates ($t_7 = 8.24$, p < 0.001, two-tailed *t*-test), 153 indicating above-chance recognition memory. (b) Overall recognition performance (d') separated by 154 confidence levels. Recognition accuracy increased with subjective confidence levels (one-way repeated-155 measures ANOVA; $F_{2.14} = 16.66$, p < 0.001). (c) Correlation between estimated and actual temporal 156 positions. Participants showed above-chance accuracy in temporal memory judgments (group-level β = 157 0.302, p < 0.001). Each color shaded line indicates a participant. (d) Individual participant's temporal 158 memory performance compared to chance level. Density plots compare the standard error of the mean 159 (SEM) of the observed temporal memory error (yellow line) to the null distribution (blue density;

160 estimated by permuting estimated temporal judgments across images within each participant, n = 1,000

161 permutations). Throughout the figure, error bars reflect mean \pm s.e.m.; dots or colors denote individual

162 participants (n=8); *** *p* < 0.001.

163 CA1 and entorhinal representational similarity across exposures predicts temporal 164 memory precision

- 165 The primary goal of the present study was to investigate whether the similarity (or dissimilarity) 166 of MTL representations across repeated stimulus encounters predicts the accuracy of temporal 167 memory judgments across long timescales. Accordingly, we examined the representational 168 similarity between exposures of each of the images that were subsequently probed in the 169 temporal memory test. Given our *a priori* interest in MTL structures, we focused on two 170 manually segmented subfields of the hippocampus (CA1 and CA2/3/dentate gyrus, hereafter 171 CA2/3/DG), along with ERC, perirhinal cortex (PRC), and parahippocampal cortex (PHC) (Fig. 172 3a). For each region of interest (ROI), we correlated the activity patterns between each pair of 173 exposures of the same image (i.e., r(E1, E2), r(E2, E3), and r(E1, E3)). As a first step, we 174 averaged across these pairwise correlations to generate a single similarity metric (across 175 exposures) for each image (Fig. 3b). We then compared these similarity metrics for images 176 associated with high versus low temporal memory precision (based on a participant-specific 177 median split). Statistical significance of the difference between high and low temporal memory 178 precision was evaluated using a permutation test that shuffles the images' temporal memory 179 identities within each participant. Among the set of MTL ROIs, CA1 and ERC exhibited
- 180 significantly greater pattern similarity across repeated exposures for high-precision images
- relative to low-precision images (Fig. 3c; CA1: p = 0.004; ERC: p = 0.004; permutation tests).
- 182 The fact that temporal memory precision was associated with greater pattern similarity across
- 183 exposures in CA1 and ERC is consistent with a context reinstatement account, wherein the
- 184 original temporal context is reinstated (and strengthened) during subsequent exposures.
- 185 We next performed several control analyses. First, because temporal memory precision increased
- 186 as a function of the session position in which the first exposure occurred (recency effect, see
- 187 Supplementary Fig. 3), we repeated the analyses for CA1 and ERC while explicitly accounting
- 188 for temporal lag information (Fig. 1d). Specifically, we ran a mixed-effects logistic regression
- 189 model that predicted temporal memory precision from pattern similarity across exposures with
- 190 temporal lags (lag 0-3) included as fixed effects and participant included as a random effect. This
- analysis confirmed that the relationship between pattern similarity in CA1/ERC and temporal
- 192 memory precision remained significant when accounting for temporal lag information (Fig. 3d;
- 193 CA1: $\beta = 2.134$, p = 0.005; ERC: $\beta = 3.207$, p = 0.008).
- 194 Second, we repeated the foregoing analyses for an early visual cortex ROI (V1) that would be
- 195 sensitive to low-level visual information but would not be expected to code for temporal context.
- 196 As expected, V1 pattern similarity across exposures did not differ for high- versus low-precision
- images (Fig. 3c; p = 0.25; permutation test) and was not a predictor of temporal memory
- 198 precision (Fig. 3d; p = 0.376; logistic mixed-effects regression). Likewise, an additional,

199 exploratory whole-brain analysis did not identify any cortical areas outside the MTL for which

200 the relationship between pattern similarity and temporal memory was significant after correction

201 for multiple comparisons (Supplementary Table 1).



203



Figure 3. CA1 and entorhinal representational similarity predicted temporal memory precision, but
 not recognition confidence. (a) Manually drawn ROIs for MTL subregions of an example participant:
 CA1 (purple), CA2/3/DG (red), ERC (yellow), PRC (blue), and PHC (green). LH/RH: left/right
 hemisphere. (b) Schematic depiction of representational similarity analysis. (c) Pattern similarity
 difference between high- and low-precision images (median split) across MTL subregions and a control

209 early visual region (V1). CA1 and ERC showed greater pattern similarity across exposures for high-

210 precision images relative to low-precision images (CA1: p = 0.004; ERC: p = 0.004; permutation tests, n

211 = 1,000). CA2/3/DG showed similar effect but did not survive correction for multiple comparisons

(p(uncorrected) = 0.023). (d) Pattern similarity across exposures as a function of temporal memory precision while accounting for temporal lag information. Pattern similarity across repeated exposures in

214 CA1 and ERC predicted temporal memory precision while accounting for temporal lag information

215 (CA1: $\beta = 2.134$, p = 0.005; ERC: $\beta = 3.207$, p = 0.008). A similar effect was also observed in

216 CA2/3/DG (*p(uncorrected)* = 0.037), but did not survive correction for multiple comparisons. (e) Pattern

- similarity across exposures as a function of recognition confidence while accounting for temporal lag
- 218 information. Pattern similarity across repeated exposures in PHC predicted recognition confidence ($\beta =$
- 219 0.799, p < 0.001). Throughout the figure, error bars reflect mean \pm s.e.m.; dots denote individual
- 220 participants; $\sim p < 0.10$; *p < 0.05; **p < 0.01; ***p < 0.001. Parentheses indicate ROIs that did not
- 221 survive multiple comparison correction.

222

223 Third, and critically, we next tested whether the effects observed in CA1 and ERC were specific

to temporal memory. To this end, we repeated the same mixed-effects regression model but now

225 used recognition confidence as the dependent variable instead of temporal precision. Neither

- 226 CA1 nor ERC exhibited significant relationships between pattern similarity and recognition
- 227 confidence (ps > 0.10). In contrast, pattern similarity was a significant predictor of recognition 228 confidence in PHC (Fig. 3e; $\beta = 0.799$, p < 0.001). A follow-up control analysis which included
- recognition confidence together with pattern similarity as fixed effects in a mixed-effects
- regression model confirmed that pattern similarity in CA1 and ERC predicted temporal memory
- precision when accounting for recognition confidence (ps < 0.001). These results provide
- important evidence that the relationships between CA1/ERC pattern similarity and temporal
- 233 memory precision were not a secondary consequence of stronger overall memory for the images;

rather, pattern similarity across exposures in CA1 and ERC specifically predicted better memory

for when (in time) images were first encountered.

236 Similarity between first and second exposures uniquely predicts temporal memory

Having demonstrated that CA1 and ERC pattern similarity across repeated exposures predicts

temporal memory for an image's first exposure, we next sought to determine which pair of image

exposures was most predictive of temporal memory. From a context reinstatement perspective,

similarity between the first exposure (E1) and the second exposure (E2) should be uniquely

- important because E2 provides the first opportunity to reinstate the temporal context from E1. To
- test this, we first compared pattern similarity for high- and low-precision images for each pair of
- image exposures (E1-E2, E2-E3, and E1-E3). Statistical significance of the difference between
- high- and low- precision images for each exposure pair was computed a permutation analysis in
- which, for each participant and exposure pair, we randomly shuffled the images' temporal
- 246 memory precision labels. For both CA1 and ERC, E1-E2 similarity was significantly greater for
- high- than low-precision images (Fig. 4a; CA1: p = 0.015; ERC: p = 0.007; permutation tests).

- However, both regions also exhibited similar effects for E2-E3 similarity (Fig. 4a; CA1: p =
- 249 0.025; ERC: p = 0.036, permutation tests). Neither region exhibited a significant effect for E1-E3
- 250 similarity (Fig. 4a; ps > 0.28).

251 To further explore this pattern of results, we performed three follow-up sets of analyses. First, in

- order to control for potential temporal lag effects (Supplementary Fig. 3), we ran a mixed-effects
- 253 logistic regression model that predicted temporal memory from pattern similarity of each
- exposure pair (E1-E2, E2-E3 and E1-E3 as separate dependent variables in one regression
- 255 model) while including lag information. For both CA1 and ERC, E1-E2 similarity significantly
- 256 predicted temporal memory (Fig. 4b; CA1: $\beta = 1.048$, p = 0.014; ERC: $\beta = 1.565$, p = 0.022).
- Effects were marginally significant for E2-E3 similarity (ps < 0.10), and not significant for E1-
- 258 E3 similarity (ps > 0.68).

259 Second, in order to more directly assess whether E1-E2 similarity contained predictive power

above and beyond that of other exposure pairs, we compared the performance of several models

that did or did not include various exposure pairs. That is, we tested whether model performance

- 262 was significantly improved when E1-E2 similarity was added to models that only included E2-
- E3 and E1-E3 similarity. For both CA1 and ERC, adding E1-E2 as a predictor significantly
- 264 improved the model's performance (CA1: $\chi^2 = 6.147$, p = 0.013; ERC: $\chi^2 = 5.315$, p = 0.021).
- 265 In contrast, adding E2-E3 and E1-E3 similarity as predictors to models with just E1-E2 similarity
- 266 did not improve the model's performance (ps > 0.15). These results established that E1-E2
- 267 similarity was uniquely important for subsequent temporal memory judgments, as would be
- 268 predicted by a context reinstatement account.
- 269 Third, it is possible that these patterns of results reflect the contribution of some overall
- 270 facilitation to memory provided by E1-E2 similarity. However, although PHC pattern similarity
- 271 across exposures was highly predictive of subsequent recognition memory confidence (Fig. 3e),
- this effect was not driven by E1-E2 similarity (Fig. 4c; p = 0.482, permutation test; Fig. 4d; p =
- 273 0.225; linear mixed-effects regression). Instead, E1-E3 similarity in PHC significantly predicted
- 274 recognition confidence (Fig. 4c; p = 0.002; Fig. 4d; $\beta = 0.473$, p = 0.018). Taken with these
- above results, these findings provide a qualitative dissociation between the predictors of

temporal memory versus recognition memory. That is, they are consistent with the interpretation

- that reinstating the temporal context of the first exposure is critical for remembering when that
- 278 image was first encountered, but it is relatively less important for recognizing whether an image
- 279 was previously encountered.



282 Figure 4. Pattern similarity between the first and second exposure in CA1 and ERC was uniquely 283 important for temporal memory. (a) CA1/ERC pattern similarity between high- and low-precision 284 images for each pair of image exposures. CA1 and ERC showed greater pattern similarity for high-285 precision images relative to low-precision images in E1-E2 (CA1: p = 0.015; ERC: p = 0.007; 286 permutation test, n = 1,000) and E2-E2 (CA1: p = 0.025; ERC: p = 0.036; permutation test). (b) PHC 287 pattern similarity between hits and misses in recognition memory for each pair of image exposures. PHC 288 showed greater pattern similarity for hits relative to misses in E1-E3 (p = 0.002; permutation test, n = 289 1,000). (c) CA1/ERC pattern similarity as a function of temporal memory precision for each pair of image 290 exposures while accounting for temporal lag information. For both CA1 and ERC, E1-E2 pattern 291 similarity was significantly predictive of temporal memory precision (CA1: $\beta = 1.048$, p = 0.014; ERC: β 292 = 1.565, p = 0.022). (d) PHC pattern similarity as a function of recognition memory confidence for each 293 pair of image exposures while accounting for temporal lag information. Recognition confidence was 294 predicted by E1-E3 pattern similarity in PHC ($\beta = 0.473$, p = 0.018). Error bars reflect mean \pm s.e.m.; 295 dots denote individual participants; $\sim p < 0.10$; *p < 0.05; **p < 0.01.

296

297 CA1 and ERC predict temporal memory via image-specific representations

298 While all of the preceding representational similarity analyses were performed by correlating

- 299 activity patterns across repeated exposures of the same stimulus (i.e., image-specific
- 300 correlations), these analyses do not guarantee that the information that predicted temporal
- 301 memory precision was specific to individual images. Namely, it is possible that temporal
- 302 memory precision benefited from generic memory processes or attentional states that generalized
- 303 across images (e.g., states optimized for memory encoding²⁸). While this possibility would still

304 support a role for CA1 and ERC in encoding temporal information, a temporal context

- 305 reinstatement account fundamentally predicts reinstatement of the specific temporal context in
- 306 which an image was encoded.

307 To assess whether temporal memory was predicted by image-specific pattern similarity, we

- 308 conducted two additional analyses (restricted to E1-E2 similarity). First, for all of the images
- tested in the temporal memory test, we permuted the E1-E2 mappings by shuffling images' E2
- 310 within each participant. We then calculated the resulting E1-E2 pattern similarity scores and a
- 311 corresponding distribution of beta values reflecting the relationships with temporal memory (see
- 312 Methods for details). Critically, for both CA1 and ERC, the relationship between 'intact' E1-E2
- 313 similarity and temporal memory was significantly stronger (higher beta values) than the
- permuted values (Fig. 5a; CA1: p = 0.019; ERC: p = 0.025). These data provide important
- 315 evidence that temporal memory precision was predicted by image-specific pattern similarity in
- 316 CA1 and ERC.

317 As a follow-up to the preceding analysis, we ran a final analysis to address whether apparent

- 318 image-specific effects might be due to general memory states and/or differences in coarse
- temporal context information (i.e., session effects). Thus, for each image included in the
- 320 temporal memory test (a 'target'), we identified control images ('foils') such that the targets and
- 321 foils shared the same E1 session number, but not scanning run (to avoid potential contamination
- from autocorrelation in the fMRI data), and the same E2 session number (but not run; Fig. 5b).
- 323 To match recognition memory with targets, foils were only included in this analysis if they were
- 324 correctly rejected at E1 and successfully recognized at E2 and E3 (see Methods for details). This
- 325 allowed us to compute similarity between target E1 and target E2 (target similarity) and target
- E1 and foils E2 (foil similarity). The difference between these measures (target similarity foil
- 327 similarity) was then used as a predictor of temporal memory precision. Indeed, this similarity
- difference score significantly predicted temporal memory precision for CA1 (Fig. 5c; $\beta = 0.893$,
- 329 p = 0.028), with a similar but marginal effect for ERC (Fig. 5c; $\beta = 1.240$, p = 0.058). These
- 330 findings lend further support to the idea that temporal memory precision was related to image-
- 331 specific pattern similarity measures and specifically argue against potential confounds due to
- 332 generic memory-related processes or session effects. The fact that these effects held when
- carefully controlling for session effects (albeit marginally in ERC) is notable because it provides
- evidence against the possibility that pattern similarity only captured coarse-level temporal
- 335 context (session information). Rather, to the extent that the pattern similarity measure captured
- temporal context information, these findings suggest a relatively 'local' temporal context
- representation that differentiated between images within the same session (day).



339

340 Figure 5. Representational image-specificity analyses. (a) Intact compared to permuted similarity 341 effect. E1-E2 pattern similarity compared to permuted similarity exhibited a stronger effect on temporal 342 memory precision in both CA1 and ERC (CA1: p = 0.019; ERC: p = 0.025; permutation tests, n = 1,000). 343 (b) Schematic illustration showing how target similarity and foil similarity were computed for an example 344 image (see Methods for details). (c) Image-specific pattern similarity (target similarity – foil similarity) as 345 a function of temporal memory precision. Image-specific pattern similarity in CA1 was significantly 346 predictive of temporal memory precision ($\beta = 0.893$, p = 0.028). ERC showed a similar but marginal 347 relationship between image-specific pattern similarity and temporal memory ($\beta = 1.240, p = 0.058$). Error 348 bars reflect mean \pm s.e.m.; $\sim p < 0.10$; *p < 0.05.

349

350 **DISCUSSION**

351 The ability to remember when events occurred in time is fundamental to human experience.

352 However, retaining precise temporal memories is complicated by the fact that real-world

353 episodic memories span long timescales (days, weeks, months and beyond) and by the fact that

354 events may recur in multiple contexts over those long timescales (e.g., a movie you have viewed

355 several times over the past year). To date, there is remarkably little evidence characterizing how

356 the human brain preserves temporal memories in the face of these challenges. Here, we show

357 that when events recur over long timescales (at lags up to several months), the re-expression of

- distributed, event-specific activity patterns in CA1 and ERC preserves memory for the original
- temporal context of an event (i.e., memory for when an event first occurred). These findings are
- 360 consistent with and bridge between prior human and rodent studies implicating CA1 and ERC in
- 361 temporal processing and temporal memory. However, our findings also go beyond existing
- 362 evidence by providing a mechanistic account of how CA1 and ERC preserve temporal memories
- 363 and demonstrating these relationships at uniquely long timescales.
- 364 While there is a rich history characterizing temporal memory in human behavioral and
- 365 neuroimaging studies^{29,30}, it is striking how few of these studies have considered temporal
- 366 memory across timescales that exceed a single experimental session. Indeed, our approach of
- 367 testing temporal memory for images that were distributed across dozens of experimental
- 368 sessions/scans spanning 8-10 months is unprecedented. Considering that the overwhelming
- 369 majority of real-world episodic memories span days, weeks, months and years, it is imperative to
- 370 understand the neural mechanisms that support temporal memory at these timescales. Although it
- is intuitively obvious that humans can and do retain temporal memories over long timescales, it
- is nonetheless remarkable that participants in the current study were generally successful at
- 373 recalling the initial temporal context for images presented at the final memory test given that (a)
- these images were drawn from a pool of tens of thousands of images, (b) the delay between the
- initial exposure and the final memory test ranged from days to almost a year, and (c) each image
- 376 was presented in multiple temporal contexts, creating potential interference. Thus, by simulating
- 377 the challenges that are inherent to real-world temporal memory, our experimental paradigm
- 378 provides a unique opportunity to characterize the underlying neural mechanisms.
- 379 By leveraging representation-based analyses to track patterns of activity across repeated stimulus
- 380 exposures and distinct temporal contexts, we were able to gain critical insight into the
- 381 mechanisms through which CA1 and ERC contribute to temporal memory. In particular, our
- 382 findings strongly align with a context reinstatement account. According to temporal context
- 383 models^{25,26}, context representations—reflected in distributed patterns of neural activity—
- 384 gradually change over time and are reinstated when an item is subsequently remembered^{31–37}.
- 385 From this perspective, our finding that greater pattern similarity across exposures preserved
- 386 memory for an event's original temporal context can be explained in terms of the original
- 387 context representation (elicited during E1) being reinstated during subsequent exposures (E2,
- E3). In fact, this account also readily explains our finding that similarity between the first and
- 389 second exposure (E1, E2) was uniquely important for temporal memory. Namely, E2 represented
- 390 the first potential 'reminder' of E1's temporal context. Interestingly, although we tested for re-
- 391 expression of E1's activity patterns by explicitly re-exposing participants to the same stimulus
- 392 multiple times (E2, E3), our findings likely generalize to situations where stimuli are not
- 393 explicitly re-exposed (or re-encountered). Indeed, human neuroimaging studies (unrelated to

temporal memory) have found that offline, spontaneous reinstatement of episodic memories not
 only occurs, but it strengthens memories in much the same way that online, cued reinstatement
 does³⁸.

397 While a context reinstatement account makes a clear prediction that better memory for the 398 original temporal context should be associated with greater representational similarity across 399 exposures, it is notable that a memory interference account²³ suggests an entirely opposite 400 prediction: that temporal memory would benefit from greater contextual distinctiveness across 401 exposures (i.e., less similarity). More specifically, greater contextual distinctiveness would 402 putatively be expected to reduce interference between the various temporal contexts in which an 403 event occurred (E1, E2, E3). That said, there are several examples in the memory interference 404 literature where reinstatement of prior experiences during new learning can, in fact, protect memories from interference^{39,40}. Moreover, it is important to note that a context reinstatement 405 406 account for CA1 and ERC does not exclude the possibility that other MTL regions (e.g., CA3) 407 might simultaneously contribute to temporal memory by emphasizing differences between

408 temporal contexts⁴¹⁻⁴⁴.

409 The fact that we specifically identified CA1 and ERC as being important for temporal memory at

410 long timescales—and the implication that these regions supported temporal context

411 reinstatement—is striking in light of accumulating evidence documenting time cells within

412 rodent CA1 and ERC $^{12-14}$. It has been speculated that ensembles of time cells allow for the

413 coding of gradually-drifting temporal context representations which become bound to individual

414 events¹⁸ and reinstated when events are remembered^{25,26}. Moreover, while much of the evidence

415 for time cells has focused on very short timescales (seconds), there is evidence that time cell

416 ensembles can reflect temporal information over multiple, longer timescales—from minutes to

417 days⁴⁵. Here, we did not directly measure or identify time cells, but the representation-based

418 analyses we employed are well-suited to capturing gradually-changing context

419 representations^{24,32,33,46–49}. In contrast, although several prior studies of human memory have also

420 implicated CA1 and ERC in memory for when events occurred^{19,20}, most of these studies have

421 not employed representation-based analyses and, therefore, are not amenable to testing or

422 capturing temporal context representations. Thus, our approach and findings uniquely bridge

423 between evidence of time cells in rodents, theoretical models of temporal context, and prior

424 studies of temporal memory in humans.

425 An additional essential consideration in understanding neural mechanisms that specifically relate

426 to temporal memory is to establish that any apparent effects related to temporal memory were

427 not derivative from more general effects of memory strength. Specifically, as memories decay

428 over time, temporal judgments could potentially be inferred from the strength of memories

- 429 themselves 50-52. This is of particular concern given the very long timescales involved in the
- 430 current study. However, several theoretical perspectives propose that memory for time is
- 431 dissociable from memory strength 30,53,54 . Here, our final memory test separately measured
- 432 recognition confidence (a proxy for overall memory strength) and temporal memory, allowing us
- 433 to conduct several targeted analyses aimed at teasing apart these two expressions of memory.
- 434 First, we found that the relationships between CA1/ERC and temporal memory precision
- 435 remained significant in a regression model that included recognition confidence as a covariate.
- 436 Second, consistent with prior arguments that distinct MTL subregions are involved in 'item-
- 437 based' versus 'context-based' memory⁵⁵, we found that pattern similarity measures in PHC
- 438 predicted recognition confidence but not temporal memory, whereas pattern similarity measures
- 439 in CA1 and ERC predicted temporal memory but not recognition confidence. Finally, when
- 440 considering pattern similarity across specific pairs of image exposures, temporal memory
- 441 (defined here as memory for when the first exposure occurred) was best predicted by pattern
- similarity between the first and second exposures, consistent with a context reinstatement
- 443 account. In contrast, recognition confidence was best predicted by pattern similarity between the
- 444 first and third exposures, potentially indicating that the last (third) exposure was relatively more
- 445 influential to memory strength (also see Supplementary Fig. 3). Together, these data points
- 446 provide important, converging evidence that temporal memory judgments in the current study
- 447 were not derived from the overall memory strength. More generally, our findings reinforce
- theoretical accounts that emphasize the distinction between memory for 'when' an event
- 449 occurred versus 'whether' an event occurred^{5,6,56,57}.
- 450 In conclusion, here we show that memory for the temporal context in which an event initially
- 451 occurred is preserved via the re-expression of activity patterns in human CA1 and ERC.
- 452 Critically, we show that these dynamics operate across—and support memory at—long
- 453 timescales (from days to months). These findings complement yet significantly advance existing
- 454 evidence from rodents and humans implicating the hippocampal-entorhinal system in
- 455 representing and remembering time. In particular, our findings suggest that distributed patterns
- 456 of activity in CA1 and ERC encode and reinstate temporal context information, thereby
- 457 preserving memory for when events occurred.

459 AUTHOR CONTRIBUTIONS

- 460 F.Z., I.C., J.B.H., and S.D. conceived and designed the final memory test. K.K. and T.N.
- 461 conceived and designed the NSD main experiment. W.G. performed manual segmentations of
- 462 the medial temporal lobe. E.J.A. and Y.W. collected the data. F.Z. analyzed the data. F.Z.,
- 463 B.A.K., J.B.H., and S.D. wrote the paper.
- 464

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- 472

473 DECLARATION OF INTERESTS

- 474 The authors declare no conflicting interests.
- 475

476 DATA AND CODE AVAILABILITY

477 Information on the NSD dataset is available at <u>http://naturalscenesdataset.org</u>. The final memory

- 478 data will be made publicly available upon manuscript publication. Custom analysis scripts for the
- 479 current manuscript are available upon request to the corresponding author (F.Z.).
- 480

481 METHODS

482 **Participants**

- 483 Eight participants took part in the study (two males, six females; age range: 19–32). All
- 484 participants were right-handed with no known cognitive deficits nor color blindness and with
- 485 normal or corrected-to-normal vision. Participants were naïve to the experimental manipulation
- 486 and were not involved in the design nor planning of the study. Informed written consent was
- 487 obtained from all participants before the start of the study, and the experimental protocol was
- 488 approved by the University of Minnesota Institutional Review Board.

489 **Design and procedure**

- 490 Data used in this study were collected as part of the Natural Scenes Dataset (NSD;
- 491 http://naturalscenesdataset.org), and included two parts: a continuous recognition phase
- 492 conducted in the fMRI scanner and a behavioral final memory phase (Fig. 1a).
- 493 *Continuous recognition phase.* A detailed description of the continuous recognition phase has
- 494 been reported in a previous publication²⁷. Briefly, for each participant, the continuous
- 495 recognition phase was split across 40 scan sessions in which 10,000 distinct color natural scenes
- 496 would be presented three times spaced pseudo-randomly over the course of all scan sessions.
- 497 Each scan session consisted of 12 runs (750 trials). Distributions of image presentations were
- 498 controlled such that both short-term and long-term re-exposures were probed (see Stimuli section
- below). Four of the participants completed the full set of 40 NSD scan sessions. Due to
- 500 constraints on participant and scanner availability, each of the other four participants completed
- 501 30-32 scan sessions. In these collected data, each participant viewed 9,209-10,000 distinct
- 502 images and participated in 22,500-30,000 trials. Each trial lasted 4 s, consisting of the
- 503 presentation of an image for 3 s and a following 1-s gap. Participants were instructed to perform
- 504 a continuous recognition task in which they reported whether the current image had been seen at
- 505 any previous point in the experiment.
- 506 *Final memory phase.* At least two days (range: 2-7 days) after completion of the continuous
- 507 recognition phase, a final memory test was administered outside of the scanner. Participants were
- 508 not informed about the final memory test in advance. During the final memory phase,
- 509 participants viewed a subset of old images (220 per participant) from the continuous recognition
- 510 phase randomly intermixed with novel images (100 per participant) and completed different
- 511 types of memory probes. The final memory phase consisted of 320 trials, with up to three
- 512 judgements per trial. Each trial began with a recognition test in which participants performed an
- old or new judgment with a confidence rating on a scale of 1 to 6 (1: 'high confidence new', 2:
- 514 'medium confidence new', 3: 'low confidence new', 4: 'low confidence old', 5: 'medium

- 515 confidence old', 6: 'high confidence old'). For images judged as "old", a frequency test followed
- 516 in which participants were asked to indicate how many times they had seen each image (1, 2, 3, 3)
- 517 or 4 or more times). Following the frequency test, participants performed a temporal memory test
- 518 using a timeline. In this test, participants were asked to indicate, on a continuous timeline with
- 519 tick marks to represent each session, when in the experiment they thought each image was first
- 520 encountered (Fig. 1c, right). The length and labels of the timeline vary across participants,
- 521 depending on how many sessions they completed in the continuous recognition phase.
- 522 Participants were encouraged to use the full length of the scale, with the left endpoint
- 523 representing the beginning of the continuous recognition phase and the right endpoint
- 524 representing the end. Participants used a cone to mark the temporal location on the line and were
- 525 instructed to indicate their confidence in response via adjusting the size of the cone, with smaller
- 526 cones representing higher confidence and bigger cones representing lower confidence (see
- 527 Supplementary Video 1 for depiction of example trials). Given the primary focus of the present
- 528 study concerns temporal memory precision, we only analyzed the estimates of temporal location
- as illustrated in Fig. 1c. All tests in the final memory phase were self-paced with a timeout of 30
- 530 s.

531 Stimuli

532 All images used in this study were taken from the Microsoft Common Objects in Context

533 (COCO) database⁵⁸.

534 *Continuous recognition phase.* For the continuous recognition phase, a total of 73,000 images

- 535 were prepared with the intention that each participant would view 10,000 distinct images (9,000
- 536 unique images and 1,000 shared images across participants) three times each over the course of
- 537 40 scan sessions. To prevent the recognition task from becoming too difficult (and risking loss of
- morale), each image was randomly placed three times on a circle according to a probability
- 539 distribution created by mixing a relatively narrow von Mises distribution and a uniform
- 540 distribution. Across all scan sessions, the mean number of distinct images shown once, twice,
- and all three times within a typical session is 437, 106, and 34, respectively.
- 542 *Final memory phase.* For the final memory phase, a total of 320 images were used for each
- 543 participant, including 220 old images viewed in the continuous recognition phase and additional
- 544 100 novel images from the COCO dataset. All old images used in the final memory phase were
- selected from the set of images that a given participant saw each image three times during fMRI
- 546 scanning. There were two additional sets of criteria to select the old images. First, 120 out of the
- 547 220 old images were selected based on three main criteria: (1) Each image exposure was judged
- 548 with correct responses in the continuous recognition phase, that is correct rejection, hit, and hit
- 549 for the first, second, and third exposure, respectively. (2) To promote the overall temporal

- 550 memory performance, images were first selected based on the session location of their first
- 551 exposure, with approximately half of these images were selected from the last eight scan sessions
- that each participant participated in (it was adjusted to last ten scan sessions for one participant to
- 553 have enough trials given their performance in the continuous recognition phase), and the other
- half were selected from the rest of the scan sessions. (3) For each half, images were then selected
- 555 based on the spacing between exposures, with one-third with all three exposures within one scan
- session, one-third with the last two exposures in the same session, and the rest either with the
- 557 first two exposures in the same session or with three exposures across different sessions. Second,
- the remaining 100 old images were selected to maximally span semantic space (see the NSD data
- 559 paper²⁷ for details). Briefly, this was done by computing shifted inverse frequency sentence
- 560 embeddings for the sentence captions, and using a greedy approach to determine the subset of
- 561 100 images that maximize the average distance between each image's embedding and its closest
- 562 neighbor.

563 In order to equate prior memory outcome with the other images, only old images that received 564 correct responses all three times in the continuous recognition phase were included in further

analyses (143-170 images for each participant).

566 MRI data acquisition and preprocessing

567 The imaging data was collected as part of the NSD at the Center for Magnetic Resonance

- 568 Research at the University of Minnesota. In brief, functional data and a few additional
- anatomical measures were collected using a 7T Siemens Magnetom passively-shielded scanner
- 570 with a single-channel-transmit, 32-channel-receive RF head coil (Nova Medical, Wilmington,
- 571 MA). Functional data was acquired using whole-brain gradient-echo echo-planar imaging (EPI)
- at 1.8-mm resolution and 1.6-s repetition time. In addition to the EPI scans, for the purposes of
- 573 hippocampal segmentation, a high-resolution T₂-weighted scan was acquired during one of the
- 574 T scan sessions. T_1 and T_2 -weighted structural scans were collected using a combination of a
- 575 3T Siemens Prisma scanner and a standard Siemens 32-channel RF head coil.
- 576 Functional data were pre-processed by performing one temporal resampling to correct for slice
- 577 time differences and one spatial resampling to correct for head motion within and across scan
- 578 sessions, EPI distortion and gradient non-linearities. Two versions of the functional data were
- 579 prepared: a 1.8-mm standard-resolution preparation (temporal-resolution, 1.333s) and an
- 580 upsampled 1.0-mm high-resolution preparation (temporal-resolution, 1.000s). The latter
- 581 preparation exploits the benefits of small head displacements and preserves as much spatial
- detail as possible⁵⁹. Analyses in the current paper used the 1.0-mm high-resolution preparation of
- 583 the NSD data.

- 584 Parameter estimates (beta weights) reflecting fMRI response amplitudes evoked by each trial
- 585 were estimated using a general linear model (GLM) approach as described in the NSD data
- 586 paper. We used the beta version 2 from NSD for all the analyses in the current paper. Briefly, the
- 587 pre-processed time-series data was fitted multiple times with a single-trial GLM, each time using
- a different hemodynamic response function (HRF) from a library of HRFs. For each voxel, we
- 589 identified which HRF provided the best fit to the data and used for that voxel the single-trial
- 590 betas associated with that HRF. Betas were then converted to units of percent BOLD signal
- 591 change by dividing amplitudes by the mean signal intensity observed at each voxel and
- 592 multiplying by 100.

593 **Regions of interest (ROIs)**

594 The medial temporal lobe (MTL) ROIs were manually drawn on the high-resolution T₂ images

- obtained for each participant, following a 7T protocol for segmentation of MTL subregions⁶⁰.
- Labels were defined on the raw high-resolution T₂ volume, and were mapped via an affine
- transformation to subject-native anatomical space. The MTL ROIs included bilateral CA1,
- 598 CA2/3/dentate gyrus, entorhinal cortex (ERC), perirhinal cortex (PRC), and parahippocampal
- 599 cortex (PHC). Example MTL ROIs from one participant were depicted in Fig. 3a. We also
- 600 included the primary visual cortex (V1) as a control region. The bilateral V1 ROI was manually
- drawn on cortical surfaces based on results of a population receptive field experiment from the
- NSD, and were then mapped to volumetric format. Cortical ROIs for the whole-brain parcel level
- analysis were defined by a multi-modal cortical parcellation from the Human Connectome
- 604 $Project^{61}$.

605 Behavioral data analyses

- 606 Overall performance for the temporal memory test was quantified by regressing each
- 607 participant's subjective estimate of when an image was first encountered against the actual
- 608 (objective) time (Fig. 2c). Note that there is a general response bias among participants toward
- the center of the timeline ("raw estimated position", see Supplementary Fig. 2). To account for
- 610 this response bias and potential non-linearity, the estimated and actual temporal positions used in
- all analyses in the current paper were converted to ranks according to each individual's marked
- 612 positions on the timeline and the actual temporal positions in the continuous recognition phase,
- 613 respectively. To quantify item-wise temporal memory error, we calculated the absolute
- 614 difference between the ranked estimated temporal position and the ranked actual position (Fig.
- 615 1e). To test whether each participant had above-chance temporal memory performance, we
- 616 compared the observed temporal memory error against a null distribution of permutations (1,000
- 617 iterations), in which the subjective estimates were randomly shuffled across trials for each
- 618 participant and the temporal memory error was recomputed for each iteration. To facilitate

- 619 subsequent analyses, for each participant we divided temporal memory trials into 'high-
- 620 precision' and 'low-precision' based on the absolute temporal memory error (median split).
- 621 To control for temporal lag information and test for relationships between lag and subsequent
- 622 memory performance (Supplementary Fig. 3), as illustrated in Fig. 1d, four temporal lags were
- 623 calculated for each image: the lag between the beginning of the continuous recognition phase and
- 624 the first exposure (lag 0), the lag between the first and second exposure (lag 1), the lag between
- 625 the second and third exposure (lag 2), and the lag between the third exposure and the final
- 626 memory phase (lag 3). The first scan session of the continuous recognition phase for each
- 627 participant corresponds to Day 0. Because memory is observed to abide by an exponential rule
- 628 rather than linear time⁶², all temporal lags were quantified by expressing time intervals in
- 629 seconds and transforming these intervals with the natural logarithm. Lag effects were then tested
- 630 using mixed-effects regression models with either recognition confidence or temporal memory
- 631 precision as a dependent variable and with each temporal lag as a separate predictor.

632 **Representational similarity analyses**

- 633 Representational similarity analyses were conducted on functional data (single-trial betas) from
- 634 the continuous recognition phase, and were performed by assessing patterns of neural activity
- 635 across voxels within each ROI evoked during single trials. Pattern similarity of all possible
- 636 exposure pairings (Fig. 3b; r(E1, E2), r(E2, E3), and r(E1, E3)) for each image was computed
- 637 using Pearson correlation. The resulting correlation coefficients were then Fisher-transformed for
- 638 further analyses. To avoid potential contamination of similarity from scanner-induced
- 639 autocorrelation of signals, only correlations between image exposures that occurred across runs
- 640 were considered (range of the trials excluded for each participant: 12-35).

641 Image-specificity analyses

642 We used two approaches to assess image-specificity in CA1 and entorhinal representations that 643 predicted temporal memory.

- 644 *Intact versus shuffled pattern similarity analysis.* Our first analysis tested whether temporal
- 645 memory precision was predicted by image-specific pattern similarity (restricted to E1-E2
- 646 similarity) in CA1 and ERC using images tested in the temporal memory test (which were a
- subset of the full image set). Specifically, we randomly shuffled the E1-E2 mappings within each
- 648 participant, such that each image's E1 was paired with a different image's E2. We then
- 649 computed the pattern similarity of these shuffled exposure pairs and the new corresponding
- 650 temporal lags. The shuffled E1-E2 pattern similarity scores and temporal lag information were
- 651 then submitted to a mixed-effects logistic regression model predicting temporal memory

precision. This procedure was performed 1,000 times, resulting in a null distribution of patternsimilarity effects (betas values) for each ROI.

654 Target versus foil pattern similarity analysis. Our second approach examined whether pattern 655 similarity effects observed in CA1 and ERC were specific to individual images or were driven by 656 general memory-related processes that could be shared across different images and/or differences 657 in coarse temporal information (i.e., session effects). To do this, for each image included in the 658 temporal memory test (a 'target'), we identified control images ('foils') according to two criteria: 659 (1) targets and foils shared the same E1/E2 session number, but not run number, respectively 660 (Fig. 5a); (2) to control for generic memory states (recognition memory performance at each encounter), foils had to receive the same memory judgments as targets (i.e., to be responded 661 662 correctly all three times), which were correctly rejected at E1 and hit at E2 and E3. We then 663 computed pattern similarity between target E1 and target E2 ('target similarity') and target E1 664 and foils E2 ('foil similarity'). This selection procedure resulted in different numbers of foils for 665 each target image. For images with two or more foils, we used the median value of those foil 666 similarity scores. To index the extent to which pattern similarity captures image-specific 667 representations, foil similarity was subtracted from target similarity for each image (target 668 similarity – foil similarity). This difference score between target and foil similarity was then 669 submitted to a mixed-effects logistic regression model as a predictor of temporal memory 670 precision, where a significant positive relationship would indicate that the pattern similarity that

671 predicted temporal memory precision was driven by image-specific representations.

b/1 predicted temporal memory precision was driven by image-specific representation

672 Statistical analyses

- 673 Behavioral and fMRI data were analyzed using a combination of permutation tests, paired *t* tests,
- 674 repeated-measures ANOVA and mixed-effects regression models. Trial-level relationships
- between similarity measures and final memory performance were tested with mixed-effects
- 676 linear/logistic regression models (for recognition confidence and temporal memory precision,
- 677 respectively). For all permutation analyses, we used 1,000 permutations and assessed
- 678 significance by computing the proportion of values in the null distribution that were higher/lower
- than the observed values. All *t* tests were two-tailed. For mixed-effects regression models, we
- 680 used the participant as a random effect and other variables as fixed effects. A threshold of p < p
- 681 0.05 was used to establish statistical significance for all analyses. fMRI analyses were corrected
- 682 for multiple comparisons with Bonferroni corrections when applicable. Only ROIs that survived
- 683 correction are reported except where otherwise noted.
- 684

685 SUPPLEMENTARY FIGURES



686



688 During the frequency test, participants were asked to indicate how many times they had seen each image

689 (1, 2, 3, or 4 or more times). No participant preferentially chose the correct response (i.e., three times).

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692 **Supplementary Figure 2. Raw estimated and actual temporal positions for each participant.** Each dot indicates a temporal memory judgment. Temporal judgments for each participant were divided into

694 'high temporal precision' and 'low temporal precision' on the basis of temporal memory error (median

695 split). Histograms on sides indicate distributions of raw estimated (vertical) and actual (horizontal)

temporal positions (overlaid across high- and low- temporal precision). Colors denote temporal memory

697 precision (blue: high temporal precision; gray: low temporal precision).



700 Supplementary Figure 3. Lag effects on behavioral measures of final memory. (a) Lag effects on

701 recognition confidence. There were spacing effects in recognition confidence such that confidence 702 increased as a function of increasing temporal lags between exposures (lag 1: $\beta = 0.051$, p < 0.001; lag 2:

703 $\beta = 0.039$, p < 0.001; in a mixed-effects linear regression model with recognition confidence as

dependent variable and with each temporal lag as a separate predictor), and a forgetting effect wherein

recognition confidence diminished as the lag between the last exposure and the final memory test

increased (lag 3: $\beta = -0.303$, p < 0.001). (b) Lag effects on temporal memory precision. There was a

recency effect across months with temporal memory precision increasing the later in the experiment an

image was first encountered (lag 0: $\beta = 0.098$, p = 0.021; in a mixed-effects logistic regression model

with temporal memory precision as dependent variable and with each temporal lag as a separate

710 predictor). Error bars reflect mean \pm s.e.m.; $\sim p < 0.10$; *p < 0.05; ***p < 0.001.

711

Cortical ROIs (HCP-MMP1 atlas)	z-value	<i>p</i> -value (uncorrected)
L Frontal Eye Fields	2.027	0.043
L Supplementary and Cingulate Eye Field	2.693	0.007
L Area 6m anterior	2.761	0.006
L Area IFJp	2.356	0.018
L Area IFSp	2.043	0.041
L Area posterior 9-46v	2.020	0.043
L Entorhinal Cortex	2.001	0.045
L Perirhinal Ectorhinal Cortex	2.912	0.004
L Area 31pd	-2.011	0.044
R Area 31p ventral	-2.369	0.018
R Frontal Opercular Area 1	-2.062	0.039
R Entorhinal Cortex	2.082	0.037
R Area TG dorsal	2.109	0.035
R AreaTemporoParietoOcci pital Junction 1	2.119	0.034
R Area 31a	-1.963	0.050

712 Supplementary Table 1. Whole-brain representational similarity analysis in cortical ROIs. A

713 mixed-effects logistic regression predicting temporal memory with pattern similarity as the main fixed

effect of interest was conducted for each parcel of the HCP-MMP1 atlas⁶¹ to determine whether cortical regions outside of the MTL also exhibit pattern similarity effects on temporal memory. This table

summarizes the whole-brain parcel level analysis with cortical ROIs showing significant relationships

717 summarizes the whole-brain parcel level analysis with cortical ROIs showing significant relationships 717 between pattern similarity and temporal memory before correcting for multiple comparisons

718 (p(uncorrected) < 0.05). No regions survived correction for multiple comparisons.

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