


RESEARCH ARTICLE

Neural oscillations suggest periodicity encoding during auditory beat processing in the premature brain

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Funding information

Fondation pour l'Audition Grant BabyMusic, Grant/Award Number: RD-2021-11

Abstract

When exposed to rhythmic patterns with temporal regularity, adults exhibit an inherent ability to extract and anticipate an underlying sequence of regularly spaced beats, which is internally constructed, as beats are experienced even when no events occur at beat positions (e.g., in the case of rests). Perception of rhythm and synchronization to periodicity is indispensable for development of cognitive functions, social interaction, and adaptive behavior. We evaluated neural oscillatory activity in premature newborns ($n = 19$, mean age, 32 ± 2.59 weeks gestational age) during exposure to an auditory rhythmic sequence, aiming to identify early traces of periodicity encoding and rhythm processing through entrainment of neural oscillations at this stage of neurodevelopment. The rhythmic sequence elicited a systematic modulation of alpha power, synchronized to expected beat locations coinciding with both tones and rests, and independent of whether the beat was preceded by tone or rest. In addition, the periodic alpha-band fluctuations reached maximal power slightly before the corresponding beat onset times. Together, our results show neural encoding of periodicity in the premature brain involving neural oscillations in the alpha range that are much faster than the beat tempo, through alignment of alpha power to the beat tempo, consistent with observations in adults on predictive processing of temporal regularities in auditory rhythms.

KEYWORDS

alpha oscillations, EEG, music, neurodevelopment, phase amplitude coupling, rhythm

Research Highlights

- In response to the presented rhythmic pattern, systematic modulations of alpha power showed that the premature brain extracted the temporal regularity of the underlying beat.

Laurel J. Trainor and Sahar Moghimi contributed equally to this paper.

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- In contrast to evoked potentials, which are greatly reduced when there is no sound event, the modulation of alpha power occurred for beats coinciding with both tones and rests in a predictive way.
- The findings provide the first evidence for the neural coding of periodicity in auditory rhythm perception before the age of term.

1 | INTRODUCTION

Neural encoding of auditory rhythms is present from early stages of neurodevelopment (Cirelli et al., 2016; Edalati et al., 2023; Flaten et al., 2022; Lenc et al., 2022; Winkler et al., 2009). In adults, evidence suggests that while listening to temporally structured auditory inputs, the observed neural oscillations do not merely reflect the evoked responses following sound events (Doelling et al., 2019; Herbst & Obleser, 2019), and do not simply mimic the temporal characteristics of the sound sequences (Nozaradan et al., 2012a, 2012b). Rather, neural oscillations appear to reflect internal processing and temporal expectations based on both the temporal organization of sound sequences and prior knowledge and experience (Doelling et al., 2023; Nozaradan et al., 2011; Tal et al., 2017; Zalta et al., 2024). Some of these neural capacities appear to be present even during early development (Edalati et al., 2023; Flaten et al., 2022; Lenc et al., 2022).

Rhythmicity in different sensory domains can lead to temporal predictions of when future events are expected, which in turn can facilitate preparation and coordination at both neural and behavioral levels (Arnal & Giraud, 2012; Arnal et al., 2015; Chang et al., 2019; Henry & Herrmann, 2014; Large & Jones, 1999; Lumaca et al., 2019; Schroeder & Lakatos, 2009). This in turn, is highly advantageous as it enables adaptive and proactive behaviors. When adults listen to a typical musical rhythm with temporal regularity, they can spontaneously extract, feel and tap to its *beat*, an (typically) isochronous series of pulse onsets (Merchant et al., 2015). That the perceived beat (i.e., pulse onsets) is derived in the brain is evident in that beats can be perceived even during rests (or silences) in the repeating rhythmic pattern, and when there is little energy at the beat frequency in the stimulus (Tal et al., 2017). At the macroscopic level, ongoing neural activity is predictively aligned to anticipated events of the rhythmic sequence (Doelling & Poeppel, 2015; Snyder & Large, 2005). One of the cortical manifestations of this phenomenon in adults is periodic fluctuations in the power of beta band activity (15–30 Hz), orchestrated by the rhythmic structure of the auditory sequence (Chang et al., 2019; Fujioka et al., 2012) in a predictive manner, as these fluctuations reach maximum power at the expected time of the next events across different tempos (Fujioka et al., 2015).

Auditory rhythms typically have a hierarchical (metrical) structure in that perceived beats at one level are grouped (typically into groups of 2 or 3) at higher metrical levels, creating beat tempos at half or one-third, respectively, of that level. Analyzing electroencephalography (EEG) responses using a low-frequency tagging approach (Nozaradan

et al., 2012) to repeating rhythmic patterns, we have recently demonstrated neural responses to beat and beat grouping (meter) frequencies in premature newborns at 30–34 weeks gestational age (wGA), in particular, showing that slow neural oscillations in the range of 1–3 Hz phase align to the envelope of the rhythmic sequences (Edalati et al., 2023). However, it is difficult to determine from such analyses whether the responses reflect periodicity encoding and neural representation of the temporal regularity or whether they are simply event-related responses to events on the previous beat. Following previous studies in adults suggesting that higher frequency neural responses reflect predictive beat tracking (Arnal et al., 2015; Doelling & Poeppel, 2015; Fujioka et al., 2015), in the present paper we revisited this previously published dataset and analyzed power fluctuations in higher frequency neural oscillatory activities in response to the six-beat stimulus of Edalati et al. (2023). This enabled us to examine evidence consistent with hypotheses related to the presence of periodicity encoding and neural temporal prediction at this early developmental stage. We are agnostic as to whether the mechanism of prediction involves some kind of neural resonance or explicit coding of temporal expectations. Particularly, as we do not have behavioral evidence of anticipation in premature infants, here we use the term “neural prediction” to refer specifically to the alignment of neural oscillations to beats, regardless of whether they coincide with a stimulus event onset or an internally generated beat onset where there is no stimulus (as in silent “rests”).

During the third trimester of gestation, the brain undergoes rapid structural and functional development (Kostović et al., 2019; Kostović et al., 2021). This period also marks the initiation of the cortical processing of exogenous stimulation, through the first thalamic afferents reaching the cortex around 28 wGA (Kostović & Jundaš, 2010). Interestingly, premature newborns already respond to various auditory stimuli and demonstrate neural coding of certain (Edalati et al., 2022; Mahmouzdadeh et al., 2013; Panzani et al., 2023). The neurodevelopmental journey during this period, including factors such as preterm birth, significantly influences the subsequent capacities observed in full-term newborns and infants (Alex et al., 2024; Kostilainen et al., 2020; Routier et al., 2023). Due to the importance of time and rhythm processing from the developmental point of view (Ladányi et al., 2020; Lense et al., 2021; Nguyen et al., 2023; Trainor et al., 2018), it is important to further investigate the early neural capacities for encoding temporal regularities and the underlying mechanisms during this critical phase of neurodevelopment.

We first hypothesized that exposure to a repetitive rhythmic stimulus would result in the encoding of periodicity, thereby eliciting power



modulations in higher frequency neural oscillations at the beat frequency. These modulations would be temporally synchronized with the stimulus beats, implying neural anticipation of the beat, mirroring observations in adults. As the stimulus envelope contains little energy at higher frequencies, this evidence would indicate that beat timing is encoded in cortical oscillatory activity. To examine this hypothesis, we quantified the synchronization between the power fluctuation of alpha-band oscillations measured in EEG and the beat (i.e., isochronous pulse train derived from the rhythmic stimulus) by computing the strength of phase-amplitude coupling (PAC) between the phase of a sinusoid representing the beat and neural alpha-band power. Second, we hypothesized that these modulations should be equivalent whether or not the beat onset times coincided with a sound event (tone) or a rest. This is important because neural event-related responses (that follow) sounds are greatly attenuated or absent when no sound stimulus is present. If alpha power modulations align to rests, and to tones following rests, this would strongly suggest neural prediction of beat onset times. To examine this hypothesis, we analyzed evidence for the equivalence of alpha power modulations around rests, tones following rests, and tones following tones. Third, one line of evidence for prediction in adults is that they tend to anticipate the beat (Repp & Su, 2013; Roman et al., 2019), so we hypothesized that our premature infants would show maximum power at a phase that slightly preceded the beat (for both tone and rest onset times).

2 | MATERIALS AND METHODS

2.1 | Participants

Nineteen healthy premature neonates (five males) with mean gestational age at birth of 32 ± 2.59 wGA, who participated in our recent study (Edalati et al., 2023), were reconsidered in this study. EEG was recorded (mean recording age: 33.57 ± 2.21 wGA) in an incubator at the neonatal intensive care unit of the Amiens University Hospital (Amiens, France) during sleep. In brief, all neonates had appropriate birth weight, size, and head circumference for their gestational age and normal auditory and clinical neurological assessments. None were considered to be at risk of brain damage. One or both parents were informed about the study and provided their written informed consent. The local ethics committee (CPP Ouest I) approved the study (ID-RCB: 2019-A01534-53).

2.2 | Auditory stimuli and the experimental paradigm

To create the rhythmic patterns, rock drum sounds composed of snare and bass were used. The stimuli were created using the open-source software Audacity 2.2.2 program and exported as WAV files. The original stimulus used in our previous study consisted of two rhythmic patterns (Edalati et al., 2023). In the present analysis, we only reconsidered the Duple/Triple Rhythm, which consisted of a six-beat

rhythmic pattern based on Cirelli et al. (2016) and Phillips-Silver and Trainor (2005). Briefly, onset-to-onset intervals between successive tones were either 330 or 660 ms, such that successive tone or silence onset-to-onsets were 330 ms, which translated to a beat frequency of 3 Hz. The pattern duration was 1980 ms (Figure 1a, Top). This pattern was repeated 19 times for 38-s long trials. The 38-s long trials were repeated 50 times across two separate blocks. Based on previous evidence, this rhythm induces the perception of a meter, based on grouping by two (i.e., 2×333 ms = 666 ms, hence a duple meter frequency of 1.5 Hz) or three beats (i.e., 3×333 ms = 999 ms, hence a triple meter frequency of 1 Hz) (Cirelli et al., 2016; Phillips-Silver & Trainor, 2005). Note that there were not sound events on every “beat.” Each experimental session started with 20 min of silence, during which the spontaneous neural activity of the neonate was recorded as a baseline condition. The stimuli were delivered through a speaker at 65 dB SPL, which was located at the feet of the neonates, using Psychtoolbox for MATLAB (Kleiner et al., 2007). The total duration of the experiment was 63 min. The recordings were stopped if the infants woke up, started to cry, or moved.

2.3 | EEG acquisition and preprocessing

EEG signals were collected using a 124-channel HydroCel GSN net with an Electrical Geodesic NetAmps 200 amplifier. The EEG was recorded at a 1000-Hz sampling rate, referenced to the electrode Cz. The recorded signals were analyzed in MATLAB using FieldTrip (Oostenveld et al., 2011), EEGLAB (Delorme & Makeig, 2004), and custom MATLAB functions and codes. A two-pass 0.5- to 45-Hz finite impulse response (FIR) filter (order = 3 cycles of the low-frequency cut-off) and a 50-Hz notch filter were applied to remove low- and high-frequency artifacts, and also the line noise from the EEG signals. Next, the data were down-sampled to 512-Hz. The electrodes belonging to the outer ring were removed from further analysis. The first and last 5 s of recording was also removed. The EEG signals were then visually inspected and bad electrodes were removed from the data. Next, in each trial, every electrode was examined and excluded from further analysis if the average absolute value exceeded $30 \mu\text{V}$. If the number of excluded electrodes in a trial exceeded 50% of the total number of electrodes, the entire trial was discarded. Two participants were removed after this process due to the small number of remaining trials. The average number of remaining trials after preprocessing was 44.53 ± 5.65 . We corrected the remaining local and transient artifacts, using the Artifact Blocking algorithm (Fujioka et al., 2011), and a threshold of $100 \mu\text{V}$. Subsequently, the EEG data were re-referenced to the average reference.

2.4 | Time-frequency representation (TFR)

Neural response at the beat and meter frequencies were quantified in our previous study (Edalati et al., 2023) using the frequency-tagging approach (Figure 1a, Bottom). Here, to investigate oscillatory activities

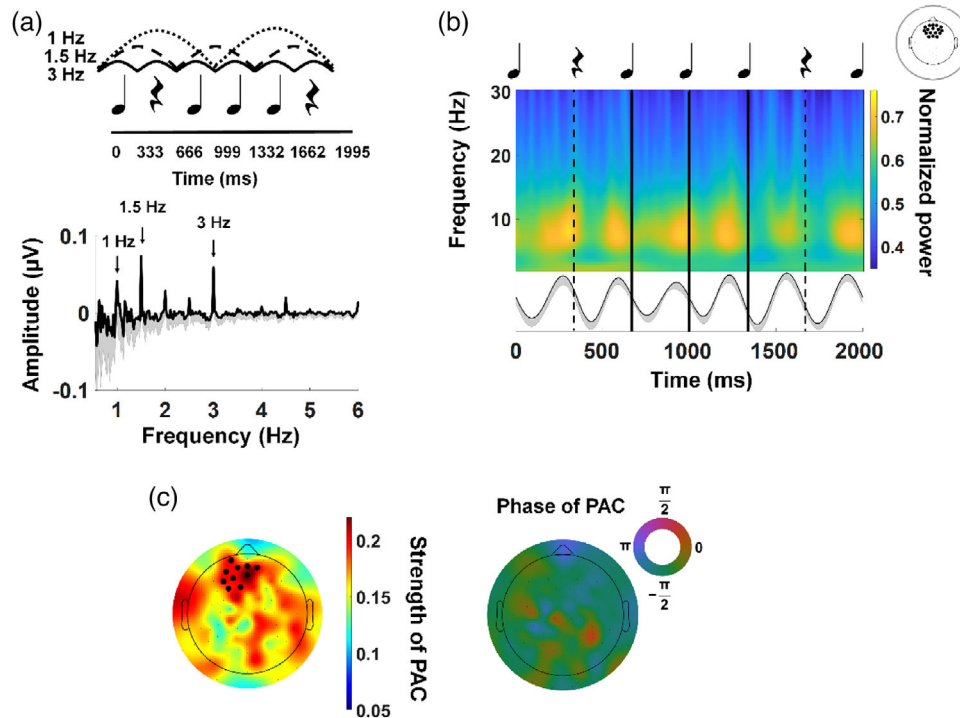


FIGURE 1 Phase-amplitude coupling analysis. (a) Frequency spectrum of the EEG (bottom) while listening to Duple/Triple Rhythm (top). (b) The top figure presents the power modulation in the course of the six-beat sequence in the frequency range of 2–30 Hz. The bottom figure presents the power fluctuations averaged in the frequency range 7–12 Hz (baseline corrected) after 3 Hz narrow band filtering for better visualization. (c) The topographical distribution of the strength of PAC (left), and the preferred phase of coupling (right; green represents alpha power phase leading stimulus phase) of the power of oscillations in the frequency range 7–12 Hz to the beat (modeled by a simulated 3 Hz sinusoidal) averaged over subjects. The dots represent the cluster where the PAC was significant in comparison with surrogate data.

related to the beat, we calculated the TFR over each 38-s long trial using the Morlet wavelet from the Fieldtrip toolbox. Wavelet cycles were set at three cycles on frequencies ranging from 2 to 30 Hz in steps of 0.5 Hz across all electrodes. We eliminated 2 s (equivalent to one repetition of the rhythmic pattern) from both ends of the trial to avoid aliasing caused by time-frequency analysis.

To establish an appropriate baseline, we randomly selected 10 windows of the same length as those of the trials (38 s) from the pre-stimulus silence period. After calculating the TFR for each window, we averaged the results across the windows and time samples inside each window and then over windows, resulting in a baseline value for each frequency step of the TFR. Time-locked TFRs of all trials were then normalized to the obtained baseline. For visualization in Figure 1, TFRs were averaged over all the repetitions of the six-beat rhythmic pattern per participant, resulting in a time-frequency map of 2 s.

After visual inspection of the normalized TFR (Figure 1b) and observation of alpha-band power fluctuations, we further analyze the temporal characteristics of the alpha-band power modulation for the beat (higher frequency bands were also analyzed in the proceeding section). Toward this, we computed the time courses of alpha-band power by calculating the mean across the frequency steps from 7 to 12 Hz. To describe the latency of alpha-band modulation, we averaged the obtained signals across the expected auditory events (tones and rests). In the resulting alpha-band waveforms, the 95% confidence interval of

the grand average as a representation of subject variability was estimated with bootstrap resampling ($N = 1000$) (Fujioka et al., 2015). The latency of the peak and the subsequent decrement and the peak amplitude of the alpha-band waveform within the -166.5 to 166.5 ms window around the beat event were then calculated.

2.5 | Phase-amplitude coupling between the beat phase and amplitude of neural alpha oscillations

To investigate whether the fluctuations in the power of alpha oscillations (7–12 Hz, selected based on the observed TFR) were locked to the beat, we analyzed the PAC between the beat and the power of alpha-band oscillations (Canolty & Knight, 2010). To investigate the specificity of the PAC between the beat and power fluctuations in the alpha-band, we conducted the same analyses on PAC between the beat and power fluctuations in frequency bands of 15–20 Hz and 20–30 Hz.

We approximated the beat dynamics with a sinusoid oscillating at 3 Hz, in which each cycle corresponded to the duration between two successive beat events (tone or rest), with the beat event corresponding to phase $\varphi = 0$. For EEG data processing, we calculated the TFR per trial (Morlet wavelet (cycles = 3) from the Fieldtrip toolbox) for frequencies 7–12 Hz in steps of 0.5 Hz. Subsequently, the time course of the alpha-band oscillation was computed by averaging across the

alpha-band frequencies. To ensure proper phase estimation, the EEG time series were filtered beforehand in the range of the modulated frequency of interest (two pass FIR bandpass filter; order = 3 cycles of the low-frequency cut-off). To calculate the phase information of both the alpha-band power signal and the 3 Hz signal representing the beat, we applied the Hilbert Transform. Toward this, the alpha power signal was first narrow band filtered around 3 Hz (2–4 Hz, order = 2) to avoid the impact of the rapid fluctuation on the temporal evolution of the phase signal. We then eliminated two seconds from both ends of each trial. The synchronization index (SI) (Cohen, 2008) between the two-phase time series was then calculated for each time sample and then averaged over time samples and trials, at each electrode location. The SI is a complex number, the radius of which indicates the strength of locking between the sinusoidal beat signal and alpha power fluctuations, and the angle of which represents the “preferred phase” of synchronization (Gonzalez et al., 2018; Moghimi et al., 2020; Staresina et al., 2015), that is, the phase at which the alpha power is greatest over time. The SI is calculated as

$$SI = \frac{1}{NT} \sum_{i=1}^N \sum_{t=1}^T e^{j[\varphi_{\sin}(t) - \varphi_{\alpha_{\text{power}}}(t)]}$$

where N is the number of trials, T is the number of samples in one trial, $\varphi_{\alpha_{\text{power}}}(t)$ is the phase value of the fluctuations in the alpha-band power time series at trial i and sample t , and $\varphi_{\sin}(t)$ is the phase value of the sinusoidal 3 Hz beat signal at sample t .

2.6 | Lissajous curve

As a complementary method to visually examine the synchronization between the phase of the beat and the power of alpha-band oscillations, we utilized the Lissajous curve (Lense et al., 2022). The Lissajous curve effectively captures how two time-varying signals vary with respect to one another, allowing us to visualize synchronization between two continuous signals and determine the phase shift from one signal to another. In this analysis, the phase of the beat was estimated as a continuously varying 3 Hz cosine function (Figure 2, Top) at a -166.5 to 166.5 ms window (i.e., -180 to 180°) centered around the tone/rest position. The power of alpha-band oscillations was defined as the mean power in the 7–12 Hz frequency range in the TFR, averaged over 333 ms windows centered around the tone/rest positions. To ensure comparability across subjects, the calculated alpha-band oscillation power was normalized between -1 and 1 . With the measure of the alpha-band oscillation power together with the cosine function specifying the phase of beat, we obtained two continuous time-varying signals that could be directly compared using the Lissajous curve.

2.7 | Statistical analysis

Statistical analyses were performed in MATLAB (MathWorks), using the FieldTrip (Oostenveld et al., 2011) and CircStat (Berens, 2009) toolboxes as well as custom MATLAB functions. Different statistical

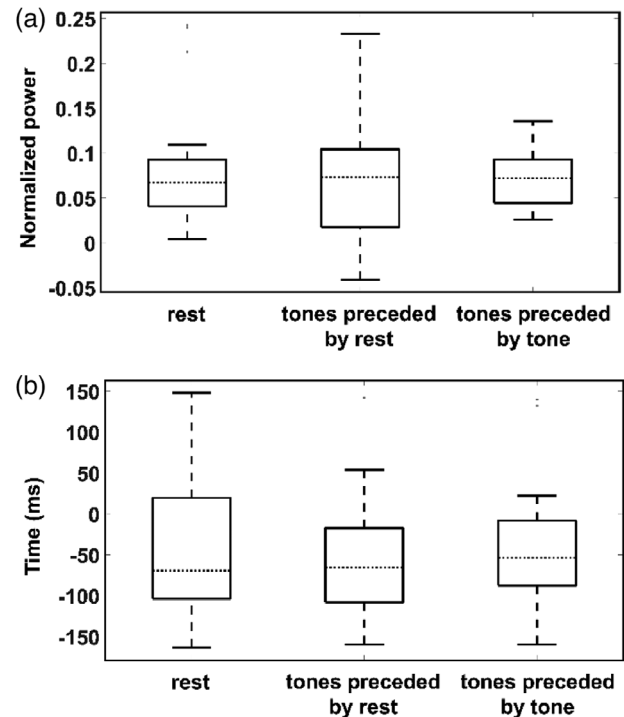


FIGURE 2 Comparison between the alpha-band power modulations around three specific beat conditions: (1) rests, (2) tones preceded by a rest, and (3) tones preceded by a tone. (a) There were no significant differences in the peak value of the alpha-band power among the three conditions as shown in a one-way ANOVA with factor condition ($F(2,14) = 0.32$, $p = 0.7276$, Bayes factor = 0.134). (b) There was no significant difference in the peak latency of the alpha-band power among the three conditions as shown by a one-way ANOVA with factor ANOVA ($F(2,14) = 0.09$, $p = 0.9123$, Bayes factor = 0.111).

analyses were conducted to address the three hypotheses raised in the Introduction.

Hypothesis 1. To evaluate the significance of beat to alpha power PAC across participants, we generated surrogate data by randomly shuffling the sinusoidal 3 Hz beat signal 1000 times. Subsequently, we calculated the PAC strength between the shuffled 3 Hz signal and the alpha-band power trials for each repetition, generating 1000 surrogate SI values from which we could infer the SI chance distribution. By comparing the observed PAC strengths with those corresponding to the surrogate datasets, we obtained electrodes over which the PAC was significantly above the chance level ($p < 0.05$). Next, we detected spatial clusters with a significant PAC. The initial threshold for cluster definition and the minimum number of neighbors were set to $p < 0.05$ and three, respectively.

The consistency of phase locking values across participants was assessed by performing the basic Rayleigh test (Berens, 2009). This test allowed us to evaluate the nonuniformity of the circular histogram of the phase difference across participants, which provides a measure of consistent phase locking to the sinusoidal 3 Hz signal representing the beat.

Hypothesis 2. To examine if alpha power modulations were equivalent whether or not the beat onset times coincided with a sound event (tone) or a rest, we compared the latencies and amplitudes of the alpha power peaks across beats coinciding with (1) rests, (2) tones that were preceded by a rest, and (3) tones that were preceded by a tone. We then used one-way ANOVA to compare the peak/latency values for the three conditions, with a particular interest in evidence in favour of the null hypothesis (evaluated with Bayesian statistics, using Akaike Information Criterion).

Hypothesis 3. To examine whether the peak latency of the alpha-band waveform was before the beat and if the following decrement was after the beat, a one-tailed one-sample *t*-test was performed. Normality was tested using the Lilliefors test (Lilliefors, 1969). The corresponding effect size was defined using Cohen's *d*.

3 | RESULTS

3.1 | Hypothesis 1: Is alpha-band power fluctuation orchestrated by the beat?

The normalized TFR over frontal and fronto-central electrodes revealed periodic fluctuations in the neural activity in the alpha frequency range (712 Hz) aligned with the beat (both tone and rest) (Figure 1b). Visual inspection of the TFR did not reveal similar power fluctuations at higher frequencies. To address the synchronization between the power fluctuation of alpha-band oscillations and the beat, we evaluated the strength of PAC between the phase of the simulated sinusoidal 3 Hz signal representing the beat (including tones and rests) and the amplitude of the alpha-band power. The topographical distribution of the strength and phase of PAC is shown in Figure 1c. In agreement with the TFR depicted over the rhythmic sequence, there was a significant PAC across participants over a number of frontal electrodes compared to surrogate data ($p = 0.0203$; Figure 1c, Left), with a consistent phase delay between the beat and alpha-band power modulations and over time and trials. To evaluate the specificity of the PAC to the beat uniquely to the alpha-band power, we conducted the same analysis by setting the modulated frequency to 15–20 Hz and 20–30 Hz. Consistent with the TFR results showing no periodic fluctuation of power at these frequency bands, no significant PAC cluster emerged while contrasted to surrogate data (Figure S1), indicating that the periodic fluctuation of power by the beat was limited to the alpha-band.

3.2 | Hypothesis 2: Is alpha-band power fluctuation equivalent for beats aligned with tones and rests?

There was no significant difference between the alpha power peak for beats aligned with (1) rests, (2) tones that were preceded by a rest, and (3) tones that were preceded by a tone (Figure 2a), as revealed by a one-way ANOVA ($F(1,14) = 0.32$, $p = 0.7276$, Bayes factor = 0.134).

Post hoc *t*-tests revealed strong evidence favoring the null hypothesis ($t_{(16)} = 0.578$, $p = 0.571$, Bayes factor = 0.289 comparing conditions 1 and 2; $t_{(16)} = 0.708$, $p = 0.489$, Bayes factor = 0.311 comparing conditions 1 and 3; $t_{(16)} = 0.1552$, $p = 0.879$, Bayes factor = 0.252 comparing conditions 2 and 3). In addition, there was no significant difference between the peak latency for beats aligned with the three aforementioned conditions (Figure 2b), as revealed by a one-way ANOVA ($F(2,14) = 0.09$, $p = 0.9123$, Bayes factor = 0.111). Again, post hoc *t*-tests revealed strong evidence favoring the null hypothesis ($t_{(16)} = 0.421$, $p = 0.679$, Bayes factor = 0.269 comparing conditions 1 and 2; $t_{(16)} = 0.004$, $p = 0.996$, Bayes factor = 0.249 comparing conditions 1 and 3; $t_{(16)} = 0.376$, $p = 0.712$, Bayes factor = 0.265 comparing conditions 2 and 3).

If the alpha oscillations were reactive (rather than predictive) and related to the neural response to tones, we should have observed a significant reduction for rests compared to tones, and also a reduction for tones preceded by a rest compared to tones preceded by a tone.

3.3 | Hypothesis 3: Does alpha-band power peak precede the beat?

The signal corresponding to alpha-band power fluctuations showed a phase lead with respect to the beat as shown in Figure 3a,b. The phase lead was consistent over the electrodes belonging to the frontal cluster identified above, as revealed with a phase difference between 0° and 90° within the significant cluster (mean phase difference over the cluster = 76.58°; Figure 3a). In addition, the Rayleigh test revealed consistent phase relationships among participants ($R = 4.3605$, $p = 0.0108$) over these frontal electrodes. The temporal distribution of the phase differences relative to the onset of the beat event for each participant is presented in Figure 3b. A complementary analysis conducted with the Lissajous curve (Figure 3c) also showed phase coupling between the beat sinusoid and the alpha-band oscillations power. The leading phase of the alpha-band oscillations power with respect to that of the beat is illustrated by the clockwise direction of the Lissajous curve.

We further examined the temporal dynamics of the alpha-band power fluctuations extracted from the TFR averaged over the electrodes belonging to the significant cluster at three specific time periods, similar to those studied for Hypothesis 2 (Figure 4); (1) around rests, (2) around tones that were preceded by a rest, and (3) around tones that were preceded by a tone. The statistical analysis revealed that for each period, the latency of the peak of the alpha-band waveform was before the beat onset (see also Figure 2), and the latency of its subsequent decrement was after the beat onset. In condition 1, the peak was located at -49.84 ± 91.91 ms, indicating that the latency was significantly earlier than the beat onsets ($t_{(16)} = -2.2357$, $p = 0.02$, Cohen's $d = 0.52$). Similarly, in conditions 2 and 3, the peak was located at -39.35 ± 77.41 ms ($t_{(16)} = -2.0959$, $p = 0.0262$, Cohen's $d = 0.48$) earlier than the rest-beat onset, and in condition 3 it was -34.07 ± 78.76 ms ($t_{(16)} = -1.78$, $p = 0.0467$,

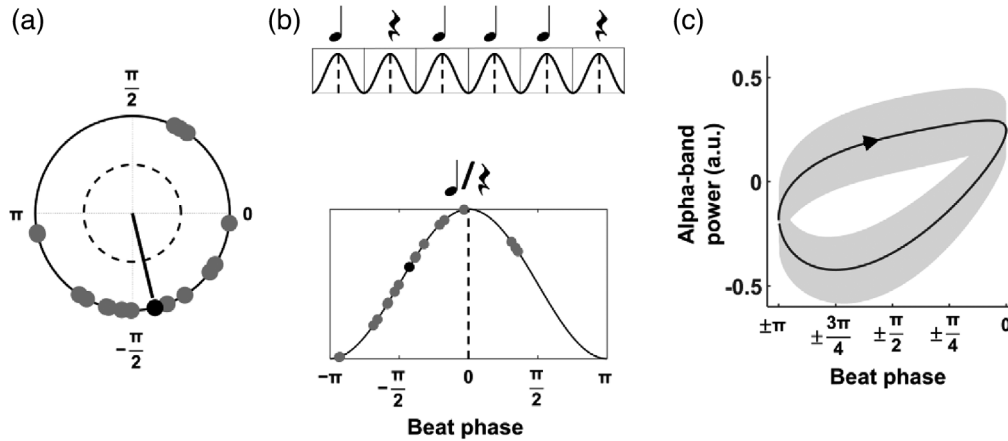


FIGURE 3 Phase analysis of PAC. (a) Individual phase of PAC (power of alpha oscillations to the beat) averaged over all events. (b) Individual phase of PAC over one beat cycle (same data as a, but presented over one cycle for temporal visualization). Both (a) and (b) are presented over the significant frontal electrodes belonging to the cluster shown in Figure 1c, which have consistent phase relationships among participants, verified by the Rayleigh test ($R = 4.3605$, $p = 0.0108$). Each gray dot in (a) and (b) corresponds to one participant. The black dot represents the average phase among participants. (c) The Lissajous curve for the alpha-band oscillation power versus beat phase averaged across participants is shown by the black line. The gray areas show the standard error across participants. Arrowhead shows the direction of travel, illustrating a phase lead for the alpha-band power fluctuations.

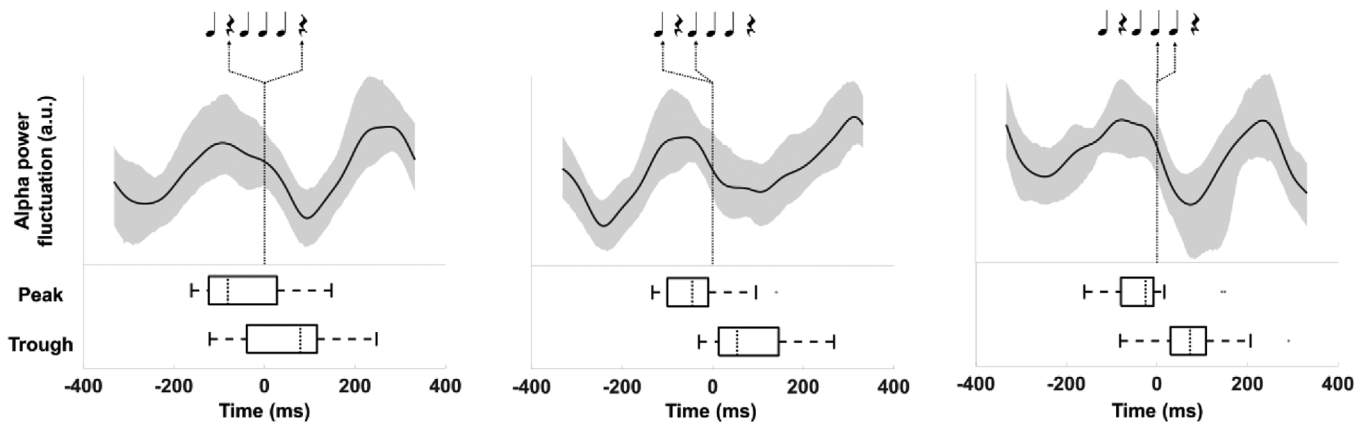


FIGURE 4 Latency of beat-related modulation of alpha power. Average of power in the frequency band 7–12 Hz around all events (a), rest events (b), and tone events preceded by rest (c). The shaded area represents the 95% confidence interval of the mean over participants. The boxplots show the distribution of the peak and trough positions around each aforementioned event. The peak position is in the range of -49.84 ± 91.91 ms ($t_{(16)} = -2.2357$, $p = 0.02$, Cohen's $d = 0.52$) for rest events (a), -39.35 ± 77.41 ms ($t_{(16)} = -2.0959$, $p = 0.0262$, Cohen's $d = 0.48$) for tone events preceded by a rest (b), and -34.07 ± 78.76 ms ($t_{(16)} = -1.78$, $p = 0.0467$, Cohen's $d = 0.41$) for tone events preceded by a tone (c). The trough position is in the range of 49.95 ± 99.59 ms ($t_{(16)} = 2.0681$, $p = 0.0276$, Cohen's $d = 0.48$) for rest events (a), 77.95 ± 87.33 ms ($t_{(16)} = 3.6803$, $p = 0.001$, Cohen's $d = 0.85$) for tone events preceded by a rest (b), and 76.68 ± 87.76 ms ($t_{(16)} = 3.5944$, $p = 0.001$, Cohen's $d = 0.83$) for tone events preceded by a tone (c).

Cohen's $d = 0.41$) earlier than the tone-following-a-rest beat onset. Furthermore, the subsequent decrement was consistently located after the beat event for all the three conditions (49.95 ± 99.59 for condition 1, 77.95 ± 87.33 for condition 2, and 76.68 ± 87.76 for condition 3) and the latencies were all significantly positive in comparison with the beat timing ($t_{(16)} = 2.0681$, $p = 0.0276$, Cohen's $d = 0.48$ for condition 1, $t_{(16)} = 3.6803$, $p = 0.001$, Cohen's $d = 0.85$ for condition 2, and $t_{(16)} = 3.5944$, $p = 0.001$, Cohen's $d = 0.83$ for condition 3).

4 | DISCUSSION

Previous studies have provided neural evidence that infants track the beat of rhythmic patterns (Cirelli et al., 2016; Flaten et al., 2022; Lenc et al., 2022; Winkler et al., 2009) and our previous study showed that already in premature newborns, slow neural oscillations phase align with beat frequencies (Edalati et al., 2023). However, studies in adults demonstrate that in addition to phase alignment between slow neural oscillations and beat frequencies, periodic fluctuations in power



at higher frequencies (specifically, beta power, 15–30 Hz) phase align to the perceived beat of rhythmic stimuli (Fujioka et al., 2009, 2012) and are modulated by perception (Iversen et al., 2009), suggesting that this beat-phase/beta-power coupling relates to intrinsic predictive processes (Large et al., 2023). The present study extends our understanding of early rhythmic capacities by showing that similar PAC is already present in premature newborns more than a month before full term. Further, the present study shows that this coupling occurs at a somewhat lower neural frequency in the premature infant brain (alpha power, 7–12 Hz) than in adults. Importantly, this PAC indicates that the premature brain encodes an isochronous beat when presented with a nonisochronous rhythm to which adults perceive a strong beat.

Two features of the alpha-band power modulation response are consistent with the premature brain engaging in prediction of underlying beat onsets. First, the modulation of alpha power occurred in response to beats coinciding with both tones and rests and, for beats coinciding with tones, the peak amplitude of the modulation was independent of whether the event was preceded by a tone or rest. That this systematic modulation of alpha power occurred around both tone and rest events makes it unlikely that these modulations were simply elicited as responses to individual sound events. Indeed, this is in contrast to evoked potentials, which are greatly reduced, if not absent altogether, when there is no sound event. This suggests that it is the timing of the beat, rather than the acoustic energy coinciding with tones, that orchestrated the power modulation. Second, the periodic alpha-band fluctuations demonstrated a phase lead with respect to the periodic signal presenting the beat (i.e., the neural alpha power peak preceded the beat onset and its trough followed the beat onset), suggesting that the response was predictive of beat onsets rather than reactive to them. This is consistent with adult data showing that during motor synchronization to an auditory rhythm, adults tend to tap before the beat (Roman et al., 2019), but this finding has to be treated with caution. As the stimuli consisted of repeated tones and rests, the small phase lead might also be considered as a large phase lag with respect to the preceding event. However, the lack of a significant difference between the alpha power characteristics corresponding to rest and tone events suggests that even if the phase was represented a large phase lag, it still represents neural coding of the timing of the beats. Evaluating and comparing phase relationships at different tempi, which modulate the interevent intervals, might help to clarify this question. In any case, the current results provide the first evidence for the possible existence of similar temporal predictive mechanisms before the age of term, although further studies are required confirm this initial hypothesis.

Studies conducted in adults have proposed different hypotheses for the role of beta oscillations in encoding temporal predictions. One hypothesis is that beta oscillations during rhythm processing originate from interactions and coupling between the auditory and motor cortices (Zalta et al., 2023, 2024). Another hypothesis is that beta oscillations are related to top-down predictions driven by temporal regularities. Evidence suggests that these predictions can modulate the strength and timing of beta oscillation during rhythm processing (Fontolan et al., 2014; Morillon & Baillet, 2017; Spitzer & Haegens,

2017). In the present paper, we observed similar stimulus aligned modulation in the premature infant brain, but at a lower frequency around 7–12 Hz. We propose that these observed alpha oscillations in premature newborns may indicate neural predictions of the timing of the beat. However, we do not have evidence about the cortical sources of the oscillations, so this remains to be investigated in future research.

We can only speculate as to why the alpha-band appears to support phase/amplitude coupling for beat processing in the premature brain, whereas the beta band serves this role in adults. Generally, in the mature adult brain low frequency and high-frequency oscillations are thought to support different aspects of information flow and encoding. In early development of neural hierarchies for information processing, various factors likely contribute to the involvement of different frequencies than in adults. It is well known that the frequency of spontaneous neural oscillations undergoes an evolution during early neurodevelopment, reflecting the maturation and refinement of neural communication and information processing. The development of inhibitory mechanisms and the developmental increase in the strength of inhibition play a crucial role in shaping neural circuits and refining neural activity (Chini & Hanganu-Opatz, 2021; Chini et al., 2022). As inhibitory interneurons and GABAergic currents mature, they contribute to the establishment of balanced neural networks and the regulation of excitation-inhibition dynamics, contributing to a transition in brain dynamics from early highly synchronous activity patterns to decorrelated neural activity later in life. In neural mass models, the frequency of oscillation in a network depends on the strength of inhibitory-excitatory and inhibitory-inhibitory connections (Ghorbani et al., 2012; Hashemi et al., 2019). However, hypotheses about the direct role of premature inhibition on the frequency of rhythmic power fluctuations are highly speculative as many other developmental factors can also impact neural strategies for temporal processing. For instance, considering structural neurodevelopment, the microstructures of the cortical columns undergo rapid evolution before the age of term in an inside-out manner (Rakic, 1988). Differences in neural responses to stimuli from early stages to later mature states can also be related to the remodeling of initial circuitry and development of more mature neural structures. In the same vein, the functional role of such alpha oscillations in the premature brain can be different from those observed in the mature brain during temporal processing (Cabral-Calderin & Henry, 2022; Grabot et al., 2019; Milton & Pleydell-Pearce, 2016; Spaak et al., 2014; Van Wassenhove, 2016). In addition, sustained alpha oscillations are absent in premature EEG, which is characterized by bursts of oscillatory activities of different frequencies (the spectral content goes through a rapid evolution with age) separated by quiescent periods (Wallois et al., 2021).

Fujioka and colleagues (Fujioka et al., 2009, 2012) found evidence in adults that the slope of the beta-band power increase predicted the expected onset time of the upcoming beat across isochronous sequences at different tempos. Here, we were only able to test one tempo in premature infants. However, we found that the phase of the neural alpha power fluctuations led the phase of the stimulus beat, with

the peak of maximum power located slightly before and the trough after the beat. Arnal et al. (2015) also found bursts of beta band oscillations preceding auditory targets in a rhythmic sequence, where the difference in the relative phase was suggested to be related to the cortical region of interest. The phase of beta band temporal dynamics observed by Fujioka et al. (2012), also varied among different brain regions, most notably between auditory and motor regions, suggestive of oscillatory communication between these regions. In the current study, the alpha-band fluctuations observed over the fronto-central region (where the activity was maximum), could be a superposition of activities with different cortical origins, making interpretation of the role of different regions in the phase relationship impossible. It thus remains for future studies to examine whether different cortical regions in the premature brain exhibit different phase relations, and how they interact during rhythmic processing. In general, hypotheses about the role of alpha oscillations in temporal predictions need to be tested in additional study designs that allow evaluating the relation between alpha power modulation and temporal prediction directly, such as, for example, examining the neural response to occasional temporal deviations (Arnal et al., 2015) and the persistence of oscillations once the stimulation ceases (Kösem et al., 2018). Until such studies are conducted it is prudent not to over interpret the underlying mechanisms of the oscillations we observed.

Time related processing is of high importance from the developmental point of view (Lense et al., 2021), for the development of language (Goswami, 2022), and musical capacities (Trainor & Hannon, 2013), as well as for communication, interpersonal coordination, and social affiliation (Cirelli et al., 2018; Nguyen et al., 2023). Predictive temporal processing is essential for adaptation to dynamic environmental changes and efficient perception, cognitive abilities necessary for learning, and the development of higher-order cognitive functions. The present study suggests that neural predictive time processing in response to a rhythmic sequence is present more than a month before the age of term, implying that rhythmic processing is likely an important early building block of neurodevelopment. The prenatal auditory world is characterized by omnipresent rhythmic sounds, such as the maternal heart beat and respiration, the fetal heart beat, and maternal speech and singing. However, premature birth can result in sensory deprivation for patterned input as these natural rhythmic inputs in the womb are not present in an incubator. Combined with exposure to the loud sounds of medical machines in the neonatal intensive care unit, this may impact the early development of neural hierarchies (Ibrahim et al., 2021). Premature birth is generally associated with various pathologies that can impact neurodevelopment. While the present study indicates that rhythm encoding through neural oscillations is evident in the premature infant brain soon after birth, the effects of the subsequent poverty of rhythmic input between premature birth and 40 weeks gestation remains unknown, as does possible benefits of rhythmic interventions during this period.

AUTHOR CONTRIBUTIONS

Conceptualization: Laurel J. Trainor, Sahar Moghimi, and Fabrice Wallois; *Methodology:* Mohammadreza Edalati, Laurel J. Trainor, and Sahar

Moghimi; *Investigation:* Mohammadreza Edalati, Ghida Ghostine, and Guy Kongolo; *Visualization:* Mohammadreza Edalati, Laurel J. Trainor, Sahar Moghimi, and Fabrice Wallois; *Supervision:* Laurel J. Trainor and Sahar Moghimi; *Writing – original draft:* Mohammadreza Edalati, Laurel J. Trainor, and Sahar Moghimi; *Writing – review & editing:* Mohammadreza Edalati, Laurel J. Trainor, Sahar Moghimi, and Fabrice Wallois.

ACKNOWLEDGMENTS

We thank Amiens University Hospital EEG technicians for data acquisition and the parents and families who consented to take part in the study. This work was supported by Fondation pour l'Audition Grant BabyMusic RD-2021-11.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The stimuli and data that support the findings of this study are available on reasonable request from the corresponding authors (S.M. and L.J.T). The data are not publicly available because of participants not providing consent to share their data outside our research consortium on the consent form. MATLAB code and data matrices are available on GitHub (<https://github.com/mredalati/Rhythmic-temporal-prediction-in-the-premature-brain>).

ETHICAL APPROVAL STATEMENT

One or both parents were informed about the study and provided their written informed consent. The local ethics committee (CPP Ouest I) approved the study (ID-RCB: 2019-A01534-53).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Edalati, M., Wallois, F., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi, S. (2024). Neural oscillations suggest periodicity encoding during auditory beat processing in the premature brain. *Developmental Science*, e13550. <https://doi.org/10.1111/desc.13550>