

Episodic boundaries affect neural features of representational drift in humans

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Abstract

A core feature of episodic memory is representational drift, the gradual change in aggregate oscillatory features that supports temporal association of memory items. However, models of drift overlook the role of episodic boundaries, which indicate a shift from prior to current context states. Our study focuses on the impact of task boundaries on representational drift in the parietal and temporal lobes in 99 subjects during a free recall task. Using intracranial EEG recordings, we show boundary representations reset gamma band drift in the medial parietal lobe, selectively enhancing the recall of early list (primacy) items. Conversely, the lateral temporal cortex shows increased drift for recalled items but lacked sensitivity to task boundaries. Our results suggest regional sensitivity to varied contextual features: the lateral temporal cortex uses drift to differentiate items, while the medial parietal lobe uses drift-resets to associate items with the current context. We propose drift represents relational information tailored to a region's sensitivity to unique contextual elements. Our findings offer a mechanism to integrate models of temporal association by drift with event segmentation by episodic boundaries.

eLife assessment

This **valuable** study presents a novel analysis of a large human intracranial electrophysiological recording dataset. The study challenges the traditional view that neural responses to word lists exhibit smoothly drifting contexts over time, showing that items just after a boundary have a characteristic response that occurs repeatedly. The evidence is **incomplete**, however, leaving open the possibility for alternative explanations.

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Introduction

A defining feature of episodic memory is the contextual information that associates and differentiates item representations. Temporal relationships are a key component of contextual information (*Tulving and Markowitsch, 1998* ; *Fortin et al., 2002* ; *Sederberg et al., 2008* .

The successful encoding of these temporal relationships has been tied to a drifting pattern in neural activity ([Folkerts et al., 2018](#); [Mau et al., 2020](#)). However, temporal relationships are also influenced by large context shifts, called boundaries ([Zacks et al., 2001, 2007](#); [DuBrow and Davachi, 2013](#); [Ranganath, 2019](#)). On an intuitive level, relational information may be encoded through both mechanisms: association with preceding items, represented by drift, and the association with shifts in context, represented by boundaries. However, it remains unclear how a drifting signal, characterized by gradual changes in neural activity, accommodates large shifts in context represented by boundary signals. The primary focus of this study is to reconcile these mechanisms of context and clarify how the brain simultaneously represents item-specific temporal information and item-independent boundary information to form a rich contextual background to encode new memories.

The Temporal Context Model (TCM) suggests an item's temporal context is built from items that immediately precede it ([Howard and Kahana, 2002](#)). When a new item is introduced, it updates the context state and gradually changes the contextual representation. The degree of item similarity *drifts* such that items presented close together have high contextual overlap while items far apart have less overlap. This drifting context offers a mechanism for robust behavioral effects observed in memory.

Drift in context representation provides a compelling explanation for the recency and contiguity effects. The recency effect arises from the proximity of recency events to the recall period. The temporal context state at the recall period has not drifted significantly from the context state while encoding the recency items ([Lohnas et al., 2015](#)); therefore, items presented most recently share the highest similarity to the context state at retrieval allowing recency items to be most easily remembered. While retrieving a specific event, the recollection process not only reinstates that item's encoding representation but also reinstates preceding item representations as context ([Manning et al., 2011](#)). Reinstated context serves as a cue mechanism for nearby items resulting in tendency to cluster items presented together, referred to as the contiguity effect ([Folkerts et al., 2018](#)).

However, these models do not inherently capture primacy effects as convincingly, which have been hypothesized to arise from rehearsal ([Tan and Ward, 2000](#)) or less well understood processes such as neural fatigue ([Serruya et al., 2014](#); [Lohnas et al., 2020](#)). Updated versions of TCM model primacy using terms that lack an obvious neural correlate ([Polyn et al., 2009](#); [Lohnas et al., 2015](#)) creating a need for a coherent integration of primacy and drifting information for context representation.

Boundary-related information provides a potential mechanism for understanding primacy. In parallel with a gradually drifting context representation, episodic experience is also segmented by sharp shifts in context, known as boundaries. Boundaries are created after large changes in stimuli, task-goals, or context information ([Kurby and Zacks, 2008](#); [Baldassano et al., 2017](#); [Griffiths and Fuentesmilla, 2019](#)). Event segmentation theory holds that boundaries segment continuous experience into "events", resulting in improved memory within the current event but worsened memory of a prior event. Boundaries may exert this effect by disrupting contextual associations between items separated by a boundary ([DuBrow and Davachi, 2013](#); [Ezzyat and Davachi, 2014](#)). Conversely, random boundary insertions improve memory of subsequent items and induce a novel primacy-like effect ([Mau et al., 2020](#); [Ranganath, 2019](#)). The ability of boundaries to disrupt associations of prior items but improve associations of subsequent items suggests they may play a role in defining context. However, the effect of boundaries on a drifting context signal is still unclear. Ranganath and colleagues suggest boundaries reset a portion of temporal context and drift occurs relative to a reinstated boundary signal ([Pu et al., 2022](#)). Alternatively, boundaries may accelerate the rate of drift inducing a greater contextual dissimilarity between boundary separated items ([Horner et al., 2016](#); [DuBrow et al., 2017](#)).

Strong evidence supports the presence of boundary representations within the medial temporal regions. Aggregate regional activity ([Baldassano et al., 2017](#)) and individual neurons ([Yoo et al., 2022](#); [Zheng et al., 2022](#)) show sensitivity to embedded boundaries in several tasks of episodic memory. However, boundary representations are not confined to just the MTL, studies across multiple cognitive domains highlight their presence in the parietal lobe. In studies of spatial navigation, boundary vector neurons are specifically sensitive to spatial boundaries ([Alexander et al., 2020](#)). These spatial boundaries help create a generalized map of the surrounding area ([Bicanski and Burgess, 2020](#)). Similarly, in episodic tasks, parietal regions demonstrate content-invariant activation at conceptual boundaries ([Zacks et al., 2001](#); [Baldassano et al., 2017](#)). These boundary representations play a key role in the construction of situational models ([Kurby and Zacks, 2008](#)). Whether spatial or episodic, the parietal lobe's ability to represent boundaries may underlie its role in constructing an abstract contextual framework as described by the posterior medial-anterior temporal (PMAT) framework ([Ranganath and Ritchey, 2012](#)). With these (non-invasive) findings as motivation, we sought to analyze neural evidence of drift-like and boundary related information recorded from temporal (hippocampus and lateral temporal cortex) and medial parietal (precuneus and posterior cingulate cortex) regions in 99 human intracranial EEG patients. We find recalled items drift at a higher rate than non-recalled items. Across multiple lists, boundary items share significant spectral similarity mainly in the parietal lobe. Our findings suggest that these regions provide complementary representations of temporal context and boundary-related activity, with medial parietal areas exhibiting unique sensitivity to boundary-related information linked with memory performance. Our data align with experiments in rodents that link parietal activity to boundary-representations in spatial navigation, suggesting a more generalized role of the parietal regions in event segmentation which supports multi-scale contextual associations in episodic memory.

Results

We analyzed depth electrode recordings from participants performing the delayed free recall task (**Figure 1A**). The task's robust contiguity effect as well as its predictable internal structure allowed us to study both item-boundary and item-item relationships. Participants had an overall recall rate of $24\% \pm 11\%$ (mean $\pm$ std; **Figure 1D**). Our analysis focused on gamma band (30 to 100 Hz) power from electrodes in the medial parietal lobe (MPL; precuneus and posterior cingulate cortex), the lateral temporal cortex (LTC; superior and medial temporal gyri), and the hippocampus (HC). We focused on gamma power due its strong association with single neuron activity ([Umbach et al., 2020](#)), local excitatory-inhibitory feedback loops ([Buzsaki and Wang, 2012](#); [Wang, 2010](#)), and order. These regions were chosen because structural and functional studies suggest the posterior medial (PM) and anterior temporal (AT) regions represent different features of episodic memory that are integrated by the hippocampus ([Ranganath and Ritchey, 2012](#)). Additionally, these regions have robust electrode coverage in patients intracranial EEG monitoring. To evaluate the relatedness of item representations, we used principal component analysis (PCA) to identify common features of gamma band covariance and quantified the similarity of between items with cosine similarity as a function of positional distance between item pairs, see Methods.

Enhanced drift rate increases distinctiveness of spectral representations for recalled items

First, we focus on neural similarity between words in the same list. Previous work consistent with temporal context models suggests neural pattern similarity reduces as a function of distance between related memories ([Hsieh et al., 2014](#); [Hsieh and Ranganath, 2015](#); [El-Kalliny et al.,](#)

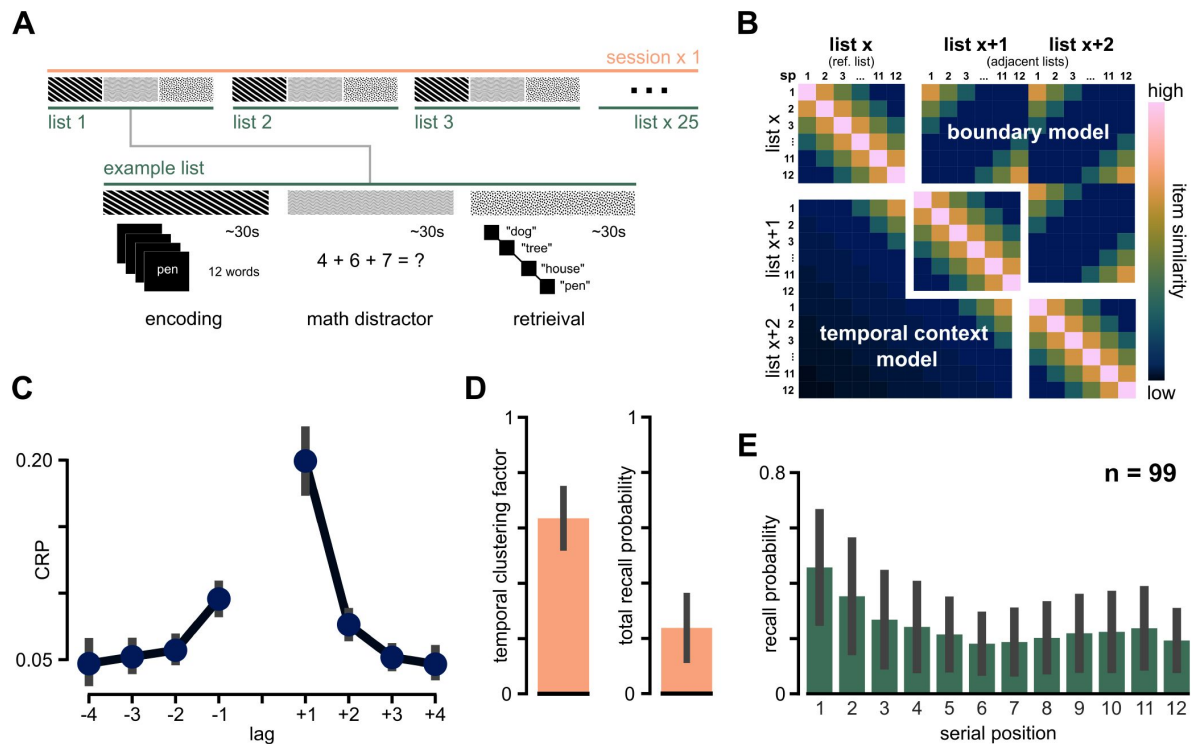


Figure 1.

Illustration of task and behavioral summary

A. Diagram of the delayed free recall task. **B.** Schematic of the predicted similarity between items across in the same list (*list x*) and 2 adjacent lists (*list x+1*, *x+2*). Items presented close together in time show the most representational similarity, shown by the drifting reduction in similarity perpendicular to the diagonal. TCM predicts item representations should continue to decay across lists due to increased temporal distance shown as blue transitions to black (bottom left). A boundary-oriented representation would show similarity between boundary items across multiple lists (top right). **C.** The average proportion of recalled events for each serial position for each participant ($n=99$). **D.** The average recall probability (left, $n=99$, mean $\pm$ sd: 0.24 ± 0.11) and the average temporal clustering factor (TCF; right, 0.64 ± 0.10) of all study participants. **E.** The lagged conditional response probability (CRP) is shown for 4 lags in either direction characterizing the contiguity in our data. The error bars in (E) represent ± 1 SEM. Error bars denote ± 1 SD unless otherwise noted.

2019). In concert with previous work, we refer to this phenomenon as neural drift. To quantify drift in our data, we calculated a similarity value between every item in the same list (Figure 2A).

Figure 2B shows the average similarity of every pair of items in a list for electrodes in the LTC. We found item similarity was reduced with increasing inter-item distance, aligning with prior findings (Hsieh et al., 2014; El-Kalliny et al., 2019). However, words at different serial positions are recalled at different rates. To understand how item-item similarity is affected based on successful recall, we compare item pairs where both items are recalled to pairs where both are not recalled (2C) using a linear mixed effects model (LME). The LME compared similarity of each serial position (SP) in reference to the first item with an interaction term for recall success, see Methods. In the lateral temporal cortex, we found that similarity decreased with increasing inter-item distance and that recalled pairs tended to be less similar than non-recalled pairs (LME, $n=81$; $\beta_{SP}=-0.005$, CI:[-0.007, -0.003], $p_{SP} < 0.001$; Interaction: SP x recalled items=-0.004, [-0.007, -0.002], $p_{interaction} = 0.001$). In terms of drift, items drifted at a higher rate such that individual item representations were less similar, or more distinct, when participants recalled both items.

Strong boundary representation in medial parietal lobe augments recall of initial list items

Next, we were interested in how boundaries affect item representations. In our behavioral task, the beginning of each list serves as a consistent boundary marking the initiation of a new encoding period. We hypothesized that a boundary signal would be most strongly represented in the first item of each list and its representation would be similar across multiple lists.

To test this hypothesis, we extended the item-item comparisons described in Figure 2 to compare items across adjacent lists. The schematic in Figure 1B visualizes the predicted similarity between items in the reference list (denoted list x) and multiple adjacent lists (denoted list $x+1$ and $x+2$). We contrast two possible models of association in the same schematic. Models based on continuous effects of new items on neural similarity (namely, the temporal context model) suggest that item-item associations would show decreasing similarity with increased positional distance, even across lists, without any evidence of enhanced similarity across lists for boundary-adjacent items. An alternative model that makes distinct allowance for boundary information would show evidence of recurring activity features near boundaries, (ie. the beginning and end of the item lists) with consistently decreasing similarity across lists for middle-list items. The schematic provides a visualization of our predictions captured in the models we applied to neural data, described below.

We began by calculating similarity between serial position (SP) 1 and every item in the same list (list x) and the 3 adjacent lists (list $x+1$, $x+2$, $x+3$), shown in Figure 3A. The similarity of SP1 items compared to each item in the adjacent lists for the medial parietal lobe, averaged by subject, is shown in Figure 3E. To calculate the degree of boundary representation, we built a general linear model with two predictor variables: boundary proximity, the distance of an item to the beginning of the list, and list distance, the distance of the target list from the reference list. An example subject's averaged similarity data is shown in Figure 3D with the model-fit superimposed. We fit the GLM to the average similarity of list x , SP1 to every item in list $x+1$, $x+2$ and $x+3$ for each subject individually in each region of interest. We found SP1s across adjacent list were most similar in the medial parietal lobe as compared to the lateral or medial temporal cortex (Figure 3B; t-test: MPL-LTC, $t(83,81)=4.05$, $p=8.0 \times 10^{-5}$; MPL-HC, $t(83,76)=3.27$, $p=1.3 \times 10^{-3}$). The similarity of list x , SP1 to subsequent boundary items in these regions is less pronounced (3-figure supplement 1 A,C). We repeated the same analysis to contrast recalled item pairs with non-recalled item pairs to assess the effect of recall success on boundary representation. We observed the similarity of boundary items across item lists was higher for recalled pairs (Figure 3B, right;

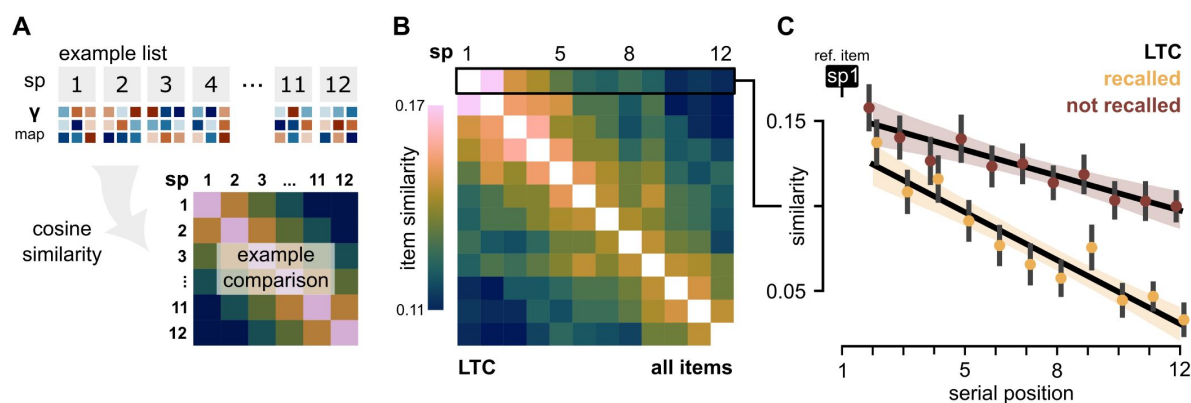


Figure 2.

Neural drift is enhanced between recalled item pairs within the lateral temporal cortex

A. Schematic of similarity analysis between item pairs in the same list. (sp: serial position; y map: gamma spectrum, PCA-optimized, time-frequency map) **B.** Similarity of all item pairs regardless of recall status, averaged by subject, across all electrodes in the LTC. **C.** Similarity of serial position 1 to each subsequent item in a list contrasting when both items are recalled (yellow) to when both items are not recalled (red). The error bars demonstrate variation in average similarity between participants. The trend lines are for visualization purposes only, the LME used to statistically test the result is described in the results section. Error bars indicate ± 1 SEM.

Figure 2—figure supplement 1. Drift rate does not differ between recalled and non-recalled items in the hippocampus and lateral temporal cortex

paired t-test, $t(83)=2.45$, $p=0.02$). This finding suggests an elevated boundary representation is incorporated for strongly encoded items, and it stands in contrast to lower similarity observed for recalled items across item lists in the LTC and HC. Finally, we asked whether the strength of boundary similarity correlated with the proportion of successful SP1 recalls per participant. We found participants with stronger boundary item similarity in the medial parietal lobe tended to recall a greater proportion of presented SP1 items (linear regression, $r=0.41$, $t(83)=4.08$, $p=1.1 \times 10^{-4}$).

The boundary representation is conserved in multiple primacy events

Our analysis thus far of adjacent SP1 items supports the presence of conserved boundary representation apart from drift-like changes in neural activity. This pattern is specific to the MPL suggesting this region represents item context relative to a boundary. To further investigate the role of boundary information in episodic encoding, we tested whether neural activity for boundary-adjacent serial positions (ie. SP2 and SP3, items which are subsequent to the boundary item within an encoding list) exhibited persistent boundary information using the same cross-list analysis as described above.

We modified our prior analysis to test the similarity of *list x*, SP2 and SP3 to every item in the adjacent three lists for recalled item-pairs only (**Figure 4A**). We tested for boundary representation in these serial positions to distinguish the role of the medial parietal lobe in representing contextual features. If the MPL is specifically sensitive to boundary information, SP2 and SP3 should show greater similarity to the boundary item than any other items in the same list. In support of our hypothesis, we found both SP2 and SP3 shared more similarity to the adjacent lists' SP1 rather than the adjacent lists' SP2 or SP3, respectively (**Figure 4**). We tested this by comparing the average similarity per subject of *list x*, SP2 to SP2 in each of the 3 adjacent lists. For SP2, we found SP2 was more similar to SP1 than SP2 in list $x+3$ (4C, top; two-sided, paired t-test, $t(83)=2.98$, $p=0.003$). We also found SP3 from list x was more similar to SP1 in both list $x+2$ and list $x+3$ than to SP3 in the same list (4C, bottom; list $x+2$: $t(83)=2.49$, $p=0.015$, list $x+3$: $t(83)=2.31$, $p=0.023$). In summary, multiple items in primacy positions share a strong similarity to boundaries in other lists. Importantly, this cross-list similarity appears to be greater than the degree of similarity to their own serial position in other lists. We examine the potential implications for this finding more thoroughly and within the temporal context framework (versus other serial encoding models) in the Discussion section.

Non-recalled items show increased boundary representation at the end of the list

Our results so far support the presence of a recurring boundary signal at the beginning of each list. Next, we were interested in whether a similar boundary representation existed at the end of each list. We repeated the same analysis described in **Figure 3** but for *list x*, SP12 to each item in the adjacent lists (**Figure 5A**). When comparing the similarity of all items pairs, we found later serial positions in adjacent lists shared a gradually increasing similarity to SP12 (**Figure 5B**). However, when we filtered for recalled items only, this trend disappeared (SD, pink). When recalled items from *list x*, SP12 were compared to adjacent recalled items, the items did not demonstrate any position dependent pattern. To test this trend, we fit a similar GLM to **Figure 3D**, with boundary proximity as a linear predictor (see **Figure 5**—figure supplement 1C), which showed a significantly higher boundary parameter estimate for non-recalled item pairs (**Figure 5C**, right; paired t-test, $t(74)=-3.39$, $p=1.1 \times 10^{-3}$). These findings suggest end-list items are represented more distinctly, or less similarly, to all succeeding items. Stated another way, while our analysis identifies persistent boundary-information across items lists for both beginning of list (primacy) and end of list (recency) items, these two classes diverge in terms of the apparent

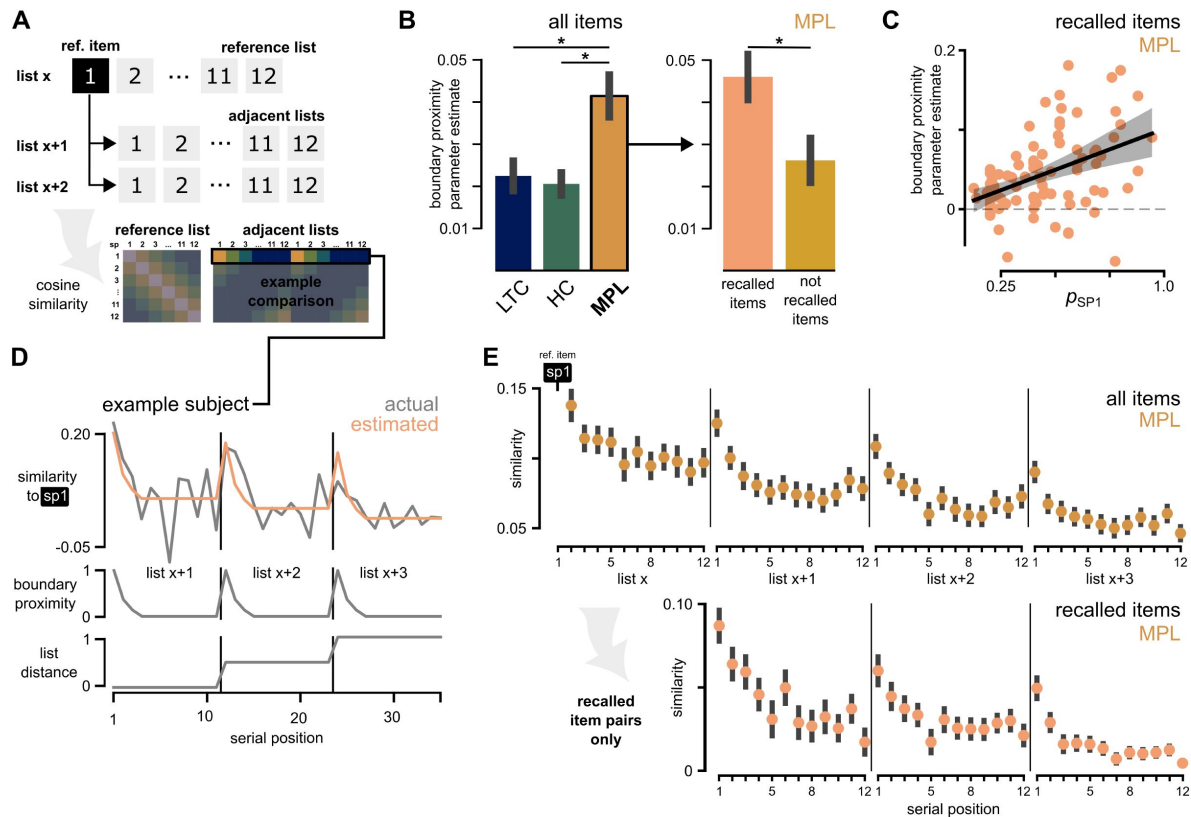


Figure 3.

The first items (SP1) across adjacent lists share a boundary representation.

A. A schematic showing the comparison of SP1 to every item in the adjacent three lists. **B.** The mean parameter estimate of the predictor for boundary proximity contrasted by region for all item pairs (left; LTC: $n=81$, mean $\beta=0.020$; HC: $n=76$, mean $\beta=0.022$; MPL: $n=83$, mean $\beta=0.042$). The parameter estimate of recalled-only pairs and non-recalled pairs is also shown for the MPL (right; recalled: pink, mean $\beta=0.045$; non-recalled: orange, mean $\beta=0.027$). **C.** Correlation of proportion of recalled SP1 by subject to the parameter estimate for boundary proximity (ordinary least squares regression, $r=0.41$, $p=1.1 \times 10^{-4}$). **D.** Design of the GLM used to fit adjacent list similarity in the MPL. The response variable (similarity to list x, SP1; gray, top) shown for an example subject with the model prediction (orange, top) overlaid. The predictor variables, boundary proximity (middle) and list distance (gray, bottom), are also shown. **E.** Mean similarity of all serial positions to the reference item (list x, SP1) regardless of recollection (top). Below, the mean similarity of only instances where both list x, SP1 and the target item are recalled are shown for all serial positions in adjacent lists (list x+1, x+2, x+3; bottom). The error bars demonstrate variation in average similarity between participants. All error bars indicate ± 1 SEM. * $p < 0.05$

Figure 3—figure supplement 1 [DOI:10.7554/eLife.90576.2](#). Serial position 1 does not show boundary representation in the hippocampus and lateral temporal cortex.

Figure 3—figure supplement 2 [DOI:10.7554/eLife.90576.3](#). Boundary information is represented in multiple principal components

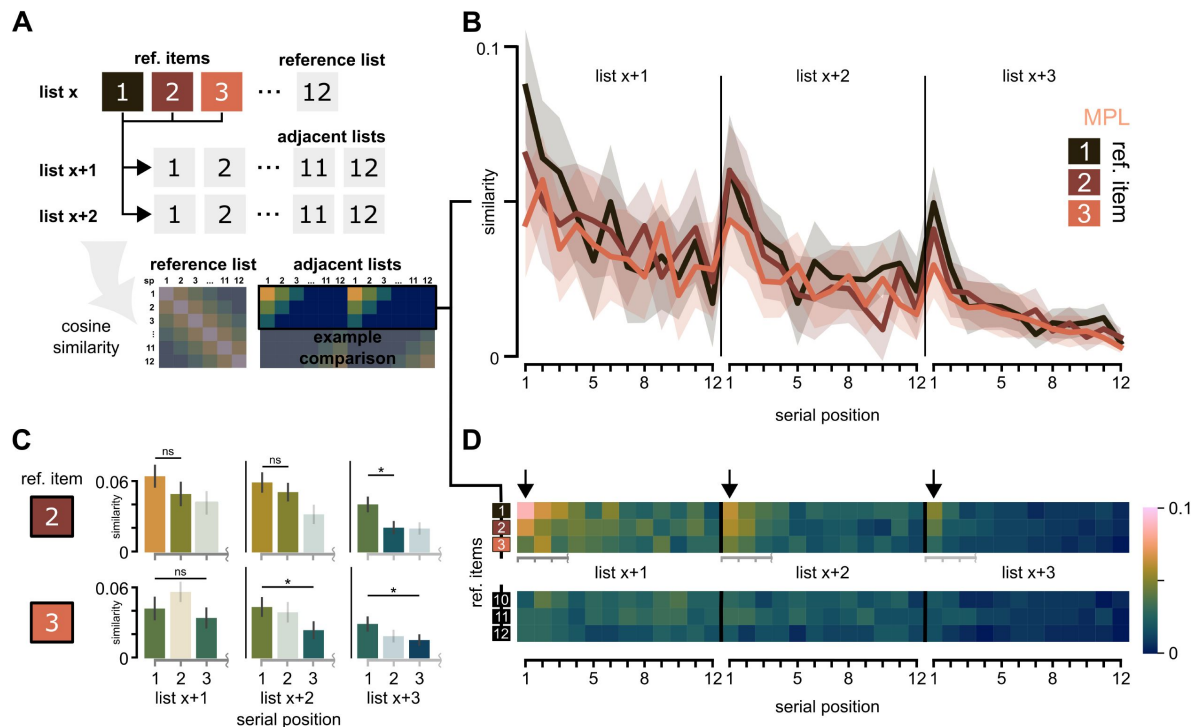


Figure 4.

Multiple primacy items retain similarity to the boundary representation in the MPL

A. A schematic of showing comparison of the reference and target items (top). The highlighted portion of the matrix demonstrates hypothesized trend in the boundary model presented as a part of 1B (bottom). **B.** Averaged similarity of only recalled item-pairs comparing the reference items: *list x*, SP1-3 to each item in *list x+1*, *x+2*, *x+3*. A representation of boundary would be supported by *list x*, SP2 showing more similarity SP1 in the adjacent lists rather than its own serial position. Alternatively, positional coding, the similarity of the same serial position between adjacent lists, would show greater similarity between *list x*, SP2 and SP2 in adjacent lists. Note the similarity of *list x*, SP2 and SP3 to SP1 in list *x+3* rather than SP2 and SP3 in list *x+3*. The confidence interval demonstrates $\pm 1\text{SEM}$ of variation in average similarity between participants. **C.** Comparison of the similarity between reference items: *list x*, SP2 and SP3 to the first three serial positions in the adjacent lists. The bar graphs demonstrate the similarity between SP2 and SP3 to the boundary item compared to the same serial position in the corresponding list. The bar colors reflect the magnitude of similarity as shown in (D). **D.** Same as (B) shown in matrix form for *list x*, SP1-3 and SP10-12 to demonstrate the lack of boundary similarity of end-list items. The black arrows indicate the first serial position (SP1) of the adjacent lists and emphasize the presence of boundary representation. The similarity of *list x*, SP2 and SP3 to the boundary is statistically tested in (C) (gray axes). All error bars indicate $\pm 1\text{SEM}$.

connection to recall success. Non-recalled items tended to show higher boundary similarity at the end of the list. Conversely, recalled items showed greater boundary similarity at the beginning of the list but not at the end of the list. Taken together, the greater preservation of boundary-related information seems to support recall for primacy items but not recency items.

Discussion

In the present study, we explored the role of task boundaries in shaping the contextual representation in episodic memory. In a delayed free recall task, we used the beginning and end of the list as repeated boundaries to investigate their influence on drift, specifically examining regional variation. In the medial parietal lobe, we discovered items adjacent to boundaries shared remarkable similarity across multiple lists, indicative of a recurring boundary signal. The strength of the boundary signal correlated with the successful recollection of boundary items. Next, we show the boundary signal is also present in serial positions two and three items removed from the boundary, further supporting the role of a boundary as a key feature of (associative) context for these items. Finally, we demonstrate evidence of recurring feature similarity for end of list boundaries (recency). However, unlike primacy items, we did not observe enhanced similarity for successfully recalled items raising the possibility that recency boundaries interfere with (rather than enhance) encoding processes. Overall, our study suggests a regional sensitivity to distinct contextual elements which, depending on the serial position, can variably affect item recall.

We began by presenting evidence that drift in the gamma spectrum is a memory relevant phenomenon. Our findings corroborate existing evidence suggesting neural drift is a marker of association between related memories ([Howard and Natu, 2005](#); [Buzsaki and Tingley, 2018](#)). Previous investigations found drift in the lateral temporal context contributed to successful recall of related items ([El-Kalliny et al., 2019](#)). Gamma oscillations also coordinate contextually relevant neuronal assemblies ([Umbach et al., 2022](#)). Our results build on this finding by characterizing drift in gamma oscillations and further describing how gamma activity is associated with context.

We also found a higher rate of gamma signal drift between successfully recalled items. This elevated drift rate might allow the representations of recalled items to remain distinct but ordered in memory. These findings align with several previous studies describing drift in item representations only when temporal order information is preserved ([Hsieh et al., 2014](#); [Hsieh and Ranganath, 2015](#); [Howard and Eichenbaum, 2015](#)). More generally, our findings support the mnemonic relevance of high frequency oscillations.

Next, we asked how gamma spectral activity reflects contextual association between items. In the medial parietal lobe, we observed recurring similarity between items distant in time but adjacent to boundaries. This pattern suggests spectral activity may carry information about an item's relationship to a boundary. These observations align with the Context Maintenance and Retrieval model ([Polyn et al., 2009, 2012](#)) which extends the predictions of TCM to encompass broader relationships among items. Our results specify the spectral and regional properties of boundary-related features and demonstrate boundaries as an important aspect of context in episodic memory.

Our main finding shows specific similarity of serial position 1 across multiple lists (**Figure 3**). Notably, this position lacks a preceding item, leading us to propose that the context for the first item may be the boundary itself. The behavioral association between boundary-related features in medial parietal cortex and recall fraction for serial position 1 items further supports the importance of this information in memory. Then, in accordance with TCM, the context for the second item would be derived from the first item, supported by the pronounced boundary signal in SP2 and SP3 (**Figure 4**). These results suggest that boundary representation might hold a

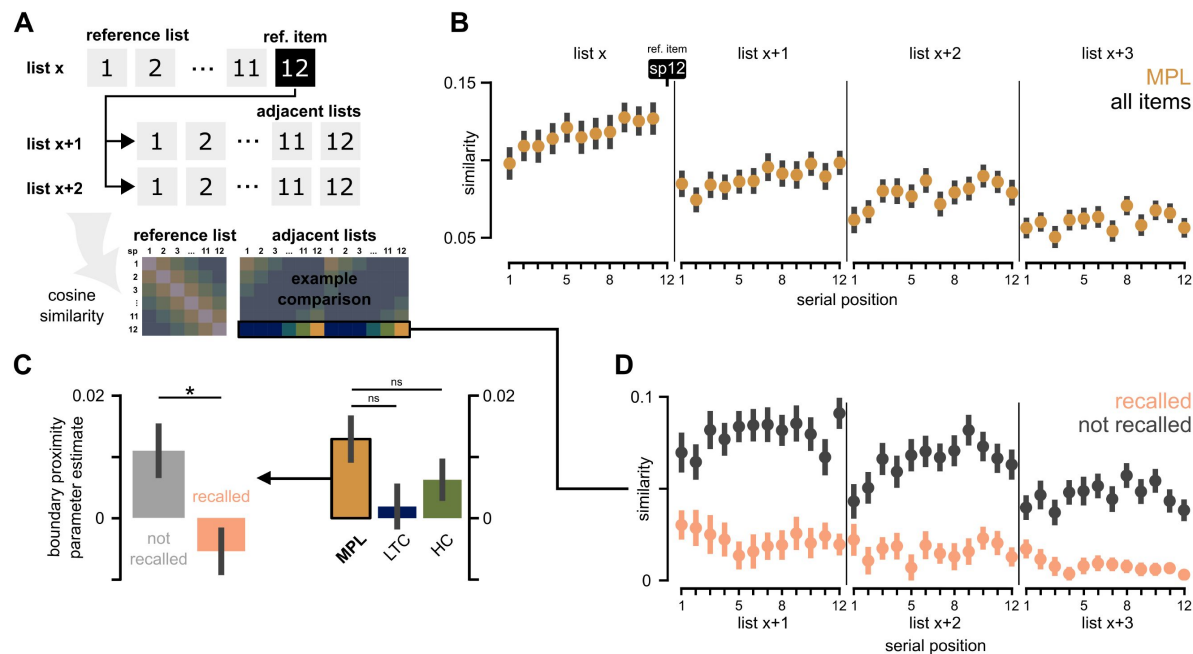


Figure 5.

The last item shares similarity to other items at the end of adjacent lists in the MPL.

A. Schematic of the predicted similarity between the last item in a list *list x*, SP12 to each item in the adjacent lists. **B.** Mean similarity of all serial positions to the reference item (*list x*, SP12) regardless of recollection (top). This shows the similarity of end-list items to other end-list items across adjacent lists. Importantly, the last item in each list (SP12) is not similar to SP1 of the adjacent list despite the temporal proximity. The error bars demonstrate ± 1 SEM of variation in average similarity between participants. **C.** The mean parameter estimate of the predictor for boundary proximity fit to average similarity data from the MPL for recalled versus non-recalled items (left; recalled: pink, mean $\beta = -0.006$; non-recalled: orange, mean $\beta = 0.012$). Additionally, the mean parameter estimate for all items between regions. (Right; MPL: $n = 83$, mean $\beta = 0.011$; LTC: $n = 81$, mean $\beta = 0.005$; HC: $n = 76$, mean $\beta = 0.003$). **D.** Same as **B** for recalled pairs only. All error bars indicate the ± 1 SEM.

Figure 5—figure supplement 1 [DOI:10.7554/eLife.90576.2](#). End-list items show partial boundary similarity to end-list items across multiple regions

critical role in primacy items specifically. Previous work also supports the idea of boundaries as drivers of primacy memory ([Pu et al., 2022](#); [Polyn et al., 2012](#)). Pu and colleagues introduced random boundaries in a task of ordered memory and reported an enhanced recollection of items immediately after the boundary, which they coined a local-primacy effect. Taken together, boundary representation may hold a critical role in consolidating primacy items in memory, introducing a new facet to our understanding of the primacy effect.

Conversely, an opposite effect of boundary representation was present for end of list items, showing an unexpected relationship of the end-list boundary with recall success. We found spectral similarity among these items when they are not recalled. Yet, when an end-of-list item is recalled, the item shares minimal similarity to succeeding items. This suggests distinctiveness is more important for recency items than their association with a boundary. Stated another way, for recency items, drift-like features consistent with predictions of the temporal context model may principally provide a cue for recall rather boundary information. Our findings suggest a broader scope of contextual association than just prior items, where temporal proximity as well as task structure in the form of boundaries, play intertwined roles in contextual construction. Our data therefore have implications for updated iterations of the temporal context model incorporating (perhaps) specific terms for boundary information. This may in turn provide a more systematic prediction of primacy effects in behavioral data.

Next, we propose drift is governed by varying contextual features. In the medial parietal lobe, spectral activity aligned closely with task boundaries. Drift between item pairs seemed to reset at each boundary, leading to renewed similarity after each boundary. This observation aligns with previous work suggesting boundaries reset temporal context ([Pu et al., 2022](#)). In the temporal cortex, our findings extend prior studies which suggest the temporal lobe may play a role in associating adjacently presented items ([Yaffe et al., 2014](#); [El-Kalliny et al., 2019](#)). We found items encoded in distant serial positions, but within the same list, drifted significantly more than items from nearby serial positions (**Figure 2C**). Consistent with the predictions of the temporal context model, the reduced similarity between distant items may reflect reduced contextual overlap proportional to the time elapsed between them. However, across task boundaries, our study did not detect a robust change in drift pattern in the medial or lateral temporal cortex. This finding contrasts with significant work ([Ben-Yakov and Henson, 2018](#); [Ezzyat and Davachi, 2014](#); [Griffiths and Fuentemilla, 2019](#)) which shows hippocampal sensitivity to event-boundaries. One interpretation would be that boundary representations in the hippocampus are quite sparse and represented by populations of time-sensitive cells whose activity is indexed to task-related boundaries ([Umbach et al., 2020](#)). While the sparse representations may not be detectable in gamma activity, perhaps it suggests drift in these regions represents a more abstract set of contextual features accumulated from multiple brain regions ([Baldassano et al., 2017](#)).

Finally, we build on the idea of boundary-modulated drift by proposing region-specific drift rates that occurs relative to distinct contextual features. The presence of boundary representations in the medial parietal lobe aligns with prior suggestions that the posterior medial network plays a role in constructing situational models ([Ranganath and Ritchey, 2012](#)). This differential sensitivity to contextual features may underlie more complex, multi-dimensional contextual associations. In free recall, temporal relationships are thought to dominate. However, our work suggests the incorporation of an additional, boundary-oriented feature of context plays an equally crucial role in organizing episodic memory.

Methods and Materials

Participants

This study included 99 human adult subjects (age: 39.0±11.1 years old, mean±sd; 45 female) from the University of Texas Southwestern Medical Center (UTSW) who underwent intracranial electroencephalographic (iEEG) electrode implantation for drug-resistant epilepsy. Electrode locations were chosen by a clinical team for seizure mapping. The UTSW institutional review board approved this study and each participant provided informed consent.

Experimental design

Participants performed a delayed free recall task. Each session consisted of 25 lists of 12 common nouns, selected at random without replacement (<http://memory.psych.upenn.edu/WordPools>). During the encoding phase, each item in a list was shown for 1.6 seconds interspersed with a 1-second cross between events followed by a 30 second arithmetic distractor task. Participants were then asked to recall as many words as possible from the immediately preceding list in a 30 second retrieval period.

Intracranial recordings

iEEG signal was recorded continuously for all implanted electrodes (Ad-tech or PMT depth electrodes, 0.8 mm) at 1000Hz for an entire session on a Nihon-Kohden 2100 clinical system. Contacts were localized by manual review by a clinical radiologist. The set of included participants included in this study had at least 1 electrode in the lateral temporal cortex (LTC; superior and medial temporal gyri), medial parietal lobe (MPL; posterior cingulate cortex and precuneus), or hippocampus (HC). Any electrodes in epileptogenic tissue or showing inter-ictal patterns were excluded from the dataset. Continuous iEEG data was time stamped at the beginning of each encoding event, distractor task, and retrieval event. Only encoding data, the 1600ms during which the word was on-screen, was considered in subjects who recalled at least 20 words in a session.

Power and similarity analyses

Signal pre-processing and oscillatory power analyses were performed with MATLAB (The MathWorks, Inc., Natick Massachusetts, United States) and Python using a combination of custom scripts and established EEG analysis toolboxes. EEG signals were downsampled to 500Hz and filtered using a band-pass filter between 2Hz and 100Hz. The spectral power was calculated by convolving with a complex Morlet wavelets (wave number = 6) for 10 linearly spaced frequencies in the gamma band (30-100Hz) excluding 1 frequency (63Hz) due to its proximity to 60Hz line noise were included in further analysis. Spectral data was log-transformed and z-scored per frequency in reference to baseline activity (-450ms to -250ms prior to item presentation). These methods align closely to established pre-processing pipelines ([Long et al., 2017](#); [Tan et al., 2020](#); [Cohen, 2014](#)).

The gamma time-frequency matrix was collapsed into a feature vector per event for principal component analysis (PCA) in MATLAB. PCA was applied to all encoding events per electrode. The 3 principal components with the highest explained variance were then used to reconstruct the power spectrum in time-frequency space ([Buzzell et al., 2022](#)). Each item-item comparison described below was calculated using cosine similarity according to the formula:

$$\text{cosine similarity} = \frac{A \cdot B}{\|A\| \|B\|},$$

where *A* and *B* are the PCA-reconstructed gamma signal collapsed into a 1-dimensional time-frequency vector for the entire encoding duration of an event (1.6 seconds).

Within list and across lists analyses

We conducted an item-item similarity analysis with a focus on change in similarity with increasing distance between items. We refer to a reference item within a reference list (see 3A) and compare that item's spectral map to subsequent items, which we refer to as the target item in a target list. In **Figure 2**, each item in a reference list, denoted *list x*, was compared to every other item in the same list. In **Figures 3** to 5, each reference item was also compared to the items in presented in the next 3 lists, denoted *list x+1*, *x+2*, or *x+3*. Similarity values of item-item comparisons were averaged within electrodes in the region of interest, then within each subject per serial position.

Statistical analysis

In our within-list analysis (**Figure 2**), we employ a mixed effects model to examine the relationship between serial position and similarity amongst items in the same list. The fixed effects in the model were serial position, ranging from 1 to 12, and recall status, included as a binary categorical variable, to capture the interaction between serial position and successful recollection. Random nested terms for each electrode and subject were included to account for group level heterogeneity.

Across **Figures 3** to 5, we used a General Linear Model (GLM) to approximate the relationship between the response variable: cosine similarity between item pairs of increasing inter-item distance, and two predictor variables: boundary proximity and list distance. The goal was to assess the impact of positional distance between items on the spectral similarity of the items. Boundary proximity captured the proximity of each serial position to the beginning or end of a list. For SP1, boundary proximity was quantified according to the equation:

$$\text{boundary proximity}_{sp1} = e^{1-d}$$

where d is the serial position of the target item within its respective list (**Figure 3C**). For SP12, we noted a linear increase in similarity for end-list events. Therefore, the boundary proximity predictor was defined as:

$$\text{boundary proximity}_{sp12} = \frac{d}{SP_{max}}$$

where d is the serial position of the target item in its respective list and SP_{max} is the number of items in each list (**Figure 1C**). The second predictor variable, list distance, quantified the overall decrease in similarity of distant lists. Items in list $x+1$, $x+2$, and $x+3$ were assigned values of 0, 0.5, and 1 respectively. The described GLM was fit to each subject's averaged positional similarity individually and parameter estimates were compared using an unpaired, two-sided t-test between the parameter estimates for each subject across two regions of interest in **Figures 3B** and **5C**.

Behavioral metrics

We calculated temporal clustering factor (TCF) according to previously published methods ([Polyn et al., 2009](#)). For all retrieved words in a list, we determined the encoding serial position. We calculated the difference in encoding position for successively recalled items. If the first two recalled words were from encoding position 1 and 4, the difference would be 3. If the third recalled word was encoded in position 2, the next transition would be -2 (SP4 to SP2). Each transition received a score based on its rank amongst all remaining possible transitions. This metric yields a value per list which was averaged by session to generate an aggregate score of temporal clustering tendency for every subject.

The lagged conditional response probability (CRP) was similarly calculated according to prior studies ([Polyn et al., 2009](#); [Healey et al., 2019](#)). The CRP value at each lag is calculated by dividing the counts of actual transitions at encoding by the counts of possible transitions for each lag. The actual transition is the encoding positional distance between two items at encoding (eg. recalling item 3 then item 1, transition: -1). The possible transitions are calculated from all orders in which the recalled events could have been recalled. By dividing the actual transition count with the possible transition count, a proportion is calculated for each lag. Lagged CRP was calculated for all possible transitions (-11 to 11). The list level calculation is averaged per session at each lag for a subject. This metric quantifies the degree to which items presented together are recalled together and describes the contiguity effect in each participant.

Figures Citations

Acknowledgements

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Figure 2—figure supplement 1.

A. Similarity of serial position 1 to each subsequent item in the same list contrasting when both items are recalled (pink) to when both items are not recalled (green) for electrodes in the medial parietal lobe (LME, $n=83$; $\beta_{SP}=-0.001$, CI:[-0.008, -0.003], $p_{SP}=5.6 \times 10^{-4}$; interaction term: SP x recalled items= -9.2×10^{-4} , CI:[-0.003, 0.004], $p_{interaction}=0.23$). **B.** Same as (A) except for electrodes in the hippocampus (LME, $n=76$; $\beta_{SP}=0.004$, CI:[-0.007, -0.001], $p_{SP}=0.004$; interaction term: SP x recalled items= -0.004 , [-0.008, 0.000], $p_{interaction}=0.054$). All displayed trend lines are for visualization purposes only, the described LME was used to quantify the interaction effect. All error bars indicate ± 1 SEM.

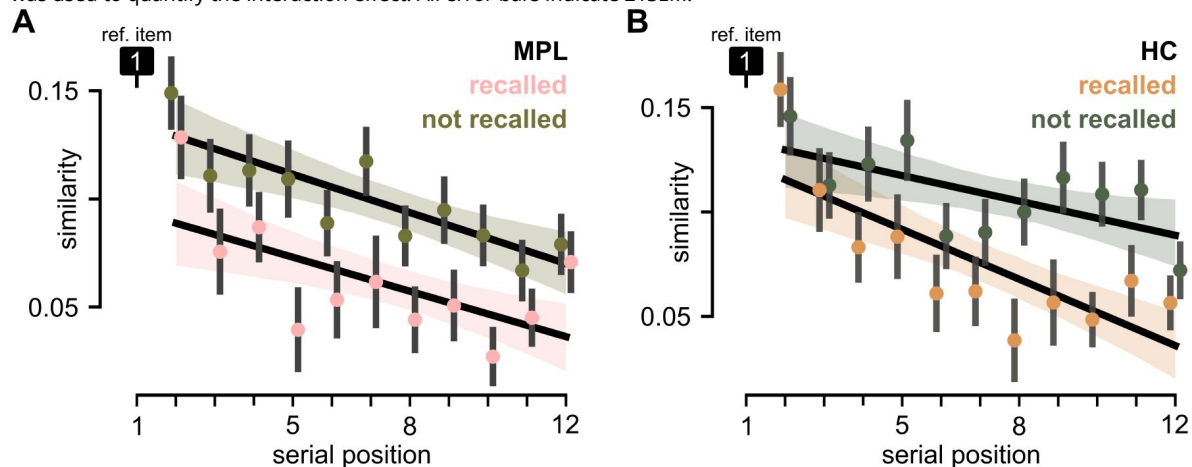
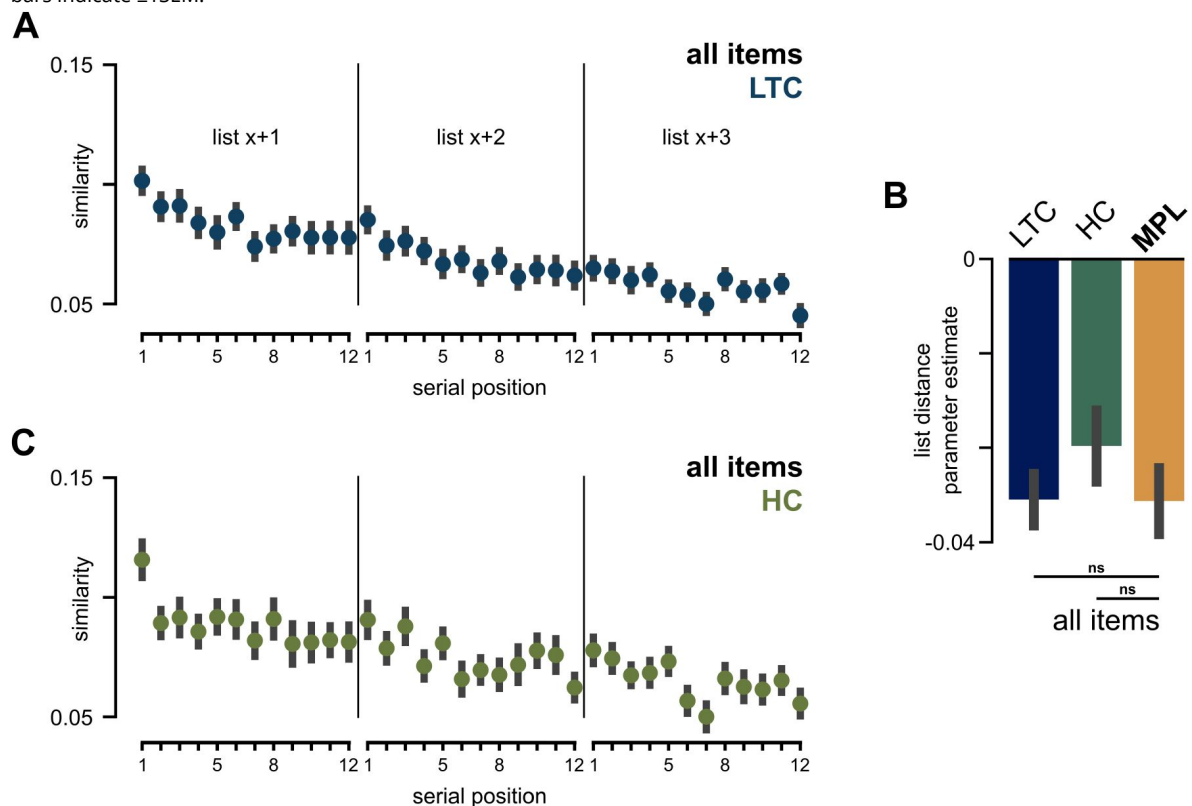


Figure 3—figure supplement 1.

A. Averaged similarity of all item-pairs comparing *list x*, SP1 to each item in *list x+1*, *x+2*, *x+3* for electrodes in the lateral temporal cortex. **B.** The mean parameter estimate of the predictor for list distance contrasted by region for all item pairs (t-test: MPL-LTC, $t(83,81)=0.29$, $p=0.77$; MPL-HC, $t(83,76)=0.91$, $p=0.36$). **C.** Same as (A) for electrodes in the hippocampus. All error bars indicate ± 1 SEM.



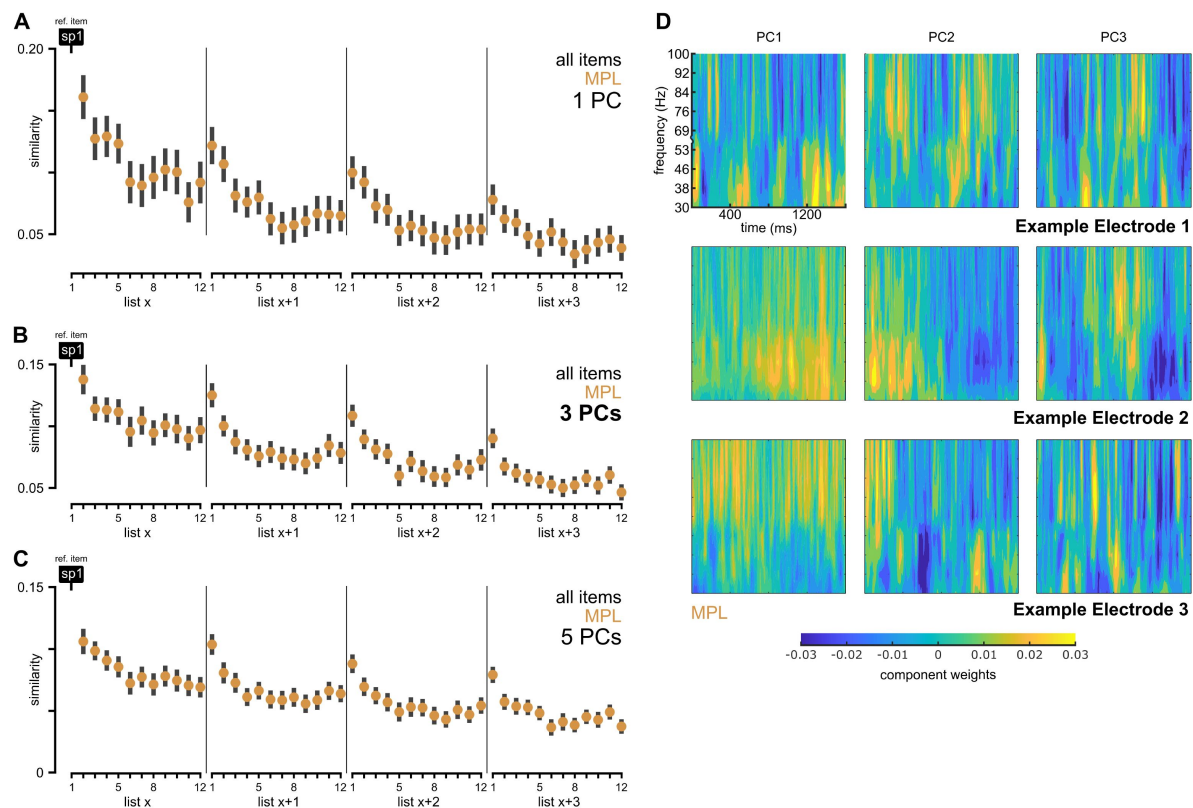


Figure 3—figure supplement 2.

A-C. Averaged similarity of all item-pairs comparing *list x*, *SP1* to each item in *list x+1*, *x+2*, *x+3* for electrodes in the MPL. The figures demonstrate the change in average similarity when 1 principal component (PC; A), 3 PCs (B), and 5 PCs (C) are included in the similarity comparison between item time-frequency representations. **D.** Example component weighting matrices for three unique patients from the MPL. Each column represents the weighting matrix for the three eigenvalues with the highest explained variance. The matrices demonstrate unique time-frequency components underlie similarity between events. All error bars indicate ± 1 SEM.

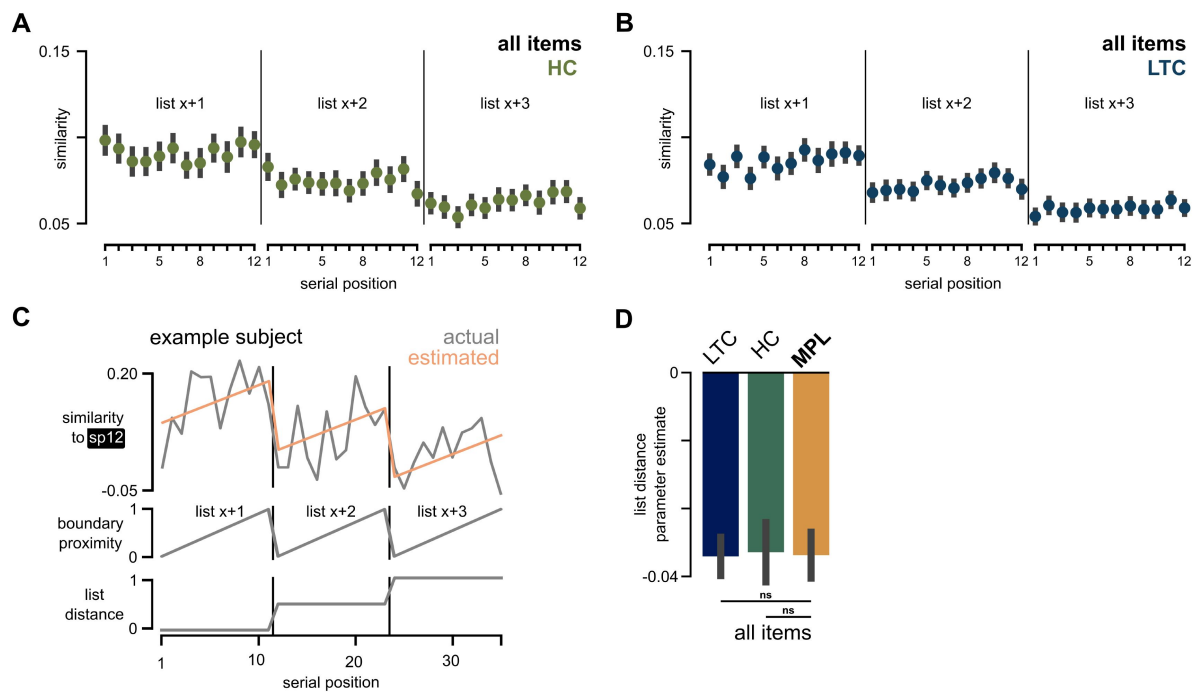


Figure 5—figure supplement 1.

A. Averaged similarity of all item-pairs comparing *list x*, *SP12* to each item in *list x+1*, *x+2*, *x+3* for electrodes in the hippocampus. **B.** Same as (A) for electrodes in the lateral temporal cortex. **C.** Design of the GLM used to fit adjacent list similarity in the MPL for serial position 12. The response variable (similarity to *list x*, *SP12*; gray, top) shown for an example subject with the model prediction (orange, top) overlaid. The predictor variables, boundary proximity (middle) and list distance (bottom), are also shown. **D.** The mean parameter estimate of the predictor for list distance contrasted by region for all item pairs (t-test: MPL-LTC, $t(83,81)=0.15$, $p=0.88$; MPL-HC, $t(83,76)=0.09$, $p=0.93$. All error bars indicate ± 1 SEM. @par

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Editors

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Reviewer #1 (Public Review):

Summary:

This study applied pattern similarity analyses to intracranial EEG recordings to determine how neural drift is related to memory performance in a free recall task. The authors compared neural similarity within and across lists, in order to contrast signals related to contextual drift vs. the onset of event boundaries. They find that within-list neural differentiation in the lateral temporal cortex correlates with probability of word recall; in contrast, across-list pattern similarity in the medial parietal lobe correlates with recall for items near event boundaries (early-list serial positions). This primacy effect persists for the first three items of a list. Medial parietal similarity is also enhanced across lists for end-of-list items, however this effect then predicts forgetting. The authors do not find that within- or across-list pattern similarity in the hippocampus is related to recall probability.

Strengths:

The authors use a large dataset of human intracranial electrophysiological recordings, which gives them high statistical power to compare neural activity and memory across three important memory encoding regions. In so doing, the authors seek to address a timely and important question about the neural mechanisms that underlie the formation of memories for events.

The use of both within and across event pattern similarity analyses, combined with linear mixed effects modeling, is a marriage of techniques that is novel and translatable in principle to other types of data.

Weaknesses:

In several instances the paper does not address apparent inconsistencies between the prior literature and the findings. For example, the first main finding is that recalled items have more differentiated lateral temporal cortex representations within lists than not recalled items. This seems to be the opposite of the prediction from temporal context models that are used to motivate the paper-context models would predict that greater contextual similarity within a list should lead to greater memory through enhanced temporal clustering in recall. This is what El-Kalliny et al (2019) found, using a highly similar design (free recall, intracranial recordings from the lateral temporal lobe). The authors never address this

contradiction in any depth in order to reconcile it with the previous literature and with the motivating theoretical model.

The way that the authors conduct the analysis of medial parietal neural similarity at boundaries leads to results that cannot be conclusively interpreted. The authors report enhanced similarity across lists for the first item in each list, which they interpret as reflecting a qualitatively distinct boundary signal. However, this finding can readily be explained by contextual drift if one assumes that whatever happens at the start of each list is similar or identical across lists (for example, a get ready prompt or reminder of instructions). In other words, this is analogous to presenting the same item at the start of every single list, in which case it is not surprising that the parietal (or any neural) representation would be similar to itself at the start of every list. So, a qualitatively unique boundary representation would not be necessary to explain this result. The authors do not include analyses to rule this out, which makes it difficult to interpret a key finding.

There is a similar absence of interpretation with respect to the previous literature for the data showing enhanced boundary-related similarity in the medial parietal cortex. The authors' interpretation seems to be that they have identified a boundary-specific signal that reflects a large and abrupt change in context, however another plausible interpretation is that enhanced similarity in the medial parietal cortex is related to a representation of a schema for the task structure that has been acquired across repeated instances.

The authors do not directly compare their model to other models that could explain how variability in neural activity predicts memory. One example is the neural fatigue hypothesis, which the authors mention, however there are no analyses or data to suggest that their data is better fit by a boundary/contextual drift mechanism as opposed to neural fatigue.

<https://doi.org/10.7554/eLife.90576.2.sa2>

Reviewer #2 (Public Review):

Summary:

The goal of this study is to clarify how the brain simultaneously represents item-specific temporal information and item-independent boundary information. The authors report spectral EEG data from intracranial patients performing a delayed free recall task. They perform cosine similarity analyses on principal components derived from gamma band power across stimulus duration. The authors find that similarity between items in serial position 1 (SP1) and all other within-list items decreases as a function of serial position, consistent with temporal context models. The authors find that across-list item similarity to SP1 is greatest for SP1 items relative to items from other serial positions, an effect that is greater in medial parietal lobe compared to lateral temporal cortex and hippocampus. The authors conclude that their findings suggest that perceptual boundary information is represented in medial parietal lobe. Despite a robust dataset, the methodological limitations of the study design prevent strong interpretations from being made from these data. The same-serial position across-list similarity may be driven by attentional mechanisms that are distinct from boundary information.

Strengths:

- (1) The motivation of the study is strong as how both temporal contextual drift and event boundaries contribute to memory mechanisms is an important open question.
- (2) The dataset of spectral EEG data from 99 intracranial patients provides the opportunity for precise spatiotemporal investigation of neural memory mechanisms.

Weaknesses:

The goal of reconciling temporal context and event boundary mechanisms is timely and would be of interest; however, an attentional account can still be used to explain the findings. This alternative account is not considered in the manuscript.

(1) The issue related to interpreting the SP1 similarity effects as reflecting boundary specific representations remains in the revised manuscript. The authors suggest that because cross-list SP1 similarity is found in recalled items that this supports the boundary interpretation. However, the effects could still be explained by variability in attention that is not specific to an event-boundary per se. As both subsequently recalled items and primacy items tend to recruit more gamma power than non-recalled and non-primacy items, recalled items will tend to have greater similarity with one another. It does not necessarily follow though that that this similarity is due to a "boundary representation."

(2) The authors partly addressed my concern regarding the comparison of recalled pairs. How did the authors account for the fact that the same participants do not contribute equally to all ROIs? If only participants who have electrodes in all ROIs are included, are the effects consistent?

<https://doi.org/10.7554/eLife.90576.2.sa1>

Reviewer #3 (Public Review):

Summary:

In this study, the authors analyzed data from 99 individuals with implanted electrodes who were performing a word-list recall task. Because the task involves successively encoding and then recalling 25 lists in a row, they were able to measure the similarity in neural responses for items within the same list as well as items across different lists, allowing them to test hypotheses about the impact of between-list boundaries on neural responses. They find that, in addition to slow drift in responses across items within a list and changes across lists, there is boundary-related structure in the medial parietal lobe such that early items in each list show similarity (for recalled items) and late items in each list show similarity (for not recalled items).

Strengths:

The dataset used in this paper is substantially larger than most iEEG datasets, allowing for the detection of nuanced differences between item positions and for analyses of individual differences in boundary-related responses. There are excellent visualizations of the similarity structure between items for each region, and this work connects to a growing literature on the role of event boundaries in structuring neural responses.

Weaknesses:

(1) The visualization in Fig 1B claims that the prediction of the temporal context model is that nearby items in the presented sequence should have similar representations; that is, nearby items within a list should be similar, and the end of a list should look similar to the beginning of the next list. First, it's unclear to me if this is exactly what TCM would predict for this dataset, since lists are separated by ~60 seconds of distractor and retrieval tasks, rather than simply by a brief event boundary. Second, the authors do not actually test this model of continuous similarity across lists. After examining smooth drift in the within-list analysis (Fig 2), the across-list analyses (Figs 3-5) use a model with a "list distance" regressor that predicts discrete changes between lists. The authors state that it is not possible to replace this list

distance regressor with an item distance regressor (which would be a straight line in Fig 3D rather than stair-steps) because this would be too collinear with the boundary proximity regressor, but I do not understand why these regressors would be collinear at all (since the boundary proximity regressor does not systematically increase or decrease across items).

(2) There is no theoretical or quantitative justification for the specific forms of the boundary proximity models. For initial items, a model of $e^{-(1-d)}$ is used (with d being serial position), but it is not stated how the falloff scale of this model was selected (as opposed to e.g. $e^{-((1-d)/2)}$). For final items, a different linear model of d/items is used, which seems to have a somewhat different interpretation, since it changes at a constant rate across all items rather than only modeling items near the final boundary. Confusingly, the schematic in Fig 1B shows symmetric effects at initial and final boundaries, despite two different models being used and the authors' assertion in their response that they do not believe these processes are symmetric.

(3) It is unclear to me whether the authors believe that the observed similarity after boundaries is due to an active process in which "the medial parietal lobe uses drift-resets" to reinstate a boundary-related context, or that this similarity is simply because "the context for the first item may be the boundary itself", and therefore this effect would emerge naturally from a temporal context model that incorporates the full task structure as the "items."

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Author response:

The following is the authors' response to the original reviews.

Reviewer 1:

(1) In several instances the paper does not address apparent inconsistencies between the prior literature and the findings. For example, the first main finding is that recalled items have more differentiated lateral temporal cortex representations within lists than not recalled items. This seems to be the opposite of the prediction from temporal context models that are used to motivate the paper-context models would predict that greater contextual similarity within a list should lead to greater memory through enhanced temporal clustering in recall. This is what El-Kalliny et al (2019) found, using a highly similar design (free recall, intracranial recordings from the lateral temporal lobe). The authors never address this contradiction in any depth to reconcile it with the previous literature and with the motivating theoretical model.

Figure 2 supports the findings from El-Kalliny and colleagues because it shows the relationship of each list item relative to the first item (El-Kalliny et al. 2019). Items encoded adjacent to SP1 show the highest spectral similarity supporting the idea of overlapping context predicted by the Temporal Context Model. However, our figure characterizes how increasing inter-item distance affects spectral similarity. It shows that two items successfully recalled from temporally distant serial positions show reduced spectral similarity. These findings align with the predictions of the temporal context model because two temporally distant items would lack significant contextual overlap and therefore would have more distinct spectral representations.

El-Kalliny and colleagues do use a similar experimental set-up however the authors define drift differently. They identified patients with a tendency to temporally cluster, and observed those patients tend to drift less between temporally clustered items however they do not specify drift relative to a constant serial position as we do in our analysis. They define drift as spectral change between two adjacent items which is a more relative measure between any

two items rather than in relation to a fixed point like SP1. Finally, our analysis focuses only on gamma activity while El-Kalliny and colleagues identified drift across a much broader set of frequency bands.

(2) The way that the authors conduct the analysis of medial parietal neural similarity at boundaries leads to results that cannot be conclusively interpreted. The authors report enhanced similarity across lists for the first item in each list, which they interpret as reflecting a qualitatively distinct boundary signal. However, this finding can readily be explained by contextual drift if one assumes that whatever happens at the start of each list is similar or identical across lists (for example, a get ready prompt or reminder of instructions). The authors do not include analyses to rule this out, which undermines one of the main findings.

Extensions of the temporal context model (Lohnas et al. 2015) predict context at the beginning of a list will be most similar to the end of the prior list. The theory assumes a single-context state, consisting of a recency-weighted average of prior items, that is updated, even across different encoding periods.

However, our results show a boundary item representation is most similar to the prior lists first item rather than the last item. Our results conflict with the extension of TCM because the shared similarity of boundary items suggests the context state for the first item in the list is not a recency-weighted average of the items presented immediately prior. The same boundary sensitive signal is not present in other regions, namely the hippocampus and lateral temporal cortex. Those regions do not show similarity between items at the beginning of each list.

Our main conclusion from these data was that the medial parietal lobe activity seems to be specifically sensitive to task boundaries, defined by the first event or the get ready prompt, while other regions are not.

(3) Although several previous studies have linked hippocampal fMRI and electrophysiological activity at event boundaries with memory performance, the authors do not find similar relationships between hippocampal activity, event boundaries, and memory. There are potential explanations for why this might be the case, including the distinction between item vs. associative memory, which has been a prominent feature of previous work examining this question. However, the authors do not address these potential explanations (or others) to explain their findings' divergence from prior work - this makes it difficult to interpret and to draw conclusions from the data about the hippocampus' mechanistic role in forming event memories.

The following text was added and revised in the discussion to discuss hippocampal activity shown in our results and its lack of sensitivity to boundaries.

“Spectral activity in the medial parietal lobe aligned closely with boundaries. Drift between item pairs seemed to reset at each boundary, leading to renewed similarity after each boundary. This observation aligns with previous work suggesting boundaries reset temporal context. In the temporal cortex, our findings extend prior studies which suggest the temporal lobe may play a role in associating adjacently presented items (Yaffe et al. 2014, ElKalliny et al 2019). We found items encoded in distant serial positions, but within the same list, drifted significantly more than items from adjacent serial positions (Figure 2C). Consistent with the predictions of the temporal context model, the reduced similarity between distant items may reflect reduced contextual overlap proportional to the time elapsed between them. However, across task boundaries, our study did not detect a robust change in drift rate in the medial or lateral temporal cortex. This finding contrasts with significant work (Ben-Yakov et al. 2018, Ezzyat et al. 2014; Griffiths et al. 2020) which shows hippocampal sensitivity to event-

boundaries. One interpretation would be that boundary representations in the hippocampus are quite sparse and represented by populations of time-sensitive cells whose activity is indexed to task-related boundaries (Umbach et al. 2020). While the sparse representations may not be detectable in gamma activity, perhaps it suggests drift in these regions represents a more abstract set of contextual features accumulated from multiple brain regions.”

(4) There is a similar absence of interpretation with respect to the previous literature for the data showing enhanced boundary-related similarity in the medial parietal cortex. The authors’ interpretation seems to be that they have identified a boundary-specific signal that reflects a large and abrupt change in context, however, another plausible interpretation is that enhanced similarity in the medial parietal cortex is related to a representation of a schema for the task structure that has been acquired across repeated instances.

We agree our results could suggest the MPL creates a generalized situational model or schematic of the task. Unfortunately, our behavioral task does not allow us to differentiate between these ideas and pure boundary representation. However, given boundaries are a component in defining situational models, we chose to interpret our results conservatively as a form of boundary representation.

(5) The authors do not directly compare their model to other models that could explain how variability in neural activity predicts memory. One example is the neural fatigue hypothesis, which the authors mention, however there are no analyses or data to suggest that their data is better fit by a boundary/contextual drift mechanism as opposed to neural fatigue.

The study by Lohnas and colleagues does find higher HFA was greater for recalled items but does not describe a serial position specific trend (Lohnas et al. 2020). For our study, we stringently controlled for recall success in each of our analyses. Our main finding of boundary similarity compares recalled boundary items to recalled items in each of the other serial positions. We also show the similarity of nonrecalled items in all serial positions to demonstrate the lack of boundary representation in first list items, when neural fatigue is presumably least present.

In addition, their study demonstrated neural fatigue in the hippocampus. They did not find evidence of fatigue in the DLPFC, suggesting region-specific mechanisms of neural fatigue. Our results are focused on the medial parietal lobe, and we were not able to find a fatigue model of the region for further comparison. While our results do not rule out the possibility of neural fatigue driving a drifting or boundary signal, we focus on the relevance of the signal to memory performance.

(6) P2. Line 65 cites Polyn et al (2009b) as an example where ‘random’ boundary insertions improve subsequent memory. However, the boundaries in that study always occurred at the same serial position and were therefore completely predictable and not random.

The citation was removed from the corresponding sentence.

(7) P2. Line 74 cites Pu et al. (2022) as an example of medial temporal lobe ‘regional activity’ showing sensitivity to event boundaries; however, this paper reported behavioral and computational modeling results and did not include measurement of neural activity.

The citation was removed from the corresponding sentence.

(8) P.3 Line 117, Hseih et al (2014) and Hseih and Ranganath (2015) are cited as evidence that 'spectral' relatedness decreases as a function of distance, but neither of these studies examined 'spectral' activity (fMRI univariate and multivariate). The manuscript would benefit from a careful review and updating of how the prior literature is cited, which will increase the impact of the findings for readers.

The text has been updated to reflect this distinction by modifying the statement to: “Previous work consistent with temporal context models suggests neural pattern similarity reduces as a function of distance between related memories.”

(9) Several previous studies have found hippocampal activity at event boundaries correlates with memory performance (Ben-Yakov et al 2011, 2018; Baldassano et al 2017), yet here the authors do not find evidence for hippocampal activity at event boundaries related to memory. Does this difference reflect something important about how the hippocampus vs. medial parietal cortex vs. lateral temporal cortex contribute to memory formation? Currently, there is not much discussion about how to interpret the differences between brain regions. Previous work has suggested that hippocampal pattern similarity at event boundaries specifically supports associative memory across events (Ezzyat & Davachi, 2014; Griffiths & Fuentemilla, 2020; Heusser et al., 2016), which may help explain their findings. In any case the authors could increase the impact of their paper by further situating their findings within the previous literature.

We would not suggest there is no boundary-related activity in the hippocampus. Similar to an earlier point made by the reviewer, to clarify our interpretation of regional differences, the following text has been added to the discussion.

“However, across task boundaries, our study did not detect a robust change in drift rate in the medial or lateral temporal cortex. This finding contrasts with significant work (Ezzyat and Davachi, 2014; Griffiths and Fuentemilla, 2020) which shows hippocampal sensitivity to event-boundaries. One interpretation would be that boundary representations in the hippocampus are quite sparse and represented by populations of time-sensitive cells whose activity is indexed to task-related boundaries (Umbach et al 2020). While the sparse representations may not be detectable in gamma activity, perhaps it suggests drift in these regions represents a more abstract set of contextual features accumulated from multiple brain regions (Baldassano et al. 2017). “

(10) The authors mention neural fatigue as an alternative theory to explain the primacy effect (Serruya et al., 2014), however there are no analyses or data to suggest that their data is better fit by a boundary mechanism as opposed to neural fatigue. Previous studies have shown that gamma activity in the hippocampus changes with serial position and with encoding history (Serruya et al 2014; Lohnas et al 2020). Here, the authors could compare the reported pattern similarity results to control analyses that replicate this prior work, which would strengthen their argument that there is unique information at boundaries that is distinct from a neural fatigue signal.

The serial position effects described by Serruya and colleagues describe decreasing HFA with increasing serial position in the MTL, lateral temporal cortex and prefrontal cortex (Serruya et al. 2014). Despite their findings, we do not observe a strong boundary effect in those regions (see Supp Fig 3 a,b). The lack of boundary effect in regions where HFA is selectively increased for primacy items suggests the global neural fatigue model does not account for our results.

Notably, the authors do not characterize HFA trends in the MPL. Nevertheless, their findings do not rule out the possibility of a boundary effect driving the HFA. We demonstrate

boundary-relevant HFA only in the MPL but not in other regions. In addition, we show a correlation between SP1 recalls and boundary representation strength, as well as a conserved similarity of multiple boundary-adjacent items.

Next, the neural fatigue study by Lohnas and colleagues does find higher HFA was greater for recalled items but does not describe a serial position specific trend (Lohnas et al. 2015). For our study, we stringently controlled for recall success in each of our analyses. Our main finding of boundary similarity compares recalled boundary items to recalled items in each of the other serial positions. We also show the similarity of non-recalled items in all serial positions to demonstrate the lack of boundary representation in the first list items, when neural fatigue is presumably least present.

In addition, their study demonstrated neural fatigue in the hippocampus. They did not find evidence of fatigue in the DLPFC, suggesting region-specific mechanisms of neural fatigue. Our results are focused on the medial parietal lobe, and we were not able to find a fatigue model of the region for further comparison. While our results do not rule out the possibility of neural fatigue driving a drifting or boundary signal, we focus on the relevance of the signal to memory performance.

(11) For the analyses that examine cross-list similarity (e.g. the medial parietal analysis in Figure 3), how did the authors choose the number of lists over which similarity was calculated? Was the selection of this free parameter cross-validated to ensure that it is not overfitting the data? Given that there were 25 lists per session, using the three succeeding lists seems arbitrary. Why not use every list across the whole session?

Given the volume of data, number of patients, and computational time available at our facility, we extended the analysis as far as we could to characterize the observed trend.

(12) P4. Line 155 says that Figure 3C shows example subject data, but it looks like it is actually Figure 3D.

The text was updated to reference the correct figure.

(13) The t-tests on P.4 Line 159 have two sets of degrees of freedom but should only have one.

The t-tests described by Figure 3B represent the mean parameter estimate of the predictor for boundary proximity contrasted by region for all item pairs. The statistical test in this case was an unpaired t-test between parameter estimates for patients with electrodes in each of the regions. The numbers within parentheses represent the sample size, or number of subjects, contributing electrodes to each region.

Reviewer 2:

(1) Because this is not a traditional event boundary study, the data are not ideally positioned to demonstrate boundary specific effects. In a typical study investigating event boundary effects, a series of stimuli are presented and within that series occurs an event boundary – for instance, a change in background color. The power of this design is that all aspects between stimuli are strictly controlled – in particular, the timing – meaning that the only difference between boundary-bridging items is the boundary itself. The current study was not designed in this manner, thus it is not possible to fully control for effects of time or that multiple boundaries occur between study lists (study to distractor, distractor to recall, recall to study). Each list in a free recall study can be considered its own “mini” experiment such that the same mechanisms should theoretically be recruited across any/all lists. There are multiple possible processes engaged at the start of a free

recall study list which may not be specific to event boundaries per se. For example, and as cited by the authors, neural fatigue/attentional decline (and concurrent gamma power decline) may account for serial position effects. Thus, SP1 on all lists will be similar by virtue of the fact that attention/gamma decrease across serial position, which may or may not be a boundary-specific effect. In an extreme example, the analyses currently reported could be performed on an independent dataset with the same design (e.g. 12 word delayed free recall) and such analyses could potentially reveal high similarity between SP1-list1 in the current study and SP1-list1 in the second dataset, effects which could not be specifically attributed to boundaries.

The neural fatigue study by Lohnas and colleagues does find higher HFA was greater for recalled items but does not describe a serial position specific trend (Lohnas et al. 2020). For our study, we stringently controlled for recall success in each of our analyses. Our main finding of boundary similarity compares recalled boundary items to recalled items in each of the other serial positions. We also show the similarity of non-recalled items in all serial positions to demonstrate the lack of boundary representation in the first list items, when neural fatigue is presumably least present.

In addition, their study demonstrated neural fatigue in the hippocampus. They did not find evidence of fatigue in the DLPFC, suggesting region-specific mechanisms of neural fatigue. Our results are focused on the medial parietal lobe, and we were not able to find a fatigue model of the region for further comparison. While our results do not rule out the possibility of neural fatigue driving a drifting or boundary signal, we focus on the relevance of the signal to memory performance.

(2) Comparisons of recalled "pairs" does not account for the lag between those items during study or recall, which based on retrieved context theory and prior findings (e.g. Manning et al., 2011), should modulate similarity between item representations. Although the GLM will capture a linear trend, it will not reveal serial position specific effects. It appears that the betas reported for the SP12 analyses are driven by the fact that similarity with SP12 generally increases across serial position, rather a specific effect of "high similarity to SP12 in adjacent lists" (Page 5, excluding perhaps the comparison with list x+1). It is also unclear how the SP12 similarity analyses support the statement that "end-list items are represented more distinctly, or less similarly, to all succeeding items" (Page 5). It is not clear how the authors account for the fact that the same participants do not contribute equally to all ROIs or if the effects are consistent if only participants who have electrodes in all ROIs are included.

In our study, all pairs are defined by the lag between a reference and target item. The results in Figure 3 show the similarity between each serial position in relation to SP1; Figure 4 shows lag between each serial position relative to SP2 and 3; and Figure 5 shows lag relative to SP12. Each statistical model accounts for the lag by ordering the data by increased inter-item distance. Further, our definition of lag is significantly more rigorous than that used by Manning and colleagues. Our similarity results for Figures 3-5 characterize the change in similarity relative to a constant reference point, such as SP1, rather than a relative reference point, such as +1 lag, which aggregates similarity between pairs such as SP1 to SP2 with SP4 to SP5, which maybe recalled via different memory mechanisms.

In Figure 5, we agree your characterization that 'similarity with SP12 generally increases across serial position' is a more accurate description of the trend. The text has been updated to reflect this by changing the interpretation to "later serial positions in adjacent lists shared a gradually increasing similarity to SP12."

Next, we clarify the statement "end-list items are represented more distinctly, or less similarly, to all succeeding items". When recalling SP12, the subsequent items recalled exhibit significantly lower similarity to SP12 (see Figure 5D, pink). Consequently, the spectral representation of successfully recalled end-list items appears more distinct from later items in similar serial positions. This stands in contrast to our observations illustrated in Figures 3 and 4, where successfully recalled start-list items demonstrate greater similarity to later items in similar serial positions.

(3) The authors use the term "perceptual" boundary which is confusing. First, "perceptual boundary" seems to be a specific subset of the broader term "event boundary," and it is unclear why/how the current study is investigating "perceptual" boundaries specifically. Second and relatedly, the current study does not have a sole "perceptual" boundary (as discussed in point 1 above), it is really a combination of perceptual and conceptual since the task is changing (from recalling the words in the previous list to studying the words in the current list OR studying the words in the current list to solving math problems in the current list) in addition to changes in stimulus presentation.

We agree with the statement that 'perceptual' as a modifier to the boundaries described here does not add significant information. Therefore, we have removed all reference to perceptual boundaries.

(4) Although the results show that item-item similarity in the gamma band decreases across serial position, it is unclear how the present findings further describe "how gamma activity facilitates contextual associations" (Page 5). As mentioned in point 1 above, such effects could be driven by attentional declines across serial position -- and a concurrent decline in gamma power -- which may be unrelated to, and actually potentially impair, the formation of contextual associations, given evidence from the literature that increased gamma power facilitates binding processes.

We agree that our study does not elucidate a mechanistic relationship between gamma power and contextual associations. The referenced sentence has been changed to: "how gamma activity is associated with context".

Please see our response to point 1 above. In addition, studies demonstrating decreasing gamma power with increasing serial position focus primarily on the MTL, lateral temporal cortex and prefrontal cortex (Serruya et al. 2012). Despite their findings, we do not observe a strong boundary effect in those regions (see Supp Fig 3 a,b). The lack of boundary effect in regions where HFA is selectively increased for primacy items suggests the global attentional decline or neural fatigue model does not account for our results.

Notably, HFA trends in the MPL are poorly described. Further, gamma power decline does not rule out the possibility of a boundary effect driving the HFA. We demonstrate boundary-relevant HFA only in the MPL but not in other regions. In addition, we show a correlation between SP1 recalls and boundary representation strength, as well as a conserved similarity of multiple boundary-adjacent items.

(5) Some of the logic and interpretations are inconsistent with the literature. For example, the authors state that "The temporal context model (TCM) suggests that gradual drift in item similarity provides context information to support recovery of individual items" however, this does not seem like an accurate characterization of TCM. According to TCM, context is a recency-weighted average of previous experience. Context "drifts" insofar as information is added to/removed from context. Context drift thus influences item similarity -- it is not that item similarity itself drifts, but that any change in item-item similarity is due to context drift.

The current findings do not appear at odds with the conceptualization of drift and context in current version of the context maintenance and retrieval model. Furthermore, the context representation is posited to include information beyond basic item representations. Two items, regardless of their temporal distance, can be associated with similar contexts if related information is included in both context representations, as predicted and shown for multiple forms of relatedness including semantic relatedness (Manning & Kahana, 2012) and task relatedness (Polyn et al., 2012).

We revised the sentence and encompassing paragraph to describe the temporal context model more accurately and emphasize how our findings align with the stated version of CMR. The revised text is below:

“Next, we asked how gamma spectral activity reflects contextual association between items. In the medial parietal lobe, we observed recurring similarity between items distant in time but adjacent to boundaries. This pattern suggests spectral activity may carry information about an item's relationship to a boundary. These observations align with the Context Maintenance and Retrieval model which extends the predictions of TCM to encompass broader relationships among items. Our results demonstrate boundaries as an important aspect of context and specify the spectral and regional properties of these boundary-related contextual features.”

(6) Lohnas et al. (2020) Neural fatigue influences memory encoding in the human hippocampus, Neuropsychologia, should be cited when discussing neural fatigue

Thank you for your suggestion. The citation has been added to the text.

(7) A within-list, not an across list, similarity analysis should be used to test the interpretation that end-of-list items are more distinct than other list items.

We believe this recommendation refers to the following line in our text: “These findings suggest end-list items are represented more distinctly, or less similarly, to all succeeding items.” Our statement compares list x, SP12 to all succeeding items (in list x+1, x+2, etc.). Therefore, this statement refers to items in the next lists which is why we performed an across list analysis rather than within-list one.

(8) It is unclear why it is necessary to use PCA to estimate similarity between items.

PCA was used to reduce the dimensionality of the time-frequency matrix for the gamma band. This technique allowed us to compare predominant trends in gamma between items. In addition, we added a figure showing 3 example subjects in Figure 3 – supplementary figure 2D to show unique time-frequency components contribute to signal reconstructed from the PCs for each subject. Therefore, the boundary representation may be represented differently for each patient.

(9) Lags are listed as -4, 4 (Page 8), however with a list length of 12, possible lags should be 11, 11.

The listed parenthetical statement ‘(-4 to 4)’ referred to Figure 1 where Lag CRP is shown for transitions from -4 to 4. However, we did calculate lag CRP for all possible transitions. Therefore, the referenced phrase was changed to: “Lagged CRP was calculated for all possible transitions (-11 to 11).”

(10) Hsieh et al. 2014 and Hsieh & Ranganath (2015) are fMRI studies and as such, do not support the statement "Previous work consistent with temporal context models suggests

spectral relatedness reduces as a function of distance between words" (Page 3).

The statement has been revised to: "Previous work consistent with temporal context models suggests neural pattern similarity reduces as a function of distance between related memories."

(11) Although statistically one can measure "How item-item similarity is affected by recollection" (Page 3), this is logically backwards, given that similarity during study necessarily precedes performance during free recall. Additionally, it is erroneous to assume that recalled words are "recollected" without additional measurements (e.g. Mickes et al. (2013) Rethinking familiarity: Remember/Know judgments in free recall, JML).

The statement was changed to "item-item similarity is affected based on successful recall" given recollection cannot be determined in our paradigm.

Reviewer 3:

(1) My primary confusion in the current version of this paper is that the analyses don't seem to directly compare the two proposed models illustrated in Fig 1B, i.e. the temporal context model (with smooth drifts between items, including across lists) versus the boundary model (with similarities across all lists for items near boundaries). After examining smooth drift in the within-list analysis (Fig 2), the across-list analyses (Figs 3-5) use a model with two predictors (boundary proximity and list distance), neither of which is a smoothly drifting context. Therefore there does not appear to be a quantitative analysis supporting the conclusion that in lateral temporal cortex "drift exhibits a relationship with elapsed time regardless of the presences of intervening boundaries" (lines 272-3).

We could not use a smoothly drifting regressor due to its collinearity with any model of boundary similarity. Therefore, we chose our two regressors: boundary proximity, which models intra-list changes in similarity and list distance, which models a stepwise decrease in similarity from adjacent lists.

However, we agree with the comment that the presented data does not directly support the lateral temporal cortex drifts independent of intervening boundaries. Therefore, we amended the statement to: "We found successfully recalled items encoded in distant serial positions drifted significantly more than items from adjacent serial positions (Figure 2C)". Consistent with the predictions of the temporal context model, the reduced similarity between distant items may reflect reduced contextual overlap proportional time elapsed between them."

(2) The feature representation used for the neural response to each item is a gamma power time-frequency matrix. This makes it unclear what characteristics of the neural response are driving the observed similarity effects. It appears that a simple overall scaling of the response after boundaries (stronger responses to initial items during the beginning portion of the 1.6s time window) would lead to the increased cosine similarity between initial items, but wouldn't necessarily reflect meaningful differences in the neural representation or context of these items.

Our study aims to draw the connection between the neural response after boundaries with neural representation and context of these items. Prior studies (Manning et al. 2011, El Kalliny et al. 2017) have interpreted similarity in neural spectra as a memory relevant phenomenon. We use very similar methods to perform our analysis.

In addition, we compare the fit of our boundary similarity model to behavioral performance to show increased boundary representation correlates with improved boundary item recall.

While our study does not specify which time-frequency components underly the increased similarity, we do limit our analysis to the gamma band. Traditional analyses include log-scaled, broadband time-frequency data (eg. 3-100hz) from which we specify the relevance of a much narrower spectral band.

Finally, we tried to study which time–frequency components contributed to the increased similarity, but it varied greatly between patients (see Figure 3 – supplementary figure 2D). Hence, we opted to use principal component analyses to compare the features showing the most variation for each given participant. This added analytical step allows us to detect boundary effects across patients despite individual variability in boundary representation.

(3) The specific form of the boundary proximity models is not well justified. For initial items, a model of $e^{(1-d)}$ is used (with d being serial position), but it is not stated how the falloff scale of this model was selected (as opposed to e.g. $e^{((1-d)/2)}$). For final items, a different model of d/items is used, which seems to have a somewhat different interpretation (about drift between boundaries, rather than an effect specific to items near a final boundary). The schematic in Fig 1B appears to show a hypothesis which is not tested, with symmetric effects at initial and final boundaries.

The boundary proximity models were chosen empirically. Our model was intended to quantify a decreasing relationship across many patients. We acknowledge the constants and variables may not definitively describe underlying neural processes.

For start- and end-list boundaries, we used different models because primacy and recency effects are unique phenomena. Primacy memory is classically thought to arise from rehearsal during the encoding time (Polyn et al. 2009, Lohnas et al. 2015). Alternatively, recency memory is thought to arise from strong contextual cues of recency items during recall due to their temporal proximity. Therefore, we have a limited basis on which to assume their spectral representation in relation to task boundaries would be symmetric.

(4) The main text description of Fig 2 only describes drift effects in lateral temporal cortex, but Fig 2 - supplement 1 shows that there is also drift and a significant subsequent memory effect in the other two ROIs as well. There is not a significant memory x drift slope interaction in these regions; are the authors arguing that the lack of this interaction (different drift rates for remembered versus forgotten items) is critical for interpreting the roles of lateral temporal cortex versus medial parietal and hippocampal regions?

Yes. Fig 2- Supplement 1 shows that drift occurs in both the HC and MPL. However, the interaction term is not significant, which suggests that the rate of drift between recalled and non-recalled items is not significantly different.

In contrast, Fig 2C shows that recalled pairs drift at a higher rate than non-recalled pairs. For the LTC, the interaction term is negative in magnitude and statistically significant. This suggests successfully encoded item pairs encoded far apart share more distinct spectral representations, specifically in the LTC. These findings lead to our interpretation in the discussion that “elevated drift rate might allow the representations of recalled items to remain distinct but ordered in memory.”

(5) The parameter fits for the "list distance" regressor are not shown or analyzed, though they do appear to be important for the observed similarity structure (e.g. Fig 3E). I would

interpret this regressor as also being "boundary-related" in the sense that it assumes discrete changes in similarity at boundaries.

Parameter fits for the 'list distance' regressor are now shown in the supplementary portion of Figures 3 and Figure 5. The difference between regions is non-significant.

(6) To make strong claims about temporal context versus boundary models as implied by Fig 1B, these two regressors should be fit within the same model to explain across-list similarity. The temporal context model could be based on the number of intervening items (as in Fig 1B) or actual time elapsed between items. The relationship between the smoothly drifting temporal context model and the discretely-jumping list distance models should also be clarified.

We could not use a smoothly drifting regressor due to its collinearity with any model of boundary similarity. A model which included a 'temporal context regressor' would not be able to account for the presence of a boundary effect and would not allow us to demonstrate a boundary representation in the presence of drift. Therefore, we chose our two regressors: boundary proximity, which models intra-list changes in similarity and list distance, which models a stepwise decrease in similarity from adjacent lists. These regressors allow the model to differentiate between intra-list changes (the boundary regressor) versus inter-list changes (the list distance regressor).

(7) The features of the time-frequency matrix that are driving similarity between events could be visualized to provide a better understanding of the boundary-related signals. The analysis could also be re-run with reduced versions of the feature space in order to determine the critical components of this signal; for example, responses could be averaged across time to examine only differences across frequencies, or across frequencies to examine purely temporal changes across the 1.6 second window.

Figure 3 – supplementary figure 2 A-C has been added to show varying the number of principal components (PCs) does not change the trend of boundary sensitivity in the MPL. In addition, we included 3 example subjects in Figure 3 – supplementary figure 2D to show unique time-frequency components contribute to signal reconstructed from the PCs for each subject. Therefore, the boundary representation may be represented differently for each patient.

(8) If the authors are considering a space of multiple models as "boundary proximity models" (e.g. linear models and exponential models with different scale factors), this should be part of the model-fitting process rather than a single model being selected posthoc.

We agree with the reviewer's suggestion that the most ideal way to fit a model to the trend would be using a model-fitting process. However, due to a limitation on the amount of computational resources available, we were not able to perform it given the size of our dataset.

(9) The interpretation of region differences in the results in Fig 2 and Fig 2 - supplement 1 should be clarified.

In discussion, we have added the following text to clarify our interpretation of the regional differences shown in the mentioned figures.

"However, across task boundaries, our study did not detect a robust change in drift rate in the medial or lateral temporal cortex. This finding contrasts with significant work (Ezzyat

and Davachi, 2014; Griffiths and Fuentemilla, 2020) which shows hippocampal sensitivity to event-boundaries. One interpretation would be that boundary representations in the hippocampus are quite sparse and represented by populations of time-sensitive cells whose activity is indexed to task-related boundaries (Umbach et al 2018). While the sparse representations may not be detectable in gamma activity, perhaps it suggests drift in these regions represents a more abstract set of contextual features accumulated from multiple brain regions (Baldassano et al. 2017). “

(10) Whether there are significant fits for the list distance regressor, and whether these fits vary across regions, could be stated. The list distance regressor could also be directly compared (in the same model) to a temporal-context regressor, which predicts graded changes in similarity between items rather than the discrete changes between lists.

We have added parameter fits for the ‘list distance’ regressor in the supplementary portion of Figures 3 and Figure 5. The difference between regions is non-significant. Therefore, our results show very similar stepwise decrease in similarity across lists between regions (list distance regressor; Figure 3 —supplementary figure 1B).

We could not compare these parameters to a separate model which includes a smoothly drifting ‘temporal-context’ regressor due to the regressors collinearity with any representation of boundary. See our response to Reviewer 3 –comment 6.

(11) The authors should clarify their interpretation of the results, and whether they are proposing a tweak to the temporal context model or a substantially different organizational system.

In the discussion we include the following statements to clarify what we suggest regarding the temporal context model.

“Our findings suggest a broader scope of contextual association than just prior items, where temporal proximity as well as task structure in the form of boundaries, play intertwined roles in contextual construction. Our data therefore have implications for updated iterations of the temporal context model incorporating (perhaps) specific terms for boundary information. This may in turn provide a more systematic prediction of primacy effects in behavioral data.”

(12) Minor typos and corrections:

52: using -> use

108: patients -> patients' 156: list -> lists

The list distance plot is described as "pink" in Fig 3 and Fig 5 - supplement 1, but appears gray in the figures.

Each of these corrections has been corrected in the text.

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