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Rhythmic temporal cues coordinate cross-frequency phase-amplitude coupling during memory encoding

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Conflict of Interest

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Abstract

Accumulating evidence suggests that rhythmic temporal cues in the environment influence the encoding of information into long-term memory. Here, we test the hypothesis that these mnemonic effects of rhythm reflect the coupling of high-frequency (gamma) oscillations to entrained lower-frequency oscillations synchronized to the beat of the rhythm. In Study 1, we first test this hypothesis in the context of global effects of rhythm on memory, when memory is superior for visual stimuli presented in rhythmic compared to arrhythmic patterns at encoding (Jones & Ward, 2019). We found that the mnemonic benefit of rhythm was associated with increased phase-amplitude coupling (PAC) between entrained low-frequency (delta) oscillations and higher-frequency (gamma) oscillations. In Study 2, we next investigated cross-frequency PAC in the context of local effects of auditory rhythm on memory encoding, in which subsequent memory is superior for information presented in-synchrony compared to out-of-synchrony with a background beat (Hickey et al., 2020). We found that the mnemonic benefit of rhythm in this context was also associated with increased cross-frequency PAC between entrained low-frequency (delta) oscillations and higher-frequency (gamma) oscillations, and that the magnitude of gamma power modulations scaled with the subsequent memory benefit for in- versus out-of-synchrony stimuli. Together, these results suggest that it is not entrained low-frequency oscillations themselves that modulate memory encoding, but the coordination of higher-frequency gamma activity by entrained low-frequency oscillations.

Keywords: Rhythm, Entrainment, Oscillations, Music, Episodic Memory

Introduction

Rhythmically-structured sounds such as speech or music contain predictable temporal patterns, and a large body of work has demonstrated that the brain can leverage such patterns to optimize perception and action (Jones, 2019; Jones & Boltz, 1989; Large & Jones, 1999). For example, target detection and perceptual discrimination are faster and more accurate when stimuli appear in-synchrony compared to out-of-synchrony with a rhythmic beat (Barnhart et al., 2018; Bolger et al., 2013; Escoffier et al., 2010; Jones et al., 2002). Recently, these dynamic effects of rhythm have been extended to higher-level cognitive processes such as memory. For example, stimuli presented rhythmically at encoding (i.e., with a consistent interstimulus interval) are better remembered in subsequent tests of long-term memory compared to stimuli presented arrhythmically at encoding (i.e., with a variable interstimulus interval; Jones et al., 2022; Jones & Ward, 2019; Thavabalasingam et al., 2015; but see Kulkarni & Hannula, 2021). In addition, the timing of stimulus presentation *within* a rhythmic temporal stream also influences memory encoding, evident in superior subsequent memory for visual stimuli presented synchronously compared to asynchronously with a background beat (Hickey, Merseal, et al., 2020; Johndro et al., 2019). Together, these results suggest that rhythm dynamically modulates memory formation at both the global and local levels. An important outstanding question is how these mnemonic effects of rhythm are instantiated in the brain.

Prior work in the perceptual domain has suggested that the effects of rhythm on behavior result from the synchronization of neural oscillations to the timing of external rhythms (i.e., neural entrainment; Schroeder & Lakatos, 2009). For naturalistic rhythms, such as biological motion, speech, and music which contain salient slow modulations (<5Hz, see Ding et al., 2017; Shen et al., 2023), this synchronization manifests as greater power or phase coherence in lower-

frequency oscillations in the delta range (1-4Hz, see Ding & Simon, 2014; Nozaradan et al., 2016; Shen et al., 2023). Low-frequency delta oscillations are known to modulate neural excitability across time in a periodic fashion. In the context of rhythm, the phase of these oscillations shifts such that windows of heightened neural excitability occur at predictable moments (in synchrony with the beat). This alignment of internal and external rhythms has two primary effects on the brain and behavior. First, it allows the brain to conserve computational resources at the global level by shifting from a more metabolically demanding "vigilance mode" of processing to a more efficient "rhythmic mode" of processing (Schroeder & Lakatos, 2009). Additionally, low-frequency oscillatory entrainment optimizes the processing of relevant events in the environment by creating distinct temporal windows of heightened neural excitability optimized for sensory-perceptual processing (rhythmic perceptual sampling; Arnal & Giraud, 2012; Calderone et al., 2014; Lakatos et al., 2008; Schroeder & Lakatos, 2009). In this way, neural entrainment can have more sustained effects on information processing at the global level as well as more discrete effects on information processing at the local level.

Recent evidence suggests that similar entrainment mechanisms may also underlie the effects of rhythm on memory encoding. In a study by Jones and Ward (2019), participants incidentally encoded visual images that were either displayed rhythmically every 600ms (1.67 Hz) or arrhythmically (variable interstimulus interval). Stimuli that were presented rhythmically at encoding were better remembered in subsequent tests of memory compared to stimuli presented arrhythmically at encoding. Rhythmic stimulus presentation at encoding was also associated with oscillatory entrainment, evident in stronger inter-trial phase coherence (ITPC) at the same frequency as stimulus presentation (1.67 Hz). While a correlation between the magnitude of oscillatory entrainment and memory performance was not observed across

participants, this suggests that global effects of rhythm on memory encoding may reflect the rhythmic coordination of neural oscillations.

Recently, Hickey et al. (2020) found additional evidence linking entrained, low-frequency oscillations to the effects of rhythm on memory performance, this time at the local level. In this study, participants encoded visual images in the context of background, musical rhythm with a steady 1.25 Hz beat, and the timing of image presentation within this rhythmic context was manipulated such that stimuli either appeared in-synchrony or out-of-synchrony with the beat. At the behavioral level, participants demonstrated superior subsequent memory performance for stimuli presented on-beat versus off-beat at encoding. Significant neural tracking of the beat was also observed, evident in enhanced inter-trial phase coherence and steady state evoked potentials (SSEPs) at the beat frequency (1.25 Hz). Importantly, a strong positive association was found between the strength of neural entrainment at the beat frequency (1.25 Hz) and the mnemonic effects of rhythm. In addition, at the time of stimulus presentation, neural entrainment at the beat frequency was greater for images that were remembered compared to those that were forgotten on subsequent tests of memory. Together, these results suggest that entrained low-frequency oscillations dynamically modulate memory formation and enhance encoding at specific moments in time.

While the aforementioned results support the proposal that entrained low-frequency oscillations influence the temporal dynamics of memory encoding at both the global and local levels, an important outstanding question is the underlying mechanism by which this occurs. One possibility is that effects of rhythm on memory reflect entrained oscillations themselves, and it is the modulation of neural activity in sensory cortices which influences local excitability and processing efficiency in a rhythmic manner (e.g., ‘sensory gating’) (Lakatos et al., 2008;

O'Connell et al., 2015; Schroeder & Lakatos, 2009). Alternatively, mnemonic effects of rhythm could reflect the orchestration of higher-frequency oscillatory activity in networks of brain regions beyond the sensory cortices. Indeed, external rhythms have been shown to influence neural activity in widespread brain regions (Besle et al., 2011) and rhythmic stimulation in one modality (e.g., auditory) can influence behavioral performance and neural activity in a different modality (e.g., visual; Hickey et al., 2020; Lakatos et al., 2008). In addition, entrained low-frequency oscillations have been shown to modulate the power of higher-frequency oscillations outside of sensory cortices, such as the parietal and frontal cortices (Keitel et al., 2017), which may be particularly relevant to higher-order cognitive functions such as memory formation. Further support for this proposal comes from an event-related potential study by Hickey, Barnett-Young, et al. (2020), which found that the mnemonic effects of rhythm are related to electrophysiological responses relatively late in the information processing stream (post-perceptual N2 and P3 components). In this way, low-frequency oscillations entrained to external rhythmic cues could dynamically organize activity in multiple frequency bands and brain regions to influence higher-order cognitive processing.

Here, we explore the proposal that entrained low-frequency oscillations influence memory performance by imposing temporal structure on higher-frequency (gamma) oscillations that are more commonly associated with memory encoding (Hickey & Race, 2021; A. Jones & Ward, 2019). Central to this proposal is the phenomenon of cross-frequency phase-amplitude coupling (PAC), whereby the amplitudes of faster (higher frequency) rhythms, such as gamma oscillations, couple to the phase of slower (lower-frequency) rhythms entrained to environmental stimuli (Buzsáki, 2006; Canolty & Knight, 2010; Lakatos et al., 2005, 2008; Sadeh, 2014). Gamma oscillations occur across a broad range of frequencies (30-100 Hz) and are thought to

reflect local processing within cortical regions (Buzsáki & Wang, 2012; Canolty & Knight, 2010). Activity in the higher range of gamma (65-100 Hz) has been more commonly associated with memory encoding (Colgin et al., 2009; Griffiths et al., 2019), whereas low-gamma activity has been associated with response speeds on perceptual tasks. Importantly, in addition to influencing sensory and perceptual processing (Bartoli et al., 2019), gamma oscillations, and the coupling of gamma oscillations to lower-frequency oscillations, are proposed to play a key role in memory formation and subsequent memory performance (Canolty & Knight, 2010; Friese et al., 2013; Jensen et al., 2007; Köster et al., 2019; Lega et al., 2016; Osipova et al., 2006; Rieder et al., 2011; Sederberg et al., 2003, 2007; Trimper et al., 2017). Thus, entrained low-frequency oscillations in sensory-specific cortices (e.g., auditory cortex for auditory rhythms) may indirectly contribute to memory performance by modulating higher-frequency neural activity in the gamma range.

Support for this proposal comes from a prior study by (Köster et al., 2019) in which low-frequency (theta) oscillatory activity was entrained via visual flicker during the encoding of visual images into memory. While the strength of participants' entrainment to the visual flicker was positively associated with overall memory performance, it was the *coupling* between entrained oscillations and higher-frequency gamma activity which predicted memory performance on individual trials. Specifically, cross-frequency PAC was greater for images that would be later remembered compared to those that would be later forgotten. These findings support the hypothesis that while entrained low-frequency oscillations put the brain into an "optimal" state for encoding, the effect of rhythm on subsequent memory may be more closely related to the orchestration of higher-frequency gamma oscillations entrained to the pace of entrained oscillations (Köster et al., 2019).

The current experiments tested this hypothesis in the context of both global and local effects of rhythm on memory encoding. In Study 1, we re-analyzed the dataset collected by Jones and Ward (2019) to investigate whether cross-frequency PAC between entrained low-frequency oscillations and higher-frequency gamma activity was associated with memory performance at the *global* level. If this is the case, then delta-gamma PAC should be greater during encoding blocks in which visual stimuli are presented rhythmically compared to those in which stimuli are presented arrhythmically. Furthermore, the magnitude of PAC differences between rhythmic and arhythmic blocks may be related to the magnitude of the mnemonic benefit of rhythm across participants. In Study 2, we re-analyzed the dataset collected by Hickey, Merseal, and colleagues (2020) to investigate whether cross-frequency PAC between entrained low-frequency oscillations and higher-frequency gamma activity is associated with the mnemonic effects of rhythm at the *local* level. If this is the case, then significant PAC should be present during encoding in the presence of background music with a steady beat, and the magnitude of this coupling should scale with the magnitude of the memory benefit for on-beat versus off-beat stimuli. When directly comparing on-beat and off-beat trials, we predicted that gamma power would be greater for on-beat trials compared to off-beat trials, and that stronger gamma power at the stimulus level would be related to a greater mnemonic benefit of rhythm.

Study 1

Method

Experimental methods have been reported previously (Jones & Ward, 2019), but are summarized here.

Participants

A total of 24 participants (9 male, 15 female) of an average age of 23.3 years (*SD* = 2.4 years) completed the experiment. One participant was excluded from the analysis due to poor attention and performance on the task. Participants were all English speakers, had normal or corrected to normal vision, and were right-handed. Participants were compensated £20 for participation. The study was approved by the Middlesex University research ethics committee and all participants provided informed consent prior to participation.

Study Design

The experimental design is illustrated in Figure 1. Each participant completed six experimental blocks in which they first encoded images and then completed a subsequent memory test. In half of the blocks, images were presented rhythmically during encoding (consistent ISI) and in the other half, images were presented arrhythmically (variable ISI). Blocks alternated between rhythmic and arrhythmic presentations at encoding and the order of blocks (rhythmic, arrhythmic) was counterbalanced across participants.

Procedure

During encoding, participants completed a target detection task in which they were shown a series of 40 images and 120 checkerboards in each block. Participants were instructed to press the spacebar whenever they saw an image of an animal (~10% of trials). Images and checkerboards were always displayed on the screen for 600 ms and were separated by a fixation cross. During rhythmic blocks, the fixation cross duration was set at 600 ms, resulting in a rhythmic presentation of images at a frequency of 1.67 Hz. During arrhythmic blocks, the fixation cross had a variable inter-stimulus interval that was determined by randomly sampling from a uniform distribution between 70-1130 ms, but with an average inter-stimulus interval of

approximately 600 ms across the whole block.

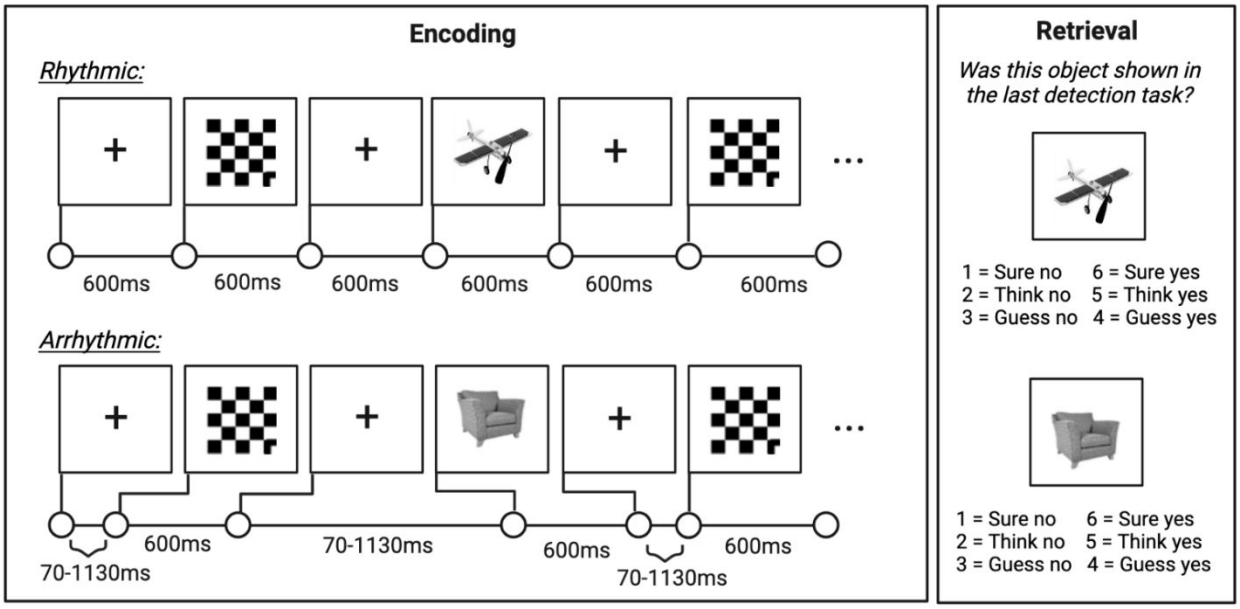

Figure 1. Experimental design for Study 1. Participants completed 6 blocks of encoding and retrieval (3 rhythmic; 3 arrhythmic). During encoding, participants were shown a series of images and checkerboards separated by fixation crosses and instructed to press the space bar each time an animal appeared. Images remained on the screen for 600ms. In rhythmic blocks, the interstimulus interval (ISI) was always 600ms, while in arrhythmic blocks the ISI was jittered between 70-1130ms. Example timelines of stimulus presentation during encoding are illustrated in the first panel. During retrieval, participants were given self-paced memory tests where they were presented with old and new images and indicated if they had seen the image during the preceding detection (encoding) task and their confidence in their memory decision.

After encoding, participants solved simple algorithmic problems for three minutes before they were given a self-paced subsequent memory test where they were shown another series of 80 images (40 images from the detection task and 40 new images). For each image, participants were asked *"Was this object shown in the last detection task?"* and indicated their response with a button press according to a response scale (6 = sure yes, 5 = think yes, 4 = guess yes, 3 = guess no, 2 = think no, 1 = sure no).

Data Analysis

Behavioral Data Analysis

Memory performance from the subsequent memory test was computed separately for each of the rhythmic and arrhythmic blocks. Responses were collapsed across confidence ratings

(1-3 = old items, 4-6 = new items) to determine the proportion of images which were correctly identified as old (hits) and of images incorrectly identified as old (false alarms). From these proportions we calculated using d-prime (d'), a measure of discriminability between previously seen and novel items to mirror the analyses in Experiment 2 and Hickey, Merseal, et al. (2020).

EEG recording and Preprocessing

EEG was recorded from 64 channels throughout the experiment using a BioSemi Active Two System (BioSemi, Amsterdam, Netherlands). EOG was also recorded to detect eye blinks. Preprocessing was completed in the EEGLab toolbox (Delorme & Makeig, 2004) and custom MATLAB scripts. First, EEG data was referenced to the average of all electrode channels. EEG signals were then downsampled from 2048 Hz (which was the sampling rate the signal was recorded with) to 512 Hz and filtered using a 0.1 Hz high pass and 120 Hz low pass filter. After, eye artifacts were removed from the signal using independent components analysis. Then, the signal was epoched into 6 second windows (Köster et al., 2019), resulting in 10 cycles of the low-frequency oscillation per epoch. In total, there were approximately 32 epochs per block. Epochs containing muscle artifacts were then removed by visual inspection. Overall, a large portion of the epochs were retained in both the rhythmic (M = 25.35; SE = .57) and the arrhythmic conditions (M = 25.17; SE = .57). The number of epochs did not differ significantly based on block number ($F(2,44) = 1.86$, $p = .19$, $\eta^2_p = .08$) or based on rhythmicity ($F(1,22) = .24$, $p = .63$, $\eta^2_p = .01$).

Phase Amplitude Coupling

Phase-amplitude coupling was calculated between neural oscillations at the rhythmic frequency (1.67 Hz) and gamma activity (30-100 Hz) in each block using the PACTools toolbox for MATLAB (Martínez-Cancino, 2020). The Modulation Index (MI; Tort et al., 2010) was

chosen as a measure of PAC based on its use in prior literature (Köster et al., 2019) and its relative accuracy when compared to other techniques (Hülsemann et al., 2019). The MI was calculated at electrodes PO7 and PO8. Electrodes PO7 and PO8 were selected given the visual nature of the entraining stimulus and previous finding by Jones and Ward (2019) of significant 1.67 Hz phase locking (entrainment) at these electrode sites. To calculate the MI, low-frequency oscillations were filtered between 1-6 Hz in .33 Hz steps, which ensured that phase-amplitude coupling could be measured at the rhythmic frequency (1.67 Hz), as well as other surrounding frequencies for comparison. High frequency oscillations were filtered between 30-100 Hz in 5 Hz steps (Köster et al., 2019) before the phase and amplitude time series were obtained using a Hilbert transform. Gamma amplitudes were sorted according to the corresponding low-frequency phase (18 bins) and the average gamma amplitude was computed in each low-frequency phase bin. Next, mean amplitudes were normalized by dividing by the average amplitude across all phase bins. The Kullback Leibler Distance (DKL) was calculated to determine if the distribution of the average gamma amplitude across phase bins (P) differs from a uniform distribution (U). The Kullback Leibler Distance (DKL) can be computed using the following equation, where j represents each phase bin, N represents the total number of phase bins:

$$\mathrm{DKL(P,U)} = \sum_{j=1}^{N}\left(\mathrm{P}(j)\log\left(\frac{\mathrm{P}(j)}{\mathrm{U}(j)}\right)\right)$$

Finally, the MI was calculated by normalizing the DKL (see equation below):

$$\mathrm{MI} = \frac{\mathrm{DKL(P,U)}}{\log(\mathrm{N})}$$

MI values range from 0 – 1, where a value of 0 indicates a completely uniform distribution of gamma amplitudes by the entrained phase (indicating an absence of phase-amplitude coupling)

and a value of 1 indicates the highest degree of modulation by the entrained phase (strong phase-amplitude coupling).

To test for statistical significance, raw MI values (MI_{raw}) were averaged across electrodes PO7 and PO8 and were compared to a surrogate distribution (MI_{surr}) (Mariscal et al., 2021). The surrogate data was generated in PACTools by randomly shuffling the amplitude time series from the original dataset, generating 200 surrogate MI values, and producing a surrogate distribution. If significant phase-amplitude coupling occurred, mean MI_{raw} values would be greater than the mean of the surrogate values (MI_{surr}). When looking at brain-behavior relationships between coupling and subsequent memory performance, MI_{raw} values were standardized (MI_z) using the mean and standard deviation of the surrogate sample.

MI values were calculated for the low gamma (30-60 Hz) and high gamma (65-100 Hz) ranges, following previous studies of memory and phase-amplitude coupling which have observed differences in the function of low versus high gamma oscillations, where higher frequency gamma activity is more closely tied to memory encoding (Colgin et al., 2009; Griffiths et al., 2019; Lega et al., 2016; Tort et al., 2008).

Statistical Analysis Plan

All statistics were completed in RStudio. Non-parametric statistics were used to determine significance of phase-amplitude coupling because the Modulation Index is on a 0-1 scale and is therefore non-linear. Analyses using normalized coupling (MI_z) and gamma power were completed using parametric statistics, except in cases where distributions were non-normally distributed. One participant had outlier MI values (> 3SD above the mean) and was excluded from the analysis.

To test the hypothesis that coupling between higher-frequency (gamma) oscillations and entrained low-frequency oscillations would occur in the context of rhythm, MI_z values were entered into 2x2x3x2 repeated measures ANOVA containing four within-subjects factors: Gamma Band (high, low), Rhythmicity (rhythmic, arrhythmic), Block (1, 2, 3), and Electrode (PO7, PO8). To evaluate the significance of phase-amplitude coupling in rhythmic and arrhythmic blocks, MI_{raw} and MI_{surr} values were averaged across blocks and electrodes and entered into a Wilcoxon Signed Rank test. Given that the primary analysis of interest was the comparison of rhythmic and arrhythmic contexts, only results involving main effects of rhythmicity are included. Pearson correlations were also used to test whether there was a relationship between PAC and the effect of rhythm on memory. Bayes Factors (BF) were also computed using JASP (Version 0.17.1; JASP Team, 2023) for all null effects including Rhythmicity which were related to our hypotheses of interest.

Results

Figure 2A depicts phase-amplitude coupling between low-frequency oscillations at the beat frequency (1.67 Hz) and higher-frequency gamma oscillations. There was not a significant main effect of Rhythmicity ($F(1,21) = 0.71$, $p = 0.41$, $\eta^2_p = 0.03$, BF10 = .281) nor Gamma Band ($F(1,21) = 0.03$, $p = 0.87$, $\eta^2_p = 0.001$, BF10 = .155), but there was a significant interaction between Gamma Band and Rhythmicity ($F(1,21) = 7.60$, $p = .012$, $\eta^2_p = .27$), indicating that rhythm had different effects on the magnitude of cross-frequency PAC for oscillations in the low-gamma (30-60 Hz) versus the high-gamma range (65-100 Hz). Indeed, follow-up analysis indicated that coupled oscillations in the low gamma range did not differ between rhythmic and arrhythmic contexts (Figure 2C; $F(1,21) = 2.67$, $p = .12$, BF10 = .702), but that coupled oscillations in the high-gamma range were numerically greater during rhythmic compared to

arrhythmic contexts (Figure 2B; $F(1,21) = 4.02$, $p = .058$, BF10 = 1.197). No other significant 2-way, 3-way, or 4-way interactions involving Rhythmicity were found (Fs < 1.98, ps > .17, BF10s < .132). Given that there was also no main effect of Block or Electrode (ps > .10, BF10s < .479), subsequent phase-amplitude coupling analyses averaged MI values across blocks and electrodes.

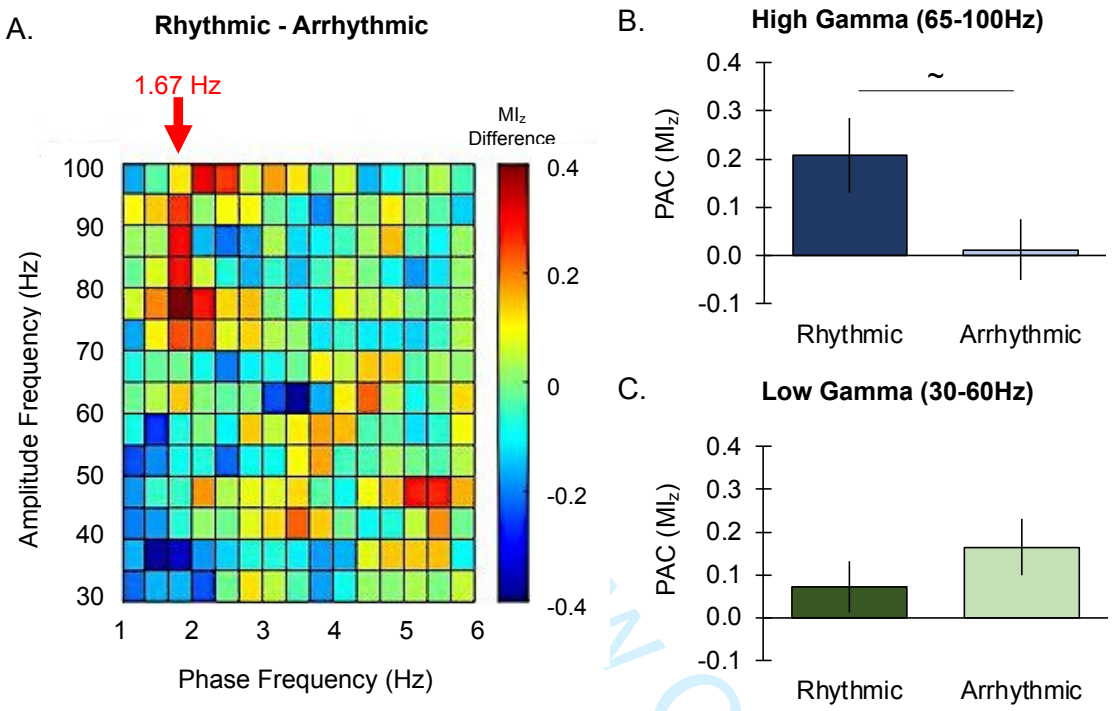

Figure 2. The difference in normalized Phase-Amplitude Coupling (PAC; measured by MI_z) between rhythmic and arrhythmic contexts. (A) The comodulogram depicts the difference in PAC between contexts (rhythmic – arrhythmic), where the third column displays coupling at the entraining frequency (1.67 Hz). (B) There was numerically greater phase-amplitude coupling at the entrained (1.67 Hz) frequency in the high-gamma (65-100 Hz) range, (C) but not in the low-gamma (30-60 Hz) range. Error bars represent SEM. ~ $p = .058$.

To evaluate the significance of phase-amplitude coupling within the rhythmic and arrhythmic blocks individually, raw MI values (MI_{raw}) were compared to a surrogate distribution (MI_{surr}) in each of condition (rhythmic, arrhythmic). In the rhythmic blocks, MI_{raw} values were significantly greater than the surrogate ($Z = -2.23$, $p = .013$, $r = .34$), whereas there was not evidence of significant coupling in the arrhythmic blocks ($Z = -1.19$, $p = .88$, $r = .18$, BF10 = .235). These results confirm that coupling between the phase of entrained 1.67 Hz oscillations

and the amplitude of higher-frequency (65-100 Hz) gamma oscillations occurs selectively in the context of rhythm (Figure 3).

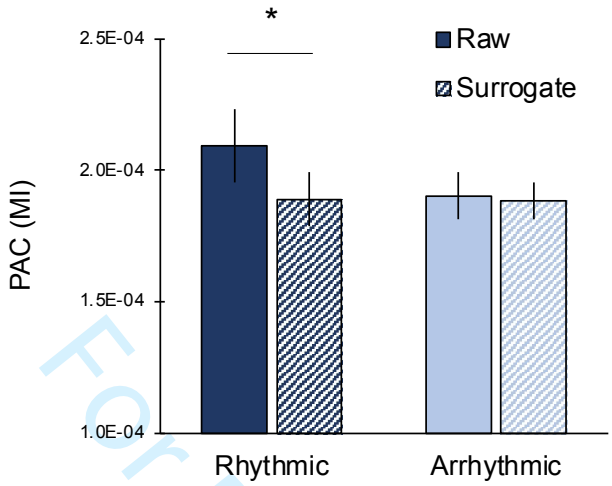

Figure 3. Significant phase-amplitude coupling (PAC; measured by MI) between the phase of entrained (1.67 Hz) oscillations and the amplitude of high-gamma (65-100 Hz) oscillations occurred in the rhythmic context only. Error bars represent SEM. * $p < .05$

Brain-Behavior Relationships

We next investigated if the effects of rhythm on the magnitude of phase-amplitude coupling between oscillations at the beat frequency (1.65 Hz) and oscillations in the high gamma range (65-100 Hz) was related to the effect of rhythm on memory performance. There was not a significant correlation between these two variables across individuals ($r(20) = .12$, $p = .59$, BF10

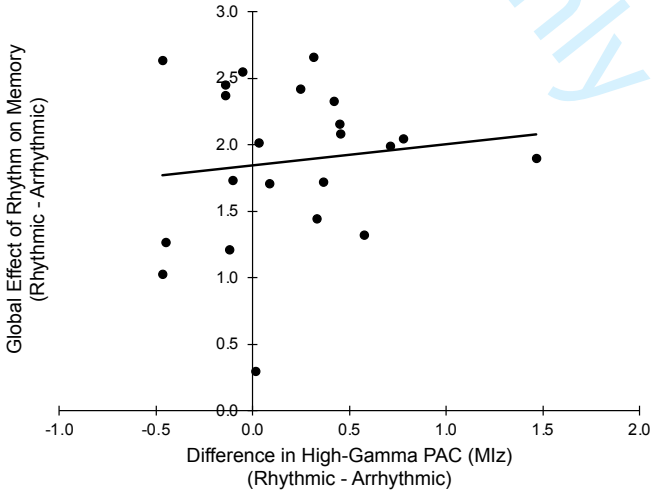

Figure 4. The difference in high-gamma phase amplitude coupling (PAC) between rhythmic and arrhythmic blocks showed a non-significant positive relationship with the global effect of rhythm on memory (d' rhythmic - d' arrhythmic).

= .303). However, the relationship was in the expected direction. One participant showed a large difference in high-gamma PAC, but their inclusion did not effect the results ($r(19) = .15$, $p = .52$, BF10 = .327).

Interim Discussion

The results from Study 1 reveal that low-frequency oscillations entrained to environmental rhythms impose temporal structure on higher-frequency (gamma) oscillations during memory encoding through a process of phase-amplitude coupling (PAC). These results support the hypothesis that in the context of rhythm, the brain operates in a 'rhythmic mode' in which gamma oscillations couple to entrained low-frequency oscillations and serve as a mechanism of selective attention that can influence both perception and cognition (Canolty & Knight, 2010; Köster et al., 2019; Schroeder & Lakatos, 2009). While we did not observe a significant relationship between the magnitude of entrained PAC and the global effect of rhythm on memory formation across participants, the directionality of the relationship was consistent with our predictions: stronger PAC was associated with greater effects of rhythm on memory. In Study 2, we turn our attention to the relationship between cross-frequency PAC and the effects of rhythm at the local level. Importantly, in contrast to Study 1 where the primary comparison was between rhythmic and arrhythmic contexts, in Study 2 stimuli were always presented in the context of rhythm but occurred either in-synchrony or out-of-synchrony with the beat. This enabled us to investigate the effects of rhythm on PAC at the local level by comparing PAC during distinct temporal windows (on-beat vs. off-beat) during the rhythmic temporal stream.

Study 2

Method

Experimental methods have been reported previously (Hickey, Merseal, et al., 2020), but are summarized here.

Participants

A total of 36 individuals (12 male, 24 female) between 18-31 years of age (M = 23, SD = 3.32) participated in Study 2. All participants were right-handed, fluent English speakers, and had normal or corrected to normal sight and hearing. Additionally, participants did not have a history of neurological illness, brain injury, or any psychiatric diagnosis. Participants were recruited from the Tufts University community and received either $15/hour or course credit for participation. All participants provided informed consent according to the procedures from the Institutional Review Board at Tufts University.

Study Design

Participants first encoded images of objects in the context of background music, half of which occurred synchronously with beat of the background music (on-beat), and half of which occurred 250ms prior to the beat (off-beat). Afterwards, participants completed a self-paced subsequent memory test in silence.

Procedure

The experimental design of Study 2 is illustrated in Figure 5. During encoding, participants viewed a series of visual stimuli in the context of instrumental background music with a steady 75 bpm beat (i.e., 1.25 Hz beat rate, inter-beat-interval = 800 ms). The music stimulus was developed using GarageBand (Apple Inc.) and was looped throughout the encoding task, lasting about 13 minutes (for more details about the musical stimulus, please see Hickey, Merseal, et al., 2020). Participants listened to the music through headphones and were informed that music would play in the background during the task. The volume of the music was set to a

comfortable listening level and kept constant across participants. In total, 120 objects were presented (60 living, 60 non-living) in the center of the screen for 750ms with a jittered inter-onset interval (IOI) between images (M = 6.4s, SD = 1.25s). Participants were instructed to decide whether each depicted a living or non-living object as quickly and accurately as possible. Importantly, images appeared either in-synchrony or out-of- synchrony with the beat of the background music (intermixed throughout the task).

Immediately after encoding, participants were administered a surprise, self-paced

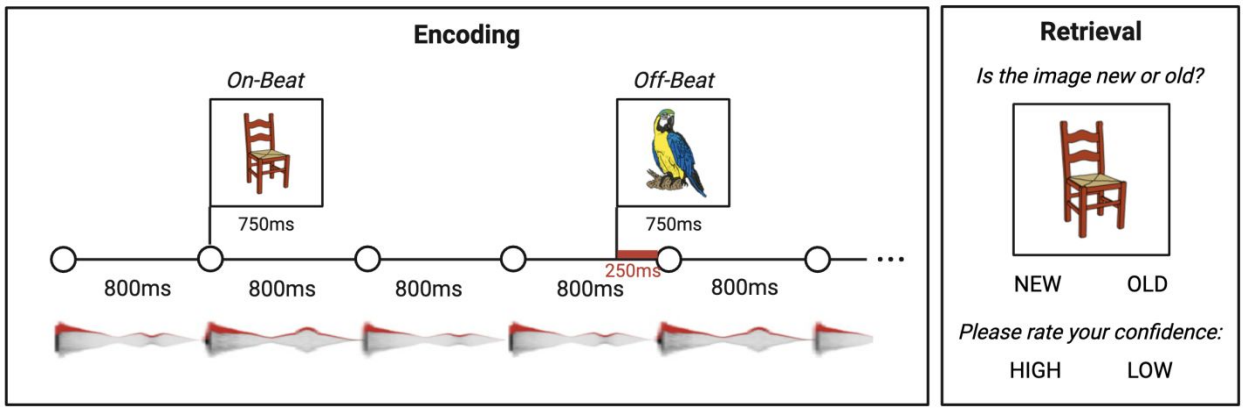

Figure 5. Experimental design for Study 2. Participants completed a single encoding (study) phase followed by a single retrieval (test) phase. During encoding, participants were shown a series of images in the context of music containing a steady 1.25 Hz beat. The beat timing is depicted using white circles above a schematic of the audio waveform of the music whose amplitude envelope is shown in red. Images were either presented synchronously (on-beat) or 250ms prior to the beat (off-beat). Each image remained on the screen for 750ms and participants were instructed to make a decision about whether the image was living or non-living. During retrieval, participants were given a self-paced memory tests where they identified if they had seen the image during the encoding task and their confidence (high, low) in their decision.

recognition memory test (in silence) in which they were shown the 120 objects from the encoding block, one at a time, intermixed with 60 novel foil objects. Participants were asked to decide whether each object had been previously seen during the encoding block (old) or not (new) and to indicate their confidence in each decision (high or low). EEG was recorded continuously throughout the encoding phase.

EEG Analysis

EEG Recording and Preprocessing

EEG was recorded from 32 channels using a BioSemi Active Two System (BioSemi, Amsterdam, Netherlands). The signal was recorded with a sampling rate of 1024 Hz and was referenced to the CMS-DRL. Two additional electrodes were placed on the mastoids and EOG was recorded from two electrodes to detect eye blinks. EEG preprocessing was completed using the EEGLab toolbox and custom MATLAB scripts. First, EEG data was referenced to the average of the mastoid electrodes. EEG signals were then downsampled to 512 Hz and filtered using a 0.1 Hz high pass and 120 Hz low pass filter. Eye artifacts were then removed from the signal using independent components analysis.

For phase-amplitude coupling analyses, EEG data was epoched into 8 second segments (approximately 97 epochs total) to allow for artifact rejection. This epoch length resulted in 10 cycles of the low-frequency oscillation (1.25 Hz) per epoch (consistent with the approach in Study 1). Epochs containing muscle artifacts were removed by visual inspection. On average, 77 epochs (SD = 14.50) per participant were retained after artifact rejection.

For gamma power analyses, EEG data was epoched around the presentation of the visual stimuli (-2:2s) and sorted based on the timing (on-beat v. off-beat). Epochs containing muscle artifacts were removed by visual inspection. A similar number of on-beat trials (M = 50.42; SD = 7.30) and off-beat trials (M = 50.89; SD = 7.31) retained after artifact rejection ($t(34) = -.74$, $p = .46$, $d = .12$).

Phase-Amplitude Coupling

Phase-amplitude coupling was calculated during encoding using the PACTools toolbox for MATLAB (Martínez-Cancino, 2020). Consistent with Study 1, phase-amplitude coupling was computed using the Modulation Index (MI; Tort et al., 2010). Details about the calculation

of the Modulation Index can be found in Study 1. In this audio-visual task, phase-amplitude coupling was computed at electrode Cz. The choice to use Cz instead of electrodes PO7 and PO8 (which were used in Study 1) was motivated by the difference in modality of the entraining stimulus (auditory rather than visual rhythm). Auditory entrainment is generally strongest in fronto-central electrode channels (Henry et al., 2014; Nozaradan et al., 2011) and significant 1.25 Hz auditory entrainment was previously analyzed by Hickey and colleagues (2020) at electrode Cz. For the low-frequency oscillation, the signal was filtered +/- 0.125 Hz around the rhythmic frequency (1.25 Hz), resulting in a signal containing information between 1.125–1.375 Hz. High frequency gamma oscillations were filtered between 30-100 Hz in 5 Hz steps (Köster et al., 2019). As described in Study 1, MI_{surr} and MI_z values were created using a surrogate distribution of MI values to determine statistical significance of phase-amplitude coupling and to use in correlations with memory performance.

Gamma Power

Gamma power at the time of stimulus presentation was computed in EEGlab between 30-100 Hz in 1 Hz bins across the entire epoch (-2s–2s) with a resolution of 10ms using a Morlet wavelet (7 cycles). The signal in each epoch at electrode Cz was baselined using a window of -900ms–100ms. This baseline was selected because it allowed for one complete cycle of the 1.25 Hz oscillation. Gamma power was averaged across narrow window surrounding stimulus presentation (-100-100ms). This window was selected in order to detect differences in on-beat and off-beat trials given that off-beat trials are relatively close in time to the beat (250ms prior). The -100ms to 100ms window ensured that there was no overlap between analysis windows for on-beat and off-beat trials. Average gamma power in the low (30-60 Hz) and high (65-100 Hz) ranges were calculated separately for on-beat and off-beat trials.

Statistical Analysis Plan

All statistics were completed in RStudio. Comparisons with the Modulation Index (MI_{raw} and MI_{surr}) were made using non-parametric statistics given the non-linear scale of the MI. Analyses using normalized coupling (MI_z) and gamma power were completed using parametric statistics, except in cases where distributions were non-normally distributed. One participant was excluded from analyses involving phase-amplitude coupling, as they had coupling that was >6SD above the mean.

We first tested for the presence of significant phase-amplitude coupling between low-frequency oscillations at the rhythmic frequency (1.25 Hz) and gamma amplitudes during encoding (which always occurred in the context of rhythm). A Wilcoxon Signed Rank test compared MI_{raw} values to the MI_{surr} values across the entire gamma range (30-100 Hz), and within the high gamma range (65-100 Hz) and low gamma range (30-60 Hz) separately. Next, we examined whether gamma power differed between on-beat and off-beat trials within participants by entering the gamma power at time of the visual stimulus presentation into a 2x2 repeated measures ANOVA containing factors of Gamma Band (high, low) and Timing (on-beat, off-beat). Finally, we investigated the relationship between phase-amplitude coupling, gamma power, and local effects of rhythm on memory using multiple linear regression. The difference in phase-amplitude coupling and gamma power (on-beat – off-beat) were used as predictors in the model, and the local memory effect (on-beat – off-beat) was used as the outcome variable. Bayes Factors (BF) were also computed using JASP (Version 0.17.1; JASP Team, 2023) for all null effects which were related to our hypotheses of interest.

Results

Phase-Amplitude Coupling

Significant coupling between low-frequency oscillations at the beat frequency (1.25 Hz) and gamma oscillations was present during stimulus encoding (Figure 6A; Z = -2.40, p = .008, r = .29). As in Study 1, this cross-frequency PAC appeared to be strongest for high gamma. Indeed, separate analysis of low gamma (30-60 Hz) and high gamma (65-100 Hz) responses confirmed that there was significant PAC between entrained oscillations and oscillations in the high gamma range (Z = -1.95, p = .025, r = .23) but not the low gamma range (Figure 6B-C; Z = -.84, p = .20, r = .10, BF10 = 1.007).

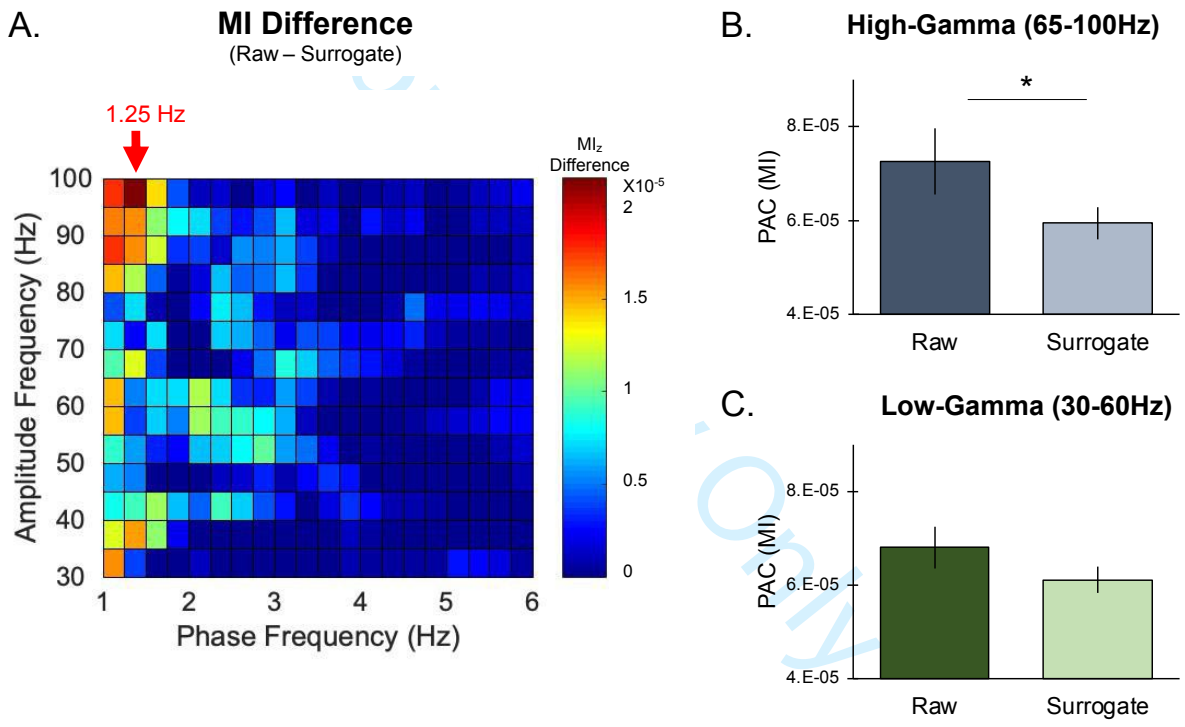

Figure 6. (A) Comodulogram displays the difference in phase-amplitude coupling (PAC; raw values – surrogate values) across the semantic decision task. Significant coupling (shown in warmer colors) is present between a range of lower (1.0-1.5 Hz) and higher (30-100 Hz) frequencies. However, peak coupling appears to occur between the entrained (1.25 Hz) oscillation and higher (80-100 Hz) frequencies. (B) Significant coupling occurred between the 1.25 Hz entrained oscillation and high-gamma (65-100 Hz) activity but, (C) not in the low-gamma range (30-60 Hz). Error bars represent SEM. * p < .01

Gamma Power

As predicted, gamma power at the time of stimulus presentation was greater for on-beat compared to off-beat trials (Figure 7A; $F(1,35) = 4.56$, $p = .040$, $\eta^2_p = .12$), with no main effect of Gamma Band (high, low; $F(1,35) = .31$, $p = .58$, $\eta^2_p = .01$, BF10 = .158) nor interaction between Timing (on-beat, off-beat) and Gamma Band ($F(1,35) = 1.81$, $p = .19$, $\eta^2_p = .05$, BF10 = .231). However, we were specifically interested in modulations of gamma power resulting from entrained low-frequency oscillations at the beat frequency (1.25 Hz). Since only high gamma demonstrated significant PAC, we reasoned that entrained oscillations may have a specific effect on the power of oscillations in the high gamma range. In support of this idea, PAC strength was positively associated with oscillatory power high in the gamma range ($r(33) = .39$, $p = .021$) (65-100 Hz; Figure 7B) and did not correlate with the power of oscillations in the low-gamma range ($rs(33) = .21$, $p = .23$, BF10 = .224). Furthermore, post-hoc exploratory analysis revealed that this positive association between PAC and gamma power was only present for on-beat trials ($r(33) = .36$, $p = .036$,) and was not significant for off-beat trials ($r(33) = -.23$, $p = .19$, BF10 = .487).

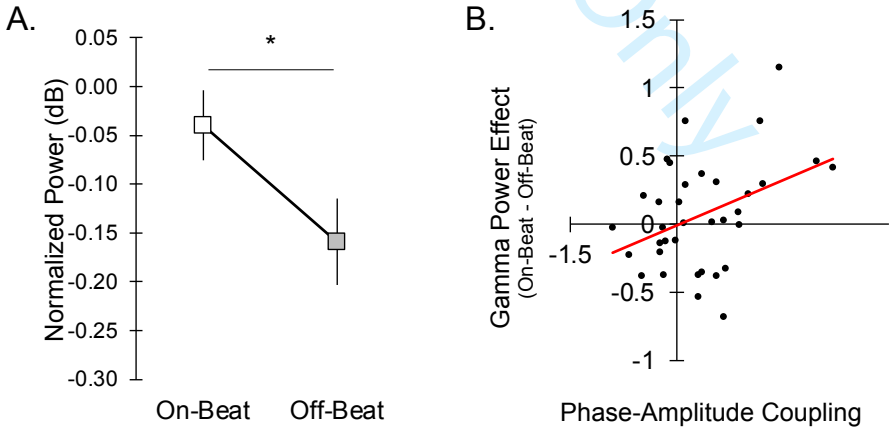

Figure 7. (A) Differences in gamma power (on-beat – off-beat). (B) At the time of stimulus presentation (-100:100ms), gamma power (30-100 Hz) is greater for on-beat compared with off-beat trials. (C) Importantly, in the high-gamma range, the strength of the coupling is related to the strength of the gamma power effects (on-beat > off-beat) in the high-gamma range. Error bars represent SEM. * $p < .05$

Brain and Behavior Relationships

Next, we investigated whether there was a relationship between PAC or gamma power and the mnemonic effects of rhythm (d'on – d'off) using multiple linear regression. The analysis was restricted to gamma oscillations in the high gamma range given that PAC and power effects were greatest for high gamma (see above). Phase-amplitude coupling was not a significant predictor of the rhythmic modulation of memory effect (B = -.10, β= -.29, p = .11, BF10 = .379). However, the difference in high gamma power between on-beat and off-beat trials did significantly predict the magnitude of the memory effect (B = .23, β= .40, p = .032). Specifically, a larger difference in gamma power for on-beat versus off-beat trials was associated with a greater memory benefit for on-beat versus off-beat trials. This suggests that the mnemonic effects of rhythm may not simply reflect the strength of PAC itself but the effect of PAC on the amplitude of high-frequency gamma oscillations. Post-hoc analysis confirmed there were no influential cases present (Cook's Distance < 1), the assumption of homoscedasticity was met, and multicollinearity between predictors was not present (Tolerance > .10; VIF < 10).

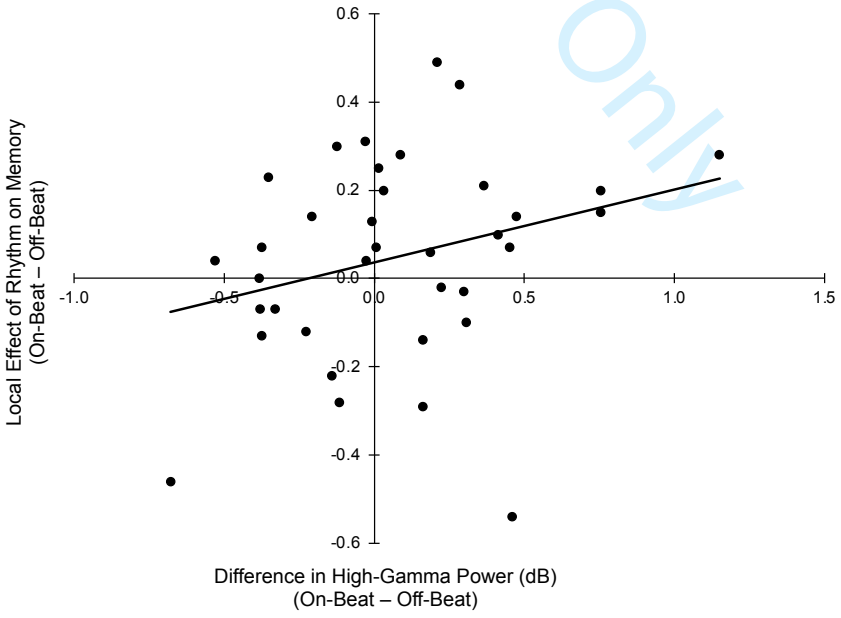

Figure 8. The difference in high-gamma phase power (dB) between on-beat and off-beat blocks showed is positively related with the local effect of rhythm on memory (d' on-beat - d' off-beat).

There has been growing recognition that environmental rhythms influence higher-order cognitive functions, such as encoding of information into long-term memory. The current study investigated potential neural mechanisms underlying this effect. Specifically, we investigated whether the effects of rhythm on memory encoding reflects the coordinated modulation of gamma oscillations by low-frequency oscillations entrained to the beat. In Study 1, we first examined this question in the context of global effects of rhythm on memory, when memory performance is enhanced for stimuli presented rhythmically compared to arrhythmically at encoding. We found that rhythmic presentation of stimuli is associated with greater phase-amplitude coupling between low-frequency oscillations at the beat frequency (1.67 Hz) and higher-frequency gamma oscillations (65-100 Hz) typically associated with episodic memory formation (Burke et al., 2014; Colgin et al., 2009; Griffiths et al., 2019). In Study 2, we next investigated this question in the context of local effects of rhythm on memory, when memory performance is enhanced for stimuli presented on-beat versus off-beat within a rhythmic context. We again found evidence for significant coupling between low-frequency oscillations at the beat frequency (1.25 Hz) and higher-frequency gamma oscillations (65-100 Hz). We also found that modulated high-frequency gamma activity was greater at the stimulus level for on-beat than off-beat trials and was positively associated with the memory benefit for on-beat versus off-beat trials. Together, these results provide novel evidence that environmental rhythms orchestrate neural activity at multiple levels during memory encoding, and that the mnemonic effects of rhythm reflect cross-frequency coupling in the brain.

The finding that entrained low-frequency oscillations influence information processing by way of modulating higher-frequency gamma oscillations complements and extends current theories of entrainment. Specifically, prior work has demonstrated that low-frequency oscillatory

entrainment and fluctuations in coupled gamma activity enhance the processing of relevant events in the environment by creating distinct temporal windows optimized for sensory-perceptual processing (rhythmic perceptual sampling) (Arnal & Giraud, 2012; Calderone et al., 2014; Lakatos et al., 2008; Schroeder & Lakatos, 2009). Here, we find that entrained oscillations and coupled gamma activity also create temporal windows optimized for memory encoding (mnemonic sampling). These results support the proposal that rhythm biases the brain into a more efficient "rhythmic mode" of processing that can influence both perception and cognition (Hickey & Race, 2021; Schroeder & Lakatos, 2009). Furthermore, while prior work has highlighted the importance of entrained oscillations for memory encoding (Hickey, Merseal, et al., 2020; A. Jones & Ward, 2019), here we specify a more precise mechanism by which this may occur. That is, our results suggest that it is not the entrained oscillations themselves that modulate memory encoding, but the coordination of higher-frequency activity by entrained oscillations. This adds to a growing body of literature emphasizing the importance of cross-frequency phase-amplitude coupling, and particularly the coupling of gamma oscillations, for the encoding of information into long-term memory (e.g., Köster et al., 2019).

An important aspect of the current results is that they provide evidence of similar memory entrainment mechanisms for both visual rhythms (Study 1) as well as auditory rhythms (Study 2), despite differences in task design and entraining frequency (1.67 Hz and 1.25 Hz, respectively). This suggests that entrainment may not need to occur in a specific modality or at a specific frequency, but instead could be a more general way for the brain leverage statistical regularities in the environment to optimize neural responsivity across time. Future work could further test this hypothesis and the generalizability of these results by investigating the effects of

different entraining modalities (e.g., effects of visual rhythms on auditory encoding) and entraining frequencies (e.g., theta rhythms) on memory performance.

Interestingly, in both Study 1 and Study 2, phase-amplitude coupling effects in the context of rhythm were most prominent for oscillations in the high-gamma range (65-100 Hz). A large body of work has demonstrated that gamma activity in different frequency ranges may result from different underlying mechanisms (Colgin et al., 2009; Crone et al., 2011), and has suggested that higher-frequency gamma activity may be closely related to attention and memory encoding (Castelhano et al., 2014; Chacko et al., 2018; Colgin et al., 2009; Griffiths et al., 2019; Ray et al., 2008). For example, a recent study by Chacko et al. (2018) found that coupling between low-frequency oscillations and gamma oscillations in the higher gamma range were associated with attentional orienting, whereas coupling between low-frequency oscillations and oscillations in the lower gamma range was associated with response speeds during a cued spatial attention task. A similar pattern has been observed in studies of gamma power, where high gamma activity has also been elicited by attentional cues in a conditional visuomotor task (Brovelli et al., 2005). It has been proposed that coupling between low-frequency oscillations and high-gamma power may be related to changes in synaptic strength (LTP/LTD) and attentional orienting that is relevant for learning and memory (Canolty & Knight, 2010; Schroeder & Lakatos, 2009). Indeed, the coupling of theta and high-gamma oscillations and the synchrony of gamma activity within the prefrontal cortex and hippocampus has been associated with spatial working memory performance (Alekseichuk et al., 2016; Carver et al., 2019; Yamamoto et al., 2014). Additionally, cross frequency coupling between low-frequency (theta) and high-frequency (high-gamma) oscillations within the hippocampus has been linked with encoding processes, whereas coupling between theta and low-gamma is more tightly associated

with memory retrieval (Colgin et al., 2009; Griffiths et al., 2019). Together with the current results, this suggests that coupled oscillations in the high gamma range may be particularly relevant for memory encoding and for directing attention to particular moments in time in order to enhance encoding.

Another important aspect of the current results is that they link entrained cross-frequency PAC to the mnemonic effects of rhythm at both the global level (Study 1) and the local level (Study 2). However, we did not find a consistent brain-behavior relationship between PAC and the mnemonic benefits of rhythm across studies. In Study 1, the lack of a relationship between the magnitude of phase-amplitude coupling and the global effects of rhythm on memory performance might reflect a lack of sensitivity at the behavioral or neural level. Study 1 utilized a blocked design, where the mnemonic benefit of rhythm was defined as the difference in memory between rhythmic and arrhythmic blocks. Previous studies have found that the effects of rhythm on memory change over time and may be most pronounced in the first blocks (Johndro et al., 2019). Therefore, averaging across blocks could have reduced our ability to detect subtle effects of rhythm on memory performance. Similarly, PAC was only evaluated at the block level, rather than at the trial level. Therefore, faster fluctuations in coupled gamma activity may have been difficult to detect or may be more closely associated with local effects of rhythm on memory. Indeed, in the original study by Jones and Ward (2019), entrainment strength was also not associated with the global effects of rhythm on memory performance.

In contrast, a significant positive relationship was observed in Study 2 between the magnitude of entrained gamma power and the mnemonic effects of rhythm at the local level (memory benefit for on-beat vs. off-beat trials). This parallels the results observed in the original study by Hickey, Merseal, and colleagues (2020), in which entrainment strength was also

positively correlated with memory performance, and suggests that brain-behavior relationships may be more easily detected using more fine-grained measurements and manipulations of rhythmic effects on behavior and neural processing. Interestingly, the magnitude of entrained PAC did not positively correlate with the mnemonic benefits of rhythm, but the magnitude of gamma power did. This suggests that it may not be the coupling itself that is relevant for encoding but rather the timing of gamma activity relative to the rhythmic stream. This was surprising given the large body of work which has found that coupled gamma oscillations influence memory encoding more broadly (Canolty et al., 2006; Friese et al., 2013; Köster et al., 2019; Lega et al., 2016; Tort et al., 2008). However, these studies have typically focused on theta-gamma coupling (rather than *delta*-gamma coupling) and have not investigated the effect of coupling on encoding *at specific moments in time*. Future work should investigate whether significant correlations are present between entrained PAC and memory performance at the global or local level when rhythms occur in the theta range. This would help to further extend theoretical models from the memory domain that emphasize theta-gamma coupling (e.g., theta-gamma neural code; Lisman & Jensen, 2013).

Limitations and Future Directions

The current study was a reanalysis of two existing datasets collected by Jones and Ward (2019) and Hickey, Merseal, et al. (2020) . These studies were selected because they allowed us to investigate the effect of coupled oscillations on memory performance at both the global and local levels. However, methodological differences across studies make it difficult to directly compare the results. For example, one major difference between the two paradigms (as mentioned previously) was the visual versus auditory entraining stimuli. Although including different entraining modalities was a unique feature of this study, it also created differences in

whether entrainment was having unimodal or cross-modal effects on memory encoding (since memory was for visual images in both paradigms). In addition, Jones and Ward (2019) used a repeated study-test design whereas participants in Hickey, Merseal, et al. (2020) only had one study block and one surprise subsequent memory test. Future work could more directly compare the effects of rhythm on global versus local processing by using more similar paradigms.

Future work should also explore whether oscillations in other frequency bands may also be relevant for rhythmic effects on memory. For example, theta-gamma coupling, which has been frequently associated with memory encoding (Buzsáki & Wang, 2012; Canolty & Knight, 2010; Lisman & Jensen, 2013), may be nested within entrained delta oscillations (Lakatos et al., 2005, 2008). The dynamic orchestration of oscillations outside the delta, theta, and gamma bands could also contribute to the temporal structuring of episodic memory. For example, alpha oscillations are thought to play an important role in the gating selective attention and are known to play role in memory formation (Hanslmayr & Staudigl, 2014; Voytek et al., 2010). Beta oscillations have also been implicated in memory tasks and are thought to control shifts in attention and neural excitability according to temporal expectations (Buschman et al., 2012; Cravo et al., 2011; Fiebelkorn & Kastner, 2019; Hanslmayr & Staudigl, 2014). In the language domain, interactions between the phase and amplitude of nested theta, gamma, delta and beta oscillations have been proposed to provide a dynamic neural code, or "neurocomputational multiplexing", central for structuring language (Murphy, 2020). Future research should investigate the degree to which nested oscillations across multiple frequency bands might also adaptively structure memory formation.

Data Availability

The data that support the findings of this study are available online through Open Science Framework (Study 1: https://osf.io/hv4j8/.; Study 2: https://osf.io/wzc2g).

Author Contributions

Paige Hickey Townsend: Conceptualization; Methodology; Formal analysis; Investigation; Writing - original draft; Writing – review & editing; Visualization. Alexander Jones: Methodology; Formal analysis; Investigation; Writing – review & editing. Aniruddh D. Patel: Methodology; Writing - review & editing; Supervision; Funding acquisition. Elizabeth Race: Conceptualization; Methodology; Formal analysis; Investigation; Resources; Writing - original draft; Writing – review & editing; Visualization, Supervision; Project administration; Funding acquisition.

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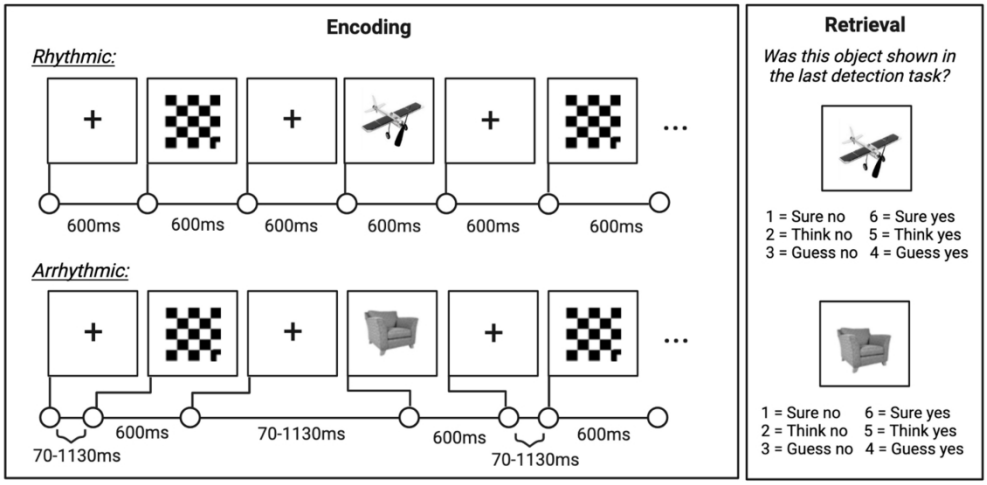

Figure 1. Experimental design for Study 1. Participants completed 6 blocks of encoding and retrieval (3 rhythmic; 3 arrhythmic). During encoding, participants were shown a series of images and checkerboards separated by fixation crosses and instructed to press the space bar each time an animal appeared. Images remained on the screen for 600ms. In rhythmic blocks, the interstimulus interval (ISI) was always 600ms, while in arrhythmic blocks the ISI was jittered between 70-1130ms. Example timelines of stimulus presentation during encoding are illustrated in the first panel. During retrieval, participants were given self-paced memory tests where they were presented with old and new images and indicated if they had seen the image during the preceding detection (encoding) task and their confidence in their memory decision.

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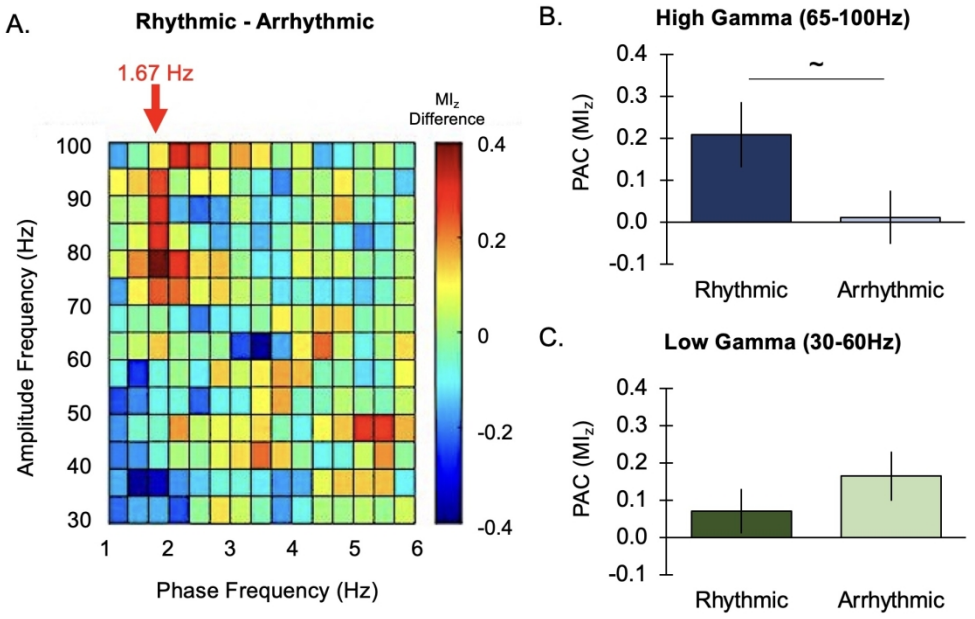

Figure 2. The difference in normalized Phase-Amplitude Coupling (PAC; measured by MIz) between rhythmic and arrhythmic contexts. (A) The comodulogram depicts the difference in PAC between contexts (rhythmic – arrhythmic), where the third column displays coupling at the entraining frequency (1.67 Hz). (B) There was numerically greater phase-amplitude coupling at the entrained (1.67 Hz) frequency in the high-gamma (65-100 Hz) range, (C) but not in the low-gamma (30-60 Hz) range. Error bars represent SEM. ~ p = .058.

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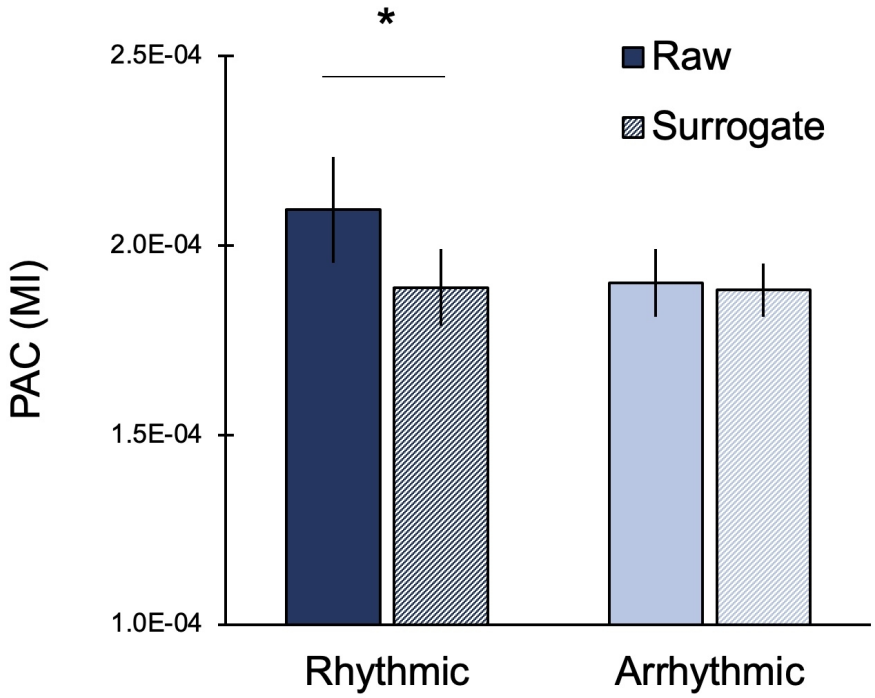

Figure 3. Significant phase-amplitude coupling (PAC; measured by MI) between the phase of entrained (1.67 Hz) oscillations and the amplitude of high-gamma (65-100 Hz) oscillations occurred in the rhythmic context only. Error bars represent SEM. * $p < .05$

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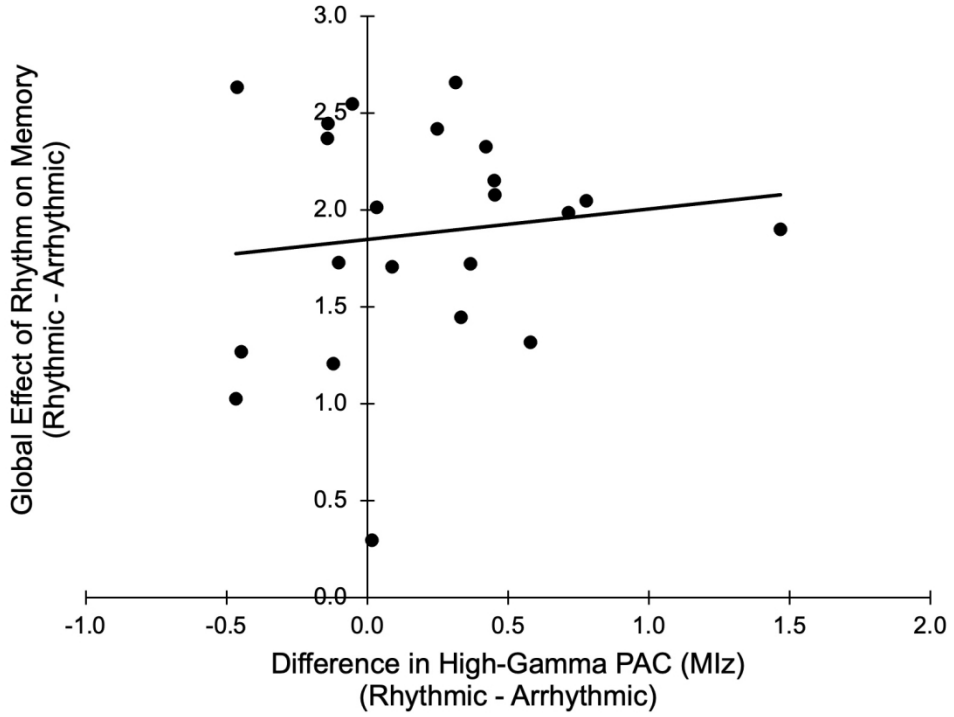

Figure 4. The difference in high-gamma phase amplitude coupling (PAC) between rhythmic and arrhythmic blocks showed a non-significant positive relationship with the global effect of rhythm on memory (d' rhythmic - d' arrhythmic).

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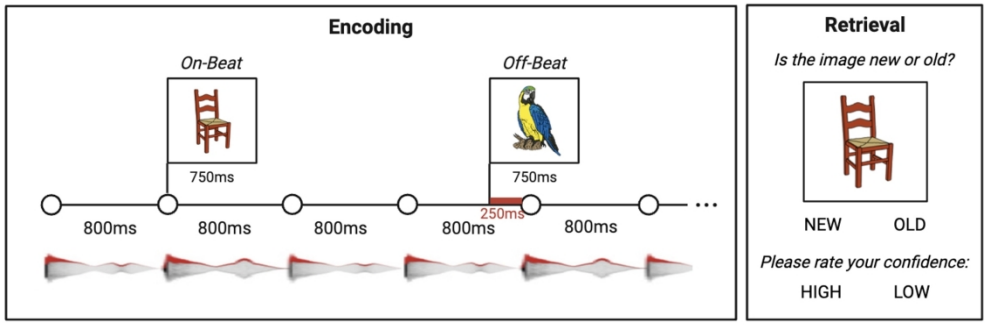

Figure 5. Experimental design for Study 2. Participants completed a single encoding (study) phase followed by a single retrieval (test) phase. During encoding, participants were shown a series of images in the context of music containing a steady 1.25 Hz beat. The beat timing is depicted using white circles above a schematic of the audio waveform of the music whose amplitude envelope is shown in red. Images were either presented synchronously (on-beat) or 250ms prior to the beat (off-beat). Each image remained on the screen for 750ms and participants were instructed to make a decision about whether the image was living or non-living. During retrieval, participants were given a self-paced memory tests where they identified if they had seen the image during the encoding task and their confidence (high, low) in their decision.

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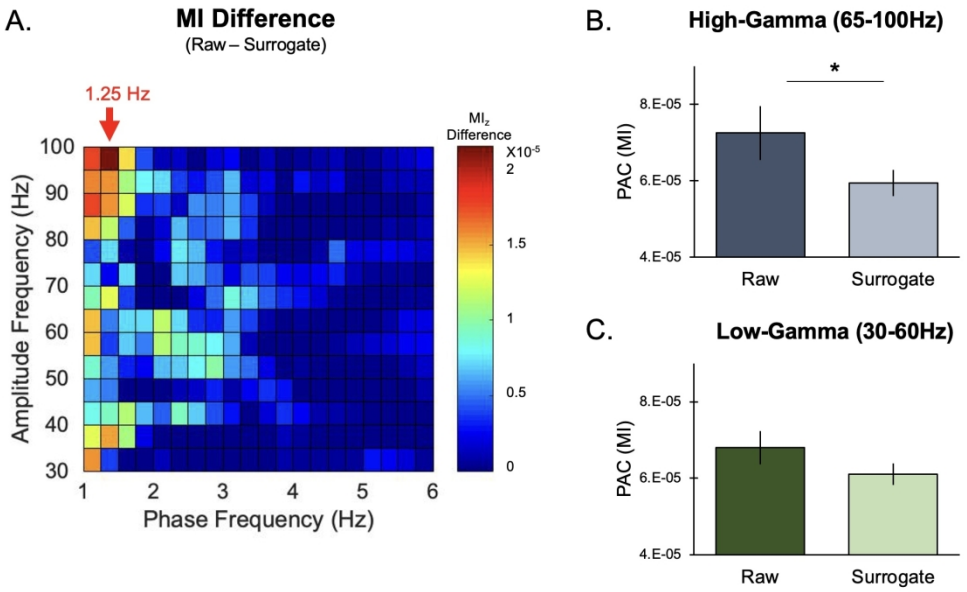

Figure 6. (A) Comodulogram displays the difference in phase-amplitude coupling (PAC; raw values – surrogate values) across the semantic decision task. Significant coupling (shown in warmer colors) is present between a range of lower (1.0-1.5 Hz) and higher (30-100 Hz) frequencies. However, peak coupling appears to occur between the entrained (1.25 Hz) oscillation and higher (80-100 Hz) frequencies. (B) Significant coupling occurred between the 1.25 Hz entrained oscillation and high-gamma (65-100 Hz) activity but, (C) not in the low-gamma range (30-60 Hz). Error bars represent SEM. * $p < .01$

376x226mm (144 x 144 DPI)

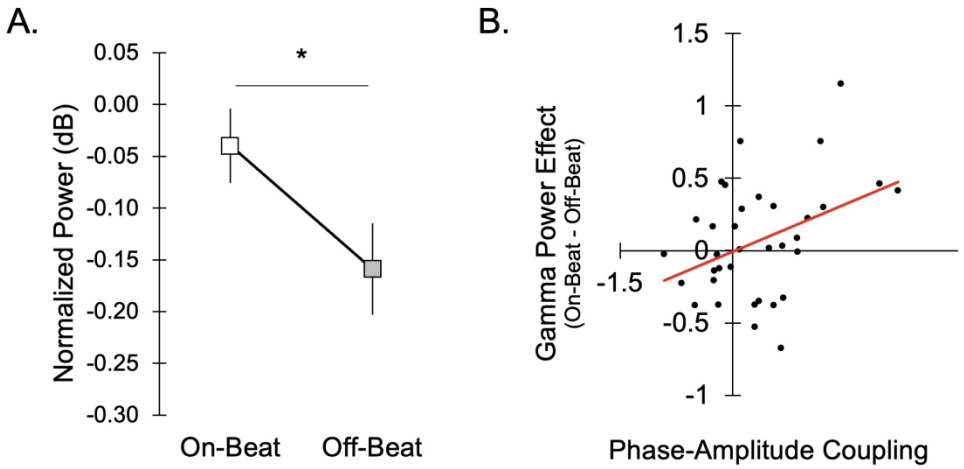

Figure 7. (A) Differences in gamma power (on-beat – off-beat). (B) At the time of stimulus presentation (-100:100ms), gamma power (30-100 Hz) is greater for on-beat compared with off-beat trials. (C) Importantly, in the high-gamma range, the strength of the coupling is related to the strength of the gamma power effects (on-beat > off-beat) in the high-gamma range. Error bars represent SEM. * $p < .05$

383x201mm (144 x 144 DPI)

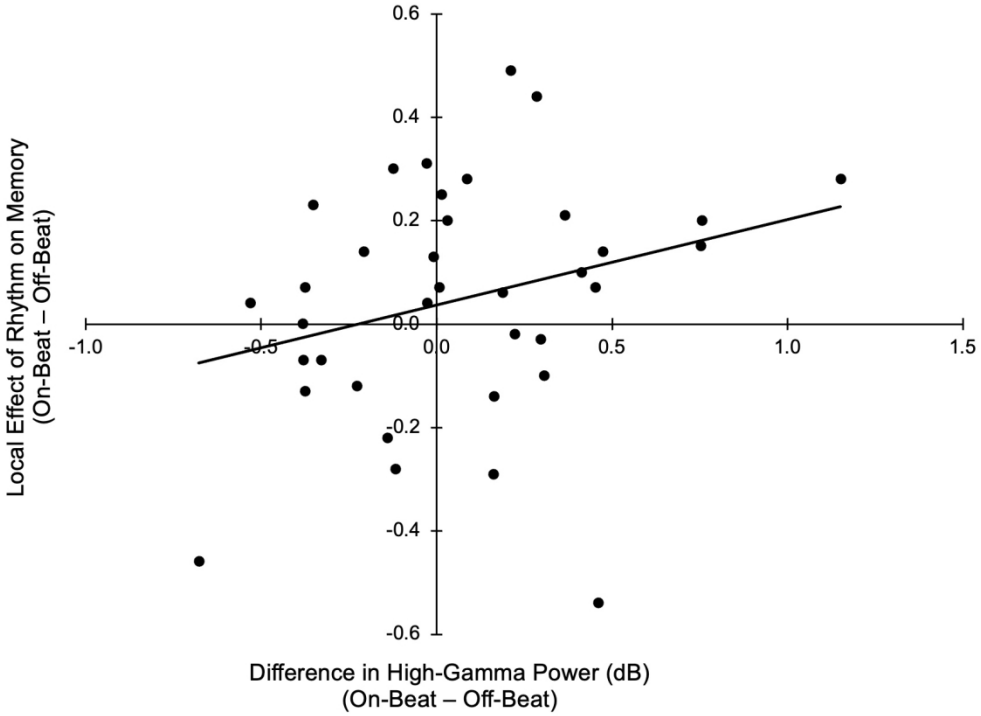

Figure 8. The difference in high-gamma phase power (dB) between on-beat and off-beat blocks showed is positively related with the local effect of rhythm on memory (d' on-beat - d' off-beat).

306x225mm (144 x 144 DPI)