Hippocampal subfields integrate information about past temporal and cognitive contexts

Halle R. Dimsdale-Zucker, Maria E. Montchal, Zachariah M. Reagh, Shao-Fang Wang, Laura A. Libby, Charan Ranganath

Abstract. The hippocampus plays a critical role in supporting episodic memory. Although we know that temporal context is a defining feature of episodic memory, we understand relatively little about how this information may be represented by the hippocampus. Research in rodents has suggested that the hippocampus represents temporal information on an absolute scale or in terms of relative temporal intervals, but cognitive models of memory have argued that temporal context in episodic memory is a consequence of changes in cognitive states and experiences. Here, we combined high-resolution fMRI imaging with voxel pattern similarity analyses to answer the question of how human hippocampal subfields represent retrieved information about cognitive states and the time at which a past event took place. As participants recollected previously presented items, activity patterns in the CA23DG subregion carried information about prior cognitive states, along with coarse-grained information about when the item was previously encountered. These findings are consistent with the idea that CA23DG supports temporal context in episodic memory by encoding an integrated representation of discrete and gradually-changing cognitive states.

Introduction. Converging evidence suggests that the hippocampus plays a critical role in memory for events and their episodic details (Eichenbaum, Yonelinas, & Ranganath, 2007; Scoville & Milner, 1957; Vargha-Khadem et al., 1997). For a memory to be considered episodic, it must be associated with a particular moment in time, or temporal context (Reiff & Scheerer, 1959; Tulving, 1983). Consistent with its integral role in

episodic memory, studies in rodents (Allen, Salz, McKenzie, & Fortin, 2016; Cai et al., 2016; Kraus et al., 2015; Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013; Salz et al., 2016), non-human primates (Naya, Chen, Yang, & Suzuki, 2017), and humans (Dimsdale-Zucker, Ritchey, Ekstrom, Yonelinas, & Ranganath, 2018; Hsieh, Gruber, Jenkins, & Ranganath, 2014; Jenkins & Ranganath, 2010, 2016; Tubridy & Davachi, 2011) have shown that the hippocampus represents information about time.

At present, there are at least two major accounts of how this might happen. One possibility is that the hippocampus maintains a continuously varying representation of temporal context, possibly via internally generated cell assembly sequences (Buzsáki & Llinás, 2017; Levy, 1996; Rodriguez & Levy, 2001; Wallenstein, Eichenbaum, & Hasselmo, 1998). Consistent with this idea, results from single-unit recording studies in rodents have suggested that cell populations in the hippocampus can faithfully represent temporal relationships across both short (Kraus et al., 2015, 2013; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Salz et al., 2016) and longer (Cai et al., 2016; Mankin, Diehl, Sparks, Leutgeb, & Leutgeb, 2015; Mankin et al., 2012; Ziv et al., 2013) intervals. Another possibly complementary account comes from cognitive theories of episodic memory that operationalize temporal context in terms of changes in cognitive *states* or experiences (Estes, 1955; Howard & Kahana, 2002). Although temporal context models generally assume that representations of temporal context change gradually, these models also predict that context can abruptly change to reflect one's current cognitive state (Lohnas, Polyn, & Kahana, 2015; Polyn, Norman, & Kahana, 2009).

The extent to which the human hippocampus represents cognitive states and temporal context is unclear, and there is reason to think that different hippocampal subfields might make distinct contributions (Dimsdale-Zucker et al., 2018). For instance, some models emphasize the role of area CA1 in encoding of temporal context (e.g., (Kesner & Rolls, 2015) others emphasize the importance of the dentate gyrus and CA3 (Levy, 1996; Lisman, 1999; Wallenstein et al., 1998), and some recent evidence has suggested that area CA2 may be disproportionately important (Mankin et al., 2015). Thus, this leaves open the question of whether temporal information may be differentially represented by hippocampus subfields.

Here, we used high-resolution functional magnetic resonance imaging (fMRI) to clarify whether or how the hippocampus encodes temporal and cognitive contexts during episodic memory retrieval. We also examined contributions of medial temporal cortical regions, as, for instance, parahippocampal cortex is known to be important for representing contextual information (Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007). We scanned participants while they recollected objects that were studied in sequentially-organized lists, and used voxel pattern similarity (PS) analyses (Dimsdale-Zucker & Ranganath, 2018; Kriegeskorte, Mur, & Bandettini, 2008) to examine whether patterns of activity in hippocampal subfields at the time of retrieval carried information about temporal and cognitive contexts instantiated at encoding.

Method.

Participants. 32 participants were recruited from the community and were compensated $50 for their time. This study was approved by the Institutional Review Board at the University of California, Davis. Four participants were excluded due to

missing behavioral data, two participants were excluded for excessive motion that prevented tracing of hippocampal subfields, one participant was excluded due to an experimenter error at data collection that resulted in the incorrect stimuli being seen, and one participant was excluded because they only had one run of usable data after discarding motion-contaminated and data-collection contaminated runs. The results below reflect data from 24 remaining participants (Mage = 22.85 years, SD = 3.06 years, Nfemale = 13). One of these 24 participants was excluded from behavioral cognitive and temporal context analyses due to partially missing data; since the brain imaging data for this participant were complete and did not depend on this behavior being recorded, they were included in all other analyses.

Encoding. Participants viewed eight 36-item lists of still pictures of everyday objects (e.g., contact lens case, french fries; http://cvcl.mit.edu/mm/uniqueObjects.html; see Figure 1). Object assignment to list and presentation order of objects within a list were uniquely randomized for each participant via the Matlab randperm function. To encourage participants to learn temporal relationships amongst items in a list (Palombo, Di Lascio, Howard, & Verfaellie, 2019), each list was presented three times in a mini-block before subjects saw items from the next list (e.g., 1, 1, 1, 2, 2, 2...8, 8, 8). Mini-blocks were separated with a self-paced break. Presentation order of objects within a list was identical for all three list presentations.

Objects remained on the screen for 2.5 seconds (timing and presentation parameters were controlled via Presentation [Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com]) while the participant made a yes/no button response to an orienting question (cognitive context). To manipulate cognitive context, each object was

associated with one of four questions: Would this item fit in a refrigerator?, Would this item fit in a bathtub?, Would you find this item in a convenience store?, Would you find this item in a supermarket?. Each of the four questions was presented equally often in each block, and question/object pairs remained the same across all three list presentations. Participants were instructed that this was a decision-making task and that there would be some repetition but to concentrate on doing the task. Participants were not aware that memory for these questions would be tested later, thus the learning of question and temporal context information was incidental.

Scanned object recognition. While in the MRI scanner, participants saw each of the 288 old objects from encoding as well as 72 new objects presented one at a time for 2.5 seconds with a jittered ITI ranging from 2-15 seconds (mean ITI jitter = 6 seconds). Objects were divided into 6 runs (60 trials per run). Object order within a run was pseudo-randomized such that objects with the same encoding question always had at least one intervening object (e.g., fridge, convenience store, bathtub, fridge, supermarket, fridge, etc.) to help minimize encoding context reinstatement biases on PS results (see Multivariate Results below). Proximity of objects from encoding mini-blocks (1-8) was not considered in the pseudo-randomization.

While in the scanner, participants were instructed to indicate via button press whether or not they remembered the object on a 4-point scale: 1=new, 2=familiar (old but no remembered details), 3=remembered non-temporal details (e.g., the encoding question, something about the object itself, or an association they made with the object), 4=remembered temporal detail (e.g., in what list or when they had seen the

object during encoding). Responses for remembered judgments were collapsed into a single response bin for behavioral and fMRI analyses.

Source memory: Cognitive context. After completing MRI scanning, participants returned to the lab where they completed a cognitive context source memory task. In this phase, participants saw all 288 studied objects from encoding and were asked to indicate which encoding question (fridge/bathtub/convenience store/grocery store) had been associated with the object. Objects were presented across four blocks of 72 trials each. Within each block, there were an equal number of objects from each encoding mini-block (1-8). Presentation order of objects was uniquely randomized by participant within each source memory block. Objects appeared on the screen until the participant had made their source memory judgment. There was no opportunity to guess or skip objects.

Source memory: Temporal context. After completing the cognitive context source memory test, participants again saw the 288 old objects from encoding and this time were asked to indicate in which mini-block (1-8) the object had appeared. Objects were again divided across four blocks of 72 trials with a different randomization order than was used in the task context source memory test. Objects remained on the screen until the participant had made their response. There was no opportunity to guess or skip temporal context judgments.

fMRI acquisition and pre-processing. Scans were acquired on a Siemens Skyra 3T scanner with a 32 channel head coil. Two sets of structural images were acquired to enable subfield segmentation: A T1-weighted magnetization prepared rapid acquisition gradient echo (MP-RAGE) pulse sequence image (1 mm isotropic voxels),

141 and a high-resolution T2-weighted image (TR = 4200 ms; TE= 93 ms; field of view =
142 200 mm^2; flip angle = 139°; bandwidth = 199 Hz/pixel; voxel size = 0.4 x 0.4 x 1.9 mm;
143 58 coronal slices acquired perpendicular to the long-axis of the hippocampus). High-
144 resolution functional (T2*) images were acquired using a multiband gradient echo planar
145 (EPI) imaging sequence (TR = 2010 ms; TE = 25 ms; field of view = 216 mm; image
146 matrix = 144 x 152; flip angle = 79°; bandwidth = 1240 Hx/pixel; partial phase Fourier =
147 6/8; parallel imaging = GRAPPA acceleration factor 2 with 72 reference lines; multiband
148 factor = 2; 52 oblique axial slices acquired parallel to the long-axis of the hippocampus
149 slices; voxel size = 1.5 mm isotropic).

150 SPM8 (http://www.fil.ion.ucl.ac.uk/spm/) was used for image pre-processing.
151 Functional EPI images were realigned to the first image and resliced. No slice timing
152 correction was performed due to the acquisition of multiple simultaneous slices with the
153 multiband sequence (capabilities to handle multiband timing do not exist in SPM8). Co-
154 registration between the native-space ROIs defined in T2 space and the functional
155 images was done with SPM's Coregister: Estimate and Reslice procedure. This
156 procedure uses a linear normalized mutual information cost-function between a
157 reference (mean functional) image and source (T2) image to compute and apply a
158 voxel-by-voxel affine transformation matrix. This transformation matrix was then applied
159 to the subfield ROIs that had been defined in T2 space (see *ROI segmentation*) to bring
160 them into register with the functional images. The T1 image was co-registered to the
161 mean EPI. Then, nonlinear spatial normalization parameters were derived by
162 segmenting the coregistered T1 image. Quality assurance included identifying suspect
163 timepoints via custom code (https://github.com/memobc/memolab-fmri-qa) defined as

time-points in excess of 0.5 mm frame displacement (based on (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012) or 1.5% global mean signal change (based on ARTRepair recommendations, (Mazaika, Whitfield-Gabrieli, & Cooper, 2005)). Runs were excluded if the frame displacement exceeded the voxel size. As reported earlier, three participants were excluded for motion in excess of these thresholds; of the 24 subjects included in the analyses, 9 had runs excluded based on these thresholds (mean number of removed runs = 0.92, SD = 1.38; ranging from 0-4 runs).

Pattern similarity analyses. PS analyses were conducted on beta maps generated from unsmoothed data in native subject space. Following the least squares separate procedure described by Mumford (2012), single trial models were generated to estimate the unique beta map for every trial in a run (N=60). Within each single trial model, the first regressor modeled the trial of interest with a stick function, the second regressor modeled all other trials in that run, six regressors were used to capture motion, and any additional spike regressors as identified by our QA scripts were used to capture additional residual variance. Voxel-wise patterns of hemodynamic activity were separately extracted for each ROI from the single trial beta images. To ensure robust ability to detect differences in PS, we required temporal signal-to-noise ratios (TSNR) in a region to be above 20 (approximately 2 standard deviations below the mean global TSNR of 50.4). This required the removal of entorhinal cortex and its subregions (mean TSNR ranged between 10-20), despite its compelling role in the representation of temporal context (Bellmund, Deuker, & Doeller, 2019; Montchal, Reagh, & Yassa, 2019)

Within each ROI, correlations (Pearson's r) were computed between these trial-wise betas to yield a trial-by-trial correlation matrix that related each voxel's signal on a

trial to all other trials across all runs. We restricted comparisons to those trials for which participants made a correct “remember” response (during MRI scanning). Correlation values were z-transformed prior to statistical analysis. Statistical analyses tested for differences in correlations between trial pairs on the basis of encoding context (cognitive context: same vs. different encoding question; temporal context: same vs. different encoding list, or similar vs. different list half). To more accurately characterize both within- and across-subject error variance (Baayen, Davidson, & Bates, 2008; Clark, 1973; Dixon, 2008; Jaeger, 2008; Mumford & Poldrack, 2007; Singmann & Kellen, in press), we implemented a mixed-modelling approach to evaluate statistical significance with the *lme4* packing in R (Bates, Mächler, Bolker, & Walker, 2014); for a similar approach, see (Dimsdale-Zucker et al., 2018). Only between-run correlations were used to maximize the number of possible trial pairs without mixing within- and between-run correlations. Trial pairs of interest were extracted from these trial-by-trial correlation matrices.

All relevant code (https://github.com/hallez/tempcon_pub), a reproducible compute environment (https://doi.org/10.24433/CO.0129473.v1), and relevant data (https://osf.io/qfcjg/) are available online.

ROI definition. Hippocampal subfields were defined following the procedure reported in (Dimsdale-Zucker et al., 2018). In short, the ASHS automated segmentation procedure was used to delineate subfields in subject-native space (Yushkevich et al., 2010). We restricted our analyses to hippocampal body where discriminating subfields is most agreed upon. Medial temporal lobe cortical regions were manually-traced (see the Libby and Ranganath protocol in (Yushkevich et al., 2015)). In accordance with prior

findings suggesting functional distinctions between anterior and posterior parahippocampal gyrus (Aminoff, Gronau, & Bar, 2007; Baldassano, Beck, & Fei-Fei, 2013; Baldassano, Esteva, Fei-Fei, & Beck, 2016), we subdivided parahippocampal cortex one slice posterior to the wing of the ambient cistern (Frankó, Insausti, Artacho-Pérula, Insausti, & Chavoix, 2014).

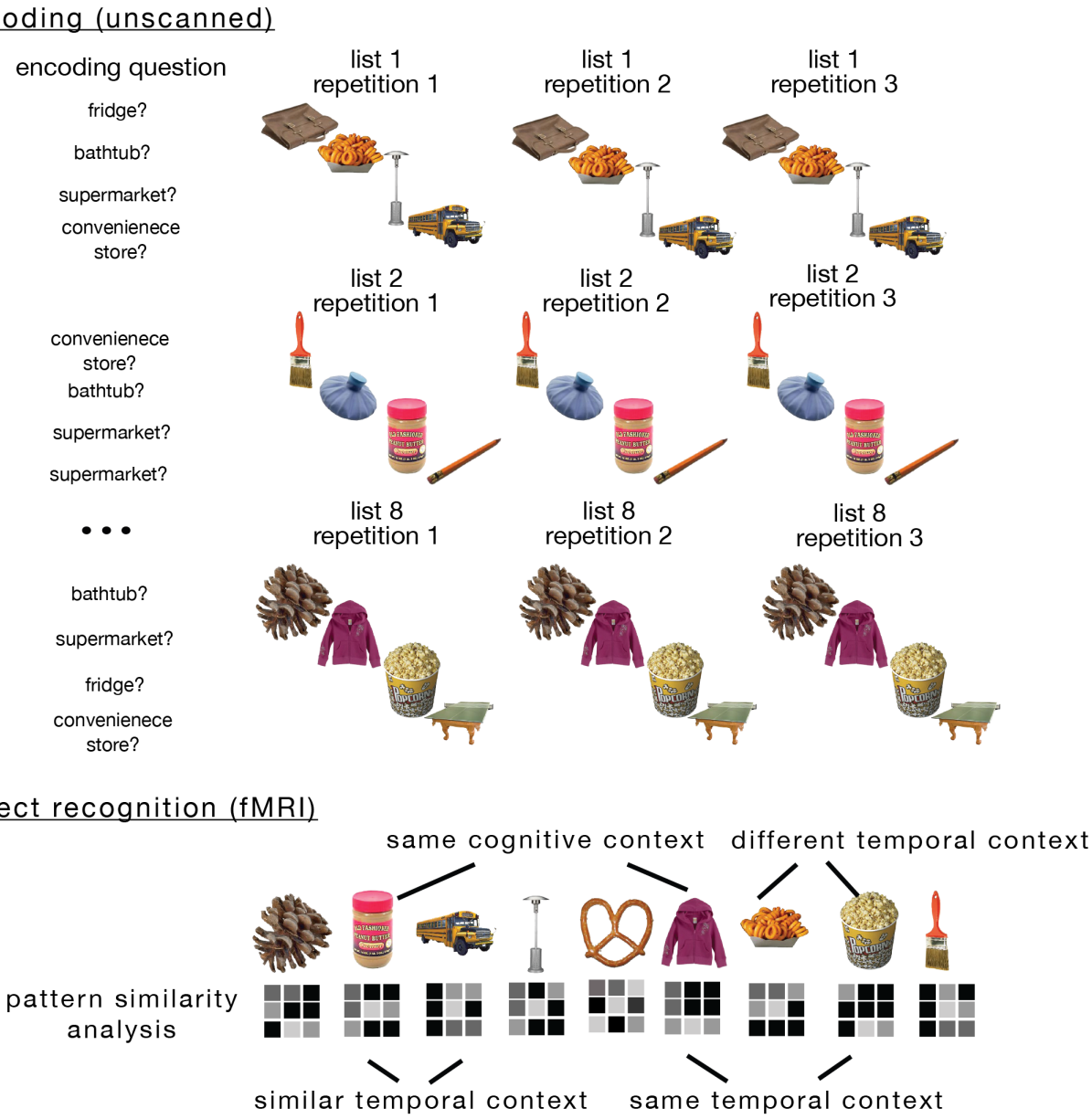

Figure 1. Task structure. During the encoding phase, each participant studied lists of 36 objects that were each randomly paired with one of four encoding questions ("Would this item fit in a fridge?", "Would this item fit in a bathtub?", "Would you find this item in a

supermarket?", "Would you find this item in a convenience store?"). Each list was repeated three times in a row to promote learning of the temporal relationships amongst the items. Objects appeared in the same order and with the same question (cognitive context) across all repetitions. High-resolution functional magnetic resonance brain imaging (fMRI) was used to examine hippocampal activity patterns during a recognition memory test for these objects, allowing us to examine activity pattern similarity as a function of whether pairs of items were encoded within the same or similar temporal contexts (i.e., studied in the same list or temporally proximal lists), and/or the same cognitive context (i.e., associated encoding question)

Results.

Behavioral results. During MRI scanning participants performed a recognition memory test requiring judgments as to whether each item was recognized on the basis of recollection of specific item and source information from the study phase (see *Method*). Pattern similarity analyses were restricted to correctly remembered items.

Correct remember judgments were the most common response (mean hit rate = 0.69, SD = 0.19), and, for these items, participants showed high accuracy at remembering the associated encoding task context (mean hit rate = 0.71, SD = 0.12). Memory for the exact ("same") temporal context (list 1-8) was poor (mean hit rate = 0.18, SD = 0.03), but, we reasoned that, even if participants were unable to recall the exact list identity, they might have memory for the "similar" temporal context associated with each item. We therefore re-scored each trial according to whether the participant could accurately determine whether it was presented in the "similar" (first half (lists 1-4) or the second half (lists 5-8)) versus "different" (across halves, i.e., list 1/list5, list 1/list 6, etc.) temporal context of the encoding phase. On this metric, memory for similar temporal context (mean hit rate for list half = 0.59, SD = 0.04) was reliably greater than chance of 0.5, $t(22) = 8.74$, $p < 0.001$. Thus, although participants did not have access

to the precise list in which an item had been studied, they were able to retrieve information about the item's temporal context at a coarse level.

fMRI results: Hippocampal Subfields We next tested whether activity patterns in the hippocampal subfields (CA1, CA23DG, subiculum) during memory retrieval carried information about the context in which the item was previously encountered. Specifically, we examined voxel PS during retrieval as a function of whether pairs of trials shared a temporal (defined either as same list vs. different list [*same* temporal context] or as same half of the experiment vs. different halves of the experiment [*similar* temporal context]) and/or cognitive (i.e., same encoding task vs. different encoding task) context when the items were originally learned.

We first considered when items came from the "same" temporal encoding context (same vs. different list). No hippocampal subfield varied its PS at retrieval with respect to the same temporal context (all $X^2 < 0.5$, all *p*s > 0.40). In CA23DG, we found that PS was higher during retrieval of items associated with the same cognitive context compared to items associated with different cognitive contexts ($X^2(1) = 4.63$, $p^{perm1000} = 0.031$). No other subfield varied its PS at retrieval with respect to cognitive context alone (all $X^2 < 0.3$, all *p*s > 0.55) nor the combination of temporal and cognitive context (all $X^2 < 0.80$, all *p*s > 0.30).

We next considered whether PS might depend on whether items shared a "similar" temporal context at encoding (same vs. different half of the encoding phase). PS levels did not vary by similar temporal context alone ($X^2(1) = 0.08$, $p^{perm1000} = 0.815$). Thus, PS levels were not modulated by same or similar temporal context alone. In CA23DG, we found that PS was higher during retrieval of items that were associated

with the same cognitive context than for items that were associated with different cognitive contexts ($X^2(1) = 4.68$, $p^{perm1000} = 0.037$; see Figure 2). Thus, irrespective of how we defined temporal context (same, similar), PS in CA23DG was higher for items that were associated with the same cognitive context. This effect was qualified by a significant similar temporal by cognitive context interaction ($X^2(1) = 8.11$, $p^{perm1000} = 0.008$), such that the effect of cognitive context was larger for items that were in similar temporal contexts (same half) than for items that were in different temporal contexts (different half) particularly when these items shared the same cognitive context.

In CA1, PS levels did not vary by similar temporal context ($X^2(1) = 2.42$, $p^{perm1000} = 0.122$), cognitive context ($X^2(1) = 0.08$, $p^{perm1000} = 0.757$), nor when we considered both temporal and cognitive context ($X^2(1) = 0.84$, $p^{perm1000} = 0.329$). In subiculum, PS levels did not vary by similar temporal context ($X^2(1) = 0.11$, $p^{perm1000} = 0.751$) or cognitive context ($X^2(1) = 0.27$, $p^{perm1000} = 0.622$), however, we found that PS was marginally higher for items that were studied relative to the same question but studied in different list halves as compared to all other conditions ($X^2(1) = 2.91$, $p^{perm1000} = 0.082$).

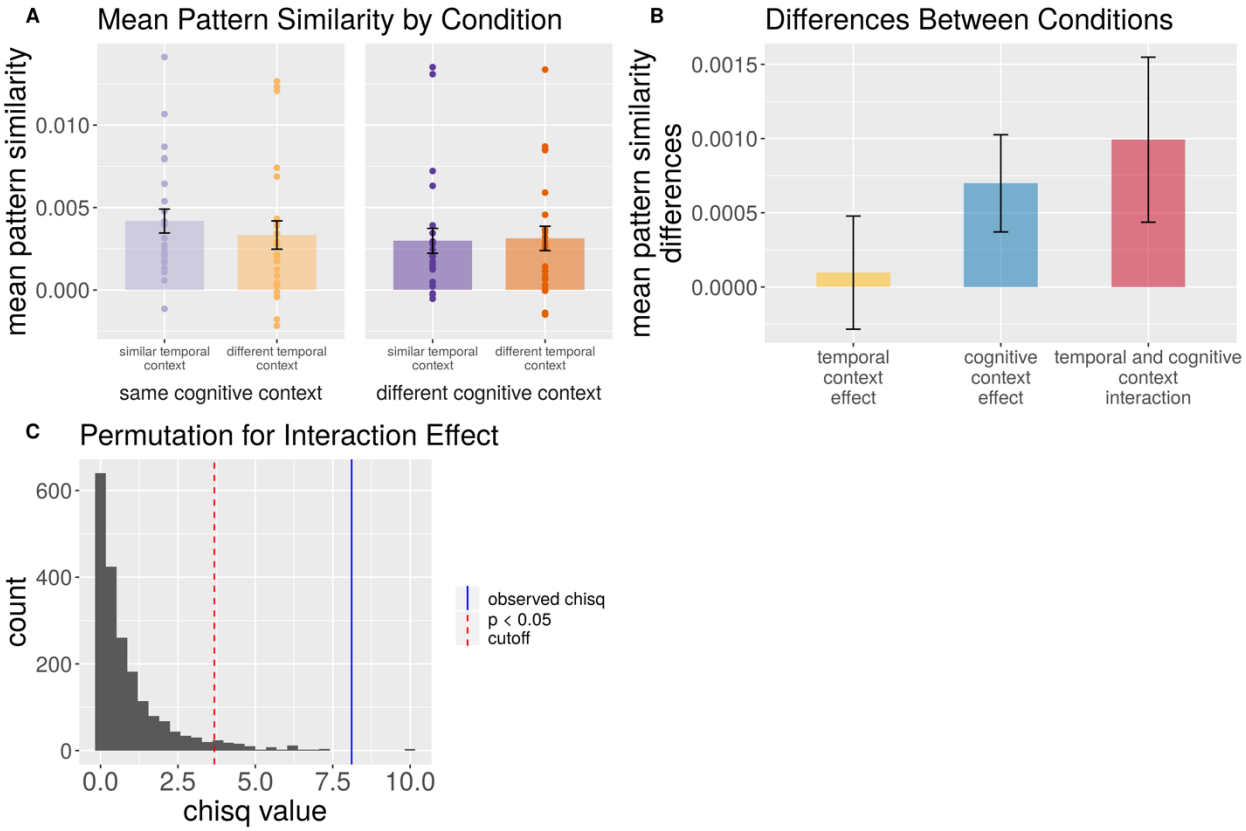

Figure 2. Pattern similarity values in CA23DG during memory retrieval carry information about temporal and cognitive encoding contexts. A. Mean pattern similarity scores, with scatter of individual subject observations for the combination of different encoding contexts. B. Differences between same/different list half ("similar" temporal context), same/different question (cognitive context), and the interaction of temporal and cognitive context ([same question, same list half – different question, same list half] – [same question, different list half – different question, different list half). C. Permuted chi-square values to determine significance of cognitive-by-temporal interaction.

fMRI Results: Medial Temporal Lobe (MTL) Neocortical Areas

Our next analyses investigated activity in MTL regions outside of the hippocampus. Previous work has suggested that regions in parahippocampal cortex (PHC) should process information about cognitive context (Diana, Yonelinas, & Ranganath, 2012, 2013; F. Wang & Diana, 2017). In anterior PHC (aPHC), we observed an interaction between cognitive context, same temporal context, and hemisphere ($X^2(3) = 8.91$, $p^{perm1000} = 0.037$). Looking across hemispheres, PS levels only varied reliably in left aPHC on the basis of cognitive context ($X^2(1) = 7.89$, $p^{perm1000}$

= 0.007). We found no other significant effects involving same temporal context (all X^2 < 0.7, all *p*s > 0.4), nor the combination of same temporal and cognitive context (all X^2 < 1.2, all *p*s > 0.2) in either hemisphere. PS in posterior PHC (pPHC) was marginally greater for items in the different as compared to same temporal context ($X^2(1) = 3.75$, $p^{perm1000} = 0.055$), but did not vary on the basis of cognitive context alone ($X^2(1) = 1.22$, $p^{perm1000} = 0.263$). This marginal effect of same temporal context in pPHC was qualified by a significant same temporal context by cognitive context interaction ($X^2(1) = 8.18$, $p^{perm1000} = 0.002$). PS levels in PRC did not vary by temporal encoding context ($X^2(1) = 0.001$, $p^{perm1000} = 0.981$), cognitive context ($X^2(1) = 0.51$, $p^{perm1000} = 0.497$), nor the combination of temporal and cognitive context ($X^2(1) = 0.82$, $p^{perm1000} = 0.354$).

We next considered whether PS in MTL neocortical areas might depend on whether items shared a similar temporal context at encoding. In aPHC, we observed an interaction between cognitive context, similar temporal context, and hemisphere ($X^2(1) = 9.17$, $p^{perm1000} = 0.028$). This reflects the fact that in left aPHC, voxel PS was greater for items studied relative to different cognitive contexts ($X^2(1) = 7.96$, $p^{perm1000} = 0.006$), as well as for items from different temporal contexts ($X^2(1) = 5.75$, $p^{perm1000} = 0.015$), but did not vary based on the combination of cognitive and temporal context ($X^2(1) = 0.88$, $p^{perm1000} = 0.349$). In right aPHC, voxel PS did not carry information about an item's cognitive context ($X^2(1) = 0.75$, $p^{perm1000} = 0.372$) or temporal ($X^2(1) = 1.49$, $p^{perm1000} = 0.226$) context, nor their combination ($X^2(1) = 0.27$, $p^{perm1000} = 0.60$). PS levels did not reliably vary for cognitive context (all X^2 < 1.2, all *p*s > 0.25), similar temporal context (all X^2 < 0.30, all *p*s > 0.60), nor the combination of cognitive and temporal context (all X^2 < 1.9, all *p*s > 0.25) in either pPHC or PRC.

Discussion.

The goal of the present study was to test the extent to which the hippocampus represents absolute temporal information and information about particular cognitive states during recollection of past events. Although cognitive states typically fluctuate over time in a continuous manner, the design of our experiment allowed us to examine the influence of these two aspects of context separately. We found that, during recollection of a study item, CA23DG activity patterns carried information about the cognitive context associated with that item during the study phase. Additionally, cognitive context information evident in CA23DG activity patterns varied over a coarse timescale, such that pattern similarity was highest for pairs of items that were associated with similar temporal and cognitive contexts. Collectively, these findings demonstrate that the hippocampus represents information about past events in a manner that is consistent with temporal context models (Howard & Kahana, 2002; Norman, Detre, & Polyn, 2008; Polyn et al., 2009; Sederberg, Howard, & Kahana, 2008).

We have long understood that context is central for recall (Clewett & Davachi, 2017; Davachi & DuBrow, 2015; Zacks & Swallow, 2007) and recollection-based recognition (Eichenbaum et al., 2007), but we do not yet understand how *temporal* context may be encoded in the brain. These representations of temporal and cognitive state contexts seem to rely on the hippocampus (Eichenbaum, 2017; Ranganath, 2019). In the hippocampus, one candidate mechanism is the coordinated firing of self-organized cell assemblies, or time cells (Lisman & Jensen, 2013; Y. Wang, Romani, Lustig, Leonardo, & Pastalkova, 2015). These cells can track how long an animal has

been running on a treadmill where distance, speed, and duration of run time can be decorrelated (Kraus et al., 2015, 2013; Salz et al., 2016), code for meaningful gaps or pauses (MacDonald et al., 2011), and represent ordered sequences and experiences even during rest periods (Pastalkova, Itskov, Amarasingham, & Buzsáki, 2008). Hippocampal ensembles also drift in their representations of space when recorded across days, thus it seems that they can encode both fine and coarse temporal information (Mankin et al., 2015, 2012; Rubin, Geva, Sheintuch, & Ziv, 2015; Ziv et al., 2013). These findings provide evidence for the idea that hippocampal neurons may encode information about temporal intervals or the passage of time. That said, available evidence indicates that hippocampal time cells are highly sensitive to changes in task context. In one such demonstration, immobilized rats learned to maintain information about specific odors across a delay period (MacDonald et al., 2013). Results showed that different cell assemblies encoded temporal intervals across the delay period depending on the odor that was to be maintained. In other words, changes in the task context led to substantial changes in the neural ensembles that encoded temporal information during the task.

In the present study, we found evidence for the idea that information about cognitive states (i.e., specific task contexts) was carried in hippocampal activity patterns during recollection, and that these patterns also carried relatively coarse-grained information about the temporal context in which the recollected item was initially encountered (see also (DuBrow, Rouhani, Niv, & Norman, 2017) for evidence that contexts can drift slowly). This is consistent with the scale of temporal information participants had access to behaviorally; they were poor at retrieving the exact list an

item had been in but had access to information about in which half of the study lists it had occurred. These findings are generally in line with what would be predicted by cognitive models of the representation of temporal context in episodic memory. Initial theories operationalized temporal context as random fluctuations in cognitive states over time (Estes, 1955), and subsequent theories have incorporated the assumption that temporal context also reflects a time-weighted average of recently processed items and experiences (Howard & Kahana, 2002; Norman et al., 2008; Sederberg et al., 2008). These models would predict that activity patterns during memory retrieval should reflect information about the temporal context associated with each study item (e.g., Manning et al., 2011; Deuker et al., 2016; Nielson et al., 2015). The Context Maintenance and Retrieval (CMR) model goes farther by incorporating information about the current task or cognitive state into the temporal context representation. CMR predicts that if there are abrupt changes in one's cognitive state (e.g., a change in the task that one is performing), items that are temporally proximal can actually have distinct contextual associations (Polyn et al., 2009). Thus, the CMR model predicts that, during memory retrieval, reinstatement of temporal context should reflect a conjunction of task-related information and information that reflects elapsed time, similar to what was observed in CA23DG. Though CMR most explicitly incorporates semantic relationships into the temporal context model, we suggest that contextual associations associated with task or cognitive states likely tap into a similar mechanism. Moreover, the model suggests that changing tasks during encoding would break up the temporal context representation during encoding of each list. This prediction is consistent with the fact that we did not see evidence of high pattern similarity across items within the same

394 list, and instead only saw representation of temporal information across coarser
395 timescales.

396 At a broader level, our findings converge with results from a number of recent
397 studies showing that hippocampal activity patterns carry information that generalizes
398 across events that share common elements (Horner, Bisby, Bush, Lin, & Burgess, 2015;
399 Schlichting & Preston, 2015). Here, we found that activity patterns in the CA23DG
400 subregion generalize across items that shared both temporal and task context. Other
401 findings, however, suggest that hippocampal representations can amplify differences
402 between overlapping experiences (Chanales, Oza, Favila, & Kuhl, 2017; Libby, Reagh,
403 Bouffard, Ragland, & Ranganath, 2018; Ritvo, Turk-Browne, & Norman, 2019; Yassa &
404 Stark, 2011). In one recent study, for instance, we found that CA23DG activity patterns
405 during memory retrieval were more different for across pairs of items that were
406 associated with the same episodic context (i.e., objects seen within the same movie)
407 than across pairs of items that were associated with different contexts. The findings of
408 Dimsdale-Zucker et al. (2018), considered alongside the present results, raise an
409 important question: When does CA23DG assign similar or distinct representations to
410 overlapping events?

411 To answer this question, it may be informative to consider the conflicting role of
412 shared context in facilitating inter-item relationships (Sederberg, Miller, Howard, &
413 Kahana, 2010) while diminishing item distinctiveness (El-Kalliny et al., 2019). During
414 recognition memory tests, people are generally more likely to recollect events that were
415 distinctive than events that were overwhelmingly similar to one another (Hunt, 1995). If
416 CA23DG represents information about one's cognitive state during an event, then we

would expect that this area would be most likely to support successful recollection when those representations are distinctive. In the present study, changes in the encoding task encouraged participants to shift cognitive states abruptly across items within a list. By attending to the task context, a participant could form distinctive memories for the different items that were in the same list. In our previous study (Dimsdale-Zucker et al., 2018), however, participants studied lists of items presented in virtual reality videos that depicted navigation through two homes. Thus, the environmental context was overwhelmingly similar across items in the same list, and the cognitive context was not explicitly controlled (i.e., cognitive context likely tracked with environments and the passage of time). To successfully encode items from the study phase, participants needed to form representations that highlighted the distinctive aspects of each item in the list in order to overcome contextual interference at the time of retrieval (Park, Arndt, & Reder, 2006). We therefore propose that, by binding information about items with information about cognitive contexts, CA23DG can support successful retrieval of overlapping memories that would otherwise be difficult to disambiguate (Yassa & Reagh, 2013).

Our findings also highlight the relative paucity of direct access to memory for temporal context at retrieval. Behavioral measures of memory for temporal context show clustered recall; that is, items studied nearer in time to one another are more likely to be recalled close together (Kahana, 1996). These findings suggest that, during episodic memory retrieval, people may be mentally transported back to a past cognitive state (Manning, Polyn, Baltuch, Litt, & Kahana, 2011; Tulving, 1983). Yet, when people are explicitly asked about temporal order information, they often cannot produce reliable

estimates (Jenkins & Ranganath, 2010). In the present study, we also found that participants had little explicit access to an item's temporal encoding context. When asked to choose in which of eight lists an item had been studied, participants were essentially at chance. This is not surprising because temporal context models only suggest that memories for temporally proximal events should be associated with similar context representations, but retrieval of context information would not automatically enable a person to determine the exact time at which a previous item was encountered. There is considerable evidence to suggest that people rely on heuristics strategies in order to roughly reconstruct the time at which an event took place (Friedman, 1993). In our study, this might have been more challenging because, as we have stated above, changes in cognitive context within a list most likely disrupted the continuity of temporal context representations (for a related finding, see (Polyn et al., 2009)).

In addition to the hippocampus, medial temporal lobe cortical regions have also been implicated in representing context. A substantial body of work has suggested a particular role for parahippocampal cortex in supporting representations of context (Davachi, 2006; Diana et al., 2007, 2013; Hsieh et al., 2014; Tubridy & Davachi, 2011; F. Wang & Diana, 2017). In line with these findings, we also saw that parahippocampal cortex carried information about cognitive and temporal contexts. Recent work has also suggested a role for lateral entorhinal cortex in absolute representations of time (Bellmund et al., 2019; Montchal et al., 2019; Sugar & Moser, 2019). Unfortunately, we could not assess whether lateral entorhinal cortex represented elapsed time because our scanning protocol was not optimized for entorhinal cortex coverage, and the temporal signal-to-noise ratio was therefore insufficient. Thus, it is possible that in this

task where participants had access to both a sense of ongoing time and fluctuating cognitive states, hippocampus and entorhinal cortex could play complementary roles.

Taken together, we have shown that that activity patterns in the CA23DG region of the human hippocampus reflected an integrated representation of cognitive and coarse temporal contexts. This finding can help explain how we represent continuously unfolding episodes in a changing world. Outside of the laboratory, we are constantly multitasking between competing goals and responsibilities. The hippocampus, and, specifically CA23DG, may allow us to differentiate between experiences that are associated with different tasks while preserving the temporal flow between experiences.

References

Allen, T. A., Salz, D. M., McKenzie, S., & Fortin, N. J. (2016). Nonspatial Sequence Coding in CA1 Neurons. *The Journal of Neuroscience*, *36*(5), 1547–1563. https://doi.org/10.1523/JNEUROSCI.2874-15.2016

Aminoff, E., Gronau, N., & Bar, M. (2007). The parahippocampal cortex mediates spatial and nonspatial associations. *Cerebral Cortex (New York, N.Y.: 1991)*, *17*(7), 1493–1503. https://doi.org/10.1093/cercor/bhl078

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Baldassano, C., Beck, D. M., & Fei-Fei, L. (2013). Differential connectivity within the Parahippocampal Place Area. *NeuroImage*, *75*, 228–237. https://doi.org/10.1016/j.neuroimage.2013.02.073

Baldassano, C., Esteva, A., Fei-Fei, L., & Beck, D. M. (2016). Two Distinct Scene-Processing Networks Connecting Vision and Memory. *ENeuro*, *3*(5), ENEURO.0178-16.2016. https://doi.org/10.1523/ENEURO.0178-16.2016

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *10.18637/Jss.V067.I01*, 1–48.

Bellmund, J. L., Deuker, L., & Doeller, C. F. (2019). Mapping sequence structure in the human lateral entorhinal cortex. *ELife*, *8*, e45333. https://doi.org/10.7554/eLife.45333

Buzsáki, G., & Llinás, R. (2017). Space and time in the brain. *Science (New York, N.Y.)*, *358*(6362), 482–485. https://doi.org/10.1126/science.aan8869

Cai, D. J., Aharoni, D., Shuman, T., Shobe, J., Biane, J., Song, W., … Silva, A. J. (2016). A shared neural ensemble links distinct contextual memories encoded close in time. *Nature*, *534*(7605), 115–118. https://doi.org/10.1038/nature17955

Chanales, A. J. H., Oza, A., Favila, S. E., & Kuhl, B. A. (2017). Overlap among Spatial Memories Triggers Repulsion of Hippocampal Representations. *Current Biology: CB*, *27*(15), 2307-2317.e5. https://doi.org/10.1016/j.cub.2017.06.057

Clark, H. H. (1973). The language-as-fixed-effect fallacy: A critique of language statistics in psychological research. *Journal of Verbal Learning and Verbal Behavior*, *12*(4), 335–359. https://doi.org/10.1016/S0022-5371(73)80014-3

Clewett, D., & Davachi, L. (2017). The ebb and flow of experience determines the temporal structure of memory. *Current Opinion in Behavioral Sciences*, *17*, 186–193. https://doi.org/10.1016/j.cobeha.2017.08.013

Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, *16*(6), 693–700. https://doi.org/10.1016/j.conb.2006.10.012

Davachi, L., & DuBrow, S. (2015). How the hippocampus preserves order: the role of prediction and context. *Trends in Cognitive Sciences*, *19*(2), 92–99. https://doi.org/10.1016/j.tics.2014.12.004

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends in Cognitive Sciences*, *11*(9), 379–386. https://doi.org/10.1016/j.tics.2007.08.001

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2012). Adaptation to cognitive context and item information in the medial temporal lobes. *Neuropsychologia*, *50*(13), 3062–3069. https://doi.org/10.1016/j.neuropsychologia.2012.07.035

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2013). Parahippocampal cortex activation during context reinstatement predicts item recollection. *Journal of Experimental Psychology. General*, *142*(4), 1287–1297. https://doi.org/10.1037/a0034029

Dimsdale-Zucker, H. R., & Ranganath, C. (2018). Representational Similarity Analyses: A Practical Guide for Functional MRI Applications. In D. Manahan-Vaughan (Ed.), *Handbook of in Vivo Neural Plasticity Techniques*. Elsevier.

Dimsdale-Zucker, H. R., Ritchey, M., Ekstrom, A. D., Yonelinas, A. P., & Ranganath, C. (2018). CA1 and CA3 differentially support spontaneous retrieval of episodic contexts within human hippocampal subfields. *Nature Communications*, *9*(1), 294. https://doi.org/10.1038/s41467-017-02752-1

Dixon, P. (2008). Models of accuracy in repeated-measures designs. *Journal of Memory and Language*, *59*(4), 447–456. https://doi.org/10.1016/j.jml.2007.11.004

DuBrow, S., Rouhani, N., Niv, Y., & Norman, K. A. (2017). Does mental context drift or shift? *Current Opinion in Behavioral Sciences*, *17*(Supplement C), 141–146. https://doi.org/10.1016/j.cobeha.2017.08.003

Eichenbaum, H. (2017). On the Integration of Space, Time, and Memory. *Neuron*, *95*(5), 1007–1018. https://doi.org/10.1016/j.neuron.2017.06.036

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152. https://doi.org/10.1146/annurev.neuro.30.051606.094328

El-Kalliny, M. M., Wittig, J. H., Sheehan, T. C., Sreekumar, V., Inati, S. K., & Zaghloul, K. A. (2019). Changing temporal context in human temporal lobe promotes memory of distinct episodes. *Nature Communications*, *10*(1), 203. https://doi.org/10.1038/s41467-018-08189-4

Estes, W. K. (1955). Statistical theory of distributional phenomena in learning. *Psychological Review*, *62*(5), 369–377. https://doi.org/10.1037/h0046888

Frankó, E., Insausti, A. M., Artacho-Pérula, E., Insausti, R., & Chavoix, C. (2014). Identification of the human medial temporal lobe regions on magnetic resonance images: Human Medial Temporal Lobe Landmarks. *Human Brain Mapping*, *35*(1), 248–256. https://doi.org/10.1002/hbm.22170

Friedman, W. J. (1993). Memory for the time of past events. *Psychological Bulletin*, *113*(1), 44–66. https://doi.org/10.1037/0033-2909.113.1.44

Horner, A. J., Bisby, J. A., Bush, D., Lin, W.-J., & Burgess, N. (2015). Evidence for holistic episodic recollection via hippocampal pattern completion. *Nature Communications*, *6*, 7462. https://doi.org/10.1038/ncomms8462

Howard, M. W., & Kahana, M. J. (2002). A Distributed Representation of Temporal Context. *Journal of Mathematical Psychology*, *46*(3), 269–299. https://doi.org/10.1006/jmps.2001.1388

Hsieh, L.-T., Gruber, M. J., Jenkins, L. J., & Ranganath, C. (2014). Hippocampal activity patterns carry information about objects in temporal context. *Neuron*, *81*(5), 1165–1178. https://doi.org/10.1016/j.neuron.2014.01.015

Hunt, R. R. (1995). The subtlety of distinctiveness: What von Restorff really did. *Psychonomic Bulletin & Review*, *2*(1), 105–112. https://doi.org/10.3758/BF03214414

Jaeger, T. F. (2008). Categorical Data Analysis: Away from ANOVAs (transformation or not) and towards Logit Mixed Models. *Journal of Memory and Language*, *59*(4), 434–446. https://doi.org/10.1016/j.jml.2007.11.007

Jenkins, L. J., & Ranganath, C. (2010). Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *30*(46), 15558–15565. https://doi.org/10.1523/JNEUROSCI.1337-10.2010

Jenkins, L. J., & Ranganath, C. (2016). Distinct neural mechanisms for remembering when an event occurred. *Hippocampus*, *26*(5), 554–559. https://doi.org/10.1002/hipo.22571

Kahana, M. J. (1996). Associative retrieval processes in free recall. *Memory & Cognition*, *24*(1), 103–109. https://doi.org/10.3758/BF03197276

Kesner, R. P., & Rolls, E. T. (2015). A computational theory of hippocampal function, and tests of the theory: new developments. *Neuroscience and Biobehavioral Reviews*, *48*, 92–147. https://doi.org/10.1016/j.neubiorev.2014.11.009

Kraus, B. J., Brandon, M. P., Robinson, R. J., Connerney, M. A., Hasselmo, M. E., & Eichenbaum, H. (2015). During Running in Place, Grid Cells Integrate Elapsed Time and Distance Run. *Neuron*, *88*(3), 578–589. https://doi.org/10.1016/j.neuron.2015.09.031

Kraus, B. J., Robinson, R. J., White, J. A., Eichenbaum, H., & Hasselmo, M. E. (2013). Hippocampal “time cells”: time versus path integration. *Neuron*, *78*(6), 1090–1101. https://doi.org/10.1016/j.neuron.2013.04.015

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational Similarity Analysis - Connecting the Branches of Systems Neuroscience. *Frontiers in Systems Neuroscience*, *2*. https://doi.org/10.3389/neuro.06.004.2008

Levy, W. B. (1996). A sequence predicting CA3 is a flexible associator that learns and uses context to solve hippocampal-like tasks. *Hippocampus*, *6*(6), 579–590. https://doi.org/10.1002/(SICI)1098-1063(1996)6:6<579::AID-HIPO3>3.0.CO;2-C

Libby, L. A., Reagh, Z. M., Bouffard, N. R., Ragland, J. D., & Ranganath, C. (2018). The Hippocampus Generalizes across Memories that Share Item and Context Information. *Journal of Cognitive Neuroscience*, 1–12. https://doi.org/10.1162/jocn_a_01345

Lisman, J. E. (1999). Relating Hippocampal Circuitry to Function. *Neuron*, *22*(2), 233–242. https://doi.org/10.1016/S0896-6273(00)81085-5

Lisman, J. E., & Jensen, O. (2013). The θ-γ neural code. *Neuron*, *77*(6), 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007

Lohnas, L. J., Polyn, S. M., & Kahana, M. J. (2015). Expanding the scope of memory search: Modeling intralist and interlist effects in free recall. *Psychological Review*, *122*(2), 337–363. https://doi.org/10.1037/a0039036

MacDonald, C. J., Lepage, K. Q., Eden, U. T., & Eichenbaum, H. (2011). Hippocampal “time cells” bridge the gap in memory for discontiguous events. *Neuron*, *71*(4), 737–749. https://doi.org/10.1016/j.neuron.2011.07.012

Mankin, E. A., Diehl, G. W., Sparks, F. T., Leutgeb, S., & Leutgeb, J. K. (2015). Hippocampal CA2 activity patterns change over time to a larger extent than between spatial contexts. *Neuron*, *85*(1), 190–201. https://doi.org/10.1016/j.neuron.2014.12.001

Mankin, E. A., Sparks, F. T., Slayyeh, B., Sutherland, R. J., Leutgeb, S., & Leutgeb, J. K. (2012). Neuronal code for extended time in the hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(47), 19462–19467. https://doi.org/10.1073/pnas.1214107109

Manning, J. R., Polyn, S. M., Baltuch, G. H., Litt, B., & Kahana, M. J. (2011). Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. *Proceedings of the National Academy of Sciences*, *108*(31), 12893–12897. https://doi.org/10.1073/pnas.1015174108

Mazaika, P., Whitfield-Gabrieli, S., & Cooper, J. C. (2005). *Detection and repair of transient artifacts in fMRI data*. Poster presented at the Human Brain Mapping.

Montchal, M. E., Reagh, Z. M., & Yassa, M. A. (2019). Precise temporal memories are supported by the lateral entorhinal cortex in humans. *Nature Neuroscience*, *22*(2), 284. https://doi.org/10.1038/s41593-018-0303-1

Mumford, J. A., & Poldrack, R. A. (2007). Modeling group fMRI data. *Social Cognitive and Affective Neuroscience*, *2*(3), 251–257. https://doi.org/10.1093/scan/nsm019

Mumford, J. A., Turner, B. O., Ashby, F. G., & Poldrack, R. A. (2012). Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. *NeuroImage*, *59*(3), 2636–2643. https://doi.org/10.1016/j.neuroimage.2011.08.076

Naya, Y., Chen, H., Yang, C., & Suzuki, W. A. (2017). Contributions of primate prefrontal cortex and medial temporal lobe to temporal-order memory. *Proceedings of the National Academy of Sciences*, *114*(51), 13555–13560. https://doi.org/10.1073/pnas.1712711114

Norman, K. A., Detre, G., & Polyn, S. M. (2008). Computational models of episodic memory. In *The Cambridge handbook of computational psychology* (pp. 189–225). https://doi.org/10.1017/CBO9780511816772.011

Palombo, D. J., Di Lascio, J. M., Howard, M. W., & Verfaellie, M. (2019). Medial Temporal Lobe Amnesia Is Associated with a Deficit in Recovering Temporal Context. *Journal of Cognitive Neuroscience*, *31*(2), 236–248. https://doi.org/10.1162/jocn_a_01344

Pastalkova, E., Itskov, V., Amarasingham, A., & Buzsáki, G. (2008). Internally generated cell assembly sequences in the rat hippocampus. *Science (New York, N.Y.)*, *321*(5894), 1322–1327. https://doi.org/10.1126/science.1159775

Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. *Psychological Review*, *116*(1), 129–156. https://doi.org/10.1037/a0014420

Power, J. D., Barnes, K. A., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2012). Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *NeuroImage*, *59*(3), 2142–2154. https://doi.org/10.1016/j.neuroimage.2011.10.018

Ranganath, C. (2019). Time, memory, and the legacy of Howard Eichenbaum. *Hippocampus*, *29*(3), 146–161. https://doi.org/10.1002/hipo.23007

Reiff, R., & Scheerer, M. (1959). *Memory and hypnotic age regression; developmental aspects of cognitive function explored through hypnosis.* New York: International Universities Press.

Ritvo, V. J. H., Turk-Browne, N. B., & Norman, K. A. (2019). Nonmonotonic Plasticity: How Memory Retrieval Drives Learning. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2019.06.007

Rodriguez, P., & Levy, W. B. (2001). A model of hippocampal activity in trace conditioning: Where's the trace? *Behavioral Neuroscience*, *115*(6), 1224–1238. https://doi.org/10.1037/0735-7044.115.6.1224

Rubin, A., Geva, N., Sheintuch, L., & Ziv, Y. (2015). Hippocampal ensemble dynamics timestamp events in long-term memory. *ELife*, *4*. https://doi.org/10.7554/eLife.12247

Salz, D. M., Tiganj, Z., Khasnabish, S., Kohley, A., Sheehan, D., Howard, M. W., & Eichenbaum, H. (2016). Time Cells in Hippocampal Area CA3. *The Journal of Neuroscience*, *36*(28), 7476–7484. https://doi.org/10.1523/JNEUROSCI.0087-16.2016

Schlichting, M. L., & Preston, A. R. (2015). Memory integration: neural mechanisms and implications for behavior. *Current Opinion in Behavioral Sciences*, *1*, 1–8. https://doi.org/10.1016/j.cobeha.2014.07.005

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, *20*(1), 11–21.

Sederberg, P. B., Howard, M. W., & Kahana, M. J. (2008). A context-based theory of recency and contiguity in free recall. *Psychological Review*, *115*(4), 893–912. https://doi.org/10.1037/a0013396

Sederberg, P. B., Miller, J. F., Howard, M. W., & Kahana, M. J. (2010). The temporal contiguity effect predicts episodic memory performance. *Memory & Cognition*, *38*(6), 689–699. https://doi.org/10.3758/MC.38.6.689

Singmann, H., & Kellen, D. (in press). An introduction to mixed models for experimental psychology. In D. H. Spieler & E. Schumacher, *New Methods in Neuroscience and Cognitive Psychology*. Psychology Press.

Sugar, J., & Moser, M.-B. (2019). Episodic memory: Neuronal codes for what, where, and when. *Hippocampus*, *0*(0). https://doi.org/10.1002/hipo.23132

Tubridy, S., & Davachi, L. (2011). Medial temporal lobe contributions to episodic sequence encoding. *Cerebral Cortex (New York, N.Y.: 1991)*, *21*(2), 272–280. https://doi.org/10.1093/cercor/bhq092

Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Paesschen, W. V., & Mishkin, M. (1997). Differential Effects of Early Hippocampal Pathology on Episodic and Semantic Memory. *Science*, *277*(5324), 376–380. https://doi.org/10.1126/science.277.5324.376

Wallenstein, G. V., Eichenbaum, H., & Hasselmo, M. E. (1998). The hippocampus as an associator of discontiguous events. *Trends in Neurosciences*, *21*(8), 317–323.

Wang, F., & Diana, R. A. (2017). Neural correlates of temporal context retrieval for abstract scrambled phrases: Reducing narrative and familiarity-based strategies. *Brain Research*, *1655*, 128–137. https://doi.org/10.1016/j.brainres.2016.11.017

Wang, Y., Romani, S., Lustig, B., Leonardo, A., & Pastalkova, E. (2015). Theta sequences are essential for internally generated hippocampal firing fields. *Nature Neuroscience*, *18*(2), 282–288. https://doi.org/10.1038/nn.3904

Yassa, M. A., & Stark, C. E. L. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, *34*(10), 515–525. https://doi.org/10.1016/j.tins.2011.06.006

Yushkevich, P. A., Amaral, R. S. C., Augustinack, J. C., Bender, A. R., Bernstein, J. D., Boccardi, M., … Hippocampal Subfields Group (HSG). (2015). Quantitative comparison of 21 protocols for labeling hippocampal subfields and parahippocampal subregions in in vivo MRI: towards a harmonized segmentation protocol. *NeuroImage*, *111*, 526–541. https://doi.org/10.1016/j.neuroimage.2015.01.004

Yushkevich, P. A., Wang, H., Pluta, J., Das, S. R., Craige, C., Avants, B. B., … Mueller, S. (2010). Nearly Automatic Segmentation of Hippocampal Subfields in In Vivo Focal T2-Weighted MRI. *NeuroImage*, *53*(4), 1208–1224. https://doi.org/10.1016/j.neuroimage.2010.06.040

Zacks, J. M., & Swallow, K. M. (2007). EVENT SEGMENTATION. *Current Directions in Psychological Science*, *16*(2), 80–84. https://doi.org/10.1111/j.1467-8721.2007.00480.x

Ziv, Y., Burns, L. D., Cocker, E. D., Hamel, E. O., Ghosh, K. K., Kitch, L. J., … Schnitzer, M. J. (2013). Long-term dynamics of CA1 hippocampal place codes. *Nature Neuroscience*, *16*(3), 264–266. https://doi.org/10.1038/nn.3329