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### Authors

Dimsdale-Zucker, Halle R  
Montchal, Maria E  
Reagh, Zachariah M  
[et al.](#)

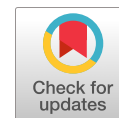
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# Representations of Complex Contexts: A Role for Hippocampus

Halle R. Dimsdale-Zucker<sup>1</sup>, Maria E. Montchal<sup>2</sup>, Zachariah M. Reagh<sup>3</sup>,  
Shao-Fang Wang<sup>4</sup>, Laura A. Libby<sup>5</sup>, and Charan Ranganath<sup>5</sup>

## Abstract

■ The hippocampus plays a critical role in supporting episodic memory, in large part by binding together experiences and items with surrounding contextual information. At present, however, little is known about the roles of different hippocampal subfields in supporting this item–context binding. To address this question, we constructed a task in which items were affiliated with differing types of context—cognitive associations that vary at the local, item level and membership in temporally organized lists that linked items together at a global level. Participants made item recognition judgments while undergoing high-resolution fMRI. We performed 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 associated with these items. We found no evidence to suggest reinstatement of information about temporal context at the level of list membership, but exploratory analyses revealed representations of temporal context at a coarse level in conjunction with representations of cognitive contexts. Results are consistent with characterizations of CA23DG as a critical site for binding together items and contexts in the service of memory retrieval. ■

## INTRODUCTION

Converging evidence suggests that the hippocampus (HC) plays a critical role in memory for events and their episodic details (Eichenbaum, Yonelinas, & Ranganath, 2007; Vargha-Khadem et al., 1997; Scoville & Milner, 1957). The HC is a circuit of interconnected subfields with different anatomical (Kesner & Rolls, 2015; Burwell, 2000; Lavenex & Amaral, 2000; Witter, Wouterlood, Naber, & Van Haefen, 2000; Amaral & Witter, 1989) and computational (Schapiro, Turk-Browne, Botvinick, & Norman, 2017; Norman & O'Reilly, 2003; Treves & Rolls, 1994; Marr, 1971) properties. Evidence from animal models has suggested that different hippocampal subfields uniquely contribute to memory through different computational specializations (e.g., pattern separation and completion; for reviews, see (Liu, Gould, Coulson, Ward, & Howard, 2015; Yassa & Stark, 2011) that enable one to encode the spatial and task variables that create a context for episodic memories (Kesner & Rolls, 2015; Mankin, Diehl, Sparks, Leutgeb, & Leutgeb, 2015; Norman & O'Reilly, 2003; Wallenstein, Eichenbaum, & Hasselmo, 1998; Lisman, 1999; Levy, 1996). This is particularly true when task demands highlight the need to bind together item-in-context representations, such as learning where

to search for a reward given an animal's current location (McKenzie et al., 2014).

Evidence in humans generally corroborates the research in animal models, suggesting that, as a whole, the HC supports episodic memory by binding together information about items and the context in which they were encountered (Zheng, Liu, Nishiyama, Ranganath, & O'Reilly, 2022; Ranganath, 2010; Eichenbaum et al., 2007; Davachi, 2006; Eacott & Gaffan, 2005; O'Keefe & Nadel, 1978). At present, however, there is little known about the roles of different hippocampal subfields in item–context binding. Many studies have used high-resolution fMRI to examine item recognition (Suthana et al., 2015; Reagh, Watabe, Ly, Murray, & Yassa, 2014; LaRocque et al., 2013; Chen, Olsen, Preston, Glover, & Wagner, 2011; Lacy, Yassa, Stark, Muftuler, & Stark, 2011; Yassa et al., 2011; Carr, Rissman, & Wagner, 2010; Viskontas, Carr, Engel, & Knowlton, 2009; Bakker, Kirwan, Miller, & Stark, 2008; Zeineh, Engel, Thompson, & Bookheimer, 2003) or representations of spatial contexts (Zheng, Gao, McAvan, Isham, & Ekstrom, 2021; Dimsdale-Zucker, Ritchey, Ekstrom, Yonelinas, & Ranganath, 2018; Chanales, Oza, Favila, & Kuhl, 2017; Stokes, Kyle, & Ekstrom, 2015; Brown, Hasselmo, & Stern, 2014; Copara et al., 2014; Suthana, Ekstrom, Moshirvaziri, Knowlton, & Bookheimer, 2011).

Cognitive theories of episodic memory have conceptualized context in at least two ways. One view emphasizes context as a variable that changes over time (Howard

<sup>1</sup>Columbia University, <sup>2</sup>University of California, Irvine, <sup>3</sup>Washington University in St. Louis - Danforth Campus, <sup>4</sup>Stanford University, <sup>5</sup>University of California, Davis

& Kahana, 2002; Estes, 1955) because of ongoing fluctuations in the participant's environment and cognitive state (e.g., the frank passage of time, changes in stimuli, shifting mental and physical states). Some high-resolution imaging studies have revealed evidence suggesting that the HC can represent information about temporal context associated with particular items or associations between items based on temporal contiguity (Dimsdale-Zucker et al., 2018; Deuker, Bellmund, Schröder, & Doeller, 2016; Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015; Copara et al., 2014; Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013).

Another view is that episodic memories are associated with “cognitive contexts” (Diana, Yonelinas, & Ranganath, 2012, 2013)—relatively discrete cognitive states that are tied to attentional priorities, task demands, or currently relevant goals (Antony et al., 2021; Aly & Turk-Browne, 2016a, 2016b; Diana et al., 2012; Diana, Yonelinas, & Ranganath, 2008). These views are not mutually exclusive, and some models suggest that context in episodic memory may be represented through a combination of temporal context and cognitive representations of task states (Lohnas, Polyn, & Kahana, 2015; Polyn, Norman, & Kahana, 2009).

To understand whether shifting cognitive contexts affiliated with encoding items could drive differences in representations across hippocampal subfields, we constructed a task in which we experimentally manipulated the cognitive context affiliated with studied items by varying the encoding question associated with an item (Ritchev, Montchal, Yonelinas, & Ranganath, 2015; Diana et al., 2008, 2012, 2013; Johnson, McDuff, Rugg, & Norman, 2009; McDuff, Frankel, & Norman, 2009; Polyn et al., 2009; Dzulkipli & Wilding, 2005; Ranganath et al., 2004; Davachi, Mitchell, & Wagner, 2003; Nolde, Johnson, & D'Esposito, 1998; Johnson, Kounios, & Nolde, 1997). To manipulate temporal context, we organized items into repeated lists, such that items in the same list would be expected to have stronger intralist temporal associations than items in different lists. This allowed us to test the extent to which hippocampal subfields represent information about cognitive (i.e., encoding question) and temporal (i.e., list membership) contextual associations. We then scanned participants while they recollected these objects and used voxel pattern similarity (PS) analyses (Dimsdale-Zucker & Ranganath, 2018; Kriegeskorte, Mur, & Bandettini, 2008) to examine patterns of activity in hippocampal subfields that reflected spontaneous retrieval of information from the study phase about the temporal and cognitive context associated with each item.

## METHODS

### Participants

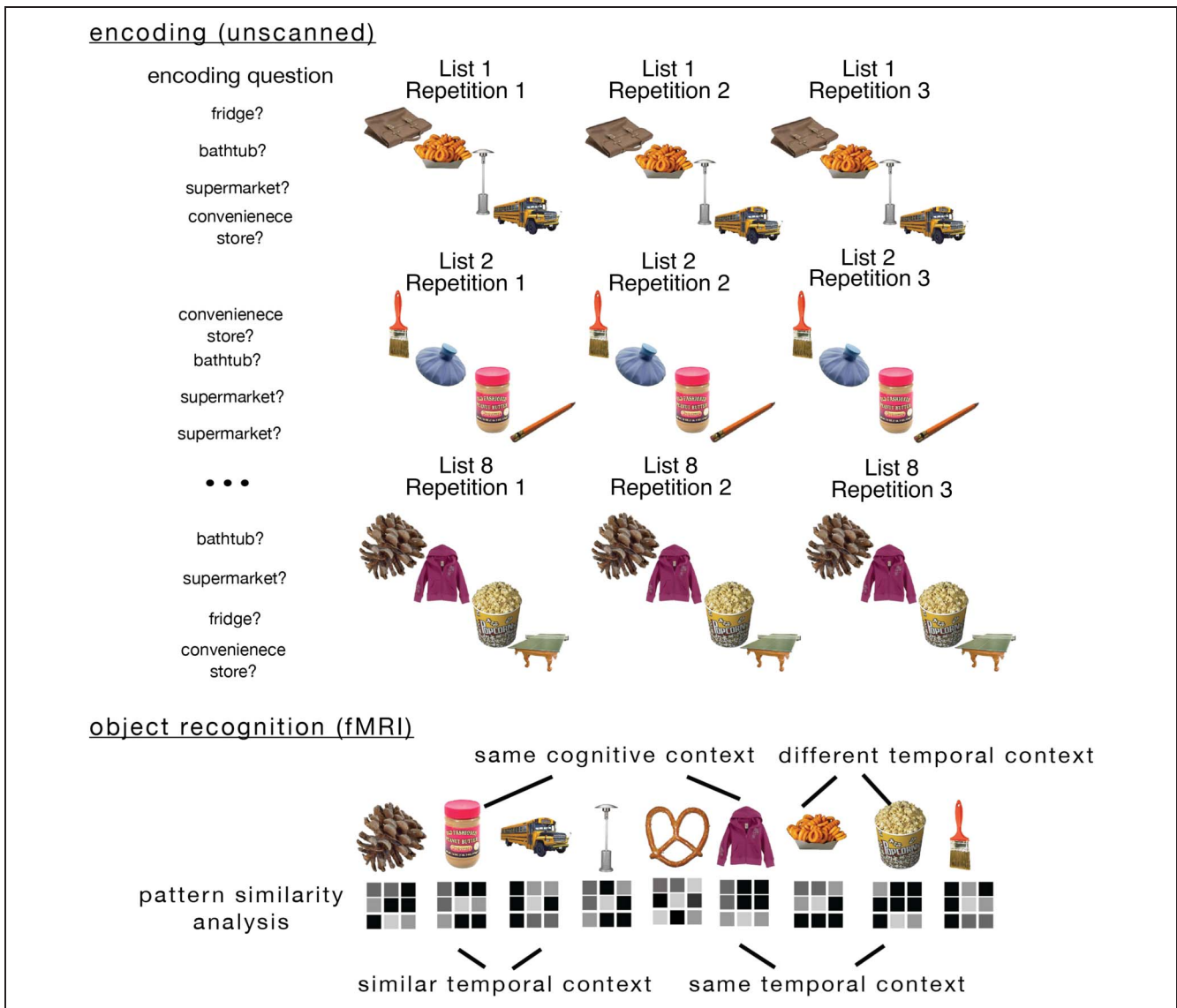
Thirty-two participants were recruited from the community and were compensated \$50 for their time. This study was approved by the institutional review board at the

University of California, Davis. Four participants were excluded because of missing behavioral data, two participants were excluded for excessive motion that prevented tracing of hippocampal subfields, one participant was excluded because of 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 ( $M_{\text{age}} = 22.85$  years,  $SD = 3.06$  years,  $N_{\text{female}} = 13$ ). One of these 24 participants was excluded from behavioral cognitive and temporal context analyses because of partially missing data; because 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; [cvcl.mit.edu/mm/uniqueObjects.html](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 among items in a list (Palombo, Di Lascio, Howard, & Verfaellie, 2019), each list was presented three times in a mini-block before participants saw items from the next list (e.g., 1, 1, 1, 2, 2, 2 ... 8, 8, 8). A label with a list number (e.g., “List 1”) appeared at the beginning of each list before seeing any objects. 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 sec (timing and presentation parameters were controlled via Presentation [Neurobehavioral Systems, Inc., [www.neurobs.com](http://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 (cognitive) and temporal context information was incidental. Grouping items into lists was meant to induce a shared context representation for items in the same list. We reasoned that repetition of lists during the study phase would enhance contextual relationships between items in the same list. A similar temporal grouping strategy has been used previously to encourage



**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 among the items. Objects appeared in the same order and with the same question (cognitive context) across all repetitions. High-resolution fMRI was used to examine hippocampal activity patterns during a recognition memory test for these objects, allowing us to examine activity PS 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).

connections between items in this fashion (Palombo et al., 2019). In contrast to the interitem links facilitated by list membership, previous work has shown that interspersing questions throughout the encoding phase can result in fast, shifting variations in context that are aligned to changes in cognitive state (Polyn et al., 2009). Thus, to target cognitive context, each item was affiliated with one of four orienting questions (for a similar manipulation of cognitive context, see Diana et al., 2012). We note that because we did not collect fMRI data during the encoding phase, we are limited to looking at reactivated representations of cognitive and temporal contexts at the time of retrieval.

### 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 sec with a jittered intertrial interval ranging from 2 to 15 sec (mean intertrial interval jitter = 6 sec). Objects were divided into six runs (60 trials per run). Object order within a run was pseudorandomized such that objects with the same encoding question always had at least one intervening object (e.g., fridge, convenience store, bathtub, fridge, supermarket, fridge) to help minimize encoding context reinstatement biases on PS results (see Multivariate Results section below).

Proximity of objects from encoding mini-blocks (1–8) was not considered in the pseudorandomization.

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 nontemporal details* (e.g., the encoding question, something about the object itself, or an association they made with the object), and 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 laboratory 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 presented centrally on the screen, and a number line displaying the numeric options 1–8 appeared below. Participants were told to use the numbers at the top of the keypad to make their response. 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 Preprocessing

Scans were acquired on a Siemens Skyra 3-T 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 pulse sequence image (1-mm isotropic voxels) and a high-resolution T2-weighted image (repetition time = 4200 msec, TE = 93 msec, field of view = 200 mm<sup>2</sup>, flip angle = 139°, bandwidth = 199 Hz/pixel, voxel size = 0.4 × 0.4 × 1.9 mm, 58 coronal slices acquired perpendicular

to the long axis of the HC). High-resolution functional (T2\*) images were acquired using a multiband gradient EPI sequence (repetition time = 2010 msec, TE = 25 msec, field of view = 216 mm, image matrix = 144 × 152, flip angle = 79°, bandwidth = 1240 Hz/pixel, partial phase Fourier = 6/8, parallel imaging = GRAPPA acceleration factor 2 with 72 reference lines, multiband factor = 2, 52 oblique axial slices acquired parallel to the long axis of the HC slices, voxel size = 1.5 mm isotropic).

SPM8 ([www.fil.ion.ucl.ac.uk/spm/](http://www.fil.ion.ucl.ac.uk/spm/)) was used for image preprocessing. Functional EPI images were realigned to the first image and resliced. No slice timing correction was performed because of the acquisition of multiple simultaneous slices with the multiband sequence (capabilities to handle multiband timing do not exist in SPM8). Coregistration between the native-space ROIs defined in T2 space and the functional images was done with SPM's Coregister: Estimate and Reslice procedure. This procedure uses a linear normalized mutual information cost function between a reference (mean functional) image and a source (T2) image to compute and apply a voxel-by-voxel affine transformation matrix. This transformation matrix was then applied to the subfield ROIs that had been defined in T2 space (see ROI segmentation) to bring them into register with the functional images. The T1 image was coregistered to the mean EPI. Then, nonlinear spatial normalization parameters were derived by segmenting the coregistered T1 image. Quality assurance included identifying suspect time points via custom code ([github.com/memobc/memolab-fmri-qa](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, nine had runs excluded based on these thresholds (mean number of removed runs = 0.92, *SD* = 1.38; ranging from 0 to 4 runs).

### PS 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, Turner, Ashby, and Poldrack (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 quality assurance 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 (TSNRs) in a region to be above 20 (approximately 2 *SDs* below the mean global TSNR of 50.4). This required the removal of entorhinal cortex and its subregions (mean TSNR ranged between 10 and 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). Trials were sorted on the basis of encoding context (cognitive, temporal); however, source memory for these contexts was not taken into consideration. Correlation values were *z*-transformed before 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 (Singmann & Kellen, 2019; Baayen, Davidson, & Bates, 2008; Dixon, 2008; Jaeger, 2008; Mumford & Poldrack, 2007; Clark, 1973), we implemented a mixed-modeling approach to evaluate statistical significance with the lme4 package in R (Bates, Mächler, Bolker, & Walker, 2015); for a similar approach, see Dimsdale-Zucker et al. (2018). We used an alpha of  $p < .05$  and performed permutation testing for all of the PS results

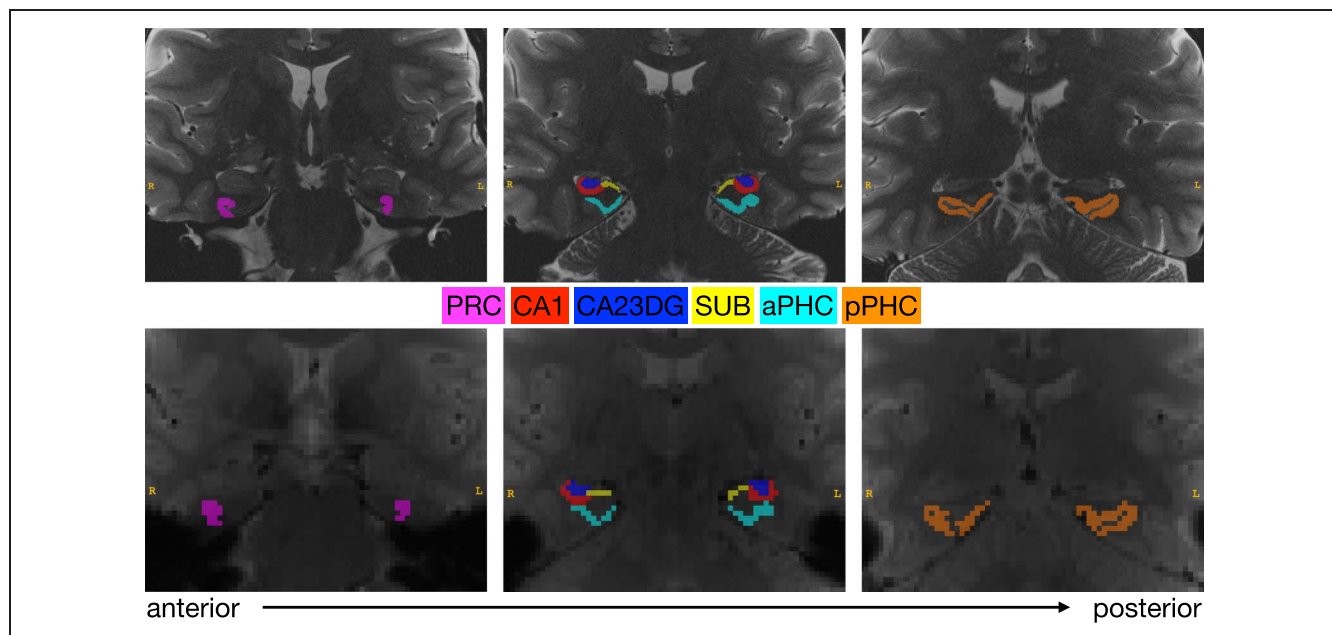
reported in the article. Only between-run correlations were used to maximize the number of possible trial pairs without mixing within- and between-run correlations. Trial pairs of interest were extracted from these trial-by-trial correlation matrices.

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

## ROI Definition

Hippocampal subfields were defined following the procedure reported in Dimsdale-Zucker et al. (2018; see Figure 2). In short, the automated segmentation of hippocampal subfields 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 (Baldassano, Esteva, Fei-Fei, & Beck, 2016; Baldassano, Beck, & Fei-Fei, 2013; Aminoff, Gronau, & Bar, 2007), we subdivided parahippocampal cortex one slice posterior to the wing of the ambient cistern (Frankó, Insausti, Artacho-Pérula, Insausti, & Chavoix, 2014).

Because ROI definition and selection for comparisons was a priori, we performed independent analyses on each ROI. As Poldrack and Mumford (2009) suggest, taking



**Figure 2.** (Top) Segmentations of hippocampal subfields (cornu ammonis [CA] 1; a combined CA2, CA3, and dentate gyrus [CA23DG] region; and subiculum [SUB]) as well as cortical medial temporal lobe regions (perirhinal cortex [PRC], anterior parahippocampal cortex [aPHC], and posterior parahippocampal cortex [pPHC]). Segmentations are depicted for a representative participant in the coronal plane of a T2 image. Slices move from anterior to posterior from left to right. (Bottom) Segmentations following reslicing to functional (EPI) space displayed on a mean functional image from the same individual.

this approach does not necessitate multiple-comparison correction. Furthermore, we were primarily interested in characterizing the content of reactivated encoding contextual information within each subfield rather than making direct comparisons between the similarities or differences in what types of information each subfield primarily represented.

## 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 Methods). PS analyses were restricted to correctly remembered items. On average, this yielded 200 trials ( $SD = 51.9$ ; minimum trials = 71, maximum trials = 282) from which we constructed all possible trial pairs and then compared activity patterns (see fMRI Results section).

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 (Lists 1–8) was poor (mean hit rate = 0.18,  $SD = 0.03$ ). Memory for task context and exact temporal context for items that were correctly remembered as studied were not significantly correlated with one another ( $r = -0.31$ ,  $p = .16$ ).

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. Visual inspection of temporal source errors indicated that participants were more likely to incorrectly identify an item as coming from a list near in time to when it was actually studied as compared to lists further away (e.g., if an item was actually studied in List 3, participants would have been more likely to incorrectly say it had been in List 2 or 4 than lists further away in time; see Appendix A).

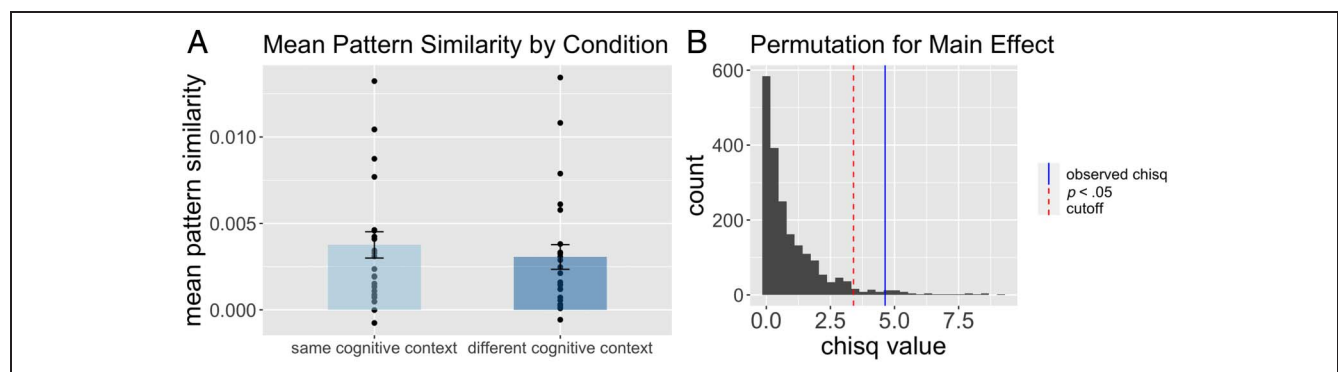
We therefore performed an exploratory analysis in which we rescored each trial according to whether the participant could accurately determine whether it was presented in the “similar” (first half [Lists 1–4] or the second half [Lists 5–8]) versus “different” (across halves, i.e., List 1/List 5, List 1/List 6) temporal context of the encoding phase. On this metric, memory for similar temporal context (mean accuracy for list half = 0.59,  $SD = 0.04$ ) was reliably greater than chance of 0.5,  $t(22) = 8.74$ ,  $p < .001$ . 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

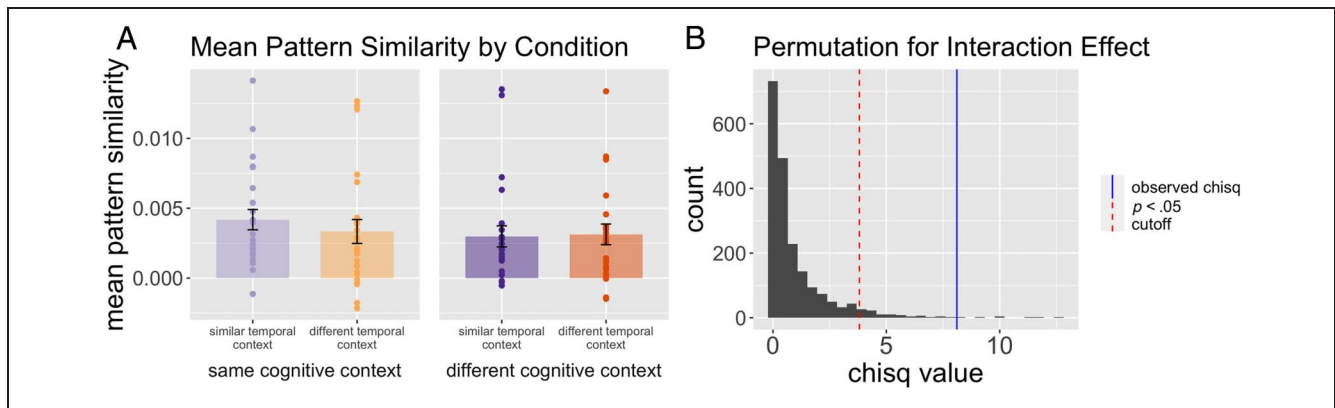
We next tested whether activity patterns in the hippocampal subfields (CA1, CA23DG, subiculum<sup>1</sup>) during memory retrieval carried information about the context in which the item was previously encountered. Specifically, we examined voxel PS during retrieval as a function of whether pairs of trials shared a temporal (same list vs. different list [“same” 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 showed significant PS differences between retrieval of items from the same list as compared with items from different lists (all  $\chi^2 < 0.5$ , all  $ps > .40$ ; see Appendix C for statistics and Appendix B for visualization of PS values between lists).

We next considered whether hippocampal voxel patterns during recollection of studied items carried information about the cognitive context (encoding question) associated with the item during encoding. 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,  $\chi^2(1) = 4.63$ ,  $p^{\text{perm}1000} = 0.031$  (Figure 3).<sup>2</sup> No other



**Figure 3.** PS values in CA23DG during memory retrieval carry information about cognitive encoding contexts. (A) Mean PS scores, with scatter of individual subject observations for the combination of different encoding contexts. Mean PS values were greater for same as compared to different cognitive contexts. (B) Permuted chi-square values to determine significance of cognitive context main effect. Observed chi-square value is depicted in blue, and the significance threshold ( $p = .05$ ) is plotted in a dashed red line.  $\text{chisq} = \text{chi-square}$ .



**Figure 4.** PS values in CA23DG during memory retrieval carry information about similar temporal and cognitive encoding contexts. (A) Mean PS scores, with scatter of individual subject observations for the combination of different encoding contexts. (B) Permuted chi-square values to determine significance of Cognitive  $\times$  (Similar) Temporal interaction. Observed chi-square value is depicted in blue, and the significance threshold ( $p = .05$ ) is plotted in a dashed red line.

subfield showed significant effects of cognitive context (all  $\chi^2 < 0.3$ , all  $ps > .50$ ; see Appendix D) nor the combination of same versus different temporal and cognitive contexts (all  $\chi^2 < 0.80$ , all  $ps > .30$ ; see Appendix D) on PS.<sup>3</sup>

We next performed a series of exploratory analyses to consider whether PS might depend on whether items shared a “similar” temporal context at encoding (same vs. different half of the encoding phase). The choice of list half was informed by the fact that participants were behaviorally able to discriminate coarse temporal context reliably greater than chance; however, we present these analyses as exploratory because participants were not explicitly asked to make temporal source judgments at the granularity of list half. This analysis revealed no significant effects of similar temporal context alone (all  $\chi^2 < 2.5$ , all  $ps > .10$ ; see Appendix D).

We next considered whether hippocampal voxel patterns during recollection of studied items carried information about the cognitive context (encoding question) associated with the item during encoding when we defined temporal context as “similar.” Consistent with our previous analysis, in CA23DG, PS for pairs of items that were associated with the same cognitive context was higher than for pairs of items that were associated with different cognitive contexts,  $\chi^2(1) = 4.68$ ,  $p^{\text{perm}1000} = .031$ . This effect was qualified by a significant similar Temporal  $\times$  Cognitive Context interaction,  $\chi^2(1) = 8.11$ ,  $p^{\text{perm}1000} = .004$  (see Figure 4), such that the effect of cognitive context in CA23DG 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. No other subfield showed significant effects of cognitive context (all  $\chi^2 < 0.30$ , all  $ps > .80$ ; see Appendix D) nor the combination of similar versus different temporal and cognitive contexts (all  $\chi^2 < 3$ , all  $ps > .080$ ; see Appendix D) on PS.

## DISCUSSION

The goal of the present study was to test whether hippocampal subfields represent information about experimentally manipulated cognitive and temporal contexts (i.e., encoding task and list identity) during recollection of studied items. Results showed that cognitive context significantly influenced activity patterns in CA23DG. We saw no evidence for a precise representation of temporal (list) context, although exploratory analyses revealed that when using a coarse definition of temporal context (first vs. second half of the study phase), CA23DG carried information about the conjunction of cognitive and temporal contexts. This suggests that patterns of activity within CA23DG may support successful memory retrieval by enabling recollection of task-relevant cognitive states or goals.

### Cognitive Context Representation in CA23DG

The HC is a prime example of how form can influence function. Computational models (Marr, 1971; for a non-Hebbian instantiation, see Zheng et al., 2022) propose that the combination of sparse coding in DG and the dense recurrent collaterals that make up most of the inputs to CA3 (Amaral & Witter, 1989) enable the HC to retrieve or recover a memory trace given a noisy or incomplete retrieval cue (i.e., “pattern completion” [Yassa & Stark, 2011; O’Reilly & McClelland, 1994; Marr, 1971]). A second factor that is key to understanding hippocampal function is that CA3 and DG are critical sites for binding of information about items and contexts (Zheng et al., 2022; Knierim, Lee, & Hargreaves, 2006). Considerable evidence suggests that lateral and medial entorhinal cortex receives distinct cortical inputs carrying information about items and contexts, respectively, and this information is subsequently integrated via convergent inputs in DG and CA3 (Libby, Ekstrom, Ragland, & Ranganath, 2012; Eichenbaum



et al., 2007; Rolls & Kesner, 2006; Burwell, 2000; Amaral & Witter, 1989). On the basis of these characteristics, we would expect that the DG–CA3 circuit should play a crucial role in recollecting contextual information about previously encountered items.

Using a paradigm adapted from Diana et al. (2012, 2013), in which different objects were encoded with unique cognitive context questions, we demonstrated that activity patterns in CA2/3DG carried information about an item's cognitive context during retrieval. PS values were greater for items that had been affiliated with the same, as compared to different, cognitive tasks at encoding. This result is striking, given that participants were only shown items from the study phase, and they were not instructed to explicitly recall information about the study tasks. Our results therefore accord with the idea that CA2/3DG plays an important role in linking item and context information, such that encountering a familiar item can trigger the recovery of contextual information via pattern completion (see also Grande et al., 2019).

Our findings are relevant to the idea that, during conscious recollection, the HC reinstates representations of discrete cognitive contexts that encompass one's current attentional priorities, task set, and/or goals (Libby, Reagh, Bouffard, Ragland, & Ranganath, 2019; Aly & Turk-Browne, 2016a, 2016b; Ritchey et al., 2015; Diana et al., 2012; Johnson et al., 2009; Eichenbaum et al., 2007; Davachi, 2006; Ranganath et al., 2004; Davachi et al., 2003). For instance, Aly and colleagues (Aly & Turk-Browne, 2016a, 2016b) found that voxel patterns in hippocampal subfields carried information about attentional orientation during a memory encoding task ("attend to artistic features" vs. "attend to spatial layout"). Converging evidence in rodents also suggests that task-relevant contextual features were the most salient factor in describing hippocampal ensemble activity similarity (conceptually analogous to the PS metrics used in human fMRI; McKenzie et al., 2014). Our results build on this idea by highlighting CA2/3DG as a site where binding of cognitive contextual information occurs in the service of episodic memory retrieval.

An intriguing possibility that could be addressed in future work is whether representational patterns would change if cognitive contexts were designed to systematically relate to features of the items. In the present design, item/question pairing was uniquely randomized for each participant, and thus, this question cannot be explored here. However, prior work has suggested that the HC may play a particular role in representing an item's context (e.g., the type of associated judgment) whereas, when context is posed as a feature of the item (e.g., its color), that medial temporal cortical regions such as perirhinal cortex are engaged (Staresina & Davachi, 2008; although see Diana et al., 2008, for some suggestions that perirhinal involvement in item/context unitization may be limited to familiarity). Thus, if cognitive context questions were selected to represent features of the items, it seems that

there would be competing hypotheses about whether the HC would still treat this information as an item's context or whether medial temporal lobe cortical regions would additionally be recruited.

### Contributions of Temporal Context

According to Tulving's definition (Tulving, 1972, 1983, 1984), episodic memories are organized by temporal context. Temporal context has been formally operationalized in terms of random fluctuations in cognitive states over time (Estes, 1955) and a time-weighted average of recently processed items and experiences (Norman, Detre, & Polyn, 2008; Sederberg, Howard, & Kahana, 2008; Howard & Kahana, 2002). These models would predict that activity patterns during memory retrieval should reflect information about the temporal context associated with each study item (e.g., Deuker et al., 2016; Jenkins & Ranganath, 2016; Nielson et al., 2015; Manning, Polyn, Baltuch, Litt, & Kahana, 2011).

In the present study, when asked to choose in which of eight lists an item had been studied, participants were essentially at chance. This is not surprising because models suggest that temporal context is relative, not absolute (Manning et al., 2011; Kahana, 1996). In other words, people can use recovered context to gauge the relative recency of two previously encountered items, but this might not be sufficient for precise memory for the temporal position of an item (Montchal et al., 2019; Jenkins & Ranganath, 2010, 2016; DuBrow & Davachi, 2013, 2014; Ezzyat & Davachi, 2014; Hintzman, 2001, 2004, 2005; Lewandowsky & Murdock, 1989) without the use of additional heuristics and reconstructive strategies (Friedman, 1993).

If the HC carries information about the relative temporal context of past events, we might expect that hippocampal activity patterns would be more similar during recollection of items that were learned in close temporal proximity than for items that were studied far apart in time. Consistent with this prediction, fMRI studies have shown that recollection of items encountered either in virtual reality (Dimsdale-Zucker et al., 2018; Deuker et al., 2016; Copara et al., 2014) or in the real world (Nielson et al., 2015) yields activity patterns within the HC that show graded similarity on the basis of both temporal and spatial contextual features.

Here, we found no evidence to suggest that activity patterns in any subfield carried information about list context. There are a number of potential reasons for this null result, but we suspect that the most important factor is that, unlike previous studies that reported temporal context representations in the HC, we manipulated cognitive contexts independently of temporal information.

Our task was designed such that participants changed cognitive contexts often within a list. Prior work has shown that, when ongoing temporal contexts are interrupted by changes in item-level cognitive contexts, both behavioral

(Polyn et al., 2009) and neural (Polyn, Kragel, Morton, McCluey, & Cohen, 2012) responses are shaped by both these local and global contextual features. Thus, by varying the encoding question within each study list, participants might have segmented each list into micro-contexts (Clewett & Davachi, 2017; DuBrow, Rouhani, Niv, & Norman, 2017; Zacks & Swallow, 2007; Zacks, Tversky, & Iyer, 2001), thereby disrupting associations based on temporal contiguity. A related possibility is that, during encoding, participants might have prioritized cognitive context over temporal contiguity because the encoding questions were more salient and relevant.

Although we did not find evidence of precise temporal context representation in the HC, an exploratory analysis did reveal evidence to suggest conjunctive representation of temporal context—“similar” or “coarse” temporal context—and cognitive context in CA23DG. In this analysis, temporal context was operationalized on the basis of which half of the study phase that an item had been previously encountered (first half: Lists 1–4; second half: Lists 5–8). Results revealed that activity patterns in CA23DG were shaped by the conjunction of coarse temporal context and cognitive context, which aligns with the binding role CA3 is thought to play (Eichenbaum et al., 2007; Rolls & Kesner, 2006; Burwell, 2000).

### **Shared versus Distinct Contextual Representations in the HC**

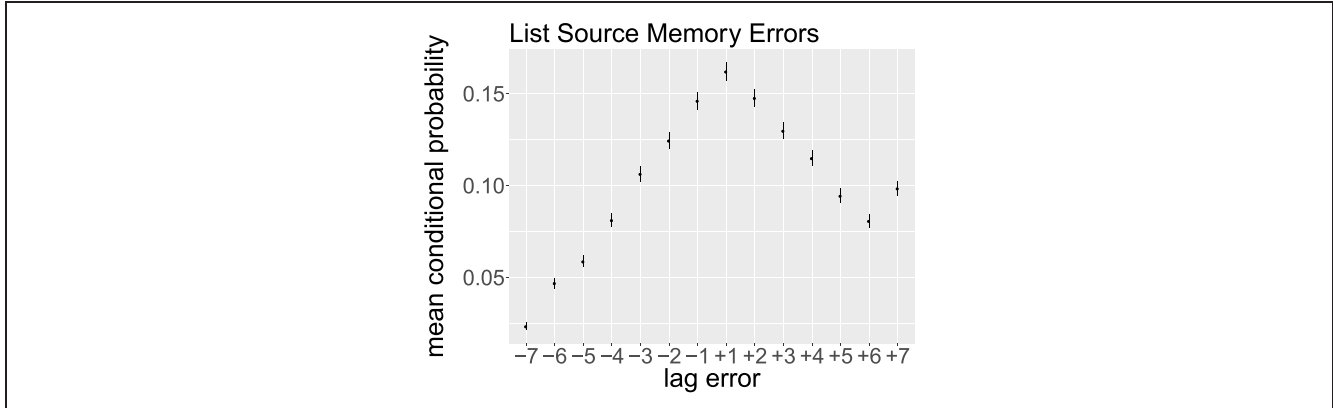
Our results conflict with a prior study, in which we found that CA23DG activity patterns during memory retrieval were less similar across pairs of items that were associated with the same episodic context (i.e., objects seen within the same movie) than across pairs of items that were associated with different spatial or episodic contexts (Dymsdale-Zucker et al., 2018). The contrast between the present results and those of Dymsdale-Zucker et al.

(2018) is relevant to many standard-resolution fMRI studies showing that hippocampal activity patterns are sometimes more similar across events that have a shared context (Libby et al., 2019; Pidgeon & Morcom, 2016; Horner, Bisby, Bush, Lin, & Burgess, 2015; Milivojevic, Vicente-Grabovetsky, & Doeller, 2015; Schlichting, Mumford, & Preston, 2015) and sometimes less similar between overlapping events (Zheng et al., 2021; Chanales et al., 2017; Kim, Norman, & Turk-Browne, 2017; Favila, Chanales, & Kuhl, 2016; Schlichting et al., 2015). Computational work by Ritvo, Turk-Browne, and Norman (2019) suggests that these different results may be because of competition between items that are to be learned. If there is relatively low competition, then CA23DG might assign similar representations to overlapping events, whereas if competition is high, the representations can be orthogonalized. We speculate that dynamic might be at play in our studies. In Dymsdale-Zucker et al. (2018), multiple sequences of items were encoded in the same two virtual reality contexts, potentially creating a significant degree of interference across items, but, in the present study, the use of multiple encoding tasks probably reduced contextual overlap across items, thereby reducing competition. This explanation can be directly tested in a future high-resolution imaging study.

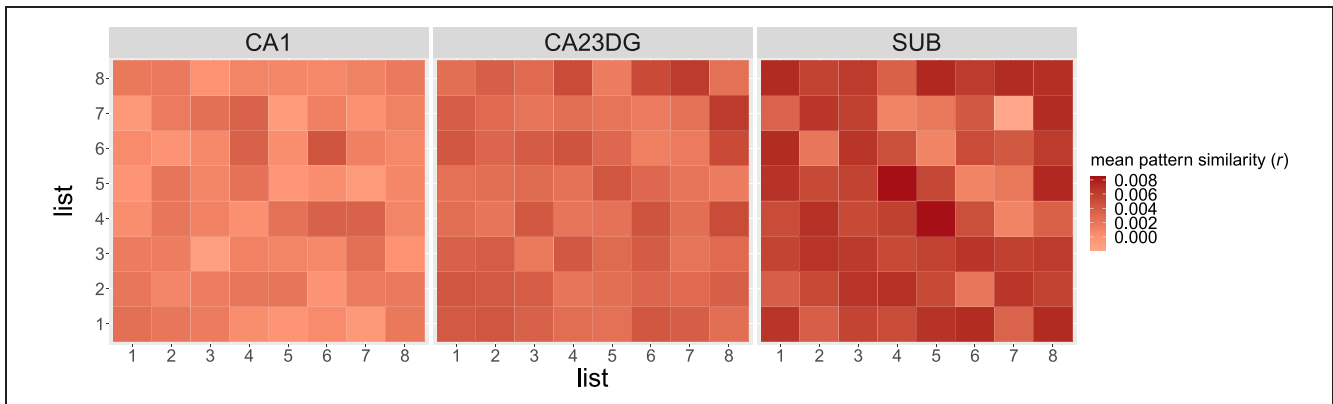
### **General Conclusions**

Our results show that activity patterns in the CA23DG region of the human HC carry information about cognitive contexts. This finding can help explain how we represent continuously unfolding episodes in a changing world. Outside the laboratory, we are constantly multi-tasking between competing goals and responsibilities. The HC, and specifically CA23DG, may allow us to differentiate between experiences that are associated with different tasks.

## APPENDIX



**Appendix A.** Temporal (list) source memory errors were more likely to occur at nearer than further lags. That is, items were more likely to be incorrectly attributed to a list that was closer in time ( $\pm 1$  or  $\pm 2$  lists) to the list in which it was actually located at encoding. We take this as evidence that, although exact memory for which of the eight encoding lists an item was studied in was relatively poor, participants had access to the relative temporal context of an item at encoding.



**Appendix B.** PS split by list across subfields of interest. No subfield showed a reliable relationship in PS levels across list. We take this as evidence that list membership was not a salient feature that participants reactivated at the time of retrieval. This aligns with participants' poor source memory for the list in which an item was studied during encoding.

**Appendix C. PS Findings in Hippocampal Subfields**

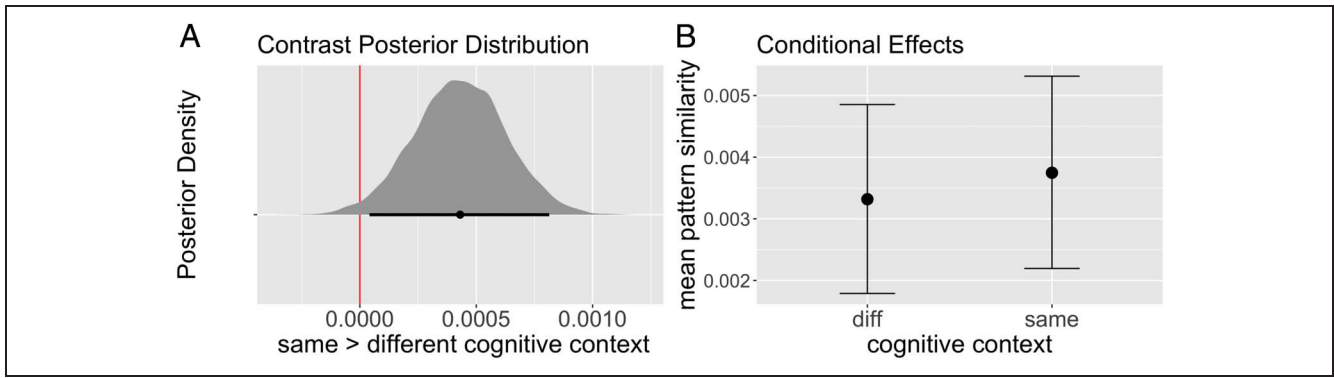
	<i>“Same” Temporal Context</i>			<i>“Similar” Temporal Context</i>		
	<i>Cognitive</i>	<i>Temporal</i>	<i>Cognitive × Temporal</i>	<i>Cognitive</i>	<i>Temporal</i>	<i>Cognitive × Temporal</i>
CA1	PS levels did not vary by cognitive context, $\chi^2(1) = 0.08$ , $p^{\text{perm1000}} = .773$	PS levels did not vary by same/different temporal context, $\chi^2(1) = 0.11$ , $p^{\text{perm1000}} = .744$	PS levels did not vary by the interaction between same temporal and cognitive contexts, $\chi^2(1) = 0.03$ , $p^{\text{perm1000}} = .871$	PS levels did not vary by cognitive context. $\chi^2(1) = 0.08$ , $p^{\text{perm1000}} = .776$	PS levels did not vary by similar temporal context, $\chi^2(1) = 2.42$ , $p^{\text{perm1000}} = .120$	PS levels did not vary by the interaction between similar temporal and cognitive contexts, $\chi^2(1) = 0.84$ , $p^{\text{perm1000}} = .360$
CA23DG	<i>PS values were greater for same as compared to different cognitive contexts, <math>\chi^2(1) = 4.63</math>, <math>p^{\text{perm1000}} = .031</math></i>	PS levels did not vary by same/different temporal context, $\chi^2(1) = 0.44$ , $p^{\text{perm1000}} = .505$	PS levels did not vary by the interaction between same temporal and cognitive contexts, $\chi^2(1) = 0.71$ , $p^{\text{perm1000}} = .400$	<i>PS values were greater for same as compared to different cognitive contexts, <math>\chi^2(1) = 4.68</math>, <math>p^{\text{perm1000}} = .031</math></i>	PS levels did not vary by similar temporal context, $\chi^2(1) = 0.08$ , $p^{\text{perm1000}} = .783$	<i>PS was greater for items that shared a similar temporal context as well as a cognitive context but was lower when these items did not share a cognitive context, <math>\chi^2(1) = 8.11</math>, <math>p^{\text{perm1000}} = .004</math></i>
Subiculum	PS levels did not vary by cognitive context, $\chi^2(1) = 0.27$ , $p^{\text{perm1000}} = .605$	PS levels did not vary by same/different temporal context, $\chi^2(1) = 0.13$ , $p^{\text{perm1000}} = .721$	PS levels did not vary by the interaction between same temporal and cognitive contexts, $\chi^2(1) = 0.03$ , $p^{\text{perm1000}} = .856$	PS levels did not vary by cognitive context, $\chi^2(1) = 0.27$ , $p^{\text{perm1000}} = .602$	PS levels did not vary by similar temporal context, $\chi^2(1) = 0.11$ , $p^{\text{perm1000}} = .745$	PS was <i>marginally</i> higher for items that were studied relative to the same question but studied in different list halves as compared to all other conditions, $\chi^2(1) = 2.91$ , $p^{\text{perm1000}} = .088$

*Italics* indicate significant modulation of PS values by cognitive, temporal, or interaction of cognitive and temporal encoding contexts.

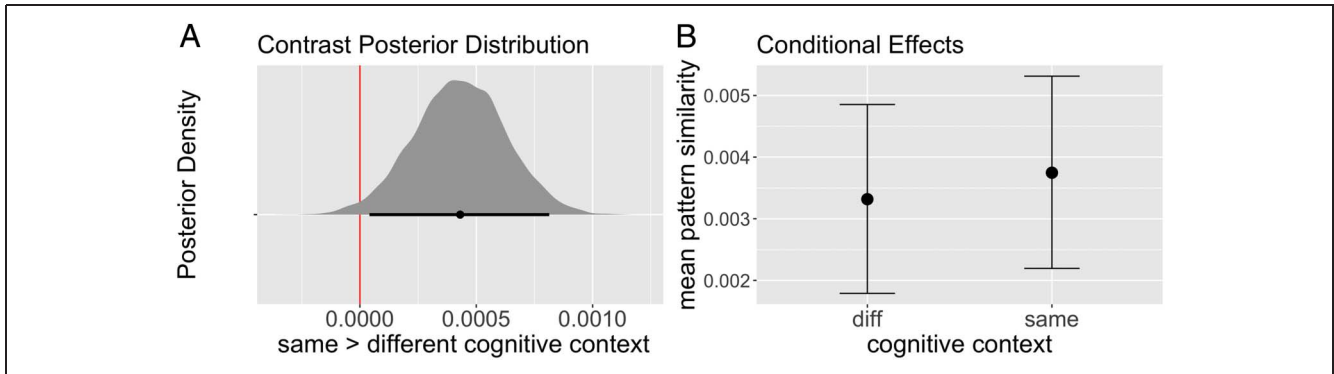
**Appendix D.** Bayesian Model Results for PS Findings in CA23DG

	"Same" Temporal Context			"Similar" Temporal Context		
	<i>Cognitive</i>	<i>Temporal</i>	<i>Cognitive × Temporal</i>	<i>Cognitive</i>	<i>Temporal</i>	<i>Cognitive × Temporal</i>
CA23DG	<i>PS values were greater for same as compared to different cognitive contexts; same &gt; different cognitive context estimate = 0.0004, PI = (0.00005, 0.0008)</i>	PS levels did not vary by same/different temporal context; different > same list estimate = 0.000182, PI = (-0.0003, 0.0007)	PS levels did not vary by the interaction between same temporal and cognitive contexts; different list and same cognitive context > same list and different cognitive context estimate = -0.0005, PI = (-0.002, 0.00007)	<i>PS values were greater for same as compared to different cognitive contexts; same &gt; different cognitive context estimate = 0.0004, PI = (0.00005, 0.0008)</i>	PS levels did not vary by similar temporal context; different half > same half estimate = 0.00005, PI = (-0.00003, 0.00004)	<i>PS was greater for items that shared a similar temporal context as well as a cognitive context but was lower when these items did not share a cognitive context. For items in different list halves, PS values were relatively similar regardless of same vs. different cognitive context; different list half and same cognitive context &gt; same list half and different cognitive context estimate = -0.004, PI = (-0.002, -0.00003)</i>

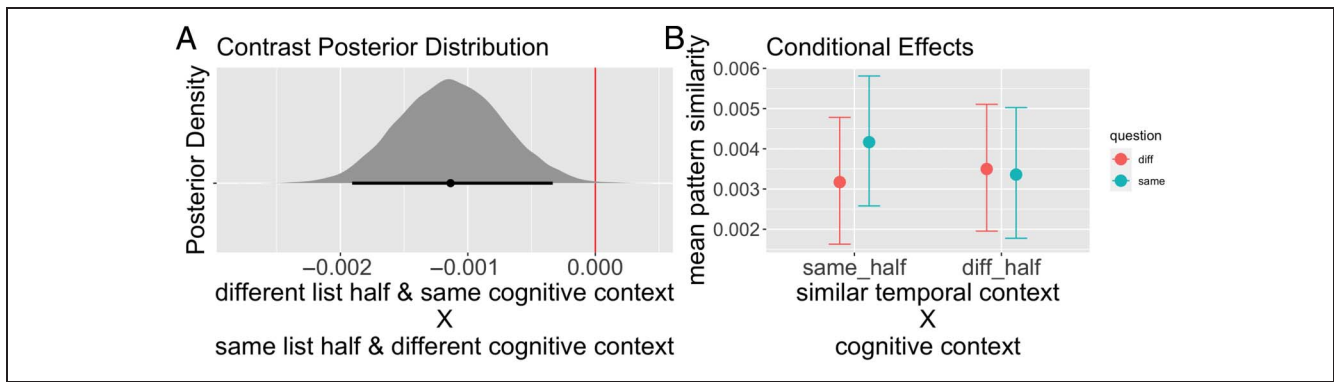
Here, we report effect estimates for contrasts as estimated by the *brms* package in the R computing environment (Bürkner, 2017). Highest density intervals (abbreviated in the table as "posterior intervals" [PI]) were calculated for each contrast. Such intervals are roughly analogous to confidence intervals and, thus, must not contain zero for the contrast to be considered significant (Turkkan & Pham-Gia, 1993). *Italics* are used to emphasize contrasts that were deemed significant based on these criteria.



**Appendix E.** Bayesian model posterior distributions and conditional effects for the influence of cognitive context (for “same” temporal context items) on PS values in CA23DG. (A) Posterior distributions for the same > different cognitive context contrast, representing differences in mean PS values between these conditions. Shaded distributions represent all posterior contrast samples, vertical red line represents zero, black points below shaded distribution represent effect estimates as determined by the model’s posterior predictive distribution for the linear predictor, and error bars around this point represent 95% credible intervals. Because the 95% CI does not overlap with zero, we can determine that cognitive context had a significant influence on PS values in CA23DG. (B) Conditional effect estimates for the influence of same and different cognitive context on PS values, accounting for other effects present in the model.



**Appendix F.** Bayesian model posterior distributions and conditional effects for the influence of cognitive context (for “similar” temporal context items) on PS values in CA23DG. (A) Posterior distributions for the same > different cognitive context contrast, representing differences in mean PS values between these conditions. Shaded distributions represent all posterior contrast samples, vertical red line represents zero, black points below shaded distribution represent effect estimates as determined by the model’s posterior predictive distribution for the linear predictor, and error bars around this point represent 95% credible intervals. Because the 95% CI does not overlap with zero, we can determine that cognitive context had a significant influence on PS values in CA23DG. (B) Conditional effect estimates for the influence of same and different cognitive context on PS values, accounting for other effects present in the model.



**Appendix G.** Bayesian model posterior distributions and conditional effects for the influence of the combined effect of “similar” temporal context and cognitive context on PS values in CA23DG. (A) Posterior distributions for the [(different list half and same cognitive context) > (same list half and different cognitive context)] contrast, representing differences in mean PS values between these conditions. Shaded distributions represent all posterior contrast samples, vertical red line represents zero, black points below shaded distribution represent effect estimates as determined by the model’s posterior predictive distribution for the linear predictor, and error bars around this point represent 95% credible intervals. Because the 95% CI does not overlap with zero, we can determine that the combined influence of similar temporal context and cognitive context had a significant influence on PS values in CA23DG. Specifically, we see that PS values were greater for items affiliated both with the same cognitive context and the same list half (“similar” temporal context) than those affiliated with different cognitive contexts (comparing teal vs. red points in the left column of the graph). PS values were relatively equivalent for items affiliated with different list halves regardless of cognitive context (same/different). (B) Conditional effect estimates for the influence of similar temporal context and cognitive context on PS values, accounting for other effects present in the model.

**Appendix H.** PS Findings in Medial Temporal Lobe Neocortical Areas

	"Same" Temporal Context			"Similar" Temporal Context		
	Cognitive	Temporal	Cognitive × Temporal	Cognitive	Temporal	Cognitive × Temporal
Anterior PHC	<i>PS was higher during retrieval of items associated with the same cognitive context compared to items associated with different cognitive contexts, <math>\chi^2(1) = 5.92</math>, <math>p^{\text{perm}1000} = .015</math></i>	<i>PS was higher during retrieval of items associated with the same as compared to different list, <math>\chi^2(1) = 4.79</math>, <math>p^{\text{perm}1000} = .029</math></i>	PS levels did not vary by the interaction between same temporal and cognitive contexts, $\chi^2(1) = 0.22$ , $p^{\text{perm}1000} = .639$	<i>PS was higher during retrieval of items associated with the same cognitive context compared to items associated with different cognitive contexts, <math>\chi^2(1) = 5.83</math>, <math>p^{\text{perm}1000} = .016</math></i>	<i>PS was higher during retrieval of items associated with a different temporal context as compared to items with similar temporal encoding contexts, <math>\chi^2(1) = 7.39</math>, <math>p^{\text{perm}1000} = .007</math></i>	PS levels did not vary by the interaction between similar temporal and cognitive contexts, $\chi^2(1) = 1.42$ , $p^{\text{perm}1000} = .233$
Posterior PHC	PS levels did not vary by cognitive context, $\chi^2(1) = 0.64$ , $p^{\text{perm}1000} = .422$	PS levels did not vary by same/different temporal context, $\chi^2(1) = 2.88$ , $p^{\text{perm}1000} = .090$	<i>PS was greater for items that shared a temporal context as well as a cognitive context but was lower when these items did not share a cognitive context, <math>\chi^2(1) = 9.44</math>, <math>p^{\text{perm}1000} = .002</math></i>	PS in pPHC did not vary with respect to cognitive context alone, $\chi^2(1) = 0.68$ , $p^{\text{perm}1000} = .411$	PS levels did not vary by similar temporal context, $\chi^2(1) = 2.07$ , $p^{\text{perm}1000} = .150$	<i>PS was greater for items that shared a similar temporal context as well as a cognitive context but was lower when these items did not share a cognitive context, <math>\chi^2(1) = 4.67</math>, <math>p^{\text{perm}1000} = .031</math></i>
PRC	PS was <i>marginally higher</i> during retrieval of items associated with the same cognitive context compared to items associated with different cognitive contexts, $\chi^2(1) = 3.53$ , $p^{\text{perm}1000} = .060$	PS levels did not vary by same/different temporal context, $\chi^2(1) = 0.074$ , $p^{\text{perm}1000} = .786$	PS levels did not vary by the interaction between same temporal and cognitive contexts, $\chi^2(1) = 0.96$ , $p^{\text{perm}1000} = .327$	PS was <i>marginally higher</i> during retrieval of items associated with the same cognitive context compared to items associated with different cognitive contexts PRC, $\chi^2(1) = 3.55$ , $p^{\text{perm}1000} = .051$	PS levels did not vary by similar temporal context, $\chi^2(1) = 0.11$ , $p^{\text{perm}1000} = .743$	PS levels did not vary by the interaction between similar temporal and cognitive contexts, $\chi^2(1) = 0.15$ , $p^{\text{perm}1000} = .703$

*Italics* indicate significant modulation of PS values by cognitive, temporal, or interaction of cognitive and temporal encoding contexts.



## Gender, Race, and Ethnicity Bias Statement

Recent work in several fields of science has identified a bias in citation practices such that articles from women and other minority scholars are undercited relative to the number of such articles in the field (Chatterjee & Werner, 2021; Fulvio, Akinnola, & Postle, 2021; Wang et al., 2021; Bertolero et al., 2020; Dworkin et al., 2020; Dion, Sumner, & Mitchell, 2018; Caplar, Tacchella, & Birrer, 2017; Maliniak, Powers, & Walter, 2013; Mitchell, Lange, & Brus, 2013). Here, we sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, race, ethnicity, and other factors and used a standardized reporting tool to quantify those efforts here (Dworkin, et al., 2020). First, we obtained the predicted gender of the first and last authors of each reference by using databases that store the probability of a first name being carried by a woman (Zhou, 2022; Dworkin et al., 2020; Zhou et al., 2020). By this measure (and excluding self-citations to the first and last authors of our current article), our references contain 7.65% woman (first)/woman (last), 14.53% man/woman, 26.29% woman/man, and 51.53% man/man. This method is limited in that (a) names, pronouns, and social media profiles used to construct the databases may not, in every case, be indicative of gender identity and (b) it cannot account for intersex, nonbinary, or transgender people. Second, we obtained predicted racial/ethnic category of the first and last authors of each reference by databases that store the probability of a first and last name being carried by an author of color (Sood & Laohaprapanon, 2018; Ambekar, Ward, Mohammed, Male, & Skiena, 2009). By this measure (and excluding self-citations), our references contain 3.36% author of color (first)/author of color (last), 10.63% White author/author of color, 15.17% author of color/White author, and 70.84% White author/White author. This method is limited in that (a) names and Florida Voter data to make the predictions may not be indicative of racial/ethnic identity and (b) it cannot account for Indigenous and mixed-race authors, or those who may face differential biases because of the ambiguous racialization or ethnicization of their names. We look forward to future work that could help us to better understand how to support equitable practices in science.

## Acknowledgments

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Reprint requests should be sent to Halle R. Dimsdale-Zucker, Department of Psychology, Columbia University, 312 Schermerhorn, 1190 Amsterdam Avenue, New York, NY 10027-6902, or via e-mail: halledz@ucr.edu.

## Data Availability Statement

Data and code for this article have already been made publicly available (see URLs in the article).

## Author Contributions

Halle R. Dimsdale-Zucker: Conceptualization; Data curation; Formal analysis; Methodology; Software; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Maria E. Montchal: Conceptualization. Zachariah M. Reagh: Supervision; Writing—Review & editing. Shao-Fang Wang: Investigation. Laura A. Libby: Conceptualization. Charan Ranganath: Funding acquisition; Supervision; Writing—Review & editing.

## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were  $M(\text{an})/M = .407$ ,  $W(\text{oman})/M = .32$ ,  $M/W = .115$ , and  $W/W = .159$ , the comparable proportions for the articles that these authorship teams cited were  $M/M = .549$ ,  $W/M = .257$ ,  $M/W = .109$ , and  $W/W = .085$  (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows:  $M/M = .489$ ;  $W/M = .266$ ;  $M/W = .128$ ;  $W/W = .117$ .

## Notes

1. For medial temporal neocortical regions, see reported results in Appendix H.
2. For ease of visualization of the effects, for pattern similarity analyses, we have chosen to plot means with individual subject points to illustrate the observed data. This does not exactly recapitulate the way the statistical comparisons were computed because these were performed as mixed models. That is, these figures show the raw pattern similarity values for these experimental conditions but do not account for the other effects present in the models that were used to determine significance. To better visualize the observed statistical effects, we have plotted the permutation distributions that were used to determine model significance.
3. At the suggestion of an anonymous reviewer, we repeated all of our analyses for the key effects we saw in CA23DG using a Bayesian modeling framework. We fit all models using Hamiltonian Monte Carlo No-U-Turn sampling as implemented by the *brms* package in the R computing environment (Bürkner, 2017). For all models, we fit four chains of 10,000 sampling iterations (5000 warm-up) each for a total of 20,000 post-warm-up samples. This sampling iteration size was used to avoid cases where the tail effective sample size was low (as indicated by Stan warning messages). Extraction and transformation of posterior draws after models were fit was done using the *tidybayes* package and the *tidyverse* collection of packages in R (Kay, 2022; Wickham et al., 2019). This approach was informed by best practices as advised by Paul Alexander Bloom (personal communication). Results from these Bayesian analyses replicated the results we report in the main analyses in the article

that were implemented via mixed models in *lmer*. However, for full transparency, we have included the Bayesian effect estimates for all contrasts as well as the highest density interval (which can be interpreted similarly to a confidence interval; Turkkan & Pham-Gia, 1993) in Appendix D. Furthermore, we include graphical depictions of the model posterior distribution and conditional effect estimates for any contrast that was deemed significant (see Appendices E–G).

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