Phase reset dynamics of memory encoding

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Abstract

Human and animal studies have implicated oscillatory reset following a behaviorally relevant stimulus in learning and memory function. Here we asked whether phase reset predicts the dynamics of memory encoding for subsequently recalled and forgotten items. Our dataset comprised 188 neurosurgical patients (99 male, 89 female) who studied lists of common words for a subsequent delayed free recall test. We observed significant 3–21 Hz overall phase reset widespread throughout the brain in the 125–500 ms interval following stimulus presentation for both subsequently recalled and forgotten items. We found that the increased recalls of the primacy effect correlated significantly and exclusively with theta phase reset from 3–7 Hz throughout the brain. When controlling for serial position effects and examining the phase consistency differences of subsequently recalled and forgotten items, we identified both a theta (3–6 Hz) and an alpha (9–14 Hz) component of phase reset. Examined separately, early list items revealed a significant theta phase reset difference, while later list items revealed a significant alpha phase reset difference for subsequently recalled items. In regional analyses, the lateral temporal cortex exhibited a significant theta phase reset difference, while the prefrontal cortex revealed both a significant theta and a significant alpha phase reset difference for subsequently recalled items. These findings support the view that oscillatory reset serves an important role in encoding new episodic associations, and reveal differing oscillatory mechanisms across theta and alpha bands for serial position effects of phase reset versus serial position controlled subsequent recall.

Significance Statement

In 188 neurosurgical patients we examined the relationship of memory function with oscillatory phase consistency in response to word encoding events in a delayed free recall task. We innovated a new approach to computing a phase consistency score with robustness across sample size differences. Using this method, we showed a significant serial position correlate across subjects with primacy regions exhibiting a clear increase in theta phase consistency (3–7 Hz). After controlling for serial position effects, we also observed a significant effect of both increased theta phase consistency (3–6 Hz) and increased alpha phase consistency (9–14 Hz) for subsequently recalled versus forgotten items. This improves our understanding of the multi-faceted role of frequency-specific phase resetting in episodic memory encoding.

Introduction

Numerous studies have highlighted the oscillatory correlates of successful memory encoding across a wide range of frequencies from low theta (3 Hz) through high gamma (100–200 Hz), predominantly via the study of spectral power (Klimesch, 1999; Fell et al., 2001; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Khader, Jost, Ranganath, & Rösler, 2010; Düzel, Penny, & Burgess, 2010; Headley & Paré, 2017). Furthermore, studies of the causal nature of oscillations in memory function have highlighted the critical nature of phase synchronization within and across brain regions for effective memory function (Hanslmayr, Axmacher, & Inman, 2019). Recent work by ter Wal et al. (2021) has even shown that successful encoding and retrieval for cue-object associative memories corresponded to increased slow theta consistency of phase, and also that encoding and retrieval corresponded to different phases approximately half a cycle apart. This has left the field with little doubt that oscillations correspond to key memory processes, and also shows that the phase synchronizations of these oscillations must be carefully explored to fully elucidate the underlying mechanisms.

The resetting of oscillations following exposure to a stimulus has been observed in both animal (Givens, 1996) and human (Rizzuto et al., 2003) studies during working memory tasks. Rizzuto et al. (2003) presented human participants with a series of temporally jittered consonants in a Sternberg item recognition task, and observed characteristic decreases in power correlating with a phase locking identified as the reset of oscillatory phase. These results ranged from 4 Hz through 32 Hz, but were identified as most potent from about 7 Hz through 16 Hz. Rizzuto, Madsen, Bromfield, Schulze-Bonhage, and Kahana (2006) extended this item recognition analysis of reset showing theta phase differences between encoding and retrieval, and attributed this to differences in the phase coding of encoding and retrieval activity (Hasselmo, Bodelon, & Wyble, 2002).

Theoretical debate arose regarding the degree to which components of stimuli-synchronized electrophysiological responses could be attributed to the resetting of phase versus additive responses of traditional event-related potential models, whether this was clearly distinguishable, and how much these were synergistic effects (Sauseng et al., 2007; Telenczuk, Nikulin, & Curio, 2010). To avoid the exclusion of substantial portions of data with filtering approaches attempting to separate these, we take a combined approach to these two processes, examining the memory-related associates of the consistency of phase taken as a whole.

The memory processes of encoding are prominently thought to be coordinated throughout the brain by phase synchronization across broad frequency ranges from theta through gamma, with synchronization signals propagating outward from the hippocampus considered a key contributor (Axmacher, Mormann, Fernández, Elger, & Fell, 2006). Oscillatory phase is further modeled as the phenomenon which regulates the timing of information exchange in both local and global networks, with networks at numerous different frequencies operating concurrently (Sauseng & Klimesch, 2008).

Synchronization of neural spike timings with peaks of oscillatory synchronization signals are considered critical to long-term potentiation (Fell & Axmacher, 2011). Schonhaut et al. (2024) recently found, during a spatial navigation task, that neurons in the broader medial temporal lobe phase-lock to hippocampal theta by two complementary processes. One process synchronized to the local field potential, while an additional mechanism was identified that was not mediated by the local field, highlighting the need to carefully explore nuances of phase synchronization. Rutishauser, Ross, Mamelak, and Schuman (2010) also found that the strength of human memory is predicted by the degree of phase-locking between single neuron spike activity and oscillatory phase, confirming the importance of understanding the role of oscillatory phase synchronization in human memory function.

We follow this body of literature by examining the synchronization of phase, originating with phase reset following stimulus presentation, in a delayed free recall task. We found the frequencies which exhibit phase resetting in correlation with known serial position effects which strongly impact recall, and also separately found the frequencies which correspond to the subsequent free recall of items after controlling for serial position.

Methods

Experimental Design

We used data from a delayed free recall task conducted with volunteer hospital patients undergoing intracranial electroencephalogram (EEG) monitoring for medication-resistant epilepsy (Kragel et al., 2017; Long et al., 2017; Solomon et al., 2017). Each session consisted of up to 25 lists of 12 words each, presented for 1600 ms with a 0 ms to 250 ms uniform timing jitter added to the first presentation, and a random spacing of 750 ms to 1000 ms between each word. Following this word encoding period, a 20 s self-paced math distractor was provided with problems of summing 3 single digit values, followed by a 30 s free recall period. Words were selected from a previously reported wordpool of 300 common English words, with each word presented only once per session (Weidemann et al., 2019).

We included subjects from our dataset with 25 or more lists of 12 encoding words each. For our analysis of the whole brain, this resulted in 188 subjects (99 male, 89 female) with 9186 total lists. We also subdivided electrode contacts by brain region, filtering our subject pool for each analysis to subjects who had contacts available in each region. This yielded an analysis of the hippocampus (Hip.) with 122 subjects (60 male, 62 female) and 6360 total lists, an analysis of the lateral temporal cortex (LTC) with 173 subjects (93 male, 80 female) and 8424 total lists, and an analysis of the prefrontal cortex (PFC) with 174 subjects (93 male, 81 female) and 8440 total lists. Subjects were able to stop at any point, with common reasons such as fatigue or medical treatment needs, and we included partial sessions as long as total data with fully completed lists met the inclusion criteria.

Morlet Wavelet Transformation

We analyzed EEG signals from intracranial depth electrodes by using Morlet Wavelet Transformation with the PTSA library. Transformations were performed at integer frequencies from 3 Hz through 24 Hz, from -750 ms prior to word presentation through 750 ms after word presentation. As standard Morlet wavelets which exhibit biases toward 0° and 180° are incompatible with a sensitive phase consistency analysis, zero-integral complete wavelets were used, with a cycle count of 6 using the PTSA software library.

Phase Consistency

With the aim of better analyzing the properties of phase between measurements of different sample sizes, we developed a new statistical metric for representing the consistency of oscillatory phase. This phase consistency metric was intentionally designed to have the following three properties for a von Mises distribution:

1. A standardized value with a distribution mean-centered around 0 for samples from the uniform distribution, up through a value of 1 for samples with all phase values identical.
2. No systematic bias in metric values due to smaller or larger sample sizes.
3. A valid algebraic mean of metric values such that the average of large numbers of phase consistency metric values approaches the value for the phase distribution from which they were sampled.

This was achieved by first calculating the power-independent square of the average unit-normalized complex plane vectors, C and S, for each wavelet transformation frequency:

$$r^2 = \left(\frac{1}{N} \sum_i^N C_i \right)^2 + \left(\frac{1}{N} \sum_i^N S_i \right)^2 \tag{1}$$

Then we created a phase consistency metric z_s by shifting Rayleigh's z statistic (Zar, 2010) down by 1, and then scaling down by the number of degrees of freedom given sample size N:

$$z_s = \frac{Nr^2 - 1}{N - 1} \tag{2}$$

This z_s phase consistency metric provides all three of the above listed properties. These properties were further validated as reliably holding under a series of numerical simulations sampling from the wrappped normal distribution for sample sizes with N of 2 and larger.

Note that while nominal phase consistency ranges from 0 to 1, with 0 representing no consistency in phase, and 1 representing perfect consistency in phase, it is an essential property of such a metric that calculated values for individual samples can extend below 0. The most negative value which can be obtained for a sample is -1, obtainable only with N of 2, where the most negative value quickly approaches 0 for larger sample sizes. These negative values represent samples more uniform than the typical sample from a uniform distribution, and are required so that averages sampled from the uniform distribution retain an unbiased central phase consistency of 0.

For electrophysiology data with low signal to noise, phase consistency values trend toward low values, so these statistically clean properties around 0 are essential for using the stated properties in averaging and subtraction operations for combination of data and comparisons between groups.

In Fig. 1 we show simulated sampling from a wrapped normal distribution to highlight visually the amount of bias in phase corresponding to commonly encountered electrophysiological values for phase consistency.

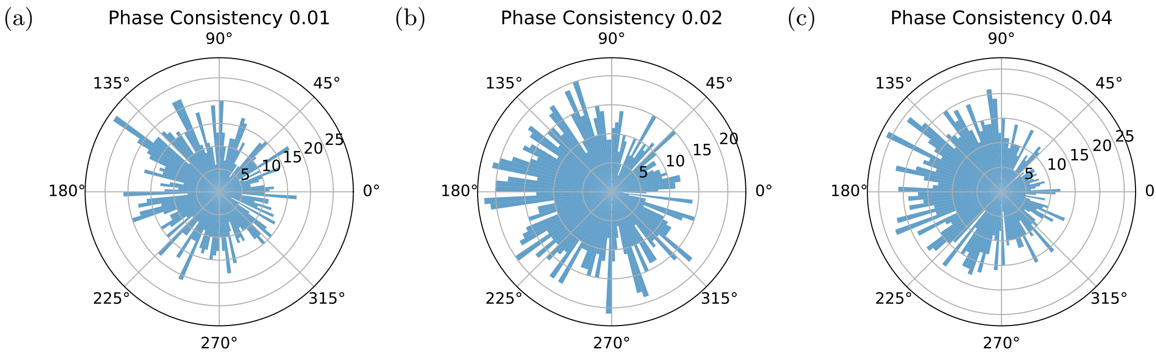

Figure 1. Simulated histograms with N=1600 showing example phase distributions that lead to phase consistency values of **a.** 0.01, **b.** 0.02, and **c.** 0.04.

Statistical Analysis

Significance testing was done as list-count weighted paired t-tests with Benjamini-Hochberg False Discovery Rate (FDR) correction. Confidence bands shown are 95% confidence intervals across subjects.

Results

We first asked whether words presented during our memory task caused a reset of ongoing oscillatory activity. We applied the phase consistency metric in Eqn. 2 to time windows from 750 ms before word presentation to 750 ms after word presentation, for frequencies from 3 Hz to 24 Hz. The results shown in Fig. 2a revealed that phase reset occurs shortly after stimulus presentation across all the frequencies of consideration. Lower frequencies exhibited a wider presentation of phase reset in the analysis, broadened both by the width of those oscillations themselves, and by the widths of the Morlet wavelets used to examine them. Due to the jittering of word presentation times built into the task design, phase consistency is driven to an average value of zero prior to the word onset, as the brain cannot synchronize phase to a future event timing that they cannot anticipate. The portions of the low frequency response which trail leftward on the plots to before stimulus presentation are due to the broadening from the Morlet wavelets. Figs. 2b–d illustrate phase reset behavior in three broad regions: Hippocampus (Hip), Lateral Temporal Cortex (LTC), and Prefrontal Cortex (PFC).

Having established that phase reset appears broadly throughout the brain following item presentation, we next asked whether the degree of phase reset would predict aspects of memory for the studied items. As the serial position of a studied item strongly modulates subsequent memory, we first examined phase reset as a function of serial position. We then consider whether — controlling for serial position — phase reset differs between the encoding of subsequently remembered and forgotten items.

Fig. 3a illustrates phase consistency both before and after item presentation as a function of serial position. Whereas the pre-word phase consistency reliably overlaps zero, the post-word phase consistency is strongly positive, and follows a pattern similar to the serial position curve of recall rates.

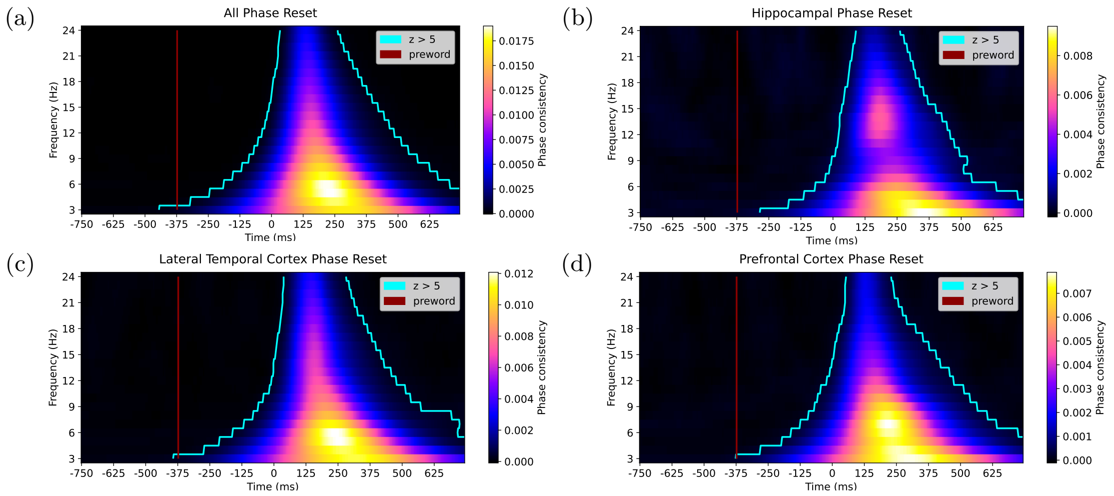

Figure 2. Average phase consistency across events for all hippocampal electrode contacts across all subjects.

Fig. 3b shows visually the relationship over all subjects between the average post-pre phase consistency difference and the average recall rate for each serial position group. We assessed the reliability of this relationship across subjects by performing correlations for each subject between the recall rate of the serial position groups and the phase consistency difference between the post-word and pre-word regions over all frequencies from 3–24 Hz. Fig. 4 illustrates the distributions of these correlation values and evaluates whether the mean correlation (across subjects) reliably differs from zero. For the entire brain we see a reliably positive correlation between phase reset and serial position – an effect that appears separately in each of the three regions of interest (hippocampus, temporal cortex and prefrontal cortex). Thus, as recall rates appear highest for early list positions we also find greater stimulus-related phase reset for early list positions.

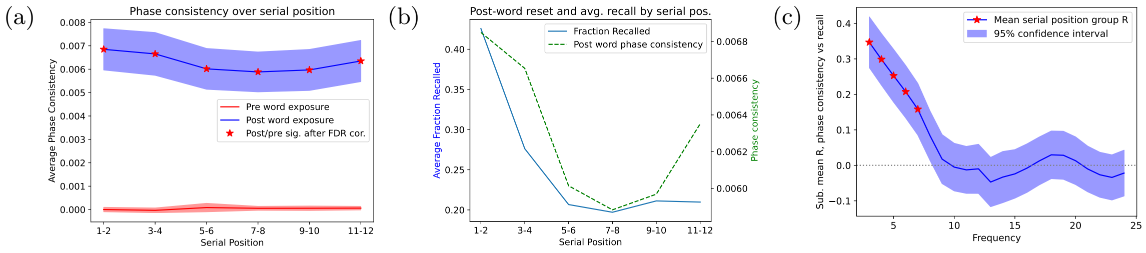

Figure 3. **(a)** Whole brain phase consistency with 95% confidence intervals averaged over all frequencies from the pre-word time window of -750 ms to -375 ms compared to the post-word time window of 125 ms to 500 ms for each serial position grouping. **(b)** Post-word phase consistency for each serial position grouping overlayed with average fraction correct for each grouping. **(c)** Mean across subjects of the correlation between serial position group recall rates and the post-pre phase consistency difference at each frequency, with 95% confidence intervals and significance marked after FDR correction.

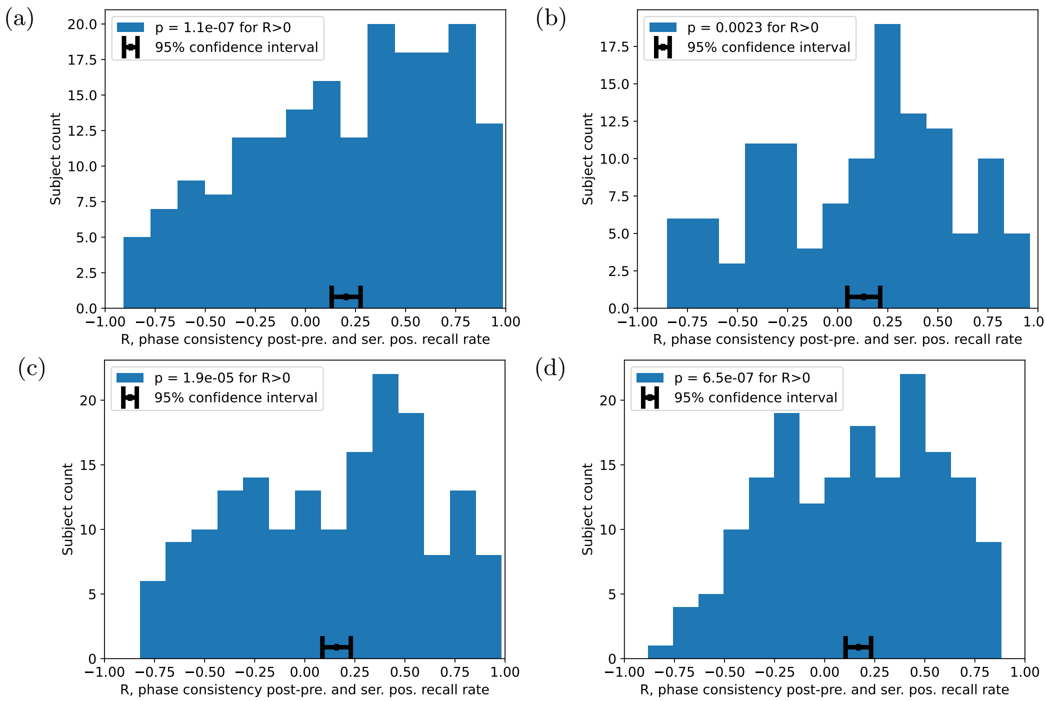

Figure 4. Histograms of subject correlation values between the successful recall fraction for serial position groups of two, and the phase consistency difference between post-word and pre-word regions. Correlations were significantly positive across subjects for each of **(a)** whole brain, **(b)** Hip., **(c)** LTC, **(d)** and PFC.

We then explored the frequency dependence of these serial position grouping correlations between post-pre phase consistency differences and recall rates, and found the results shown in Fig. 3c, which reveal that the serial position phase reset effect exists primarily within the band of 3 Hz through 7 Hz, and convincingly overlaps zero at higher frequences. In additional data not shown, this effect follows an identical pattern across the subdivided brain regions of Hip., LTC, and PFC, albeit with the significance of the matching trend not surviving FDR correction within the sparser hippocampal data. This convincingly reveals that across the brain, the phase reset correlates of serial position effects on subsequent recall rates are within the theta bands of 3–7 Hz, with the strongest effects at the lower frequencies.

Given that serial position strongly influences recall probability, we chose to first establish the nature of serial position effects of phase consistency, and then control for serial position to rule out the possibility that the serial position correlation is the exclusive driver of phase consistency effects. Fig. 5a shows the frequency distribution of the overall subsequent memory effect (SME) across the whole brain, without controlling for serial position. It can be seen that all frequencies examined contribute to the overall effect across all conditions, with sensitivity to observing phase consistency trailing off at the highest frequencies above 21 Hz. In Fig. 5b we controlled for serial position effects by grouping early list, middle list, and late list items separately, and then merging the resulting phase consistency

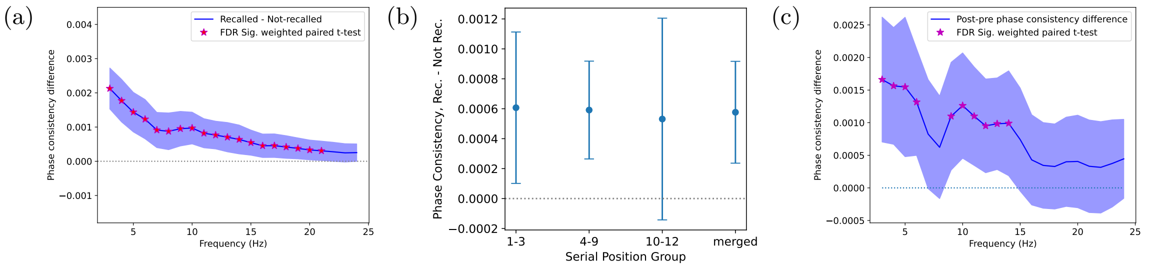

Figure 5. Whole brain phase consistency SME (recalled minus not-recalled) with 95% confidence intervals **(a)** as a frequency distribution without serial position control, **(b)** overall effect controlling for serial position grouping, and **(c)** as a frequency distribution controlling for serial position grouping.

differences between recalled and not-recalled items. This result gives high confidence in an overall remaining SME across the whole brain and all frequencies even after controlling for serial position effects.

We then performed this serial position control analysis for each frequency separately, resulting in Fig. 5c, where a significant serial position controlled SME appears across both theta (3–6 Hz) and alpha (9–14 Hz) bands. This pronounced alpha component of the phase consistency SME is distinct from the theta-only effect of the serial position correlate found in 3c.

Fig. 6a, 6b, and 6e show the detailed whole brain SME for phase reset separated out by frequency and serial position grouping, where early list items exhibit a theta SME from 3–6 Hz, middle list items include that band plus an alpha effect at 9–10 Hz and a beta effect at 16–20 Hz, and late list items have a alpha SME from 9–11 Hz. Given the serial position controlled SME effect of Fig. 5c highlighting the overall significance of the theta and alpha phase reset components, this serial position division of the data shows the theta phase reset SME appearing in the earlier list items and the alpha phase reset SME appearing in the later list items.

We also separated the SME across the other dimension of brain region without controlling for serial position. Fig. 6b shows the hippocampal contacts trending upward in their SME at lower theta frequencies as one might expect, but without significance due to the smaller number of total contacts contributing to this result. Fig. 6d shows only a significant theta phase reset (3–5 Hz) SME in the LTC, while in Fig. 6f there is a bimodal theta phase reset (3–4 Hz) and an extended alpha phase reset (6–11 Hz) SME.

Discussion

We showed that theta phase consistency rises significantly from 3–7 Hz in correlation with serial position effects primarily driven by primacy in a delayed free recall task. Furthermore we showed that after controlling for serial position, a significant subsequent memory effect of theta phase consistency increase (3–6 Hz) combined with alpha phase consistency increase (9–14 Hz). These results show differing mechanisms of oscillatory phase reset associated with the increased recall of primacy, versus increases in subsequent recall when controlling for serial position.

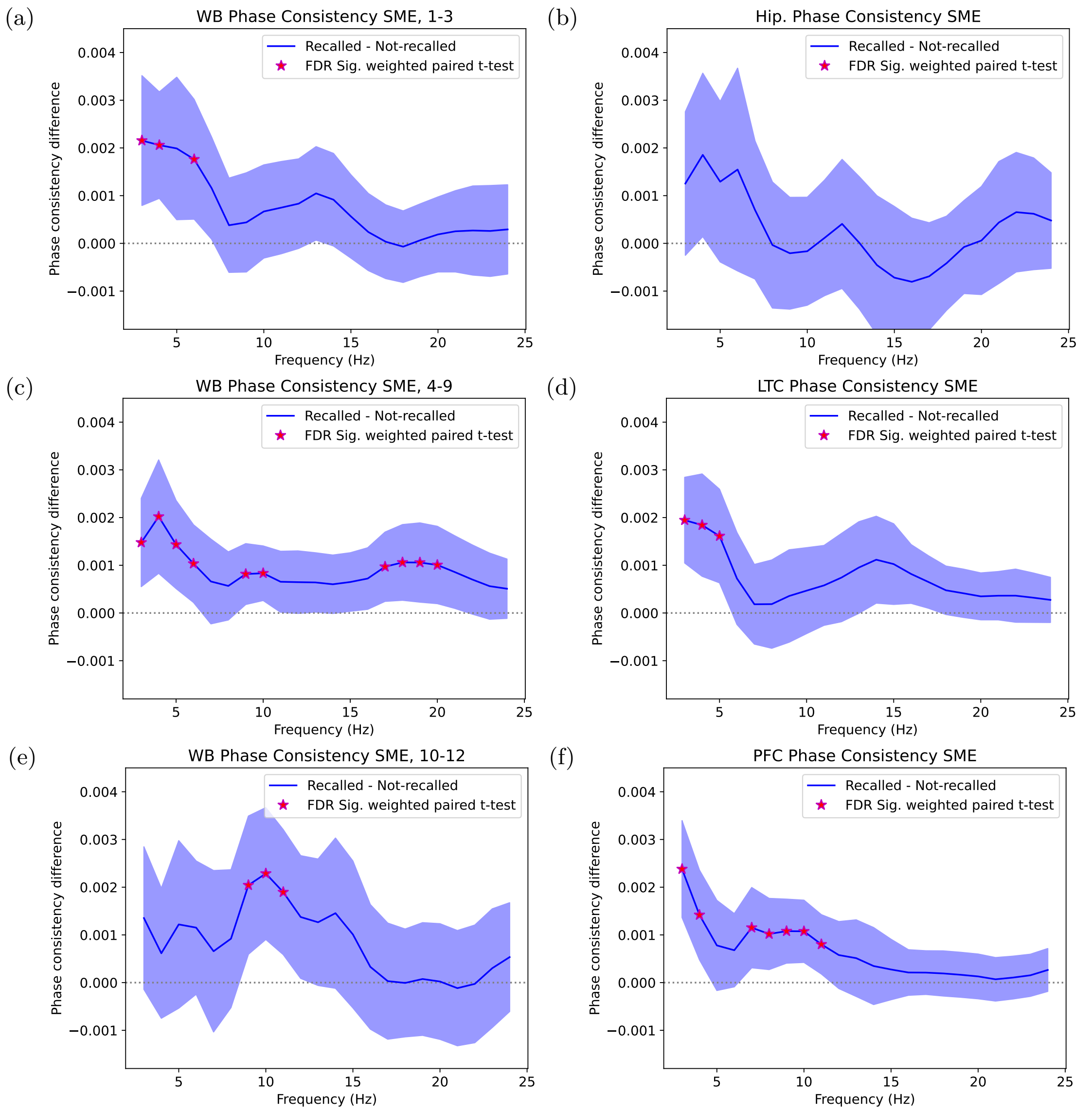

Figure 6. Phase consistency SME by serial position grouping from recalled minus not-recalled, averaged over all contacts and all subjects. **(a, c, e)** Ser. Pos. 1–3, 4–9, 10–12. **(b,d,f)** Hippocampus, LTC, PFC.

Because word presentations were jittered in their timing, we were able to conclude these results are causally due to participant responses to the word presentation events. Confirming that phase consistency values prior to the word presentation have confidence bands that strongly overlap zero and are well separated from the other effects validates the expectation that the remaining effects are specifically due to participant responses to the word presentations, as was observed clearly in Fig. 3a. We propose that this strong theoretical guarantee, with a built-in validation, provides a useful foundation for exploring oscillatory responses.

With the above results we have demonstrated the general potency of the phase consistency metric in Eqn. 2 for studying oscillatory phase relationships, and encourage its broader use. This approach is not limited to studying temporal synchronization with stimuli, but equivalently provides a convenient tool for examining the consistency of relative phase, such as between contacts.

We have shown in a free recall task that oscillatory phase reset 125 ms to 500 ms following word stimuli presentation appears throughout the brain across a broad frequency range from 3 Hz through 21 Hz. The strongest magnitudes of measured phase consistency exhibited in Fig. 2, without consideration of any memory dynamics, were found in the theta frequency range. However, interpreting the relative magnitudes of far away frequencies of phase consistency must consider the greater ease of extracting phase consistency at lower frequencies. This improved ease of extracting consistency is facilitated both by longer low-frequency Morlet wavelets having longer time periods to integrate data over, as well as a reduced sensitivity of lower frequency consistency measurements to small fluctuations in experimental synchronization or physiological fluctuations in response timing. Griffiths and Jensen (2023) recently reviewed the episodic memory role of synchronization of gamma oscillatory activity (30–80 Hz) in conjunction with theta, and it is notable that directly examining the consistency of phase with respect to a stimulus in that higher frequency band is much less sensitive due to the higher sensitivity to intertrial differences in response times. The phase consistency metric used here would extend better to higher frequencies if applied to the synchronization of relative phase between contacts, which better controls for physiological response timing fluctuations, rather than to the synchronization of phase with respect to external stimulus timing.

We demonstrated a particularly clear correspondence between theta phase reset (3–7 Hz) and the recall rates at various serial positions. There is a strong theoretical reason to have expected this correspondence for list primacy, given the hypothesis that well synchronized theta phase resetting would be a byproduct of phenomena such as attentional effects that are expected to contribute to increased recall rates during primacy portions of a list. Our results lend support to this hypothesis, and we encourage additional work in this area on studies with other modulators of attention, to further explore the details of this effect.

The apparent correspondence in Fig. 3b of phase consistency with the slightly increased recall rate in late list items in a delayed free recall task requires a more nuanced consideration, but is plausibly due to participant encoding behaviors or strategies that arise upon the expectation of approaching the end of the consistently sized lists. In Fig. 6e, the phase reset SME for this late list portion of the data showed a characteristically different frequency profile for the contribution to subsequent recalls than was observed for the primacy regions, with significance in the alpha band that was found to correspond to the SME.

This did not appear in the frequency plot of Fig. 3c, which showed only a theta effect, as due to the math distractor task in the delayed recall experiment causing the serial position curve to be dominated by primacy, the correlation examined was expected to be dominated by the much stronger primacy effect on recall probability.

Even after controlling for serial position, phase consistency showed a clear theta and alpha phase reset SME, distinct from the primacy effect, supporting the notion that phase reset plays a multi-faceted role in the processes that synchronize the brain during the task of encoding word presentation. The regional division of the data showed a theta effect in the LTC, and a dual theta/alpha effect in the PFC. A more nuanced analysis of the regional contributions to these processes was hindered by variability and reduced data counts after restricting to electrode contacts within specific brain regions. Additional analyses not shown, attempting to divide across all the axes of frequency, brain region, and serial position grouping, were washed out by the sparsity of data, but might yield interesting insights with additional data or alternative analytical approaches or modeling.

A particularly encouraging aspect of these phase consistency analyses were that the effects observed were both potent and widespread, indicating the potential of using this information as an independent data axis to oscillatory power for combined biomarkers of successful encoding in machine learning approaches.

Overall, this phase consistency approach to exploring phase reset in a delayed free recall task revealed that phase reset corresponds to successful recall in at least two different ways, a widespread theta phase reset effect associated with the primacy effect on recall, and a dual theta/alpha phase reset effect independent of serial order exhibiting portions of these components in the LTC and PFC. These results show that there are multiple mechanisms by which phase reset associates with the memory dynamics leading to the successful recall of episodic associations, and warrant further study to explore the reset of these oscillatory networks.

Data and Code Accessibility

All experimental data is on OpenNeuro at https://openneuro.org/datasets/ds004789 and our analysis code may be freely obtained from the senior author's website: https://memory.psych.upenn.edu

Conflict of Interest Statement

The authors declare no competing financial interests.

Acknowledgments

We are grateful to the patients for their generous participation in this project, and wish to thank the numerous hospital staff and researchers who were involved in data acquisition. This work was supported by the NIH grant MH55687.

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