

# Memory in time: Neural tracking of low-frequency rhythm dynamically modulates memory formation



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## ARTICLE INFO

### Keywords:

Neural oscillations  
Rhythm  
Long-term memory  
Entrainment  
Dynamic attending  
Music

## ABSTRACT

Time is a critical component of episodic memory. Yet it is currently unclear how different types of temporal signals are represented in the brain and how these temporal signals support episodic memory. The current study investigated whether temporal cues provided by low-frequency environmental rhythms influence memory formation. Specifically, we tested the hypothesis that neural tracking of low-frequency rhythm serves as a mechanism of selective attention that dynamically biases the encoding of visual information at specific moments in time. Participants incidentally encoded a series of visual objects while passively listening to background, instrumental music with a steady beat. Objects either appeared in-synchrony or out-of-synchrony with the background beat. Participants were then given a surprise subsequent memory test (in silence). Results revealed significant neural tracking of the musical beat at encoding, evident in increased electrophysiological power and inter-trial phase coherence at the perceived beat frequency (1.25 Hz). Importantly, enhanced neural tracking of the background rhythm at encoding was associated with superior subsequent memory for in-synchrony compared to out-of-synchrony objects at test. Together, these results provide novel evidence that the brain spontaneously tracks low-frequency musical rhythm during naturalistic listening situations, and that the strength of this neural tracking is associated with the effects of rhythm on higher-order cognitive processes such as episodic memory.

## 1. Introduction

Time is a critical component of episodic memory, our ability to remember past events in specific spatiotemporal contexts (Tulving, 1983). Recently, there has been a growing interest in how time is represented in the brain and how temporal representations at different timescales contribute to the formation of long-term memories (Cohn-Sheehy and Ranganath, 2017; Palombo and Verfaellie, 2017). Much of the research into these questions has focused on how sequential representations of temporal context coded in regions such as the medial temporal lobes or the posterior-medial network serve to segment and organize elements of experience into coherent episodic memories (Aly et al., 2018; Baldassano et al., 2017; Davachi and DuBrow, 2015; Ezzyat and Davachi, 2011; Gold et al., 2017; Hasson et al., 2015; Heusser et al., 2016; Howard and Kahana, 2002; Hsieh et al., 2014; Ranganath and Hsieh, 2016). Yet many temporal structures commonly found in the environment, such as biological motion, speech, or music, contain recurrent temporal patterns that unfold rhythmically over time. While a

large body of research has demonstrated that external rhythms influence how we attend to and perceive the world (for review, see Calderone et al., 2014; Haegens and Zion Golumbic, 2018; Nobre and van Ede, 2018), little is known about how the brain leverages these rhythms in the service of more complex cognitive processes such as memory.

The current study investigated whether environmental rhythms dynamically modulate memory by influencing neural processing and encoding at particular moments in time. It is well established that neural responses in the brain spontaneously synchronize to the periodicities of external rhythms, evident in increases in electrophysiological power and phase alignment at the same frequency as the external rhythmic stream (Calderone et al., 2014; for review, see Nozaradan, 2014; Thut et al., 2012). For naturalistic rhythms, such as speech and music, this occurs most prominently in the synchronization of low-frequency (<5 Hz) responses in the delta range (Zhou et al., 2016). Importantly, these low-frequency neural responses to rhythm have been shown to dynamically modulate fluctuations in cortical excitability, such that high excitability states align with the temporal pattern of the rhythmic stream

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<https://doi.org/10.1016/j.neuroimage.2020.116693>

Received 30 October 2019; Received in revised form 18 February 2020; Accepted 26 February 2020

Available online 3 March 2020

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(Large and Jones, 1999; Schroeder and Lakatos, 2009). This has led to the proposal, as formalized in the Oscillation Selection Hypothesis, that low-frequency neural responses to external rhythms prioritize processing of information at specific moments in time (e.g., in-phase with the rhythm) and thereby serve as a core mechanism of attentional selection (Calderone et al., 2014; Doelling and Poeppel, 2015; Frey et al., 2015; Henry et al., 2014; Lakatos et al., 2008; Mathewson et al., 2012; Schroeder and Lakatos, 2009; Tierney and Kraus, 2015). Support for this proposal comes from the finding that perceptual processing (e.g., target detection and discrimination) is enhanced in rhythmic contexts specifically when stimuli appear in-phase with a rhythmic beat (Escoffier et al., 2010; Jones et al., 2002; Rohenkohl et al., 2012; Barnhart et al., 2018; Bolger et al., 2013; ten Oever et al., 2014; for review see Haegens and Zion Golumbic, 2018; Henry and Obleser, 2012; Lakatos et al., 2008; Mathewson et al., 2010; Stefanics et al., 2010). This proposal also provides a neural instantiation of the Dynamic Attending Theory, which proposes that rhythm can dynamically modulate fluctuations in attention such that peaks of attention align with external rhythms in the environment (Jones and Boltz, 1989; Jones, 2019; Large and Jones, 1999). Given that what we remember is tightly linked to how, and when, we attend (Chun and Turk-Browne, 2007; deBettencourt et al., 2018), a logical extension of this proposal is that neural tracking of rhythm also dynamically modulates memory and influences the encoding of information at specific moments in time.

Recent studies investigating the effects of external rhythms on memory lend preliminary support to this proposal. Simple rhythmic auditory and visual stimulation (e.g., trains of flashes/beeps) delivered at the theta frequency have been shown to lead to global increases in theta activity in the brain and to enhance subsequent episodic memory performance (Clouter et al., 2017; Köster et al., 2019; Roberts et al., 2018; Wang et al., 2018; for review, see Hanslmayr et al., 2019). In addition, stimuli presented within structured temporal contexts (e.g., repeating ISI) are better remembered compared to stimuli presented within unstructured temporal contexts (e.g., random ISI), an effect that has been linked to facilitated sensory processing (as reflected in the reduction of early ERP amplitudes) (Jones and Ward, 2019; Thavabalasingam et al., 2016). A recent study by Johndro et al. (2019) extended these prior results by demonstrating that rhythmic temporal structures not only have global effects on memory encoding, but also influence encoding at specific moments in time. In this study, the temporal onset of to-be-remembered visual stimuli was manipulated *within* a rhythmic temporal stream (instrumental music) such that stimuli could appear either in-synchrony or out-of-synchrony with the background beat. In a subsequent test of memory, the authors found that memory performance was greater for items that had appeared in-synchrony compared to out-of-synchrony with the beat at encoding. These results reveal that cross-modal, background rhythms can influence memory encoding, and that the mnemonic benefit of rhythm depends on the timing of stimulus presentation within the rhythmic temporal stream.

The goal of the current study was to investigate the neural mechanisms by which the brain leverages low-frequency, environmental rhythms in the service of memory encoding. Specifically, we tested the hypothesis that the brain spontaneously tracks environmental rhythms and that the resulting rhythmic fluctuations in neural activity serve as a mechanism of temporal attention that influence encoding at specific moments in time. EEG was recorded while participants completed an incidental encoding task in which they classified visually-presented stimuli that were either presented in-synchrony or out-of-synchrony with the beat of background music. Participants were then given a surprise subsequent memory test (in silence) in which they made old/new judgments about novel and previously-presented stimuli. At the neural level, we predicted that cortical tracking of the auditory rhythm would be evident in increased low-frequency electrophysiological power and phase consistency, specifically at the beat frequency (1.25 Hz) and its harmonics (for review, see Calderone et al., 2014; Nozaradan, 2014; Thut et al., 2012). At the behavioral level, we predicted that memory would be

greater for stimuli presented in-synchrony compared to out-of-synchrony with the background beat (Johndro et al., 2019). Importantly, our primary hypothesis centered on the relationship between neural responses to rhythm and memory formation. If cortical tracking of rhythm dynamically modulates memory formation, we hypothesized that the effect of rhythm on subsequent memory should be related to the strength of electrophysiological responses at the beat frequency. This hypothesis was motivated by prior studies which have demonstrated that the effect of external rhythms on behavior depend on the fidelity by which these rhythms are represented in the brain. For example, Köster et al. (2019) found that participants do not respond equally well to visual stimulation at the theta frequency, and that participants' responsiveness to theta stimulation strongly predicts the beneficial effect of that stimulation on subsequent memory performance. A similar relationship between neural and behavioral responses to rhythm has also been observed in the context of rhythmic auditory stimulation: Participants with stronger neural responses to low-frequency auditory rhythms demonstrate greater effects of rhythm on perception and action (e.g., Nozaradan et al., 2016; Doelling and Poeppel, 2015; Tierney and Kraus, 2013; Herrmann et al., 2016). Thus, we predicted that the effect of rhythm on memory encoding would be positively related to participants' synchronous neural activity at the beat frequency. We also investigated whether neural tracking of rhythm predicts subsequent memory within subjects at the time of stimulus presentation. We predicted that electrophysiological responses at the beat frequency would be stronger for items that would be subsequently remembered compared to items that would be subsequently forgotten (e.g., 'subsequent memory effects'; Wagner et al., 1999; Paller and Wagner, 2002). Such results would provide additional evidence that neural tracking of low-frequency rhythm is functionally related to encoding success at particular moments in time.

## 2. Methods

### 2.1. Participants

A total of 36 individuals (12 male, 24 female) between 18 and 31 years of age ( $M = 23$ ,  $SD = 3.32$ ) participated in the current study. Our sample size was based on prior studies that have observed strong positive correlations between the effects of rhythm on neural activity and behavior (Köster et al., 2019; Nozaradan et al., 2016 and Doelling and Poeppel, 2015). 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.

### 2.2. Stimuli

#### 2.2.1. Auditory stimulus

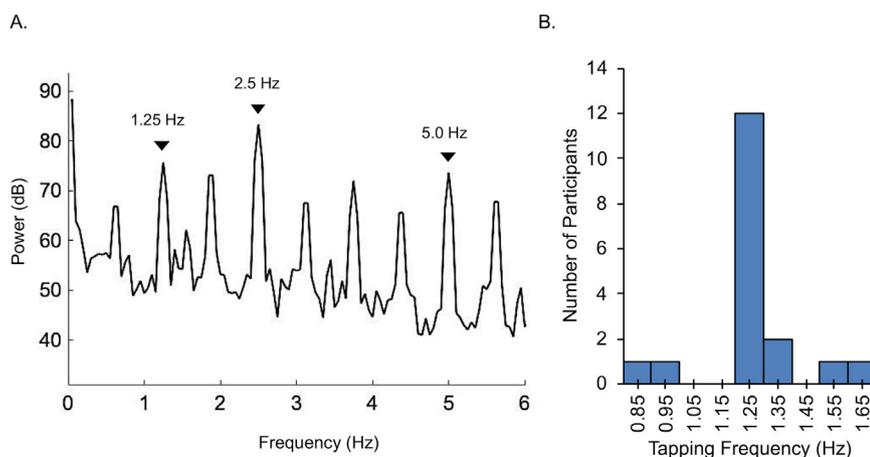
Garage Band software (Apple, USA) was used to design a novel music track with a tempo of 75 bpm or 1.25 Hz (inter-beat interval = 800 ms) and a 4/4 metrical structure. The music was instrumental in quality, did not contain any words or lyrics, and was designed to sound naturalistic without being highly complex in terms of melody, rhythm, or texture. Instrumentation samples consisted of stock Garage Band loops and were comprised of a "Basic Core Beat" as well as a "Forward Progress Guitar", "Hourglass Guitar", "Brixton Lights Lead Guitar", and "Digital Riff Guitar". The first eight beats (two measures) were composed of only the loop of the "Basic Core Beat". In total, the original music stimulus was 2 min and 15 s in length. The music track is available in the supporting materials.

**2.2.1.1. Acoustic analysis of auditory stimulus.** An acoustic analysis of the music stimulus was performed in order to confirm that acoustic energy was present at the beat frequency. The amplitude envelope of the music stimulus was obtained by performing a Hilbert transform after passing the audio file through a Hanning window. The envelope was then segmented into 20 s epochs with 5 s overlaps, submitted to a fast Fourier transform (FFT), and averaged to produce a frequency spectrum of the sound envelope. Prominent peaks at the beat and harmonic frequencies (e.g., 1.25, 2.5, 5.0 Hz) were present in the frequency spectrum of the sound envelope of the music stimulus (Fig. 1A). We next confirmed that there was no difference in the average acoustic energy during the presentation of on-beat and off-beat visual stimuli by calculating the average amplitude and power present in the music stimulus during the 750 ms that visual targets were displayed. There was no difference in the mean amplitude or power of the background music during the presentation of on-beat and off-beat images (amplitude:  $t(116) = 1.05$ ,  $p = 0.30$ ,  $d = 0.19$ ; power:  $t(118) = 0.43$ ,  $p = 0.67$ ,  $d = 0.08$ ).

**2.2.1.2. Perceived beat of auditory stimulus.** Data from a tapping task ( $n = 18$ ; see Procedures) was analyzed to confirm that participants' perceived beat corresponded to the beat frequency present in the music. Participants' mean tapping rate was 75.99 bpm ( $SD = 0.14$ ), or 1.26 Hz, confirming that participants' perceived beat frequency closely corresponded to the beat frequency present in the music (1.25 Hz) (Fig. 1B). The strong consensus among participants in perceived beat tempo contrasts with the diversity of modulation frequencies at which salient acoustic energy was present the music (Fig. 1A), which is notable given that different frequencies could theoretically have been selected by individuals as their own perceived beat (for review, see Nozaradan, 2014). These results align with the notion that the beat one perceives in music is not a simple "readout" of the chief periodicity in the stimulus itself, since the strongest peak in the envelope modulation was at 2.5 Hz. These results are also consistent with previous work showing that the strongest peak in the modulation spectrum of simulated auditory neural responses to rhythmic music is often at 2 or 4 times the frequency of the perceived beat (Ding et al., 2017).

### 2.2.2. Visual stimuli

Visual stimuli consisted of 190 pictures of objects (95 animate, 95 inanimate) from the Multilingual Picture Database (MultiPic) (Dunabeitia et al., 2018). All images were drawn by the same artist and were standardized in terms of visual complexity and concreteness. Examples of animate images included photographs of animals or plants and of inanimate images included household objects, vehicles, or tools. Both categories contained a mix of images that were both black and white and in color.



**Fig. 1.** Music stimulus attributes and tapping task performance. (A) Frequency spectrum of the sound envelope of the music stimulus. Primary peaks were observed at the beat frequency (1.25 Hz) and its harmonics (e.g., 2.5 Hz and 5.0 Hz), indicated by black triangles. (B) Tapping frequency histogram. Tapping rates produced by a subgroup of eighteen participants while listening to the music stimulus indicated that participants perceived the beat to have a frequency close to the beat frequency of the music stimulus (1.25 Hz).

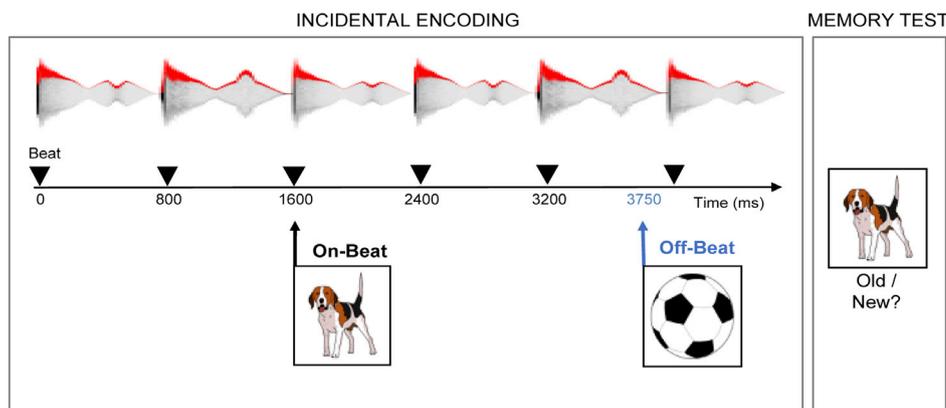
## 2.3. Procedures

### 2.3.1. Study overview

During all EEG recordings, participants were seated comfortably in a chair and were instructed to relax and avoid any head or body movement. Participants first completed two baseline EEG recordings. During a resting state recording, participants sat in silence for 5 min with eyes closed. During a passive listening recording, participants listened to the looped music stimulus for 5 min with their eyes focused on a central fixation cross displayed on a computer screen in front of them. Following the two baseline EEG recordings, participants completed a visual flanker task (Eriksen and Eriksen, 1974) in order to provide a baseline measure of inhibitory control. In addition, the flanker task acted as a temporal buffer between passive listening and the onset of the encoding task. Participants then completed an incidental encoding task (in the presence of background music) and a subsequent memory test (in silence). Finally, participants completed the beat alignment test (BAT) as a measure of their general beat perception ability (Iversen and Patel, 2008) and filled out a questionnaire about their past musical experience. Eighteen participants also completed a final tapping task in which they listened to the music stimulus and were instructed to tap along with the beat by pressing a button on a computer keyboard as soon as they perceived a steady beat. In total, the entire experiment took approximately 1 h and 15 min to complete.

### 2.3.2. Incidental encoding task

The experimental design of the memory task is depicted in Fig. 2. During incidental encoding, participants viewed a series of visual stimuli and were instructed to decide whether each depicted a living or non-living object as quickly and accurately as possible by making a button press with their right index finger on a keyboard. In total, 120 objects were presented (60 living, 60 non-living). Objects were displayed in the center of the screen for 750 ms with a jittered ISI between images ( $M = 6.4$  s,  $SD = 1.25$  s). Participants wore headphones during the task and were told that music would play in the background, but were otherwise not instructed to pay attention to the music. The volume of the music was set to a comfortable listening level and kept constant across participants. Visual objects did not appear before the third measure of the music stimulus (i.e., before 6.4 s). Importantly, images appeared either in-synchrony or out-of-synchrony with the beat of the background music (intermixed throughout the task). For the images presented in-synchrony (on-beat condition), the onset of each object was synchronized with the beat of the background music. For the images presented out-of-synchrony (off-beat condition), the onset of each object was shifted 250 ms prior to the beat. This timing for the off-beat condition was chosen such that presentation of off-beat stimuli did not align with a clear subdivision of



**Fig. 2.** Memory paradigm. During incidental encoding, participants were shown a series of pictures of objects in the context of background, rhythmic music and made a semantic decision (living/non-living) about each object. Pictures remained on the screen for 750 ms and appeared either in-synchrony (on-beat) or out-of-synchrony (off-beat) with the background rhythm (off-beat pictures were presented 250 ms prior to the beat). Participants were then given a surprise memory test in silence in which they were shown pictures of objects that had been previously viewed during the encoding block and novel objects and made a recognition memory decision for each (old/new). The top of the figure displays an example of the musical waveform (black) and amplitude envelope (red) with inverted black triangles indicating the timing of the underlying beat (800 ms ISI, or 1.25 Hz). The lower portion of the figure shows example images with a thin arrow above each image showing the time of its onset.

the inter-beat interval. The presentation order of the object stimuli was semi-randomized such that an equal number of living/non-living and on/off beat images were presented in each third of the experiment and no more than six items of the same condition (on/off) were presented in a row. The assignment of objects to conditions was counterbalanced across participants. In total, the encoding task lasted 13 min. The 2 min 15 s musical stimulus was looped so that background music was present throughout the encoding task, and the EEG was recorded continuously. Prior to beginning the task, participants completed ten practice trials in silence.

### 2.3.3. Memory test

Immediately following the encoding task, participants were administered a surprise, self-paced 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).

### 2.3.4. Beat alignment test (BAT)

Following the memory test, participants completed the beat perception portion of the Beat Alignment Test (Iversen and Patel, 2008) to measure individual differences in the ability to detect a beat in music. In the BAT, participants listen to 36 instrumental musical excerpts sampled from a variety of popular genres and judge whether or not a train of high-pitched rhythmic beeps superimposed on the music are aligned with the beat or not. The superimposed beeps in the off-beat trials contain either a tempo error (too fast or too slow) or a phase error (too early or too late) relative to the musical beat. BAT accuracy was calculated as the mean percentage of trials correctly categorized for each participant.

### 2.3.5. Music questionnaire

Participants completed a written questionnaire to assess their degree of musical experience. Years of prior musical experience was quantified using the following question: “Within the past 10 years, how many years of experience do you have playing an instrument, singing, or participating in musical training?”

### 2.3.6. EEG Recording and Preprocessing

EEG was recorded during the resting state, passive listening, and incidental encoding blocks using a BioSemi Active-Two amplifier system (BioSemi, Amsterdam, Netherlands). EEG was recorded from 32 Ag/AgCl

scalp electrodes and two additional reference electrodes placed on the left and right mastoids. Vertical and horizontal eye movements were monitored using additional electrodes placed on the outer canthi of the eyes and above the nasion. Signals were digitized using a sampling rate of 1024 Hz. EEG preprocessing and analysis were performed using EEGLab (Delorme and Makeig, 2004) and custom MATLAB scripts. EEG recordings from the 32 scalp channels were first referenced to the average of two mastoid electrodes, downsampled to 512 Hz, and filtered using a 0.1 Hz high pass and 50 Hz low pass filter. Independent components analysis was performed to remove eye-blinks and muscle artifact from the signal. For the analysis of spectral power (steady-state evoked potentials; SSEPs), the continuous data were segmented into 20-s epochs locked to a beat onset, yielding an average of 14 epochs for each subject for passive listening and 38 epochs for each subject for the encoding task with a resolution of 0.05 Hz. The first 10 s of the recording (before any objects were displayed) were excluded from analysis to account for transient evoked potentials elicited at the onset of the music stimulus and to best capture EEG responses to rhythm that may take several seconds to develop (Nozaradan, 2014). For the between-subjects analysis of phase coherence (ITPC), the continuous data were segmented into 4-s epochs of 4 beats from  $-800$  ms to  $3200$  ms around the onset of the first beat within each measure, yielding an average of 91 epochs for each subject for the passive listening and resting state conditions and 241 epochs for the encoding task (97 epochs for the encoding task when excluding epochs containing visual stimuli). For the within-subjects analysis of phase coherence, the continuous data were segmented into 4-s epochs from  $-2000$  ms to  $2000$  ms around the onset of each visual stimulus (120 epochs). Recordings from two participants during passive listening and three participants during resting state failed to save at the time of testing and were excluded from those respective analyses.

## 2.4. Data analysis

### 2.4.1. Behavioral data analysis

To analyze performance on the incidental encoding task, accuracy (percent correct) and mean response times (RT) for correct responses were calculated for each participant’s semantic (living/non-living) decisions. Trials for which reaction times were more than two standard deviation from the mean were removed prior to analysis of RTs. On average, this resulted in the removal of  $3.55$  ( $SD = 3.87$ ) trials per participant. To measure recognition memory performance, the proportion of correctly identified old items from the encoding period (hits) and incorrectly identified new lure items (false alarms) were generated.

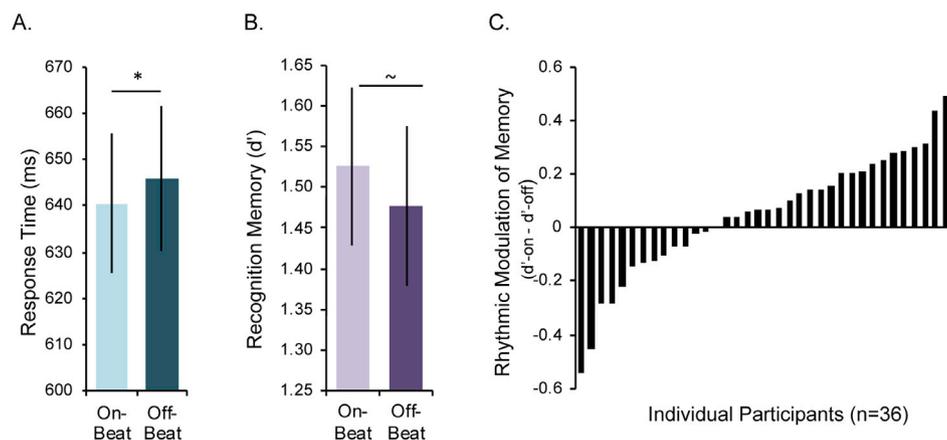
Using those proportions,  $d'$ , a measure of discriminability between previously seen and novel items, and  $C$ , a measure of response bias, were calculated for both on-beat and off-beat stimuli. To replicate prior work from [Johndro et al. \(2019\)](#) and to increase power, recognition memory analyses were collapsed over confidence ratings. Index scores were then calculated to investigate the relationship between the effect of rhythm on behavior and the effect of rhythm on neural responses. For RTs, index scores were calculated by subtracting encoding RTs for on-beat images from encoding RTs for off-beat images. For recognition memory, index scores were calculated by subtracting  $d'$  for off-beat items from  $d'$  for on-beat items.

#### 2.4.2. Electrophysiological data analysis

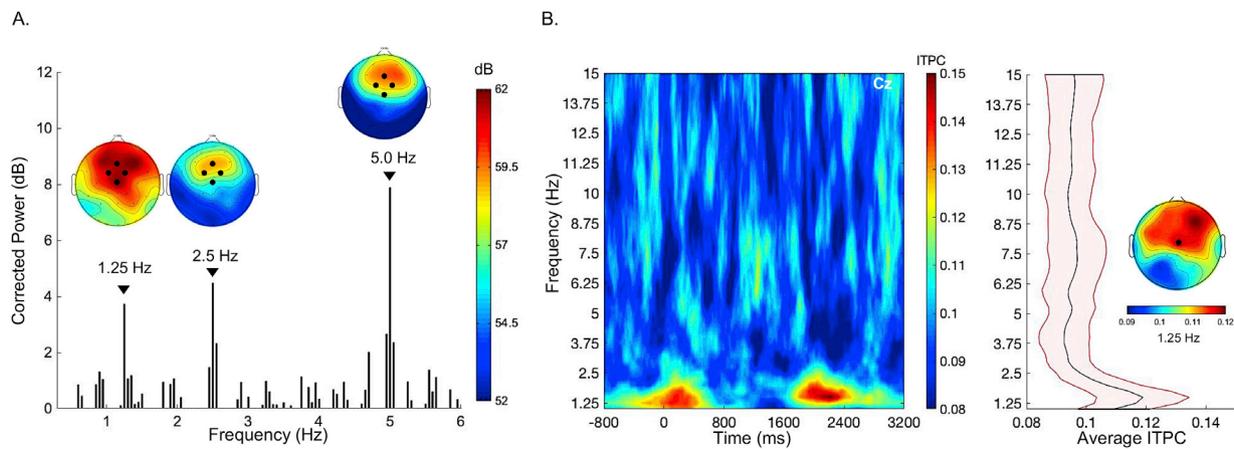
**2.4.2.1. EEG power analysis.** We first aimed to determine whether neural synchronization to the musical rhythm was evident in measures of EEG power. For both the passive listening and encoding task, a power spectrum was calculated by first averaging 20 s non-overlapped epochs (as described in EEG Recording and Preprocessing) in the time domain to maximize the signal-to-noise ratio of neural responses phase-locked to the beat. Averaged signals were then transformed in the frequency domain using a Fast Fourier Transform (Hanning window), yielding a frequency spectrum with a resolution of 0.05 Hz. The power spectrum from the passive listening condition served as an independent auditory localizer to identify electrodes at which neural tracking of beat-related rhythms was greatest. Power at the beat frequency and harmonics was greatest over a frontocentral cluster (Fz, Cz, FC1, FC2, shown as black dots on scalp plots in [Fig. 4A](#)), consistent with the topography commonly observed in the literature for auditory rhythms (e.g., [Henry et al., 2017](#); [Nozaradan et al., 2011](#); [Nozaradan et al., 2012a](#); [2012b](#); [Stupacher et al., 2016](#); [Tierney and Kraus, 2015](#)). Power spectra were averaged across this frontocentral cluster for both the encoding task and passive listening periods, and the contribution of noise was removed at each bin of the frequency spectrum by subtracting the average power measured at two frequency bins ( $\pm 0.15\text{--}0.2$  Hz) on either side of the target frequency ([Nozaradan et al., 2011](#); [Tierney and Kraus, 2015](#)), resulting in a normalized (corrected) power spectra. To determine the significance of EEG responses at the beat frequency (1.25 Hz), normalized power across the frontocentral channels during the passive listening and encoding tasks was tested against zero using a one-tailed  $t$ -test to measure neural tracking of the musical rhythm.

**2.4.2.2. Inter-trial phase coherence analysis.** In a second analysis, a time-frequency decomposition was performed on the EEG data collected

during resting state, passive listening, and incidental encoding. In order to measure the consistency with which neural responses within each EEG channel are phase-locked across epochs, the EEG time series was first convolved with a family of complex Morlet wavelets with cycles increasing linearly between 3 and 7 cycles as a function of frequency across 1–15 Hz (0.25 Hz resolution) in order to optimize the frequency resolution at low (e.g., beat-related) frequencies ([Cohen, 2014](#)). The resulting complex values were used to calculate inter-trial phase coherence (ITPC) for all time points within the epoch length and for all frequencies between 1 Hz and 15 Hz (with 0.25 Hz resolution) at electrode Cz. Electrode Cz was chosen because it contained the highest ITPC value within the frontocentral cluster during the passive listening task, which served as an independent auditory localizer (see [Fig. 4B](#)). Furthermore, previous studies have used electrode Cz when measuring phase consistency in response to rhythmic stimuli ([Henry and Obleser, 2012](#); [Stefanics et al., 2010](#); [Will and Berg, 2007](#)). ITPC values were then averaged across the time-window to produce a global ITPC value for each participant. For the music conditions (passive listening and encoding task), ITPC at the beat frequency (1.25 Hz) can be interpreted as the degree to which neural phase across epochs tracks the auditory beat. ITPC values close to 0 reflect high variability of phase angles across epochs, whereas ITPC values close to 1 reflect low variability of phase angles across epochs. If neural tracking of the beat was present in measures of EEG phase, ITPC at the beat frequency (1.25 Hz) in the context of music (encoding and passive listening) should be greater than 1.25 Hz ITPC during rest within subjects. Significant ITPC at the beat frequency during the music conditions compared to rest was first tested using non-parametric tests since the data were not normally distributed. Parametric analyses were also performed using Fisher Z transformed difference scores in which ITPC at rest was subtracted from ITPC during the music conditions (e.g.,  $\text{ITPC}_{\text{Encoding}} - \text{ITPC}_{\text{Rest}}$ ). For comparison of ITPC during the encoding block to ITPC at rest, analysis was restricted to encoding block epochs in which no visual stimulus was presented in order to equate epoch number across conditions (a similar approach was used to compare ITPC during encoding and passive listening). To examine the relationship of ITPC during the encoding block to behavioral performance, encoding-block ITPC was calculated across all encoding block epochs. For the analysis of within-subjects differences in ITPC during the time of stimulus presentation, a time-frequency decomposition was performed on the EEG data during incidental encoding as described above after randomly sub-sampling the data within participants to match the number of epochs in each subsequent memory condition (e.g., remembered, forgotten).



**Fig. 3.** Behavioral results. (A) Mean response times (RT) for semantic classifications of on-beat and off-beat stimuli during the incidental encoding task. (B) Subsequent recognition memory performance ( $d'$ ) for stimuli appearing on-beat or off-beat during encoding. Error bars indicate SEM.  $*p < 0.05$ ,  $\sim p = 0.10$ , one-tailed. (C) Individual variability in the rhythmic modulation of memory index (on-beat  $d'$  minus off-beat  $d'$ ).



**Fig. 4.** Baseline neural responses to music during passive listening. (A) EEG frequency spectrum depicting periodic neural activity during passive listening. Selective increases in power occurred at the beat frequency (1.25 Hz) and harmonic frequencies (2.5, 5.0 Hz) over frontocentral electrodes (Fz, Cz, FC1, FC2). Topoplots depict raw power across the scalp. SSEP plot depicts corrected power (dB) over frontocentral electrodes. (B) Intertrial Phase Coherence (ITPC) during passive listening at electrode Cz. Time-frequency plot of ITPC (left) and average ITPC across time (right). Red shading represents the standard deviation across participants. Significant cortical tracking of rhythm was observed specifically at the beat frequency (1.25 Hz).

#### 2.4.3. Brain-behavior relationships

A primary question of interest was whether neural activity at the beat frequency is functionally related to encoding success at particular moments in time. We predicted that stronger cortical tracking of rhythm at the beat frequency (1.25 Hz) as measured by power (SSEPs) or phase (ITPC) would be associated with stronger rhythmic modulation of memory ( $d'$ -on minus  $d'$ -off) both between and within individuals. For the interindividual analyses, separate Spearman Rank correlations were used to evaluate brain-behavior relationships due to the presence of two outliers (mean memory index scores  $< 2$  SD from the mean). We also evaluated these relationships excluding the two outliers using Pearson's correlations. In follow-up analyses investigating whether memory performance for on-beat vs. off-beat trials differed between individuals demonstrating stronger versus weaker cortical tracking (median split), groups were compared using nonparametric Mann-Whitney U tests when scores were not normally distributed. For the intraindividual analyses, cortical tracking at the beat frequency during the time of stimulus presentation (0–750 ms) was compared for subsequently remembered and subsequently forgotten trials using Fisher Z transformed difference scores. Subsequent memory analyses were only performed on ITPC measures of neural tracking given the low signal-to-noise ratio of SSEPs when stimulus-locked epochs were split by subsequent memory performance.

#### 2.4.4. Individual differences analyses

Given recent evidence that cortical entrainment to music is modulated by musical expertise (Doelling and Poeppel, 2015), we were also interested in whether neural or behavioral responses to rhythm were influenced by participants' years of musical training or beat perception abilities (BAT score) (Table 1). To investigate these relationships, correlations were performed between these latter two measures and individuals' behavioral responses to rhythm and EEG responses to rhythm (power of 1.25 Hz SSEP, and ITPC).

#### 2.4.5. Statistical analysis

All statistics were completed using SPSS (version 25) and R (version 3.5.3). Non-parametric statistical tests were used when data were not normally distributed. Where behavioral comparisons were hypothesis-driven (Johndro et al., 2019), significance was evaluated based on one-tailed tests. All other analyses significance was evaluated using two-tailed tests.

**Table 1**

Performance on the Beat Alignment Task (BAT) and years of active musical experience or training within the past 10 years in the participant group. Note that the mean BAT accuracy of the participant group falls within the 95% confidence interval reported in prior studies (e.g.,  $M = 0.81$ ,  $SD = 0.14$ ,  $CI = 0.76$ – $0.86$ ; Johndro et al., 2019) whereas the mean years of musical experience is slightly lower than that reported in prior studies (e.g.,  $M = 6$ ,  $SD = 4$ ,  $95\% CI = 4.58$ – $7.42$ ; Johndro et al., 2019).

BAT Accuracy (%)	Musical Experience (Years)
$M = 0.77$	$M = 1.93$
$SD = 0.13$	$SD = 2.89$
Range: 0.44–0.97	Range: 0–10

#### 2.4.6. Data availability

The data that support the findings of this study are available online through Open Science Framework (DOI 10.17605/OSF.IO/WZC2G).

### 3. Results

#### 3.1. Behavioral results

##### 3.1.1. Behavioral performance at encoding

Before analyzing performance on the recognition memory test, we first analyzed participants' performance on the semantic classification task during encoding. Semantic classification accuracy was high across conditions ( $M = 97\%$ ,  $SD = 3$ ) and did not differ significantly between on-beat and off-beat trials ( $Z = -0.39$ ,  $p = 0.35$ , one-tailed,  $r = 0.07$ ). In contrast, reaction times were significantly faster for stimuli presented in-synchrony compared to out-of-synchrony with the background beat ( $Z = -2.25$ ,  $p = 0.01$ , one-tailed,  $r = 0.37$ ) (Fig. 3A). These results align with prior observations of perceptual facilitation for stimuli presented in-synchrony with background rhythms (e.g., Johndro et al., 2019; Bolger et al., 2013; Escoffier et al., 2010; Kunert and Jongman, 2017).

##### 3.1.2. Recognition memory performance

To investigate whether background rhythm influenced encoding at specific moments in time, recognition memory performance was compared for on-beat and off-beat stimuli. Recognition memory was numerically greater for stimuli presented on-beat at encoding compared to stimuli presented off-beat at encoding across participants (Fig. 3B), in line with the results of the prior behavioral study by Johndro et al. (2019). However, substantial individual variability was present in the

effect of rhythm on subsequent memory (Fig. 3C) and the difference between on-beat and off-beat memory did not reach significance at the group level ( $t(35) = 1.28, p = 0.10$ , one-tailed,  $d = 0.21$ ).<sup>1</sup> This contrasts with the significant difference between on-beat and off-beat memory observed in the prior study by Johndro et al. (2019), but might be due differences in experimental design across studies (e.g., blocked vs. intermixed design; Correa et al., 2004). Importantly, the lack of a strong effect of rhythm at the group level does not limit our ability to test our primary hypothesis of interest—that the effect of rhythm on memory depends on the fidelity by which rhythm is represented in the brain. Indeed, substantial individual variability in the magnitude of the rhythmic effect on memory enables us to take an individual differences approach to investigate the relationship between behavioral and neural responses to rhythm.

### 3.2. Neural responses to rhythm

#### 3.2.1. Cortical tracking during passive listening

To examine the degree to which participants' neural activity tracked the beat of the complex music stimulus, we first investigated baseline neural responses during passive listening (Fig. 4), which served as an independent localizer for the analyses of neural tracking of rhythm during the encoding block. Peaks in the EEG spectrum (Fig. 4A) occurred specifically at the beat frequency (1.25 Hz;  $t(33) = 4.15, p < 0.001, d = 0.71$ ) and harmonic frequencies (e.g., 2.5 Hz,  $t(33) = 5.47, p < 0.001, d = 0.94$ ; and 5.0 Hz,  $t(33) = 9.53, p < 0.001, d = 1.63$ ) over frontocentral electrodes.

Inter-trial phase coherence (ITPC) during passive listening is displayed in Fig. 4B. A selective increase in ITPC was observed at the beat frequency (1.25 Hz). The statistical significance of the increase in ITPC was confirmed by comparing 1.25 Hz ITPC during passive listening to 1.25 Hz ITPC at rest ( $Z = -2.38, p = 0.02, r = 0.40$ ) at electrode Cz. Fisher's Z transformed difference scores (1.25 Hz ITPC during passive listening – 1.25 Hz ITPC at rest) also indicated an increase in phase coherence at the beat frequency ( $t(31) = 2.57, p = 0.02, d = 0.45$ ). No significant phase locking was observed at the harmonic frequencies of 2.5 Hz and 5.0 Hz.

#### 3.2.2. Cortical tracking during incidental encoding

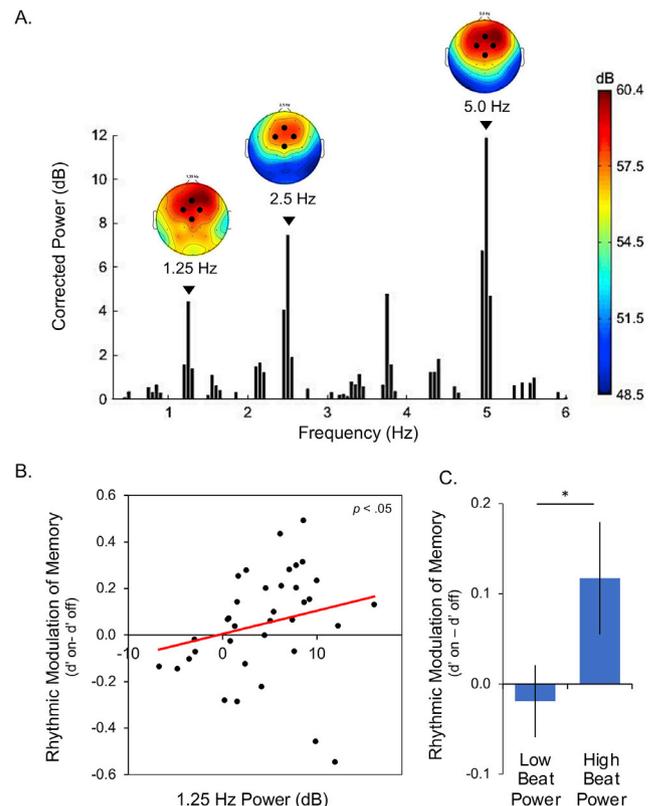
We next investigated whether participants' neural activity tracked the beat of the music during the incidental encoding task (living/non-living judgment), when the music stimulus played in the background and was task-irrelevant. The EEG spectrum during incidental encoding is displayed in Fig. 5A. Similar to passive listening, prominent peaks were observed at the beat frequency (1.25 Hz,  $t(35) = 5.17, p < 0.001, d = 0.86$ ) and harmonic frequencies (e.g., 2.5 Hz,  $t(35) = 9.66, p < 0.001, d = 1.61$ ; 5.0 Hz;  $t(35) = 9.23, p < 0.001, d = 1.54$ ) over frontocentral electrodes. Direct comparison of electrophysiological responses during incidental encoding and passive listening indicated that cortical tracking of the auditory beat was not reduced during incidental encoding compared to passive listening (no difference in power at the beat frequency during incidental encoding,  $t(33) = 0.45, p = 0.66, d = 0.08$  and greater power at the harmonic frequencies during incidental encoding,  $t(33) > 3.20, p < 0.004, d > 0.56$ ).

Inter-trial phase coherence during the encoding task is displayed in Fig. 6A. Like the measure of EEG power, increased ITPC was observed during the encoding task at the beat frequency. The statistical significance of the increase in ITPC at the beat frequency was confirmed by comparing 1.25 Hz ITPC during the encoding task to 1.25 Hz ITPC at rest (excluding epochs in which visual stimuli were presented at encoding to equate the number of epochs across conditions). Increased ITPC at the

beat frequency was significant compared to baseline ITPC at rest ( $Z = -3.98, p < 0.0001, r = 0.66$ ). A one-sample *t*-test using Fisher's Z transformed difference scores compared to rest also indicated significant 1.25 Hz ITPC during encoding ( $t(32) = -4.82, p < 0.0001, d = 0.84$ ). In contrast to ITPC during passive listening, significant ITPC during encoding was also observed at the harmonic frequencies (2.5 Hz and 5.0 Hz). Exploratory analyses revealed that ITPC at the harmonic frequencies during encoding was significantly greater than that at rest (2.5 Hz:  $Z = -4.65, p < 0.0001, r = 0.78$ ; 5.0 Hz:  $Z = -4.24, p < 0.0001, r = 0.71$ ). One-sample *t*-tests using the Fisher Z transformed difference score compared to rest also indicated significant 2.5 Hz and 5.0 Hz ITPC during the encoding block (2.5 Hz:  $t(32) = 5.85, p < 0.0001, d = 1.02$ ; 5.0 Hz:  $t(32) = 4.89, p < 0.0001, d = 0.85$ ). Direct comparison of electrophysiological responses during incidental encoding and passive listening indicated that cortical tracking of the auditory beat was not reduced during incidental encoding compared to passive listening (phase coherence at the beat frequency and harmonics during incidental encoding was greater than during passive listening,  $Z_s > -2.44, p_s < 0.02$ ).

### 3.3. Brain-behavior relationships

After establishing that significant cortical tracking of the background beat was present during incidental encoding, we next investigated



**Fig. 5.** Steady-state evoked potentials (SSEPs) during the encoding task and relationship to memory performance. (A) EEG frequency spectrum depicting periodic neural activity during the encoding task. Power increases were observed at the beat frequency (1.25 Hz) and its harmonics (e.g., 2.5 Hz and 5.0 Hz) over frontocentral electrodes. Topoplots depict raw power across the scalp. SSEP plot depicts corrected power (dB) averaged over frontocentral electrodes (Fz, Cz, FC1, FC2). (B) A positive correlation was observed between corrected SSEP power at the beat frequency (1.25 Hz) and the rhythmic modulation of memory index ( $d'$  on –  $d'$  off). (C) Greater memory for on-beat vs. off-beat stimuli was only present in individuals demonstrating higher power at the beat frequency (defined by median split). Error bars indicate SEM. \* $p < 0.05$ .

<sup>1</sup> A significant effect of rhythm on recognition memory was present at the group level after the removal of two behavioral outliers ( $d'$  difference < 2SD from group mean) ( $t(33) = 2.49, p = 0.009, d = 0.43$ ).

whether stronger cortical tracking during encoding was associated with stronger rhythmic modulation of memory across participants. We first tested the relationship between the rhythmic modulation of memory index ( $d'$ -on minus  $d'$ -off) and SSEP power at the beat frequency (Fig. 5B). A significant positive correlation was observed ( $r(34) = 0.37$ ,  $p = 0.03$ ). This positive correlation remained, and was strengthened, when two behavioral outliers were removed ( $r(32) = 0.53$ ,  $p < 0.001$ ). As part of post-hoc analysis, participants were separated into groups that demonstrated stronger vs. weaker neural tracking of the beat (as defined by median split). As depicted in Fig. 5C, the rhythmic modulation of memory index was significantly greater in the group demonstrating strong neural tracking of the beat ( $U = 85$ ,  $p = 0.01$ ,  $r = 0.41$ ). Furthermore, the memory index was significantly greater than zero only in the group demonstrating stronger neural tracking of the beat ( $Z = -1.76$ ,  $p = 0.04$ ,  $r = 0.41$ ), while the group demonstrating weaker neural tracking of the beat did not demonstrate effects of rhythm on subsequent memory ( $Z = -0.14$ ,  $p = 0.55$ ,  $r = 0.03$ ).

We next tested the relationship between the rhythmic modulation of memory index and cortical tracking of rhythm as measured by phase coherence at the beat frequency (ITPC across epochs during encoding). A significant positive correlation was observed between the rhythmic modulation of memory index and ITPC at the beat frequency during encoding ( $r(34) = 0.39$ ,  $p = 0.02$ ; Fig. 6B). The positive correlation remained, and was strengthened, when two behavioral outliers were removed ( $r(32) = 0.46$ ,  $p = 0.007$ ). As part of a post-hoc analysis, participants were separated into groups that demonstrated stronger vs. weaker neural tracking of the beat (as defined by median split of ITPC values). As depicted in Fig. 6C, the rhythmic modulation of memory

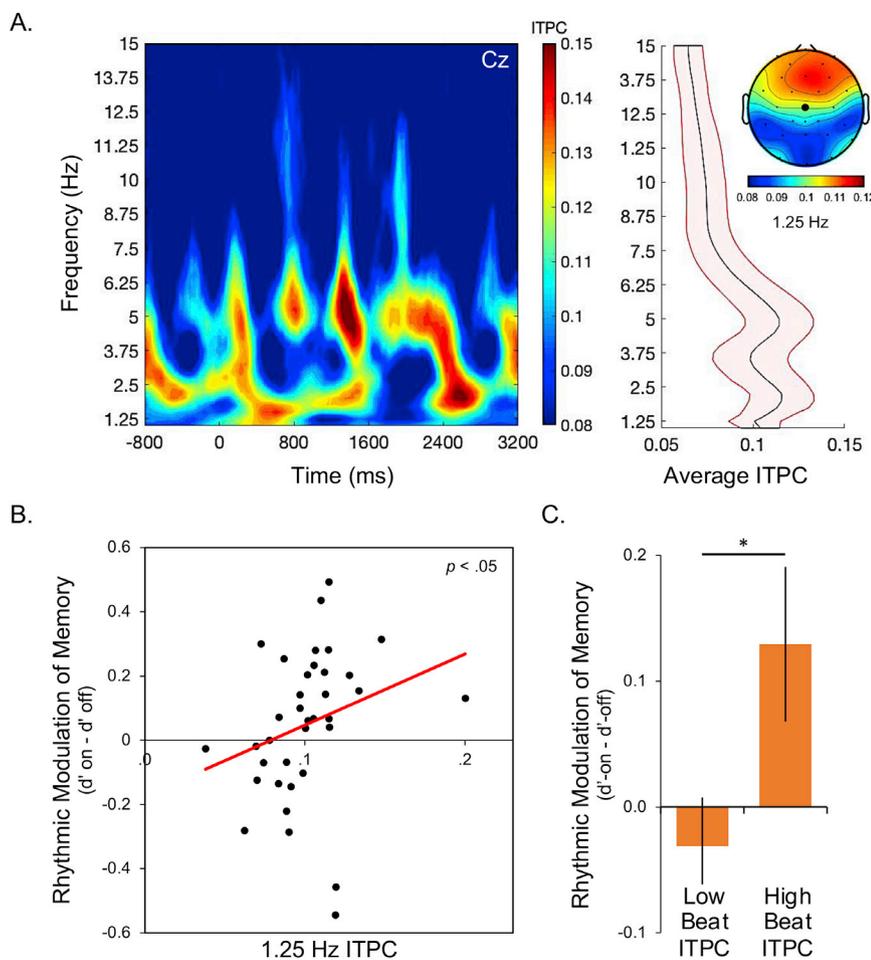
index was significantly greater in the group demonstrating stronger neural tracking of the beat ( $U = 73$ ,  $p = 0.004$ ,  $r = 0.66$ ). Furthermore, the memory index was significantly greater than zero only in the group demonstrating stronger neural tracking of the beat ( $Z = -1.96$ ,  $p = 0.02$ ,  $r = 0.46$ ), while no significant rhythmic modulation of memory was observed in the group demonstrating weaker neural tracking of the beat ( $Z = -0.30$ ,  $p = 0.38$ ,  $r = 0.07$ ).

### 3.4. Specificity of interindividual brain-behavior relationships

To investigate the specificity of the correlation between the rhythmic modulation of memory index and neural responses at the beat frequency, we next conducted an exploratory analysis of the relationship between the memory index and neural tracking measures (SSEP, ITPC) at the harmonic frequencies (2.5 Hz, 5.0 Hz; Fig. 7). No association was found between the rhythmic modulation of memory index and SSEP power at the harmonic frequencies (2.5 Hz:  $r(34) = -0.04$ ,  $p = 0.81$ ; 5.0 Hz:  $r(34) = -0.05$ ,  $p = 0.78$ ). Similarly, no association was found between the rhythmic modulation of memory index and ITPC at the harmonic frequencies (2.5 Hz:  $r(34) = -0.02$ ,  $p = 0.91$ ; 5.0 Hz:  $r(34) = -0.13$ ,  $p = 0.44$ ). These results confirm that the rhythmic modulation of memory is related to neural tracking of the rhythm specifically at the beat frequency (1.25 Hz).

### 3.5. Within-subjects effect of rhythm on subsequent memory

To investigate whether neural tracking at the beat frequency also predicts subsequent memory for individual trials, we next performed a

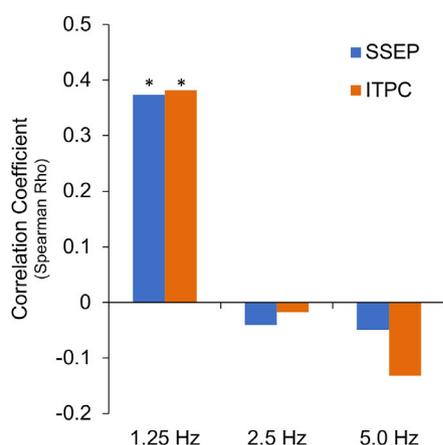


**Fig. 6.** Inter-trial Phase Coherence (ITPC) during the encoding task and relationship to memory performance. (A) ITPC across all trials (including those with visual stimuli) during the encoding task at electrode Cz. Time-frequency plot of ITPC (left) and average ITPC across time (right). Red shading represents the standard deviation across participants. Significant cortical tracking occurred at the beat frequency (1.25 Hz) and harmonics (e.g., 2.5 Hz and 5.0 Hz). Topoplot depicts raw ITPC across the scalp. (B) ITPC at the beat frequency (1.25 Hz) positively correlated with the rhythmic modulation of memory index ( $d'$  on -  $d'$  off) at the subject level. (C) Only individuals with greater power at the beat frequency (defined by a median split) demonstrated significant rhythmic modulation of memory. Error bars indicate SEM. \* $p < 0.005$ .

within-subjects subsequent memory analysis which complements and extends the between-subjects correlations. We hypothesized that neural tracking at the beat frequency during the time of stimulus presentation would be greater for trials that would be subsequently remembered compared to trials that would be subsequently forgotten. As displayed in Fig. 8A, an increase in low-frequency phase coherence was observed during the time of stimulus presentation (0–750 ms) both for subsequently remembered and for subsequently forgotten items. Importantly, direct comparison of these two conditions revealed that phase coherence at the beat frequency was significantly greater for items that would be later remembered compared to items that would be later forgotten (Fig. 8B;  $t(35) = 2.09, p = 0.04, d = 0.35$ ). Like the between-subjects correlations, exploratory analysis revealed that subsequent memory performance was related to neural tracking specifically at the beat frequency: ITPC at the harmonic frequencies did not differ for subsequently remembered and subsequently forgotten trials (2.5 Hz:  $t(35) = 1.64, p = 0.11, d = 0.27$ ; 5.0 Hz:  $t(35) = 0.50, p = 0.62, d = 0.08$ ; Fig. 8C). An additional exploratory analysis investigated whether phase coherence at the beat frequency during the time of stimulus presentation differed for on-beat and off-beat trials. A marginal reduction in ITPC was observed for off-beat compared to on-beat trials ( $t(35) = 2.02, p = 0.05, d = 0.34$ ). Together, these results reveal that in addition varying across individuals, the strength of neural responses to rhythm also fluctuates dynamically within individuals and influences encoding success at specific moments in time.

### 3.6. Individual differences

We next investigated whether neural or behavioral responses to rhythm are enhanced for individuals with superior beat perception (as measured by the BAT) or greater musical experience. Beat perception was not correlated with either the RT index ( $rs(34) = -0.14, p = 0.42$ ) or memory index ( $rs(34) = 0.18, p = 0.28$ ) and there was not a significant relationship between beat perception and the magnitude of neural responses to rhythm at the beat frequency (1.25 Hz SSEP:  $rs(34) = -0.07, p = 0.70$ ; 1.25 Hz ITPC:  $rs(34) = -0.06, p = 0.72$ ). Years of musical experience also did not correlate with the RT index ( $rs(34) = -0.08, p = 0.67$ ) or the memory index ( $rs(34) = 0.18, p = 0.30$ ) and there was not a significant relationship between years of musical experience and the 1.25 Hz SSEP power ( $rs(34) = 0.02, p = 0.90$ ) or 1.25 Hz ITPC ( $rs(34) = 0.14, p = 0.42$ ).



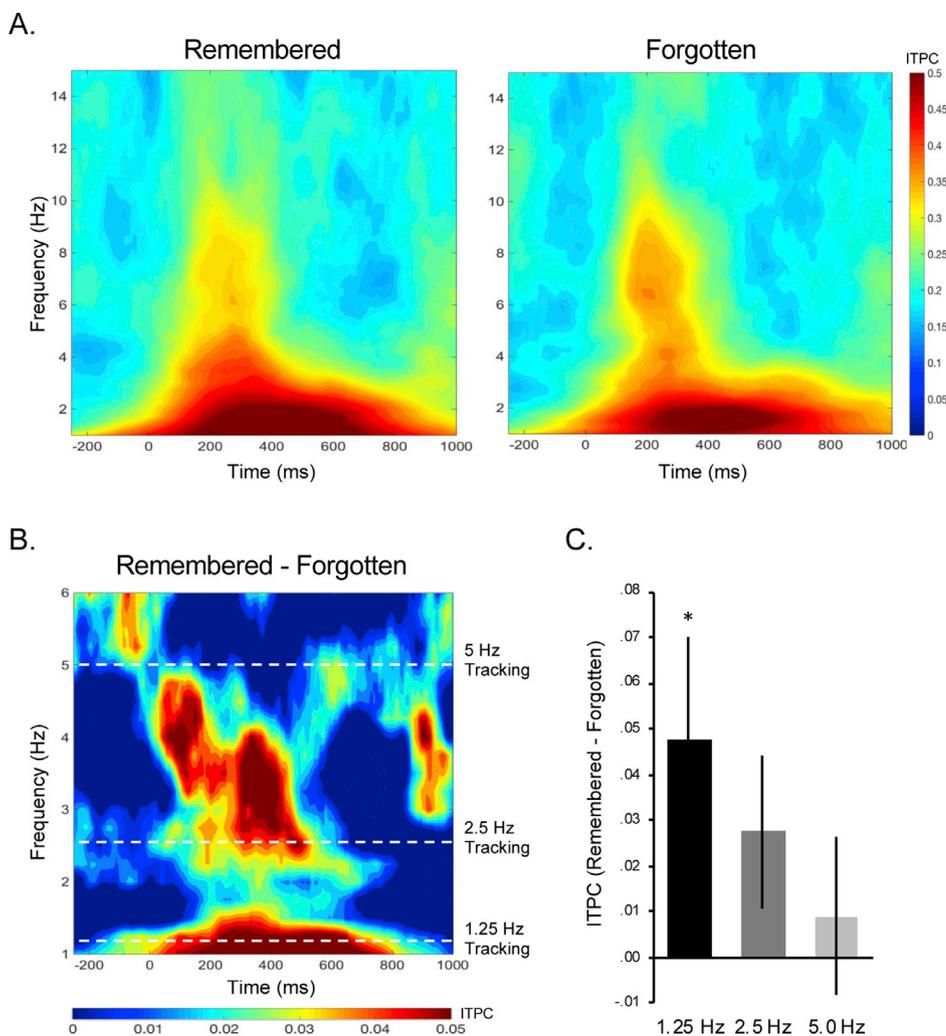
**Fig. 7.** Correlations between the rhythmic modulation of memory index ( $d'$  on  $-d'$  off) and neural tracking measures (SSEP, ITPC) at the beat frequency (1.25 Hz) and the harmonic frequencies (2.5 Hz, 5.0 Hz). The association between neural tracking of the beat and the rhythmic modulation of memory is specific to the beat frequency (1.25 Hz). \* $p < 0.05$ .

## 4. Discussion

Low-frequency rhythms abound in our natural environment. A large body of prior work has demonstrated that the brain can leverage these rhythmic temporal cues to enhance perception and action. The current study provides novel evidence that neural responses to environmental rhythms also influence more complex cognitive functions such as episodic memory. Specifically, we found that neural activity spontaneously synchronizes to low-frequency, musical rhythms during an incidental encoding task, evident in both increased electrophysiological power and phase consistency at the musical beat frequency (1.25 Hz). Importantly, stronger neural responses at the beat frequency were associated with better subsequent memory for visual events that appeared in-synchrony versus out-of-synchrony with the background beat at encoding. This relationship between neural tracking of rhythm and memory performance was present at the group level between subjects as well as on a trial-by-trial basis within subjects. These results extend prior behavioral work suggesting that rhythmic temporal cues in the environment influence memory encoding (Johndro et al., 2019; Jones and Ward, 2019; Thavabalasingam et al., 2016) and provide novel evidence that the effect of rhythm on episodic memory depends on the fidelity by which external rhythms are represented in the brain.

Prior research into the effects of external rhythms on episodic memory has primarily focused on the effects of rhythmic stimulation in the theta band (e.g. 4–8 Hz). Such effects are understandable given the established relationship between theta activity in the brain and episodic memory (e.g., Hanslmayr et al., 2016; Nyhus and Curran, 2010). For example, simple rhythmic stimulation at the theta frequency (e.g., sensory flicker or TMS) has been shown to increase electrophysiological power and phase alignment in the theta band and to enhance episodic memory (e.g., Clouter et al., 2017; for review, see Hanslmayr et al., 2019; Köster et al., 2019; Roberts et al., 2018; Wang et al., 2018). The current study extends this prior work by demonstrating a novel relationship between episodic memory and neural responses to lower-frequency (<5 Hz) environmental rhythms. Although not traditionally associated with episodic memory, such low-frequency neural responses in the delta range are thought to play a critical role in selective attention by dynamically modulating the excitability of large neuronal populations over time (Cravo et al., 2013; Henry and Herrmann, 2014; Lakatos et al., 2008; Schroeder and Lakatos, 2009). Importantly, the alignment of low-frequency neural activity to the timing of external rhythms has been shown to optimize processing at specific moments in time (e.g., in-phase with the rhythm) and has been proposed to serve as a fundamental mechanism of temporal attention (Calderone et al., 2014; Doelling and Poeppel, 2015; Frey et al., 2015; Haegens and Zion Golumbic, 2018; Henry 2014; Lakatos et al., 2008; Large and Jones, 1999; Mathewson et al., 2012; Morillon and Schroeder, 2015; for review, see Nobre and van Ede, 2018; Schroeder and Lakatos, 2009; Tierney and Kraus, 2015). The present findings suggest that in addition to influencing how we attend to and perceive the world, low-frequency neural responses to environmental rhythms also influence what we remember.

Behavioral performance in the current study was associated with increases in both electrophysiological power and phase coherence at the beat frequency, providing converging evidence supporting a relationship between neural and mnemonic responses to rhythm. Measures of EEG power and phase coherence at the beat frequency have been used in prior studies to measure the strength of neural tracking of rhythm (Doelling and Poeppel, 2015; Henry and Obleser, 2012; Henry et al., 2017; for review, see Nozaradan, 2014). Phase coherence is typically interpreted as a measure of the precision by which underlying neural oscillations are aligned to an external stimulus rhythm, whereas measures of EEG power are typically taken to measure the presence of sustained periodic EEG responses (or evoked potentials) at the rhythmic frequency. Although mathematically distinct, these power and phase coherence measures are likely not independent: power measures may also assess the stability of neural phase locking at beat and harmonically-related frequencies (Lenc



**Fig. 8.** Subsequent memory analysis. (A) Inter-trial Phase Coherence (ITPC) during the presentation of visual stimuli that will be later remembered (left) or forgotten (right) at electrode Cz. Visual stimuli are presented from time 0–750 ms. (B) Difference in ITPC for subsequently remembered versus subsequently forgotten items, zooming in on the beat-related frequencies of interest (note different Y-axis scale from plots in A). (C) Mean ITPC at the beat frequency (1.25 Hz) during the time of stimulus presentation was significantly greater for subsequently remembered compared to subsequently forgotten items. Error bars indicate SEM. \* $p < 0.005$ .

et al., 2019) and measures of ITPC can be influenced by changes in EEG power (van Diepen and Mazaheri, 2018). Indeed, in the current study we found that rhythmic modulations of EEG power and ITPC had similar frontocentral topography during encoding and that the magnitude of these responses was highly (though not perfectly) correlated across participants ( $r(34) = 0.54, p < 0.001$ ). Thus, an important outstanding question is whether the effects of rhythm on memory are related to evoked neural responses (e.g., phase-resetting) (Breska and Deouell, 2017; Capilla et al., 2011), induced responses (e.g., entrainment of endogenous oscillations), or a combination of the two (Doelling et al., 2019; for review, see Helfrich et al., 2019; Lakatos et al., 2019; van Ede et al., 2018). While we cannot distinguish between these possibilities in the present study, it is important to note that the effects of rhythm on memory performance were associated with the modulation of electrophysiological responses specifically at the beat frequency (1.25 Hz). That is, despite the presence of increased power and ITPC at other frequencies (e.g., at the 2.5 and 5.0 Hz harmonics), the effect of rhythm on memory performance was associated with the magnitude of increased power and ITPC only at the beat frequency. Thus, one can postulate that the rhythmic effects on memory seen in the current work are related to one's internal representation of the beat and the brain's ability to guide processing in a predictive manner rather than simply a reactive sensory-driven response (e.g., Nobre and van Ede, 2018).

An important aspect of the current study is the substantial individual variability present in the effect of rhythm on participants' memory

performance and neural activity. Variability in the effect of rhythmic stimulation on memory encoding has also been observed in prior studies (Köster et al., 2019; Wang et al., 2018; Johndro et al., 2019). For example, Köster et al. (2019) found that while visual theta stimulation enhanced encoding at the group level, this memory enhancement effect was only present in ~60% of individual participants (see also Wang et al., 2018). Johndro et al. (2019) also observed substantial between-subject variability in the effect of background musical rhythm on subsequent memory, and found that memory was greater for in-synchrony versus out-of-synchrony stimuli only in participants who encountered in-synchrony stimuli during the first block of the experiment (before they could habituate to the music or adopt explicit encoding strategies that directed attention away from the irrelevant rhythm). Although individual variability in the current study may have reduced the overall effects of rhythm on memory performance at the group level, this characteristic of the data also allowed us to take an individual differences approach in our analysis to test whether the effect of rhythm on memory depends on the strength of individuals' neural response to rhythm. A key finding of the current study is that the variable effects of external rhythm on subsequent memory performance can be explained by variability in neural responses to rhythm (both across individuals and within individuals at specific moments in time). These results extend prior work demonstrating that the effect of external rhythm on behavior depends on the fidelity by which rhythm is represented in the brain (e.g., Köster et al., 2019; Nozaradan et al., 2016; Doelling and Poeppel, 2015; Tierney and

Kraus, 2013; Herrmann et al., 2016) and support our hypothesis that neural tracking of rhythm dynamically modulates memory and influences encoding at particular moments in time.

An open question is why some participants demonstrated strong neural tracking of rhythm while others did not. Prior studies have demonstrated that neural tracking of low-frequency (e.g., theta/delta) auditory inputs varies substantially across individuals and is affected by factors such as an individual's amount of prior musical training (e.g., Doelling and Poeppel, 2015; Musacchia et al., 2007) or temporal prediction abilities (Nozaradan et al., 2016). Although no association was found in the current study between musical experience (or beat perception abilities, i.e., BAT performance) and the effect of rhythm on neural activity or behavior, our sample did not contain a wide range of musical experience (less than two years of musical experience on average). It is therefore possible that an even stronger association between neural and behavioral responses to rhythm would be observed if the same paradigm were run in individuals with greater musical expertise. Another possibility is that the effects of rhythm on neural activity in the current study depended on participants' level of attention to the background music, which could have varied between individuals as well as across time within individuals. Prior work suggests that attention plays a critical role in modulating neural and behavioral responses to rhythm (e.g., Henry et al., 2017; Lakatos et al., 2008; Johnidro et al., 2019). In the current paradigm, the rhythmic music present in the background at encoding was irrelevant to the task at hand and may have served as a source of distraction for some individuals. Future research should investigate the degree to which the effects of rhythm on neural activity and memory encoding are influenced by attention to, or distraction by, the external rhythmic stimulus.

Although the current results provide novel evidence for a relationship between neural responses to low-frequency rhythms in the delta range and memory encoding, the precise mechanism by which this rhythmic stimulation might influence memory remains an open question. One possibility is that the memory effects in the current paradigm occur indirectly via the modulation of higher-frequency neural responses in the theta range. Auditory cortical entrainment in the delta band has been shown to interact with oscillatory activity in distinct networks and to modulate theta power in parietal cortex (Keitel et al., 2017). Although the harmonic response in the current study that falls within the theta range (e.g., 5.0 Hz) did not correlate with memory performance, cross-frequency mechanisms may not be evident at this specific frequency and might emerge only at a wider frequency range (e.g., 5–8 Hz) or in induced theta responses that are not phase-locked to the beat. An alternative, not mutually exclusive, possibility is that the low-frequency (delta) responses have a more direct influence on visual memory encoding, for example by facilitating cross-regional communication or influencing the sensitivity of sensory neurons in other brain regions (Fries, 2015; Gregoriou et al., 2015; Helfrich et al., 2017). In support of this possibility, it has been shown that auditory stimulation can reset the phase of ongoing oscillations in the visual cortex (e.g., Naue et al., 2011). Future studies should investigate the precise mechanisms by which low-frequency, auditory rhythms influence visual memory encoding.

One limitation of the current work is the relatively small sample size. Larger samples may contain a wider range of variability in both neural and behavioral responses to rhythm and could provide a more sensitive way to assess the relationship between these two variables. Nevertheless, a significant positive relationship between the strength of neural tracking and the effect of rhythm on memory performance was observed in the current sample at both the interindividual and intraindividual levels, and this relationship was specific to neural tracking at the hypothesized frequency of interest (frequency of the perceived musical beat). Although care must be taken when interpreting significant brain-behavior correlations in the context of relatively small sample sizes (Loken and Gelman, 2017), it is important to note that our hypothesis about the positive relationship between neural tracking at the beat frequency and memory formation was determined *a priori* based on prior work demonstrating

strong positive correlations between electrophysiological and behavioral responses to rhythm (e.g., Köster et al., 2019; Nozaradan et al., 2016; Doelling and Poeppel, 2015). Analysis of the relationship between memory performance and neural activity was also restricted to frequencies and electrodes of interest defined by an independent localizer (i.e., passive listening) that occurred prior to the encoding block. Thus, despite our limited sample size, the presence and the pattern of the current results provide novel evidence that in addition to dynamically modulating perception and action, neural tracking of rhythm also dynamically modulates memory formation and influences encoding at specific moments in time. However, it is important to consider the current results as preliminary evidence and future studies should aim to replicate these results.

Future studies should also investigate nature of the processing changes that occur in the context of rhythm. It is currently unclear whether the effect of rhythm on memory reflects a processing benefit for in-synchrony stimuli, a processing cost for out-of-synchrony stimuli, or some combination of the two. Comparing behavioral performance in these two conditions to performance in a silent condition could shed light on this question. A prior study by Johnidro et al. (2019) found that subsequent memory was numerically greater for stimuli appearing in-synchrony with a background beat at encoding compared to stimuli appearing in silence, and numerically reduced for stimuli appearing out-of-synchrony with a background beat at encoding compared to stimuli appearing in silence. These results suggest that rhythm may confer both a processing benefit as well as a processing cost depending on the timing of stimulus presentation within the rhythmic stream. However, interpretation of memory performance in the context of background music versus silence is complicated by the fact that these conditions are not matched in terms of sensory input, attentional load, arousal, or the potential for distraction. Therefore, a silent condition may not provide an optimal baseline from which to assess the relative behavioral effects of rhythm. Using a control condition that is more closely matched in terms of other contextual factors (e.g., music without a clear beat) could potentially be more informative, but interpretation would still be limited by remaining differences in the rhythmic versus arrhythmic contexts that could affect performance (e.g., differences in sensory input or arousal). An alternative approach would be to control for rhythmic sensory input (e.g., musical context) and to investigate the effect of rhythm on behavioral performance in individuals who show weaker versus stronger neural tracking of the beat, under the assumption that the brain state of participants who do not demonstrate strong neural tracking most closely approximates an arrhythmic control. When we adopt this approach in our own data, we observe evidence for a mnemonic benefit for on-beat stimuli but no evidence for a mnemonic cost for off-beat stimuli (see Supplemental Results). These results align with prior studies demonstrating facilitatory effects of rhythm on behavior (e.g., Clouter et al., 2017; Escoffier et al., 2010) and provide suggestive evidence that the effects of rhythm on subsequent memory do not simply reflect a reduction in memory for off-beat stimuli. Future studies could more directly address this question by investigating the effects of rhythm on memory performance in larger samples with a greater range of variability in neural tracking or in populations who demonstrate impairments in beat detection or rhythm-based temporal prediction (e.g., Parkinson's Disease; Breska and Ivry, 2018).

## 5. Conclusion

The current study highlights the broad impact of low-frequency rhythms in our environment, and suggests that the brain can leverage these temporal signals to influence memory formation. We provide novel evidence that the brain spontaneously tracks musical rhythm during naturalistic listening situations, and that the strength of this neural tracking is related to the effect of rhythm on visual encoding at specific moments in time. The finding of a positive association between neural responses to rhythm and memory formation aligns with a growing

interest in how rhythmic sensory stimulation can be used as a tool to influence cognitive function (Obleser and Kayser, 2019; Thut et al., 2012) and opens the door for future studies to explore the potential for safe, non-invasive techniques such as musical rhythm to dynamically modulate neural activity and cognitive processing over time.

### Declaration of competing interest

The authors declare no competing financial interests.

### CRediT authorship contribution statement

**Paige Hickey:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Hannah Merseal:** Formal analysis, Investigation. **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.

### Acknowledgements

This research was funded (in part) by a grant from the GRAMMY Museum®. The authors wish to thank Dr. Molly Henry for helpful feedback and suggestions on earlier versions of this work.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2020.116693>.

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