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Successful memory formation is driven by contextual encoding in the core memory network

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ABSTRACT

To understand how memories are successfully formed, scientists have compared neural activity during the encoding of subsequently remembered and forgotten items. Though this approach has elucidated a network of brain regions involved in memory encoding, this method cannot distinguish broad, non-specific signals from memory specific encoding processes, such as associative encoding. Associative encoding, which is a key mechanism of learning, can be seen in the tendency of participants to successively recall, or cluster, study neighbors. We assessed the electrophysiological correlates of associative processing by comparing intracranially recorded EEG activity during the encoding of items that were subsequently recalled and clustered; recalled and not clustered; or not recalled. We found that high frequency activity (HFA) in left prefrontal cortex, left temporal cortex and hippocampus increased during the encoding of subsequently recalled items. Critically, the magnitude of this effect was largest for those recalled items that were also subsequently clustered. HFA temporally dissociated across regions, with increases in left prefrontal cortex preceding those in hippocampus. Furthermore, late hippocampal HFA positively correlated with behavioral measures of clustering. These results suggest that associative processes linking items to their spatiotemporal context underlie the traditionally observed subsequent memory effect and support successful memory formation.

Introduction

To investigate the neural mechanisms of successful memory formation, scientists compare brain activity measured during the encoding of subsequently remembered and subsequently forgotten items. Neuroimaging studies investigating these subsequent memory effects (SMEs) have revealed that increased activation in a network of temporal and prefrontal cortical regions predict subsequent memory (Wagner et al., 1998; Paller and Wagner, 2002; Kim, 2011; Burke et al., 2014). However, these changes in activation might be due to any number of processes, including increased attention, use of elaborative strategies, or the formation of item-to-context associations. Forgetting an item could be caused by failures of any of these processes. Therefore, to establish whether the SME is driven by memory-specific processes or a mnemonic attentional signal, it is necessary to use a more fine-grained contrast comparing items that vary in *how* they are remembered, not *whether* they are remembered.

In a free recall task, items that are effectively encoded in relation to their context exhibit strong temporal clustering, being recalled in close proximity to their study-list neighbors (Kahana, 1996). By comparing brain activity during the encoding of items that are subsequently clustered with those that are not clustered (defined here as the subsequent clustering effect, SCE), we can isolate the neural correlates of effective item-to-context associative memory encoding. To identify the memory-specific neural mechanisms supporting memory formation, we compared the SCE and SME. We hypothesized two potential outcomes. First, the SCE may be a component of the SME. Activation in the SME might be driven by items that are subsequently clustered, a prediction supported by behavioral evidence showing that increased clustering correlates with high recall success (Sederberg et al., 2010). Alternatively, the SCE and SME may be independent and while clustering may correlate with probability of recall, both may be moderated by a third unknown variable (Brown et al., 1991). In this case, the SME might instead be driven by attentional mechanisms. Elevated attention across a subset of items could enhance recall for those items, but, as clustering arises predominantly from cue dependent retrieval processes (Schwartz et al., 2005; Howard et al., 2008), enhanced attention would be unlikely to give rise to the substantial clustering effects that are typically observed.

We analyzed intracranial electroencephalographic (iEEG) data from neurosurgical patients participating in a free recall task. The recorded iEEG signals simultaneously sample local field potentials throughout the brain, and can be analyzed in terms of specific time-varying oscillatory or spectral components of neural activity. Using brain regions selected *a priori* based on previous subsequent memory studies, we measured the spectral signals during encoding of words that were later clustered; later recalled and not clustered; or later forgotten.

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To foreshadow our results, we found that high frequency activity (HFA, 44–100 Hz) in the memory network tracked effective contextual encoding with greater HFA for subsequently clustered compared to subsequently recalled non-clustered items. Furthermore, we found that the timing of this effect dissociated across regions: left prefrontal cortex clustering related increases in HFA preceded those in hippocampus and late hippocampal HFA was correlated with the behavioral tendency to cluster responses.

Materials and methods

Participants

136 participants (58 female; age range: 8–57, mean = 33) with medication-resistant epilepsy underwent a surgical procedure in which electrodes were implanted subdurally on the cortical surface and deep within the brain parenchyma. In each case, the clinical team determined electrode placement so as to best localize epileptogenic regions. Data were collected as part of a long-term multicenter study; data were collected at Boston Children's Hospital, Hospital of the University of Pennsylvania, Freiburg University Hospital, and Thomas Jefferson University Hospital. The institutional review board at each hospital approved the research protocol. We obtained informed consent from the participants or their guardians. Participants were left-hemispheric language dominant as assessed by either the participants' handedness or a clinically administered intracarotid injection of sodium amobarbital (Wada test). Clinical need determined the electrode placements and the total number of participants contributing to each region of interest ranged from 60 (left inferior frontal gyrus) to 86 (left inferior temporal cortex). Although portions of this dataset were previously reported (Burke et al., 2014; Long et al., 2014), all of the analyses and results described here are novel. The raw, de-identified data as well as the associated codes used in this study can be accessed at the Cognitive Electrophysiology Data Portal (http://memory.psych.upenn.edu/Electrophysiological_Data).

Intracranial recordings

iEEG data were recorded using a Bio-Logic, DeltaMed, Nicolet, GrassTelefactor, or Nihon Kohden EEG system. Depending on the amplifier and the discretion of the clinical team, the signals were sampled at 256, 400, 500, 512, 1000, 1024, or 2000 Hz. Signals were referenced to a common contact placed either intracranially or on the scalp or mastoid process. Contact localization was accomplished by co-registering the post-op CTs with the MRIs using FSL Brain Extraction Tool (BET) and FLIRT software packages. Contact locations were then mapped to both MNI and Talairach space using an indirect stereotactic technique. Depth electrodes were manually localized by a neuroradiologist experienced in neuroanatomical localization utilizing post-operative MRIs and CT images in order to accurately identify all depth contacts located within the hippocampus. For each participant and electrode, the raw EEG signal was downsampled to 200 Hz and a fourth order 2 Hz stopband butterworth notch filter was applied at 50 or 60 Hz to eliminate electrical line noise.

Free recall task

Participants studied lists of 15 or 20 high-frequency nouns for a delayed free recall task (Fig. 1A). The computer displayed each word for 1600 ms, followed by an 800 to 1200 ms blank interstimulus interval. Immediately following the final word in each list, participants were given a series of arithmetic problems of the form A + B + C = ??, where A, B and C were randomly chosen integers ranging from 1–9. This distractor interval lasted at least 20 s, but participants were allowed to complete any problem that they started resulting in an average retention interval of 25 s. After the distractor, participants had 45 s to freely recall as many words as possible from the list in any order. Vocalizations were digitally recorded and later manually scored for analysis. On average, participants participated in two sessions.

Data analyses and spectral power

Two concerns when analyzing bivariate interactions between closely spaced intracranial contacts are volume conduction and confounding interactions with the reference line. We used bipolar referencing to eliminate such confounds when analyzing the neural signal (Nunez and Srinivasan, 2006). We found the difference in voltage between pairs of immediately adjacent electrodes (Burke et al., 2013). The resulting bipolar signals were treated as new virtual electrodes and are referred to as such throughout the text. Analog pulses synchronized the electrophysiological recordings with behavioral events.

We applied the Morlet wavelet transform (wave number 6) to all bipolar electrode EEG signals from 300 ms preceding to 1600 ms following word presentation, across 46 logarithmically spaces frequencies (2–100 Hz). We included a 1000 ms buffer on both sides of the data to minimize edge effects. After log transforming the power, we downsampled the data by taking a moving average across 100 ms time windows and sliding the window every 50 ms, resulting in 31 time intervals (16 non-overlapping) from −300 ms to 1600 ms surrounding stimulus presentation. Power values were then Z-transformed within session by subtracting the mean and dividing by the standard deviation power. Mean and standard deviation power were calculated across all encoding events and time points in a session for each frequency. We split the Z-transformed power into six distinct frequency bands (θ_L, 3–4 Hz; θ_H, 6–8 Hz; α, 10–14 Hz; β, 16–26 Hz; γ_L, 28–42 Hz; γ_H, 44–100 Hz; Sederberg et al., 2006), by taking the mean of the Z-transformed power in each frequency band. We included two theta bands as there is evidence for distinct slow and fast theta bands (Lega et al., 2011).

Our conditions of interest were subsequently recalled clustered items, study items recalled either preceding *or* following the recall of a study neighbor (absolute lag between serial position of items was 1), subsequent recalled non-clustered items, study items recalled preceding *and* following the recall of a non-neighboring study item (absolute lag between serial position of items was 2 or greater), and subsequently not recalled items. Across participants there were on average 44 clustered items, 56 non-clustered items, and 358 not recalled items. A participant had to have a minimum of 5 items per condition to be included in the analysis, 126 participants met this criterion.

Our two contrasts were between subsequently recalled and forgotten items and between subsequently clustered and non-clustered items. For each contrast of interest and for each participant, electrode and frequency band, we calculated Z-transformed power in each of two conditions. We averaged Z-power values across electrodes within a region of interest (ROI) as we were interested in effects consistent across an ROI and not regional differences within an ROI. Therefore, each participant contributed a single Z-power value for each of two conditions for each ROI. Conditions were compared across participants within an ROI and frequency using a paired *t*-test.

Region of interest selection and analysis

The three ROIs were derived from several recent large scale studies suggesting that these are core regions in the memory network (Kim, 2011; Burke et al., 2014; Long et al., 2014). We defined ROIs using Brodmann area or neuroradiological localization and included left inferior frontal gyrus (LIFG, BA 45/47, N = 60), left inferior temporal lobe (LIT, BA 20/21, N = 86) and hippocampus (N = 64). Each participant had at least two electrode pairs in a given ROI.

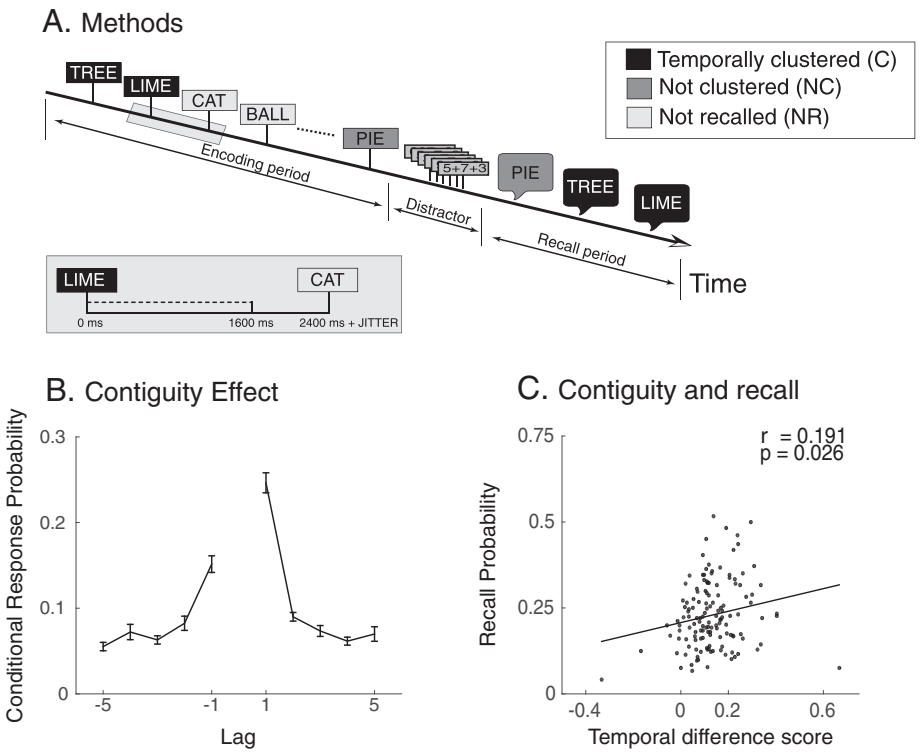

Fig. 1. Methods and behavioral results. (A) Methods. During the encoding period, participants viewed words presented for 1600 ms and separated by a variable interstimulus interval. Following the last item on the list, participants performed a math distractor task, after which they recalled the study items in any order. Encoding items were divided into three conditions based on how they were recalled: temporally clustered (C, black) or recalled preceding or following a study neighbor, e.g. tree and lime; not clustered (NC, dark grey) or recalled preceding and following non-neighboring study items; or not recalled (NR, light grey). **(B)** Conditional response probability as a function of lag (the difference in serial position of two studied items). The figure shows the likelihood of making a transition from item *i* to item *i* +/− lag. Participants are more likely to transition to nearby (small absolute lag) items than to distant (large absolute lag) items. Error bars are standard errors of the mean. **(C)** Recall probability, the overall proportion of items recalled, is positively correlated with temporal difference score, the difference in likelihood of making nearby (+/− 1 lag) relative to distant (+/− 3 to 5 lag) transitions (each point is a participant).

Peak time analysis

Using previous methods (Burke et al., 2014), we analyzed the temporal specificity of the subsequent clustering effect. Within each ROI and each participant, we found the time point of the maximum (peak) difference in Z-power between subsequently clustered and non-clustered items. As the resulting distributions of peak times were not normally distributed (see *Results*), we compared peak times across ROIs using a non-parametric Wilcoxon rank sum test.

Results

Before examining the spectral components of the subsequent memory and clustering effects, we report the basic behavioral data. Participants recalled on average 23% of studied items (SD = 10%). Participants were more likely to make recall transitions between neighboring study items than between non-neighboring study items (Fig. 1B), replicating the lag contiguity effect (Kahana, 1996). We quantified this tendency to cluster with a *temporal difference score*: the probability of making a transition of absolute lag of 1 minus the average probability of making a transition of absolute lag of 3 through 5 (Kahana, 1996). The average temporal difference score .13 was significantly greater than zero ($t(135) = 14.0$, $p < .01$) and was positively correlated with probability of recall ($r = .19$, $p = .03$, Fig. 1C), replicating previous findings (Sederberg et al., 2010). These results show that iEEG patients, like healthy controls, cluster their recalls and that the tendency to cluster is positively related to overall performance.

We characterized the spectral components of the subsequent memory and clustering effects by comparing Z-power across items subsequently recalled and forgotten (SME) or items subsequently clustered and not clustered (SCE). Clustered items were recalled either preceding *or* following the recall of a study neighbor. Non-clustered items were recalled preceding *and* following the recall of a non-neighboring study item. We ran a paired *t*-test comparing Z-power across the encoding interval (0–1600 ms) in six frequency bands (θ_L, 3–4 Hz; θ_H, 6–8 Hz; α, 10–14 Hz; β, 16–26 Hz; γ_L, 28–42 Hz; γ_H,44–100 Hz) for each contrast.

The subsequent memory analysis revealed high frequency activity (HFA, 44–100 Hz) increases and low frequency activity decreases in left inferior frontal gyrus (LIFG), left inferior temporal lobe (LIT), and hippocampus ($ts > 2.0$, $ps < .05$; Fig. 2A), replicating previous results (Burke et al., 2014; Long et al., 2014). The subsequent clustering analysis revealed HFA increases in LIFG ($t(54) = 2.0$, $p = .053$), LIT ($t(79) = 2.2$, $p = .03$), and hippocampus ($t(60) = 2.3$, $p = .02$; Fig. 2B).

We have shown that subsequent clustering is characterized by HFA increases in the SME network. To test whether these signals reflect the formation of an item-to-context association, we compared HFA across the pre- and post-stimulus intervals. A memory specific signal reflecting the formation of a bound item-to-context representation should be restricted to the post-stimulus interval, as such an association cannot be formed before an item is presented. Therefore, we tested the post-stimulus specificity of the SCE in our ROIs. Using a paired *t*-test, we compared pre-stimulus (−300 to 0 ms) to post-stimulus (0 to 1600 ms) HFA differences between subsequently clustered and non-clustered items. Pre- and post-stimulus intervals did not differ in LIFG ($t(54) = .68$, $p = .50$) or LIT ($t(79) = .38$, $p = .70$), but the SCE was significantly greater in the post- than pre-stimulus interval in hippocampus ($t(60) = 3.1$, $p < .01$).

We have identified an SCE characterized by HFA increases across our three ROIs. Fig. 3 illustrates the time course of that effect in each region. Because LIFG has been hypothesized to play a critical role in retrieval and selection processes (Thompson-Schill et al., 1997, 2005; Gold

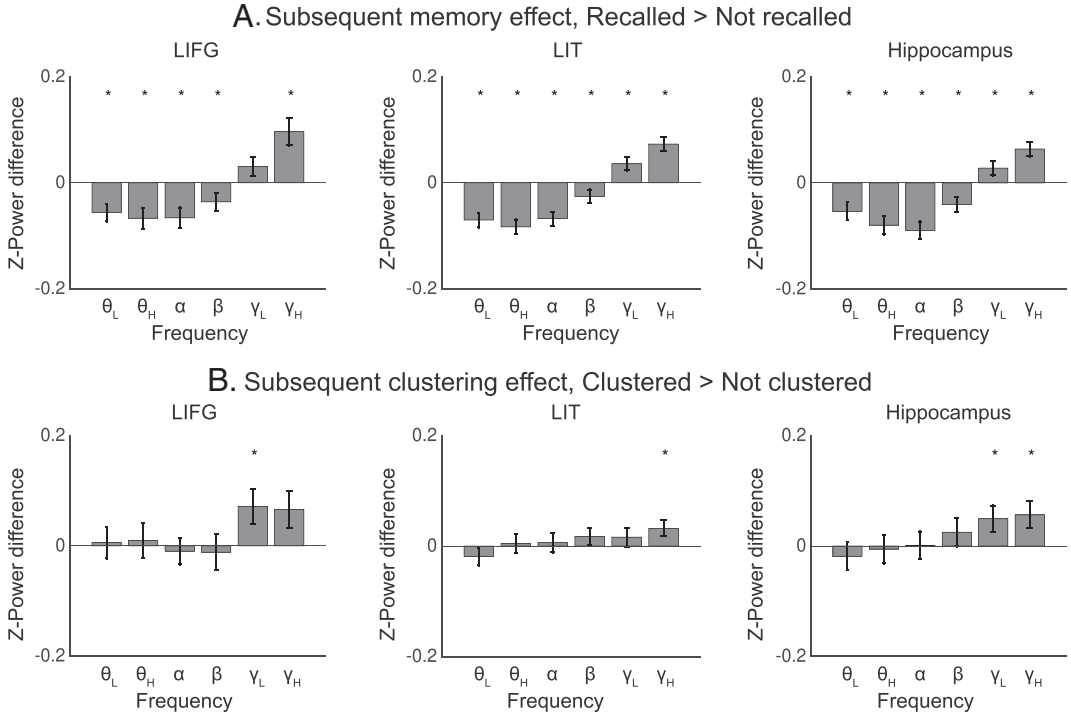

Fig. 2. Subsequent memory and clustering effects. The figure shows average across participant Z-power difference for six frequency bands (θ_L, 3–4 Hz; θ_H, 6–8 Hz; α, 10–14 Hz; β, 16–26 Hz; γ_L, 28–42 Hz; γ_H, 44–100 Hz) and three regions of interest (ROI; left inferior frontal gyrus, LIFG; left inferior temporal lobe, LIT; and hippocampus). Z-power values were generated by comparing the frequency band-specific spectral power of two conditions and averaging those difference values across electrodes within an ROI. Error bars are standard errors of the mean. Asterisks denote power differences that significantly differed ($p < .05$) from zero. **(A)** Subsequent memory effect, comparison of subsequently remembered and forgotten items. **(B)** Subsequent clustering effect, comparison of subsequently clustered and non-clustered items, where items recalled preceding or following a study neighbor (+/− 1 lag) are considered clustered and all others are not clustered.

et al., 2006; Badre and Wagner, 2007; Blumenfeld and Ranganath, 2007) and because these processes, which may update context (Polyn and Kahana, 2008), have to unfold prior to hippocampally-mediated item-to-context binding in order to support subsequent clustering, we hypothesized that clustering-related activity in LIFG should precede activity in hippocampus. To test this hypothesis, for each participant and ROI we identified the time interval during which the SCE was maximal (see *Methods*). We observed that the median peak interval in hippocampus (900–1000 ms) was reliably later than the median peak interval in LIFG (600–700 ms; non-parametric Wilcoxon rank sum test ($z = -2.27$, $p = .02$). There was no reliable difference in peak time between hippocampus and LIT (median peak time in LIT, 500–600 ms; $z = 1.65$, $p = .10$) or between LIFG and LIT ($z = -.66$, $p = .51$).

We have shown that the peak LIFG SCE precedes the peak hippocampal SCE, supporting the hypothesis that hippocampus drives item-to-context binding. If hippocampal HFA is indicative of such a process, then the amount of late HFA in the hippocampus should directly relate to behavioral measures of clustering. We selected the modal hippocampal peak time (1300–1400 ms; Fig. 3) as our interval of interest. For each participant, we extracted hippocampal HFA during this interval across all encoding trials and correlated the average signal with each participant's temporal difference score. We found a significant positive correlation ($r = .38$, $p = .002$) whereby increased HFA in the hippocampus was associated with increased temporal clustering (Fig. 4). There was no correlation with the median peak time ($r = .03$, $p = .83$).

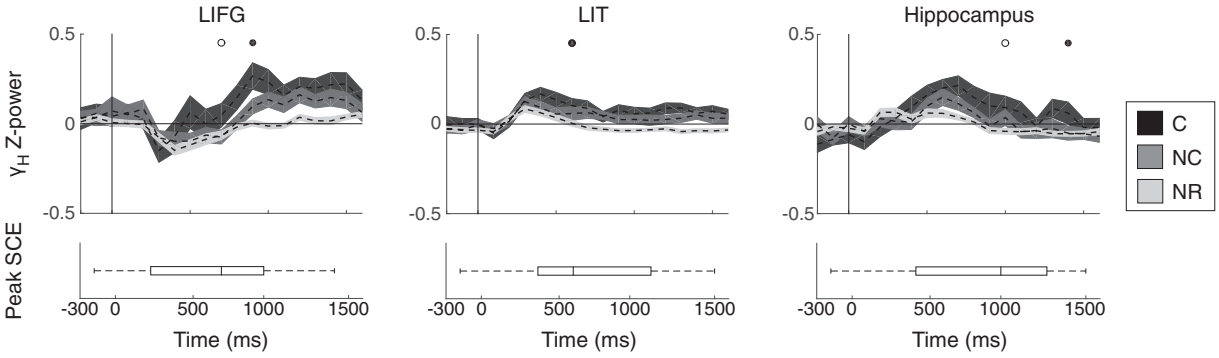

Fig. 3. Clustering effects across time. The figure shows average high gamma Z-power across the −300 to 1600 ms presentation interval where 0 is when the word is presented on screen, separately for each ROI. Z-power values are plotted separately for clustered (C, black), not clustered (NC, dark gray) and not recalled (NR, light gray) conditions. Error bars are standard errors of the mean. Below each time course is a box-and-whisker plot showing the interquartile range of peak SCE time intervals. For each participant, we found the time interval during which the HFA difference between subsequently clustered and subsequently non-clustered items was maximal. The solid black circle is the mode peak time interval and the white circle is the median peak time interval. For LIT, the median and mode peak time intervals were the same.

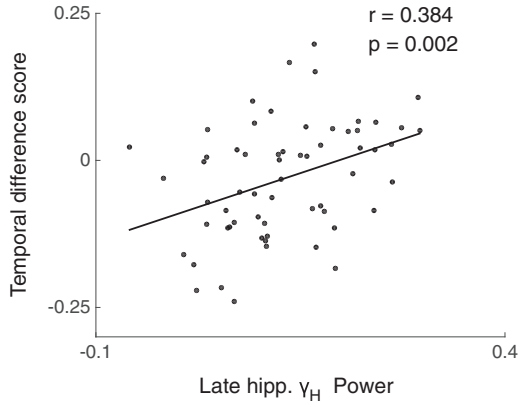

Fig. 4. Relation between hippocampal activation and temporal difference score. For each participant, we calculated the average high gamma Z-power across all encoding trials specifically for the late, 1300–1400 ms post-stimulus interval in hippocampus, as this interval was the modal peak time across participants (see *Results* and Fig. 3). We found a significant positive correlation between late hippocampal activation and temporal difference score (each point is a participant).

Discussion

The goal of the current study was to measure the neural correlates of memory encoding as they relate to subsequent clustering. Our study demonstrates three key findings. First, there is a subsequent clustering effect (SCE) whereby high frequency activity (HFA) in the left inferior frontal gyrus (LIFG), left inferior temporal lobe (LIT), and hippocampus is greater for subsequently clustered compared to subsequently recalled, but not clustered items. Second, clustering related HFA increases in LIFG precede those in the hippocampus, and the hippocampal SCE is specific to the post-stimulus interval. Finally, HFA in the hippocampus during the late interval (1300–1400 ms) across all encoding trials positively correlates with behavioral measures of clustering. Together, these results suggest that the core memory network is not simply driven by a mnemonic attentional signal and that item-to-context binding in the hippocampus supports successful memory formation.

We found increased HFA across the core memory network (Kim, 2011) for the encoding of items subsequently clustered compared to items subsequently recalled but not clustered. Though classic memory analyses (Wagner et al., 1998; Kim, 2011; Burke et al., 2014) have shown region-specific activation increases by comparing subsequently remembered and forgotten items, this activation need not be a memory signal per se. By directly comparing items based on how they were recalled, instead of whether they were recalled, we were able to relate the SME to a memory-specific mechanism of contextual encoding. Although there is a wealth of evidence showing that hippocampus is involved in both associative (Davachi and Wagner, 2002; Kirwan and Stark, 2004; Mayes et al., 2007; Mitchell and Johnson, 2009) and order memory (Jenkins and Ranganath, 2010; Ezzyat and Davachi, 2014; Davachi and DuBrow, 2015), previous studies have assessed encoding differences between items by explicitly manipulating task demands at either encoding or retrieval. An open question is whether the same mechanisms support memory formation when there are no requirements to encode or retrieve associations, as such demands could induce explicit strategy use which might obscure other processes (Carr et al., 2010). Without using an associative encoding or retrieval task, our results show that HFA in the SME network increases with effective contextual encoding, suggesting that hippocampus may readily associate items and contexts even in the absence of explicit task demands (Eichenbaum, 2004).

We found evidence that clustering related HFA increases in LIFG precede those in hippocampus. Substantial evidence has shown that LIFG engages in controlled retrieval, semantic elaboration and selection processes (Demb et al., 1995; Thompson-Schill et al., 1999; Badre and Wagner, 2007; Martin, 2007). Furthermore, communication between prefrontal and medial temporal lobe cortex has been shown to support memory formation (Dickerson et al., 2007; Preston and Eichenbaum, 2013). In our study, an encoding item's pre-existing associations could be retrieved by LIFG and integrated with the current context representation (Polyn and Kahana, 2008; Lenartowicz et al., 2010; D'Ardenne et al., 2012). This context representation would then be bound to the current encoding item by the hippocampus (Ranganath, 2010; Libby et al., 2014). Although we found early LIFG HFA increases, previous work (Burke et al., 2014) has suggested that late HFA increases in LIFG might retrieve or select stimulus-relevant information in the service of item memory (Blumenfeld and Ranganath, 2007; Kim, 2011). Therefore, the relative time course of LIFG and hippocampus may dictate whether or not an item is bound to its spatiotemporal context.

Finally, late hippocampal HFA is associated with the degree to which a participant will consecutively recall study neighbors during test. If late HFA in hippocampus is indicative of item-to-context binding, as we inferred from the time course of the SCE, then the amount of late hippocampal HFA should directly relate to participants' tendency to cluster responses during recall. We found that increases in late (1300–1400 ms) hippocampal HFA are positively correlated with temporal difference scores. This finding, coupled with the temporal dissociation of SCE across regions, suggests that hippocampus engages in item-to-context associative processes during encoding.

Two major questions not addressed by the present work include the role of theta in contextual encoding and how HFA is modulated during contextual retrieval. One may have made the *a priori* prediction that theta (3–8 Hz) would show a reliable clustering effect. Theta may signal the on-line state of the hippocampus (Buzsáki, 2002), the theta phase relates to long-term potentiation and may provide a temporal context for events (Buzsáki, 2005; Hasselmo and Stern, 2014), and theta has been implicated in tasks which manipulate context (Summerfield and Mangels, 2005; Staudigl and Hanslmayr, 2013). Theta effects in the current study may be obscured by broad asynchronous power fluctuations. The most consistent pattern associated with the SME is increased HFA coupled with decreased low frequency activity (Burke et al., 2014; Long et al., 2014); a somewhat similar pattern is present in the SCE as well (see Fig. 2). Such a pattern may be indicative of a "general activation" mechanism as it is observed outside of the memory domain (Crone et al., 2001; Miller et al., 2007; Jerbi et al., 2009) and may obscure narrowband theta signals. A promising future direction will be to investigate not only narrowband effects, but to also assess the role of theta phase in contextual encoding (Canolty et al., 2006; Axmacher et al., 2006; Nyhus and Curran, 2010; Rutishauser et al., 2010; Lega et al., in press) as there is compelling evidence that contextual mechanisms may be supported by phase amplitude coupling between theta and gamma frequencies (Staudigl and Hanslmayr, 2013).

Additionally, the current study focused on contextual processing as an indicator of effective encoding based on predictions of context models (Howard and Kahana, 2002; Polyn et al., 2009). Context models also posit that context is reinstated during retrieval, a prediction supported by recent neuro-imaging work showing evidence for content and context reinstatement (Polyn et al., 2005; Manns et al., 2007; Manning et al., 2011, 2012; Morton et al., 2013; Miller et al., 2013; Yaffe et al., 2014; Staudigl et al., 2015). A critical open question is how the univariate HFA increases observed here manifest during retrieval and how HFA increases interact with multivariate representations of items and context. One prediction is that HFA may increase prior to clustering at retrieval, and that HFA signals may be correlated with the amount of similarity between encoding and retrieval patterns.

Conclusion

We have demonstrated that HFA increases as a function of effective contextual encoding, whereby subsequently clustered items show the greatest HFA. Additionally, we have shown that the SCE dissociates across time and regions with the SCE in LIFG preceding the SCE in hippocampus.

This result supports the hypothesis that prefrontal cortex retrieves or selects contextual information and that the hippocampus associates items with this contextual representation. Finally, we have shown that late hippocampal HFA correlates with participants' tendency to consecutively recall study neighbors. Together, these results suggest that HFA increases observed in the SME network are likely the result of contextual encoding and that this contextual encoding directly supports successful memory formation.

Acknowledgments

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Conflict of interest

The authors declare no competing financial interests.

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