Please do not remove this page

Infants show enhanced neural responses to musical meter frequencies beyond low-level features

Lenc, Tomas; Peter, Varghese; Hooper, Caitlin; et.al.

https://research.usc.edu.au/esploro/outputs/journalArticle/Infants-show-enhanced-neural-responses-to/99690998902621/filesAndLinks?index=0

Lenc, T., Peter, V., Hooper, C., Keller, P. E., Burnham, D., & Nozaradan, S. (2023). Infants show enhanced neural responses to musical meter frequencies beyond low-level features. Developmental Science, 26(5), 1–15. https://doi.org/10.1111/desc.13353
Document Type: Published Version

Link to Published Version: https://doi.org/10.1111/desc.13353

UniSC Research Bank: https://research.usc.edu.au
research-repository@usc.edu.au
CC BY-NC-ND V4.0
© 2022 The Authors. Developmental Science published by John Wiley & Sons Ltd.This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
Downloaded On 2023/11/29 20:42:42 +1000

Please do not remove this page

Check for updates

Received: 2 May 2022 | Revised: 20 October 2022 | Accepted: 16 November 2022

DOI: 10.1111/desc.13353

Developmental Science WILEY

RESEARCH ARTICLE

Infants show enhanced neural responses to musical meter frequencies beyond low-level features

Tomas Lenc[1,2] | Varghese Peter[2,4] | Caitlin Hooper[2] | Peter E. Keller[2,5] | Denis Burnham[2] | Sylvie Nozaradan[1,2,3]

[1]Institute of Neuroscience (IONS), Université catholique de Louvain (UCL), Brussels, Belgium

[2]MARCS Institute for Brain, Behaviour and Development, Western Sydney University, Sydney, Australia

[3]International Laboratory for Brain, Music and Sound Research (BRAMS), Montreal, Canada

[4]School of Health and Behavioural Sciences, University of the Sunshine Coast, Queensland, Australia

[5]Center for Music in the Brain & Department of Clinical Medicine, Aarhus University, Aarhus, Denmark

Correspondence
Tomas Lenc, The Institute of Neuroscience (IONS), Université catholique de Louvain (UCLouvain), 53 Avenue Mounier, B1200 Brussels, Belgium.
Email: tomas.lenc@uclouvain.be

Funding information
Australian Research Council, Grant/Award Numbers: DP00025567, DP110105123; H2020 European Research Council, Grant/Award Number: 801872

Part of the Special Issue "Music in Development", edited by Heather Bortfeld and Samuel Mehr.

Abstract

Music listening often entails spontaneous perception and body movement to a periodic pulse-like meter. There is increasing evidence that this cross-cultural ability relates to neural processes that selectively enhance metric periodicities, even when these periodicities are not prominent in the acoustic stimulus. However, whether these neural processes emerge early in development remains largely unknown. Here, we recorded the electroencephalogram (EEG) of 20 healthy 5- to 6-month-old infants, while they were exposed to two rhythms known to induce the perception of meter consistently across Western adults. One rhythm contained prominent acoustic periodicities corresponding to the meter, whereas the other rhythm did not. Infants showed significantly enhanced representations of meter periodicities in their EEG responses to both rhythms. This effect is unlikely to reflect the tracking of salient acoustic features in the stimulus, as it was observed irrespective of the prominence of meter periodicities in the audio signals. Moreover, as previously observed in adults, the neural enhancement of meter was greater when the rhythm was delivered by low-pitched sounds. Together, these findings indicate that the endogenous enhancement of metric periodicities beyond low-level acoustic features is a neural property that is already present soon after birth. These high-level neural processes could set the stage for internal representations of musical meter that are critical for human movement coordination during rhythmic musical behavior.

KEYWORDS
development, EEG, frequency-tagging, infants, musical beat and meter perception, rhythm processing

Research Highlights

- 5- to 6-month-old infants were presented with auditory rhythms that induce the perception of a periodic pulse-like meter in adults.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
© 2022 The Authors. *Developmental Science* published by John Wiley & Sons Ltd.

- Infants showed selective enhancement of EEG activity at meter-related frequencies irrespective of the prominence of these frequencies in the stimulus.
- Responses at meter-related frequencies were boosted when the rhythm was conveyed by bass sounds.
- High-level neural processes that transform rhythmic auditory stimuli into internal meter templates emerge early after birth.

1 | INTRODUCTION

Music is a universal phenomenon observed across individuals and societies (Mehr et al., 2019; Nettl, 2000; Savage et al., 2015). Yet the evolutionary origins of human capacities for the perception and production of music, that is, musicality, remain poorly understood. Recent accounts propose that music-making has its origins in social behaviors (Mehr et al., 2021; Savage et al., 2021). These accounts predict that mechanisms allowing humans to perceive and produce high levels of interpersonal synchrony during music making (and dance) constitute a core component of musicality (see also Honing, 2012) and should appear early in development.

Despite diversity along many dimensions, music seems to have universal features that bolster temporally coordinated behaviors (Mehr et al., 2019; Savage et al., 2015). Specifically, the structure of music across cultures can be characterized by *periodic recurrence* at timescales relevant to sensory-motor coordination. At the fast end of this temporal range, this involves a small set of recurring time intervals between successive sound onsets, which are typically (but not necessarily) subdivided by a common period (Jacoby & McDermott, 2017; Mehr et al., 2019). Moreover, this finite set of short time intervals is often arranged recurrently, thus forming repeated patterns of sound onsets spanning the subsecond to suprasecond range (Agawu, 2016; Hannon et al., 2004; Margulis, 2014; Palmer & Krumhansl, 1990; Toiviainen & Snyder, 2003). Overall, this structure based on periodic recurrence facilitates the perception of a set of nested periodic beats (hereafter *meter*, for short) (Cohn, 2020; Honing & Bouwer, 2018; London, 2004). Meter is a cornerstone of musical synchronization as it provides a precise shared mental representation of time across musicians, dancers, and listeners. Humans often perceive meter in music spontaneously and tend to move the body in time with it, as when people bob the head, tap the foot, or dance periodically along with music (Burger et al., 2010; Janata et al., 2012).

Importantly, even if musical sounds lack strongly recurrent features at some level within the temporal range described above, humans seem to readily perceive and synchronize with a stable meter (Large et al., 2015; Lenc et al., 2018; Nozaradan et al., 2012b; Su & Pöppel, 2012). Indeed, music with less regular rhythmic structure is not a peculiarity of a few isolated musical genres, but appears to be ubiquitously present and synchronized to in dance contexts across cultures (Agawu, 2016; Holzapfel, 2015; Locke, 2010; London et al., 2017; van der Weij et al., 2017; Witek, 2017).

The nature of the processes that underlie meter perception, especially from less regular (or "weakly-periodic") music remains unknown. Regularity detection may be sufficient to support meter perception from music with prominent acoustic periodicities, a process that has been referred to as meter *extraction* (c.f. Kotz et al., 2018). However, meter perception cannot solely rely on regularity detection when the musical rhythm lacks prominent acoustic periodicities, that is, when there is no prominent periodic meter to be extracted from the acoustic structure of the rhythmic stimulus. In fact, in weakly-periodic music, meter perception requires endogenously generating periodicities beyond the acoustic features, a process that may rely on qualitatively and quantitatively different processes (Lenc et al., 2021). This ability may be supported by general perceptual mechanisms, such as neural resonance, which have been proposed to endogenously enhance the representation of metric periodicities as a result of connectivity and dynamics within auditory-motor cortical networks (Large et al., 2015; Tichko et al., 2022). Alternatively, this capacity could be built upon inferential processes by which individuals learn to associate a specific rhythm with a specific metric interpretation through exposure (Hannon & Trehub, 2005b; London et al., 2017; van der Weij et al., 2017).

The processes underlying meter perception may also be differentially present across species. The capacity to build an internal representation of a periodic beat from isochronous stimuli has been shown in nonhuman primates (Gámez et al., 2018; Zarco et al., 2009). In addition, several species of mammals and birds have shown the ability to synchronize to periodic regularities extracted from strongly-periodic music (Cook et al., 2013; Jao Keehn et al., 2019; Patel et al., 2009; Schachner et al., 2009), and this ability may build on low-level neurophysiological processes in the auditory pathway (Rajendran et al., 2017, 2020). However, evidence for the neural and behavioral representation of an endogenously generated beat induced with weakly-periodic input has only been observed in enculturated adult humans so far. Therefore, assuming a uniform set of neural/psychological processes supporting meter perception when listening to strongly- versus weakly-periodic rhythms may not be warranted.

In terms of human development, the processes supporting detection of temporal regularities relevant to meter perception appear early, within the first year of life. Already at 2–3 months, infants can discriminate rhythmic patterns based on the grouping of acoustic onsets (Demany et al., 1977). At 7–9 months, they show the ability to establish an internal representation of rhythmic patterns invariant to pitch and

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

tempo (Trehub & Thorpe, 1989). 7-month-old infants can discriminate rhythmic stimuli based on the meter cued by prominent periodicities in their acoustic structure (Hannon & Johnson, 2005), and detect when this regular structure is disrupted (Hannon & Trehub, 2005a, 2005b). In fact, the rudiments of meter extraction from strongly-periodic rhythms may be already present at birth. As reported in an influential study by Winkler et al. (2009), newborns show a difference in brain responses to sound omissions when these occur aligned (rather than misaligned) with beats prominently cued by the acoustic structure of a rhythm (but see Honing et al., 2014 for a discussion of possible acoustic confounds). These observations indicate a human predisposition for meter perception, particularly when cued by strongly-periodic rhythms. Indeed, regular rhythms are an important part of the environment from early infancy, particularly in the context of infant-directed songs (Hilton et al., 2022; Mehr et al., 2019) and nursery rhymes (Suppanen et al., 2019).

However, the ability to synchronize overt body movement with meter even in highly regular rhythms has a much longer developmental time course (Hannon et al., 2018; Kirschner & Tomasello, 2009; McAuley et al., 2006). Zentner and Eerola (2010) found no evidence for spontaneous synchronization of movement with the meter in infants younger than 24 months (see also Ilari, 2015 for a replication). Nevertheless, they observed precursors of sensory-motor synchronization with meter. When the stimulus contained prominent acoustic cues to a periodic beat, infants adjusted the speed of their spontaneous movements to the tempo of this physically cued beat (see also Cirelli & Trehub, 2019; Fujii et al., 2014; Provasi et al., 2014). Together, the evidence suggests that very young infants may have the ability to establish a representation of meter from prominent periodic cues even before the maturation of motor skills.

Yet, whether the ability to build an internal representation of meter from weakly periodic rhythms emerges early in development remains an unanswered question. In one study, Bergeson and Trehub (2006) showed that 9-month-old infants failed to detect temporal deviations in a 3.6-s long rhythmic pattern where the arrangement of sounds did not follow a prominent periodicity. This finding was taken to indicate that an internal representation of meter was not established. However, presenting the pattern without repetition eliminated a level of recurrence at a relatively long timescale that is typically present in weakly-periodic music. In fact, even adult performance in a comparable experimental design is rather low (Grahn & Brett, 2007; Grube & Griffiths, 2009; Povel & Essens, 1985).

Probing the processing of weakly-periodic rhythms across development poses particular methodological challenges. For instance, rhythmic stimuli in discrimination tasks must be carefully controlled for low-level features, which may significantly limit the range of rhythmic stimuli that can be investigated (e.g., Hannon & Johnson, 2005). Moreover, behavioral habituation paradigms cannot be easily employed to obtain comparable data at different time points of the developmental continuum (due to the confounds potentially introduced by task instructions and cognitive factors).

To overcome these issues, electroencephalography (EEG) can be used to measure brain activity at the millisecond scale without requiring concomitant behavioral outcome. For instance, the internal representation of meter can be investigated indirectly, extrapolating from transient EEG responses elicited by occasional changes of single acoustic events comprising a rhythmic sequence (mismatch negativity; see Bouwer et al., 2014, 2016; Honing et al., 2014). However, this approach relies on observing a differential brain response when the position of the change is aligned versus misaligned with the metric pulse prominently cued by the acoustic structure of the stimulus. Consequently, this approach cannot be easily applied to weakly-periodic rhythms, that is, to rhythms that do not systematically contain acoustic events at plausible metric pulse positions (Lenc et al., 2021; London et al., 2017).

An alternative approach to capturing the internal representation of meter is the combination of EEG with frequency-tagging (Lenc et al., 2021; Nozaradan, 2014; Nozaradan, Keller, et al., 2017). Using this approach, it has been shown that when adult humans listen to rhythmic inputs that give rise to meter perception, the elicited neural response is selectively enhanced at the frequencies related to the perceived meter periods (Lenc et al., 2018, 2020a; Nozaradan et al., 2012b, 2018; Nozaradan, Mouraux, et al., 2016; Nozaradan, Schwartze, et al., 2017; Tal et al., 2017). Importantly, this enhancement is observed even when meter-related frequencies are not prominent in the input, i.e., when periodic recurrence given by temporal arrangement of sound events is low. In other words, this enhanced neural representation of meter periodicities cannot be easily explained by the physical structure of the stimulus, thus controlling for low-level confounds. Rather, this observation suggests that the rhythmic input is transformed within the adult brain into the perceptual meter category (Lenc et al., 2021; Nozaradan, Keller, et al., 2017). There is increasing evidence that this neural transformation relies on high-level cortical processes, which allow the brain to actively build an endogenous representation of meter, beyond extraction of stimulus regularities (Lenc et al., 2020a; Nozaradan et al., 2018; Sifuentes-Ortega et al., 2022; Tal et al., 2017; see also Nozaradan, Mouraux, et al., 2016; Nozaradan, Schwartze, et al., 2017 for further evidence gathered from surface and intracranial EEG in brain-damaged patients). Hence, frequency tagging may be a powerful method to probe how neural processes critical for meter perception develop over the lifetime, without relying on overt behavioral responses.

Here, we used the frequency-tagging approach to test whether 5- to 6-month-old infants already show selective enhancement of the neural activity at meter periodicities in response to rhythms lacking prominent periodic cues to the meter (see also Cirelli et al., 2016 who used frequency-tagging in 7- and 15-month-old infants to capture neural responses to more regular rhythms). Such neural enhancement would indicate that precursors of coordinated musical behaviors, even in the face of degraded acoustic cues, are in place soon after birth. Alternatively, observing that infants' neural responses merely track the acoustic structure of rhythms without enhancing meter-related periodicities would suggest that the emergence of higher-level rhythm processing may rely on extensive (possibly multimodal) exposure to music and/or maturation of sensorimotor synchronization abilities.

We also tested whether the selective enhancement at meter periodicities was increased when the rhythms were carried by bass tones

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

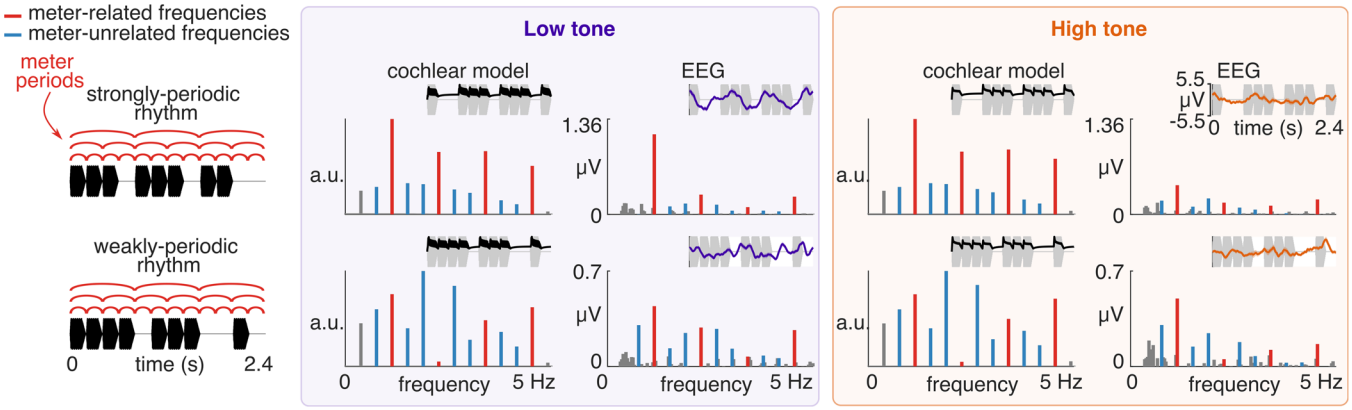

FIGURE 1 Spectra of the cochlear model output and of the EEG responses for each rhythm and tone (averaged over 28 frontocentral channels and 20 infants). Meter-related frequencies at 1.25, 2.5, 3.75 and 5 Hz are shown in red, whereas the remaining (meter-unrelated) frequencies are shown in blue. Insets depict time-domain responses averaged across all repetitions of the corresponding rhythmic pattern (in grey) for the cochlear model, or for the EEG responses averaged across all infants. Standard error of the mean for the time-domain EEG responses is indicated as shaded regions.

compared to high-pitched tones, as has been found in adults (Lenc et al., 2018). This was motivated by recent studies suggesting that bass sounds have a privileged role in making people move along with the periodic meter (Burger et al., 2018; Hove, Vuust, et al., 2019; Stupacher et al., 2016; Van Dyck et al., 2013). However, whether this bass benefit for rhythm has biological roots, or it arises from long-term exposure to music in which the rhythm is predominantly conveyed by low-frequency sounds remains unknown. Observing an enhancement effect of low tones on the neural representation of meter in infants would suggest that the link between rhythm processing and bass sounds does not rely on learning over the lifespan, but rather may derive from basic functional connections between the auditory and vestibular systems (Todd & Lee, 2015b; Trainor & Unrau, 2009), or on prenatal experience (Parncutt, 2016; Parncutt & Chuckrow, 2019).

2 | METHODS

2.1 | Participants

Twenty infants (mean age 5.7 months, from 5.03 to 6.43 months; nine females, no pre-term birth, no auditory or neurological disorder) took part in the experiment. The infants were recruited from the Babylab database at the MARCS Institute for Brain, Behaviour and Development, Western Sydney University. The research was approved by the local Ethics committee, as part of the project H9660, and informed consent was obtained from legal representatives of the infants.

Sample size was chosen based on the data from an identical experiment in adults (Lenc et al., 2018). The main aim of the current study was to evaluate the selective neural emphasis on meter-related frequencies in the weakly-periodic rhythm by comparing their standardized prominence in the EEG and in a cochlear model that estimates low-level responses at early stages of the auditory pathway. This comparison consistently yields large effects across datasets (Lenc et al., 2020b; Nozaradan et al., 2012b). To detect the effect observed in Lenc et al. (2018) (d = 1.63; average across low- and high-tone conditions), a sample size of N = 8 would be sufficient to obtain statistical power of 99% and a level of significance of 5%. In addition, simulations using the Superpower R package (Lakens & Caldwell, 2021) revealed that detecting the within-subject contrast between low- and high-tone conditions with a power of 80% would require a sample size of N = 20.

2.2 | Stimuli

The stimuli consisted of two different 2.4-s long rhythms, continuously looped for 60 s. Each rhythm was made up of twelve 200-ms long events (see Figure 1; see also Lenc et al., 2018, 2020b; Nozaradan et al., 2012b, 2018; Nozaradan, Mouraux, et al., 2016; Sifuentes-Ortega et al., 2022). The rhythmic structure of the patterns was based on a specific arrangement of eight sound events (pure tones with 10-ms rise and 50-ms fall linear ramps) and four silent events (amplitude at 0). The carrier frequency of the pure tone was either 130 Hz (low tone) or 1236.8 Hz (high tone, 39 semitones above the low-tone frequency), as in Lenc et al. (2018). These two carrier frequencies were chosen to fall within spectral bands where rhythmic fluctuations either correlate (100–200 Hz) or do not correlate (800–1600 Hz) with sensory-motor entrainment to music, as indicated by previous research (Burger et al., 2018, 2012). As in previous work (Hove et al., 2014; Lenc et al., 2018), the loudness of the low and high tone sequences was equalized to correct for the differential sensitivity of the auditory system across the frequency range. Specifically, using the Glasberg and Moore model (Moore et al., 2016), low and high tones were equalized to 70 phons by matching the maximum short-term loudness of a single 200-ms high-tone and low-tone sound. Free field parameters were used as the sequences were presented with loudspeakers. Sound intensity was held constant across infants.

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

The two rhythms used in the current study were selected based on previous evidence that they both induce perception of musical meter consistently across individuals. The induced meter is based on nested grouping of the individual event rate (200 ms) by 2 (2 × 200 ms = 400 ms), 2 (2 × 400 ms = 800 ms), and 3 (3 × 800 ms = 2400 ms) (Lenc et al., 2018; Nozaradan et al., 2012b, 2018). Importantly, although the two rhythmic patterns have been found to consistently induce perception of musical meter, they provide the listener with different amounts of direct sensory cues to this perceived metric structure (see Text S1 in the Supplementary material for details on calculation of syncopation score and counterevidence score to measure prominence of metric periodicities in the two rhythms). In particular, the tones in the first rhythm mostly occur at pulse positions of the typically perceived meter (and not otherwise), thus creating a strong periodic contrast cueing that meter. On the other hand, the sounds and silences in the second rhythm are arranged in a way that does not closely match any periodic meter. For these reasons, the first and the second rhythm are further referred to as "strongly-periodic" and "weakly-periodic" rhythm, respectively (note that various terms have also been used to describe these same rhythms, e.g., unsyncopated and syncopated; see Lenc et al., 2021).

Another way to measure the prominence of periodicities in the stimulus is to analyze the modulation spectrum of the acoustic stimulus using fast Fourier transform (FFT). This analysis allows quantification of the periodic recurrence in the continuous modulation of acoustic features of the input (here amplitude envelope). Because the stimulus consisted of seamless repetitions of the same rhythmic pattern, the modulation spectra were expected to contain energy at the frequency corresponding to the repetition of the pattern (1/2.4 s = 0.416 Hz) and harmonics of that frequency. The relative distribution of energy across these different harmonics reveals how much periodic recurrence was present in the signal modulations at rates nested within the pattern repetition period. From the set of first 12 harmonics (up to 5 Hz, i.e., the frequency of individual event rate in the rhythms), four frequencies were considered to be meter-related (1.25, 2.5, 3.75, 5 Hz), as they corresponded to the frequencies and harmonics of the perceived metric pulses. The remaining eight frequencies in the set were considered to be meter-unrelated. Note that in the current study (as in Cirelli et al., 2016) the first frequency (0.416 Hz) was excluded from further analysis, thus leaving 11 frequencies of interest (identical across the two rhythms). The lowest frequency was discarded to keep the stimulus analysis comparable with the frequency-domain analysis conducted on the EEG, as the EEG was high-pass filtered at 0.5 Hz to remove very slow drifts from the signals.

To measure the relative prominence of meter frequencies, amplitudes at the 11 frequencies of interest were converted to z-scores as follows: ([x] − [mean across the 11 frequencies])/[SD across the 11 frequencies]. A higher z-score at a specific frequency thus indicates that the amplitude at that frequency stands out prominently relative to the whole set of frequencies in the modulation spectrum. The z-scores for meter-related frequencies were averaged to obtain an index of their relative prominence in the modulation spectra.

To estimate the extent to which the neural transformation of a rhythmic acoustic stimulus could be driven by low-level stages of the auditory pathway, we simulated responses to the rhythmic stimuli using a biologically-plausible model of peripheral auditory processing. Comparing the EEG responses to these early representations thus helps disentangling the contribution of higher-level transformations that cannot be trivially explained by responses at early sound processing stages. The cochlear model used to analyze the stimuli was the same as in Lenc et al. (2018). It consisted in a Patterson-Holdsworth ERB filter bank with 128 channels (Patterson & Holdsworth, 1996), followed by Meddis' inner hair-cell model (Meddis, 1986), as implemented in the Auditory Toolbox for Matlab (Slaney, 1998). The output of the cochlear model was subsequently transformed into the frequency domain using FFT, and the obtained spectra were then averaged across cochlear channels.

2.3 | Experimental procedure

The two rhythmic patterns conveyed either by the low or the high tone were presented separately in blocks. Each of the four resulting blocks consisted in five sequences made up of 25 seamless repetitions of the same rhythmic pattern during 60 s. The order of the blocks was counterbalanced across infants. The rhythms were created in Matlab R2016b (The MathWorks, Natick, MA) and delivered by Presentation Software 14.2 (Neurobehavioral Systems, Berkeley, USA) using two loudspeakers placed approximately 50 cm from each other, 1.5 m in front of the infant's head. Under these conditions, stimulus intensity was approximately 75 dB SPL, hence presumably below adults' thresholds for direct activation of the vestibular system by low-frequency tones (Todd et al., 2000).

Infants were seated in front of the loudspeakers, on the lap of the parent and infants' EEG signals were recorded while they were presented with the stimuli, with short breaks between the 5-min. blocks. To avoid movement bias related to the rhythmic structure of the sequences, the parent listened to a playlist of irrelevant music at comfortable but relatively high intensity through headphones to mask the stimulus sequence sounds. To keep the infant still during sequence presentation, silent videos of cartoons were displayed on a computer screen placed between the two loudspeakers, and the experimenter also silently entertained the infant with puppets or bubbles. Parents were asked to not speak during the recording session and to minimize their movements.

2.4 | EEG acquisition and analysis

EEG signals were collected using a 128-channel HydroCel GSN net with an Electrical Geodesic NetAmps 200 amplifier passing a digitized signal to Electrical Geodesics NETSTATION software (v.4.3.1). Signals were recorded online at a sampling rate of 1000 Hz and with a Cz reference. Electrode impedance during recording was maintained below 50 kOhm.

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

The EEG data were preprocessed as follows. First, the data were segmented from −0.5 s to +60.5 s relative to the onset of each sequence. The obtained segments were filtered using a 0.5–30 Hz Butterwoth 4th order bandpass filter, to remove very slow drifts and higher frequencies irrelevant to the current study. The filtered segments were downsampled by a factor of 4 (to 250 Hz sampling rate), to facilitate data handling and storage. DC removal was applied to the segments, to center the amplitudes around zero. Furthermore, the electrodes located at the three external rings of the electrode net were removed (except left and right mastoid electrodes), as they are more prone to contamination with artifacts due to movement or muscle activity and capture neural activity in response to auditory rhythms to a lesser extent compared to more central electrodes (Cirelli et al., 2016), thus keeping 92 electrodes out of the 128-electrode set. The segments were then processed using the Artifact Blocking algorithm in Matlab (Mourad et al., 2007), which is especially useful for improving signal to noise ratio in continuous infant data by removing artifacts of very large amplitude (>100 microV) (see, e.g., Cirelli et al., 2016; Fujioka et al., 2011; Marie & Trainor, 2013, 2014; Rekow et al., 2021).

The spectrum of the EEG data was obtained by first cropping the segments from +2.4 to +57.6 s, thus removing EEG response to the first and last repetition of the rhythm within each sequence to avoid onset responses and possible edge effects due to the Artifact Blocking algorithm. The cropped segments were then re-referenced to the averaged mastoid electrodes, to increase signal-to-noise ratio of neural responses to auditory stimuli that are expected to project onto frontocentral electrodes (Cirelli et al., 2016). Each segment was then chunked again into two 26.4-s epochs. This allowed doubling the number of epochs to be further averaged in the time domain, which helps cancelling out signals not aligned to the rhythmic input and thus reducing background noise that can be prominent in the frequency range of interest, that is, below 5 Hz. The time-averaged epochs were then transformed into the frequency domain using FFT, yielding a spectral resolution of approximately 0.037 Hz. To obtain valid estimates of the responses, the contribution of noise was minimized by subtracting, at each frequency bin, the average amplitude at the neighboring bins (2nd to 5th on both sides), thus centering the obtained spectra around zero by correcting for the 1/f shape of the background noise (see, e.g., Mouraux et al., 2011; Nozaradan et al., 2011, 2012a, 2012b; Retter & Rossion, 2016). Finally, data quality was confirmed by checking for large residual artifacts (amplitudes larger than 10 microV in more than 10 channels within one of the conditions) within the frequency range of interest (0.5–5 Hz). As none of our participants showed such artifacts, further analyses were performed on the whole sample (N = 20).

Frequency-tagged responses to auditory rhythms in infants are expected to be located on frontocentral channels (Cirelli et al., 2016). This was confirmed by examining the topographical distribution of the mean EEG amplitude across all 11 frequencies of interest, averaged across all conditions and infants (see also Figure 2). Therefore, the values considered for further statistical tests were extracted at the 11 frequencies of interest from the EEG spectra averaged across 28 frontocentral channels (14 in each hemisphere), separately for each condition and infant. Similar results were observed by taking a set of 28 channels with largest overall response magnitude, and can be found in the Supplementary material (Text S2).

2.5 | Statistical analysis

Statistical analyses were carried out using R (R Core Team, 2022). Repeated-measures ANOVAs were conducted using the ez package (Lawrence, 2016). The significance level was set at $p < 0.05$ and the reported effect size corresponds to partial eta squared. Post-hoc comparisons were carried out using paired t-tests and the reported effect sizes correspond to Cohen's d. Confidence intervals were estimated using percentile bootstrap (1000 samples). Bonferroni correction was used to adjust for multiple comparisons.

The overall magnitude of the EEG responses to each rhythm was estimated as the summed amplitude across all 11 frequencies corresponding to the envelope modulation spectrum of the stimulus. This overall magnitude, reflecting the general gain of the response, was compared across conditions using a 2 × 2 repeated-measures ANOVA with factors Tone and Rhythm.

Most importantly for our hypothesis, we then examined the relative EEG response at meter frequencies. To this aim, amplitudes at the 11 frequencies of interest were converted to z-scores, in the same way as for the cochlear model (see Section 2.2). Higher z-score at specific frequencies indicated that the response at these frequencies stood out more prominently relative to the whole set of 11 frequencies elicited by the auditory input. The z-scores were averaged separately for the meter-related frequencies (frequencies corresponding to periods and harmonics of metric pulses consistently perceived from these rhythms across adult listeners) and meter-unrelated frequencies (the remaining eight frequencies of interest). The mean z-score at meter frequencies (or meter z-score) was taken as an index of periodicity at the rates of metric pulses in neural activity. Indeed, this value becomes larger when either the amplitude at meter-related frequencies increases or the amplitude at meter-unrelated frequencies decreases. As expected, the meter z-scores calculated from the spectrum of the cochlear model are high for the strongly-periodic rhythm, where meter-related frequencies are more prominent than meter-unrelated frequencies (1.1 for low-tone and 1.14 for high-tone). In contrast, for the weakly-periodic rhythm, the meter z-score values in the cochlear model output are low (−0.11 for low-tone and −0.07 for high-tone).

To test whether the neural representation of meter was driven by high-level endogenous processes (rather than early auditory processes), one-sample one-tailed t-tests were used to probe whether meter z-scores in the EEG responses were higher than values obtained from the cochlear model. A significant t-test would indicate a neural enhancement of periodicities where adults tend to perceive meter, beyond tracking of acoustic features of the stimulus. In addition, meter z-scores were compared across conditions using a 2 × 2 repeated-measures ANOVA with factors Tone (low vs. high) and Rhythm (strongly-periodic vs. weakly-periodic).

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

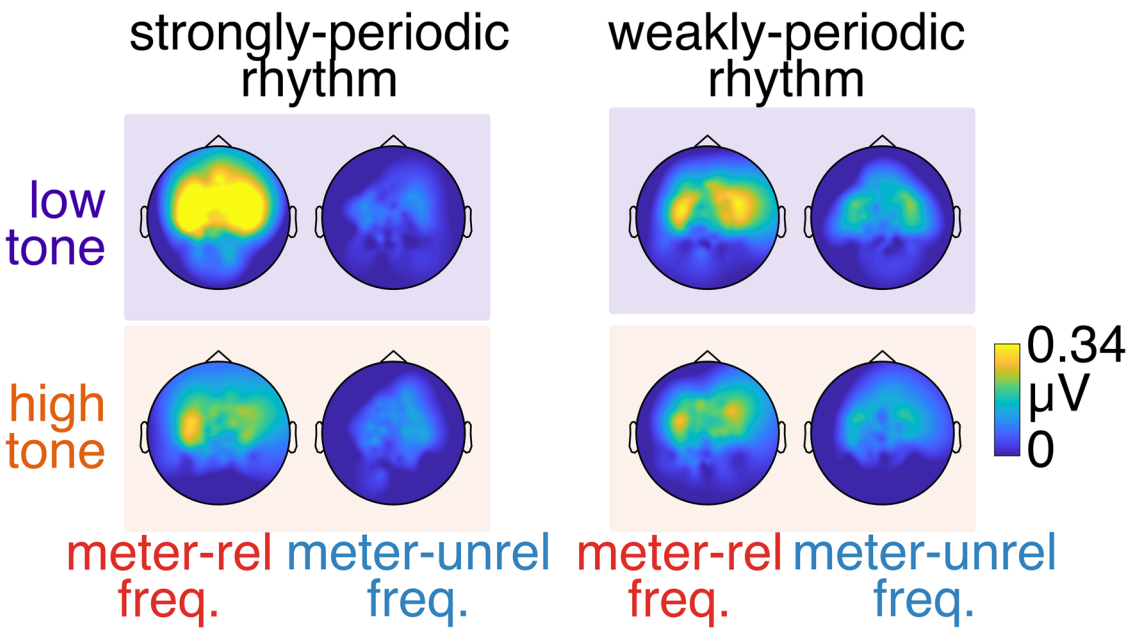

FIGURE 2 Topographical maps of the mean amplitude (microV) at meter-related frequencies and meter-unrelated frequencies across conditions (averaged across 20 infants). The maps show bilateral frontocentral distribution of the activity, as expected for responses to auditory rhythms within this frequency range, with larger activity for meter frequencies compared to meter-unrelated frequencies, even in the weakly-periodic rhythm, especially when conveyed with low tone.

3 | RESULTS

3.1 | Overall magnitude of the EEG response

Figure 1 shows the spectra of the EEG responses elicited by the rhythmic stimuli. The 2 × 2 repeated-measures ANOVA used to compare the overall EEG response magnitude across conditions did not show any significant main effects of Tone or Rhythm or the interaction between these factors (all *p*'s > 0.26). This result thus indicates similar overall magnitude of the response across conditions, in line with the results obtained in adults (Lenc et al., 2018).

3.2 | Relative amplitude at meter frequencies

As shown in Figure 3, one-sample one-tailed t-tests were used to estimate whether meter-related frequencies in the EEG were more prominent than predicted by the cochlear model. There was no significant enhancement of the relative (z-scored) amplitude at meter-related frequencies in the EEG compared to the cochlear model for the strongly-periodic rhythm (all *p*'s = 1). This was expected based on the high prominence of meter frequencies already in the acoustic structure of the strongly-periodic input. However, for the weakly-periodic rhythm, the meter-related frequencies were significantly enhanced in the EEG responses when the rhythm was conveyed with low tone (mean = 0.23, 95% CI [0.12, 0.36], $t_{19} = 5.37$, $p < 0.0001$, d = 1.2), and high tone (mean = 0.12, 95% CI [0, 0.25], $t_{19} = 2.93$, $p = 0.02$, d = 0.65).

In addition, a 2 × 2 repeated-measures ANOVA was employed to compare the relative prominence of meter frequencies across the factors Tone and Rhythm. This ANOVA revealed a main effect of Tone ($F_{1,19} = 10.25$, $p = 0.005$, $\eta_p^2 = 0.35$), with greater enhancement of meter frequencies in the low-tone condition than in the high-tone condition across both rhythms. There was also a main effect of Rhythm ($F_{1,19} = 10.63$, $p = 0.004$, $\eta_p^2 = 0.36$), as expected from the higher prominence of meter frequencies in the strongly-periodic input. The interaction between Tone and Rhythm was not significant ($p = 0.32$).

The results of the one-sample one-tailed t-tests indicate that meter frequencies can be selectively enhanced when the prominence of these frequencies in the rhythmic stimulus is low, and the results of the ANOVA suggest that this effect is boosted with low tones. In addition, the observed enhancement of meter frequencies and the effect of low tones cannot be easily explained by differences in the overall magnitude of the responses, as revealed by the ANOVA comparing the overall gain across conditions.

3.3 | Control analyses

We also tested whether the increased prominence of meter-related frequencies could be driven by non-specific effects such as high-pass or low-pass function of the response, or the shape of generic responses to sound onsets (e.g., with shorter time course compared to the shape of the individual acoustic event used to generate the stimuli). Such effects would lead to a larger gain at the highest (i.e., 5 Hz) or lowest (i.e., 0.83 Hz) frequency of interest, and thus would also affect the estimated relative prominence of meter frequencies. To test whether this was the case, we re-calculated the z-scores either after excluding 5 or 0.83 Hz

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

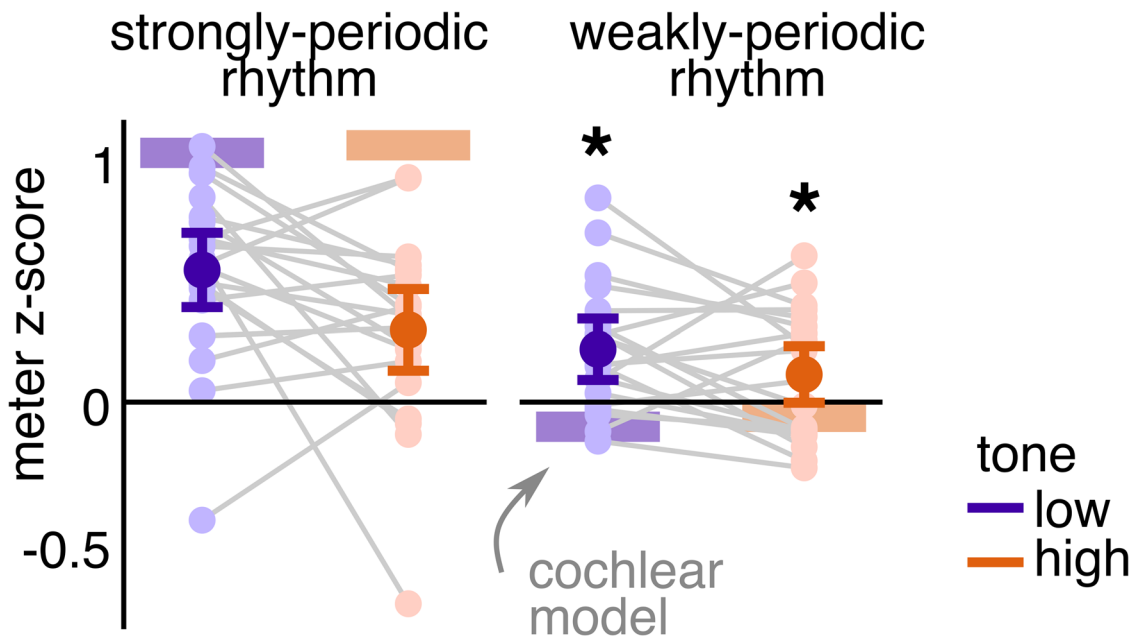

FIGURE 3 Z-score values of the meter-related frequencies across conditions (individual values in light color, and mean in dark color). Error bars indicate 95% confidence intervals (Morey, 2008). Corresponding values obtained from the cochlear model are shown as vertical lines. Asterisks on top of the points represent p-values obtained from the one-sample one-tailed t-tests of EEG against the cochlear model, *: p<0.05.

frequency from the set. In both cases, we obtained the same significant effects as in the main analysis (for a detailed description, see Supplementary material, Text S3). These results thus indicate that the boosted neural response at meter frequencies is not fully driven by non-specific transformations enhancing lower or higher frequencies irrespective of their relevance for the perceived meter.

To test whether the standardization using z-scores biased results, we used another standardization which does not take into account the variability across amplitudes as the z-score does. Specifically, for each condition and infant, the amplitudes were normalized between 0 and 1 by dividing observed amplitudes by the amplitude range, given by the maximum minus minimum amplitude measured across the frequencies of interest. These normalized values were then compared using a 2 × 2 × 2 repeated measures ANOVA comparing the meter-related versus meter-unrelated frequencies across Tone and Rhythm. There was a significant interaction between the factor Meter and Tone, ($F_{1,19}$ = 10.01, p = 0.005, η_p^2 = 0.35) and no three-way interaction (p = 0.3), thus reproducing the tone effects found with the z-scores (see Figure S1).

To control even further for a possible effect of z-scores, we tested whether the same results could be found without any normalization, that is, when just taking the raw amplitudes in microV. Here we found a three-way interaction between Rhythm, Tone and Meter ($F_{1,19}$ = 9.27, p = 0.007, η_p^2 = 0.33) (see Figure S2). While still supporting the main findings above, this control analysis highlights the importance of at least some form of standardization, given the fact that (i) EEG effects are likely multiplicative (Joon Kim et al., 2007) and (ii) the raw amplitude difference between meter-related and unrelated frequencies is much larger in the strongly- versus weakly-periodic rhythm (as shown in Figure 1).

Together, these control analyses corroborate the main results, suggesting that the effect of tone frequency is not an artifact of the chosen standardization method.

4 | DISCUSSION

In this study, we show that 5- to 6-month-old infants exhibit selective enhancement of neural activity at meter frequencies. Moreover, this enhanced neural representation of meter frequencies is increased when the rhythm is conveyed by low-pitched sounds compared to high-pitched sounds. These findings cannot be solely explained by stimulus-driven effects, as the neural emphasis on meter periodicities arose even in response to a weakly-periodic rhythm lacking prominent acoustic cues to the meter. These effects are also unlikely to be explained by low-level auditory nonlinearities, as biologically plausible cochlear modeling does not show enhanced meter frequencies in response to the weakly-periodic rhythm. Together, these results thus suggest that high-level central mechanisms may play a key role in infants' processing of rhythm, especially in establishing an internal representation of meter.

4.1 | Selective enhancement of metric periodicities beyond low-level features

In line with previous studies in adults (Lenc et al., 2018, 2020a; Nozaradan et al., 2012b, 2018; Nozaradan, Mouraux, et al., 2016), the current results provide evidence that the infant brain produces increased neural activity at meter frequencies. Moreover, this brain

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

activity is not solely stimulus-driven. In other words, components of the input that are selectively enhanced in the neural response are not necessarily the most prominent components making up the input, and sometimes even exhibit magnitudes close to zero in the input, as shown here in the weakly-periodic rhythm (e.g., activity at 2.5 Hz, see Figure 1).

In addition, nonlinearities due to subcortical auditory processes such as adaptation cannot fully explain the observed selective enhancement of meter frequencies. It should be noted that the model used in the current study to simulate the processing of the sequences at the auditory periphery was not specifically designed to simulate the cochlear processing of 5- to 6-month-old infants (Slaney, 1998). To our knowledge, there is currently no readily available cochlear model that takes into account the developmental course of the human auditory system. Nevertheless, infants in our study showed significantly greater prominence of meter-related frequencies in response to the weakly-periodic rhythm than could be expected based on adult-like cochlear processing. This suggests that cochlear nonlinearities, even at a mature stage, are unlikely to account solely for the enhanced meter representation observed here.

Therefore, it can be proposed that the enhanced neural representation of meter frequencies reflects endogenous cortical periodic activity that is phase-locked to the rhythmic inputs and whose periods correspond to the most consistently perceived meter periodicities in Western adult listeners (Lenc et al., 2018; Nozaradan et al., 2012b, 2018; Rajendran et al., 2017).

4.2 | Role of periodic recurrence at shorter and longer timescales when recurrence corresponding to the meter is weak

What are the processes underlying the selective enhancement observed here? Acoustically, the weakly-periodic rhythm used in the current study does not contain prominent periodic recurrence corresponding to the meter that the neural system can track and emphasize. However, the weakly-periodic rhythm is not random, and still contains temporal structure that can be used to build up a representation of the meter endogenously. First, the cyclic repetition of the rhythmic pattern creates a slow periodicity (here 2.4 s). If the infant neural system is sensitive to this repetition, it provides an opportunity to internally generate faster beat levels by subdivision (Repp, 2005; Repp & Su, 2013). Indeed, pattern repetition plays a role in meter perception (Brown, 1993; Longuet Higgins & Lee, 1982; Steedman, 1977; Temperley & Bartlette, 2002) and short cyclic patterns are particularly used in music characterized by weakly-periodic rhythms around the world (Agawu, 2006; London et al., 2017; Pressing, 2002; Witek et al., 2014). In addition, the set of inter-tone intervals making up the rhythmic patterns in the current study is small (three different inter-tone intervals, 0.2, 0.4, and 0.6 s), and shares a common denominator, which provides another cue for subdivision. Hence, using the temporal information available in the weakly-periodic stimulus, the brain may spontaneously generate multiple levels of periodic recurrence, and this process might be further biased by the frequency tuning curve of the neural network (Nozaradan et al., 2012b, 2018) and preference for simple frequency ratios (Bergeson & Trehub, 2006; Drake et al., 2000; Jacoby & McDermott, 2017).

There are several lines of evidence supporting this interpretation. First, sensitivity to repetition of sound patterns is already in place in neonates (Stefanics et al., 2007; Winkler et al., 2009). Second, the subdivision of periodic time intervals occurs spontaneously in adults (Repp & Jendoubi, 2009) and the tendency to do so may be present very early in development. For instance, 5-month-olds have been shown to detect temporal disruptions in rhythmic patterns based on inter-tone intervals with a 3:2 ratio, which allows subdivision into regular isochronous timespans (Hannon et al., 2011). However, disruption detection was absent for patterns with inter-tone intervals 7:4, which precludes subdivision.

Mechanistically, such processes have been described in neurodynamic models in terms of mode-locking and resonance in coupled oscillators, which can reconstruct metric periodicities that are weak (or even completely absent) in the physical stimulus (Kim & Large, 2019; Large et al., 2015; Tichko et al., 2022). These models predict that mode-locking is a fundamental emergent property of cortical dynamics, and hence should be present very early in development. However, at the same time, neurodynamic models explaining the emergence of meter from weakly-periodic rhythms rely on nonlinear coupling between an auditory and a motor network (Large et al., 2015; but see Tal et al., 2017 who failed to observe oscillatory dynamics in supplementary motor area predicted by the neural resonance theory). Given that overt sensory-motor synchronization is far from mature at 5–6 months of age (Zentner & Eerola, 2010), our current results could be taken to indicate that a mature auditory-motor system may not be necessary for endogenous enhancement of meter. Yet, it is important to note that neural architecture can be mature before the emergence of overt motor behaviors and before intense exposure. For instance, substantial evidence suggests that the dorsal stream network for speech processing develops quickly within the first months of life (Brauer et al., 2013; Choi et al., 2021; Dehaene-Lambertz, 2017; Leroy et al., 2011). Whether the dorsal brain networks implicated in meter processing (Cannon & Patel, 2020; Patel & Iversen, 2014) may have a similar developmental trajectory remains to be investigated.

Taken together, the current evidence suggests that at 5–6 months, the infant brain may well be equipped with general mechanisms supporting the ability to map weakly-periodic (i.e., syncopated) rhythmic inputs onto a stable set of metric pulses (Lenc et al., 2021).

4.3 | Role of learned rhythm-meter associations

Learned associations constitute another way in which consistent internal representations of meter could emerge even when they are not directly cued by the structure of the stimulus. This learning would not need to proceed only explicitly through formal musical training, but could also operate implicitly through exposure to a culture-specific musical repertoire (see also Hannon et al., 2012). In other words, the

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

particular meter induced by the acoustic rhythm could be shaped by long-term exposure to various multimodal cues specific to the general context in which the rhythm is most often presented within a culture (Cameron et al., 2015; Hannon et al., 2012; Hannon & Trehub, 2005b; London et al., 2017; van der Weij et al., 2017). For instance, there is evidence that within a few minutes, 7-month-old infants can form associations between a rhythmic auditory pattern and multimodal experience from periodic bouncing (Phillips-Silver & Trainor, 2005). Similarly, 6-month-olds can learn to associate periodic acoustic accents with a specific rhythmic pattern and this is reflected in subsequent brain responses (Flaten et al., 2022). In adults, moving along a rhythmic pattern in a way that emphasizes a certain periodicity leads to an enhancement of that periodicity in EEG responses during subsequent listening (Chemin et al., 2014). Hence, there is evidence that multimodal exposure has the potential to shape the association between a rhythm and its metric interpretation already at an early age (see also Tichko et al., 2021, 2022). Such associations may allow the brain to match a rhythm to a particular internal metric template, even when the rhythm acoustically lacks unambiguous periodic cues to the meter.

Even though the infants in the current study most likely had not encountered the exact rhythmic patterns before participating in the experiment (the current rhythms were not characteristic of a particular culture or genre), it remains plausible that the infants were previously exposed to rhythmic patterns with similar structural features. Thus, the neural responses to the rhythms used in the current study might have been driven by generalization of the rhythm-meter association acquired by the infant for another (sufficiently similar) rhythm (Tichko & Large, 2019; van der Weij et al., 2017; Zhao & Kuhl, 2016). If such generalization mechanisms were driving our current results, this would imply that learning to associate specific types of rhythmic figures with particular meters (i) begins soon after (or even before) birth, (ii) can be relatively robust even when purely implicit, and (iii) does not exclusively rely on the production of active body movements time-locked to the rhythm. In fact, associations between auditory rhythmic patterns and passive periodic movement could be established already before birth (Parncutt & Chuckrow, 2019). Indeed, the fetus is sensitive to the sounds in mother's environment and her movement in response to these sounds already from the third trimester (see Parncutt, 2016 for a review).

Further investigation of the "learned-association" hypothesis could be conducted by comparing the neural transformation of a rhythmic input toward a specific meter across different time points over the lifespan, including in newborns, and also across individuals with different musical enculturation. In this regard, we hypothesize that rhythm-meter association learning on a much shorter time scale may be driven by active body movement once the ability for sensorimotor synchronization is developed (as reported in adults; Chemin et al., 2014).

4.4 | Role of low tones in rhythm processing

The finding that rhythmic stimulation by low tones enhanced the neural representation of meter is in line with a growing body of evidence suggesting a privileged role of bass sounds in rhythm processing. At the behavioral level, rhythmic low-frequency sounds have been shown to elicit greater amounts (Hove, Martinez, et al., 2019; Van Dyck et al., 2013) and tighter synchronization (Burger et al., 2012) of spontaneous body movement. At the neural level, recordings from adults indicate that bass sounds boost periodicities related to the perceived meter, particularly when these periodicities are not prominent in the acoustic input (Lenc et al., 2018). The current study extends these results by showing that the low-tone benefit is already in place at 5–6 months of age and can occur even without an explicit behavioral task. Hence, these observations contribute to our understanding of the possible neurobiological basis for the convention of using bass instruments to carry the rhythmic foundations of music and to stimulate motor engagement (Hove, Vuust, et al., 2019; Stupacher et al., 2016).

The specific neurophysiological mechanisms behind the low-tone benefit are an open question. While a recent study showed that peripheral encoding of temporal modulations may be biased toward low-frequency sounds, this was only observed when isochronous low- and high-frequency pip trains were presented simultaneously at different tempi (Zuk et al., 2018). Given that the current study presented low and high tones in separate trials, the peripheral nonlinearities described by Zuk et al. (2018) cannot directly explain the observed EEG results, particularly for the weakly-periodic rhythm.

Further, our results argue against the hypothesis that the low-tone benefit arises from learned associations between bass sounds, rhythm, and movement established through long-term exposure to music. Rather, the effect may develop through prenatal learning, given the continuous exposure of the fetus to low-pass filtered sounds in the womb coupled with vestibular and proprioceptive stimulation generated by the mother's movement (Parncutt, 2016; Trainor & Unrau, 2009). Indeed, vestibular input plays an important role in meter perception (Trainor et al., 2009) and infants rapidly develop associations between the rate of periodic bouncing and an auditory rhythmic pattern (Phillips-Silver & Trainor, 2005).

Nonetheless, it remains possible that low tone effect observed here may have been partially driven by direct activation of the vestibular system by low tones. Although the sequences were presented at an intensity (approximately 75 dB) below the vestibular threshold, this threshold (90 dB sound pressure level on average) is variable across individuals (Todd & Lee, 2015b). Most importantly, the available data on the vestibular threshold are based on measures in adult participants and it remains possible that the threshold is lower in 5- to 6-month-old infants. If this is the case, then a vestibular sensorimotor neural network could have been directly activated by the rhythmic sequences conveyed by low tones in the current study (Todd & Lee, 2015a; Trainor et al., 2009). Yet, it remains unclear how this activation alone could lead to selective neural enhancement of the meter-related frequencies, especially in weakly-periodic rhythm which lacks prominent acoustic cues to the meter.

Alternatively, it has been proposed that the privileged role of bass sounds in conveying rhythm may stem from evolutionarily shaped properties of the auditory system (Hove et al., 2014). However, the results of the analysis of our stimuli with a physiologically plausible

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

cochlear model argue against this hypothesis (see also Wojtczak et al., 2017).

4.5 | Interpretation of EEG results and links to behavior

It may be tempting to interpret the EEG results of the current study as evidence for perception. Indeed, researchers sometimes interpret a differential EEG response as evidence for beat "perception" (Winkler et al., 2009). Yet, linking measures of neural activity to perception as a high-level subjective phenomenon is non-trivial (Norcia, 2013). Instead, it may be more fruitful (and valid) to think of recording neural signals as a means to isolate a particular process that contributes to overt behavior by interacting with numerous other factors (such as cognitive and affective processing). In fact, the capacity to isolate processes is an advantage, as carefully designed EEG experiments can reveal properties of the perceptual system that are not observable from behavior (Lenc et al., 2020a; Luck, 2014; Rossion et al., 2020). Hence, we prefer to interpret the results of the current study as capturing neural processing of musical meter without confounds associated with motor skills, understanding instructions, decision making, etc. (Nozaradan, Keller, et al., 2017). Our observations show that the infant brain has the capacity to endogenously enhance representations of metric periodicities that are not prominent in stimulus structure. When and how these representations are used to guide overt behavior remains to be investigated (but see, e.g., Nozaradan, Peretz, et al., 2016 for evidence linking frequency-tagged EEG responses and overt tapping). In sum, the fundamental neural processes reported in the current study may set the stage for the development of interpersonal synchronization abilities (for a related interpretation of animal electrophysiology, see, e.g., Rajendran et al., 2017), thus providing evidence of neural specialization for meter, as hypothesized by recent evolutionary accounts (Mehr et al., 2021).

5 | CONCLUSIONS

Our results demonstrate that 5- to 6-month-old infants show neural transformations of rhythmic auditory stimuli toward categorical meter in a similar manner to transformations in adults. These observations suggest that the neural processes previously observed in adults emerge early in development, before the ability to synchronize overt movement with rhythmic inputs is fully developed. In fact, these neural processes may set the stage for the development of overt sensorymotor synchronization abilities by providing the infrastructure to link spectrotemporally complex sensory inputs with invariant periodic time representations—a cornerstone of temporal coordination in musical behaviors. The basic capacity for transforming rhythmic input into internal meter templates may thus provide a foundation for a core component of human musicality (Honing, 2012; Mehr et al., 2021; Savage et al., 2021), which enables the alignment of thoughts and feelings during human interaction across the lifespan (Malloch & Trevarthen, 2018; Phillips-Silver & Keller, 2012). Our findings pave the way for future investigation of the nature of the underlying neural processes, which is particularly timely given the growing use of rhythmic auditory stimulation in diagnosis of and interventions for developmental disorders (Lense et al., 2021).

CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in the Open Science Framework (OSF) at http://doi.org/10.17605/OSF.IO/9WF5U, reference number 9wf5u.

ORCID

Tomas Lenc https://orcid.org/0000-0001-5796-1388
Varghese Peter https://orcid.org/0000-0002-4007-507X
Peter E. Keller https://orcid.org/0000-0001-7579-6515
Sylvie Nozaradan https://orcid.org/0000-0002-5662-3173

REFERENCES

Agawu, K. (2006). Structural analysis or cultural analysis? Competing perspectives on the "standard pattern" of West African rhythm. *Journal of the American Musicological Society*, *59*(1), 1–46. https://doi.org/10.1525/jams.2006.59.1.1

Agawu, K. (2016). The rhythmic imagination. In *The African imagination in music* (pp. 155–194). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780190263201.003.0005

Bergeson, T. R., & Trehub, S. E. (2006). Infants perception of rhythmic patterns. *Music Perception*, *23*(4), 345–360. https://doi.org/10.1525/mp.2006.23.4.345

Bouwer, F. L., Van Zuijen, T. L., & Honing, H. (2014). Beat processing is pre-attentive for metrically simple rhythms with clear accents: An ERP study. *PLoS ONE*, *9*(5), e97467. https://doi.org/10.1371/journal.pone.0097467

Bouwer, F. L., Werner, C. M., Knetemann, M., & Honing, H. (2016). Disentangling beat perception from sequential learning and examining the influence of attention and musical abilities on ERP responses to rhythm. *Neuropsychologia*, *85*, 80–90. https://doi.org/10.1016/j.neuropsychologia.2016.02.018

Brauer, J., Anwander, A., Perani, D., & Friederici, A. D. (2013). Dorsal and ventral pathways in language development. *Brain and Language*, *127*(2), 289–295. https://doi.org/10.1016/J.BANDL.2013.03.001

Brown, J. C. (1993). Determination of the meter of musical scores by autocorrelation. *Journal of the Acoustical Society of America*, *94*(4), 1953–1957. https://doi.org/10.1121/1.407518

Burger, B., London, J., Thompson, M. R., & Toiviainen, P. (2018). Synchronization to metrical levels in music depends on low-frequency spectral components and tempo. *Psychological Research*, *82*(6), 1195–1211. https://doi.org/10.1007/s00426-017-0894-2

Burger, B., Thompson, M. R., Luck, G., Saarikallio, S., & Toiviainen, P. (2012). Music moves us: Beat-related musical features influence regularity of music-induced movement. In E. Cambouropoulos, C. Tsougras, P. Mavromatis, & K. Pastiadis, (Eds.), *Proceedings of the ICMPC-ESCOM 2012 Joint Conference: 12th Biennial International Conference for Music Perception and Cognition and the 8th Triennial Conference of the European Society for the Cognitive Sciences of Music* (pp. 183–187). School of Music Studies, Aristotle University of Thessaloniki.

Burger, B., Thompson, M. R., Saarikallio, S., Luck, G., & Toiviainen, P. (2010). Influence of musical features on characteristics of music-induced movements. In S. M. Demorest, S. J. Morrison, & P. S. Campbell, (Eds.),

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Proceedings of the 11th International Conference on Music Perception and Cognition (ICMPC11), (pp. 425–428). Seattle, Washington USA: University of Washington.

Cameron, D. J., Bentley, J., & Grahn, J. A. (2015). Cross-cultural influences on rhythm processing: Reproduction, discrimination, and beat tapping. *Frontiers in Psychology*, *6*, 366. https://doi.org/10.3389/fpsyg.2015.00366

Cannon, J. J., & Patel, A. D. (2020). How beat perception Co-opts motor neurophysiology. *Trends in Cognitive Sciences*, *25*(2), 137–150. https://doi.org/10.1016/j.tics.2020.11.002

Chemin, B., Mouraux, A., & Nozaradan, S. (2014). Body movement selectively shapes the neural representation of musical rhythms. *Psychological Science*, *25*(12), 2147–2159. https://doi.org/10.1177/0956797614551161

Choi, D., Dehaene-Lambertz, G., Peña, M., & Werker, J. F. (2021). Neural indicators of articulator-specific sensorimotor influences on infant speech perception. *Proceedings of the National Academy of Sciences*, *118*(20), e2025043118. https://doi.org/10.1073/pnas.2025043118

Cirelli, L. K., Spinelli, C., Nozaradan, S., & Trainor, L. J. (2016). Measuring neural entrainment to beat and meter in infants: Effects of music background. *Frontiers in Neuroscience*, *10*, 229. https://doi.org/10.3389/fnins.2016.00229

Cirelli, L. K., & Trehub, S. E. (2019). Dancing to metallica and Dora: Case study of a 19-month-old. *Frontiers in Psychology*, *10*, 1073. https://doi.org/10.3389/fpsyg.2019.01073

Cohn, R. (2020). Meter. In A. Rehding, & S. Rings, (Eds.), *Oxford handbook of critical concepts in music theory* (pp. 207–233). Oxford University Press.

Cook, P., Rouse, A., Wilson, M., & Reichmuth, C. (2013). A California sea lion (Zalophus californianus) can keep the beat: Motor entrainment to rhythmic auditory stimuli in a non vocal mimic. *Journal of Comparative Psychology*, *127*(4), 412–427. https://doi.org/10.1037/a0032345

Dehaene-Lambertz, G. (2017). The human infant brain: A neural architecture able to learn language. *Psychonomic Bulletin and Review*, *24*(1), 48–55. https://doi.org/10.3758/S13423-016-1156-9/FIGURES/1

Demany, L., Mckenzie, B., & Vurpillot, E. (1977). Rhythm perception in early infancy. *Nature*, *266*(5604), 718–719. https://doi.org/10.1038/266718a0

Drake, C., Jones, M. R., & Baruch, C. (2000). The development of rhythmic attending in auditory sequences: Attunement, referent period, focal attending. *Cognition*, *77*(3), 251–288. https://doi.org/10.1016/S0010-0277(00)00106-2

Flaten, E., Marshall, S. A., Dittrich, A., & Trainor, L. J. (2022). Evidence for top-down metre perception in infancy as shown by primed neural responses to an ambiguous rhythm. *European Journal of Neuroscience*, *55*(8), 2003–2023. https://doi.org/10.1111/ejn.15671

Fujii, S., Watanabe, H., Oohashi, H., Hirashima, M., Nozaki, D., & Taga, G. (2014). Precursors of dancing and singing to music in three- To four-months-old infants. *PLoS ONE*, *9*(5), e97680. https://doi.org/10.1371/journal.pone.0097680

Fujioka, T., Mourad, N., He, C., & Trainor, L. J. (2011). Comparison of artifact correction methods for infant EEG applied to extraction of event-related potential signals. *Clinical Neurophysiology*, *122*(1), 43–51. https://doi.org/10.1016/j.clinph.2010.04.036

Gámez, J., Yc, K., Ayala, Y. A., Dotov, D., Prado, L., & Merchant, H. (2018). Predictive rhythmic tapping to isochronous and tempo changing metronomes in the nonhuman primate. *Annals of the New York Academy of Sciences*, *1423*(1), 396–414. https://doi.org/10.1111/nyas.13671

Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *Journal of Cognitive Neuroscience*, *19*(5), 893–906. https://doi.org/10.1162/jocn.2007.19.5.893

Grube, M., & Griffiths, T. D. (2009). Metricality-enhanced temporal encoding and the subjective perception of rhythmic sequences. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior*, *45*(1), 72–79. https://doi.org/10.1016/j.cortex.2008.01.006

Hannon, E. E., & Johnson, S. P. (2005). Infants use meter to categorize rhythms and melodies: Implications for musical structure learning. *Cognitive Psychology*, *50*(4), 354–377. https://doi.org/10.1016/j.cogpsych.2004.09.003

Hannon, E. E., Nave-Blodgett, J. E., & Nave, K. M. (2018). The developmental origins of the perception and production of musical rhythm. *Child Development Perspectives*, *12*(3), 194–198. https://doi.org/10.1111/CDEP.12285

Hannon, E. E., der Vanden Nederlanden Bosch, C. M., & Tichko, P. (2012). Effects of perceptual experience on children's and adults' perception of unfamiliar rhythms. *Annals of the New York Academy of Sciences*, *1252*(1), 92–99. https://doi.org/10.1111/j.1749-6632.2012.06466.x

Hannon, E. E., Snyder, J. S., Eerola, T., & Krumhansl, C. L. (2004). The role of melodic and temporal cues in perceiving musical meter. *Journal of Experimental Psychology: Human Perception and Performance*, *30*(5), 956–974. https://doi.org/10.1037/0096-1523.30.5.956

Hannon, E. E., Soley, G., & Levine, R. S. (2011). Constraints on infants' musical rhythm perception: Effects of interval ratio complexity and enculturation. *Developmental Science*, *14*(4), 865–872. https://doi.org/10.1111/j.1467-7687.2011.01036.x

Hannon, E. E., & Trehub, S. E. (2005a). Metrical categories in infancy and adulthood. *Psychological Science*, *16*(1), 48–55. https://doi.org/10.1111/j.0956-7976.2005.00779.x

Hannon, E. E., & Trehub, S. E. (2005b). Tuning in to musical rhythms: Infants learn more readily than adults. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(35), 12639–12643. https://doi.org/10.1073/pnas.0504254102

Hilton, C. B., Moser, C. J., Bertolo, M., Lee-Rubin, H., Amir, D., Bainbridge, C. M., Simson, J., Knox, D., Glowacki, L., Alemu, E., Galbarczyk, A., Jasienska, G., Ross, C. T., Neff, M. B., Martin, A., Cirelli, L. K., Trehub, S. E., Song, J., Kim, M., … Mehr, S. A. (2022). Acoustic regularities in infant-directed speech and song across cultures. *Nature Human Behaviour*, *6*, 1545–1556. https://doi.org/10.1038/s41562-022-01410-x

Holzapfel, A. (2015). Relation between surface rhythm and rhythmic modes in Turkish Makam music. *Journal of New Music Research*, *44*(1), 25–38. https://doi.org/10.1080/09298215.2014.939661

Honing, H. (2012). Without it no music: Beat induction as a fundamental musical trait. *Annals of the New York Academy of Sciences*, *1252*(1), 85–91. https://doi.org/10.1111/j.1749-6632.2011.06402.x

Honing, H., & Bouwer, F. L. (2018). Rhythm. In P. J. Rentfrow, & D. J. Levitin (Eds.), *Foundations in music psychology: Theory and research* (pp. 33–70). MIT Press.

Honing, H., Bouwer, F. L., & Háden, G. P. (2014). Perceiving temporal regularity in music: The role of auditory event-related potentials (ERPs) in probing beat perception. In H. Merchant, & V. de Lafuente (Eds.), *Neurobiology of interval timing* (pp. 305–323). Springer.

Hove, M. J., Marie, C., Bruce, I. C., & Trainor, L. J. (2014). Superior time perception for lower musical pitch explains why bass-ranged instruments lay down musical rhythms. *Proceedings of the National Academy of Sciences*, *111*(28), 10383–10388. https://doi.org/10.1073/pnas.1402039111

Hove, M. J., Martinez, S. A., & Stupacher, J. (2019). Feel the bass: Music presented to tactile and auditory modalities increases aesthetic appreciation and body movement. *Journal of Experimental Psychology: General*, *149*(6), 1137–1147. https://doi.org/10.1037/xge0000708

Hove, M. J., Vuust, P., & Stupacher, J. (2019). Increased levels of bass in popular music recordings 1955–2016 and their relation to loudness. *The Journal of the Acoustical Society of America*, *145*(4), 2247–2253. https://doi.org/10.1121/1.5097587

Ilari, B. (2015). Rhythmic engagement with music in early childhood: A replication and extension. *Journal of Research in Music Education*, *62*(4), 332–343. https://doi.org/10.1177/0022429414555984

Jacoby, N., & McDermott, J. H. (2017). Integer ratio priors on musical rhythm revealed cross-culturally by iterated reproduction. *Current Biology*, *27*(3), 359–370. https://doi.org/10.1016/j.cub.2016.12.031

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Janata, P., Tomic, S. T., & Haberman, J. M. (2012). Sensorimotor coupling in music and the psychology of the groove. *Journal of Experimental Psychology: General*, *141*(1), 54–75. https://doi.org/10.1037/a0024208

Jao Keehn, R. J., Iversen, J. R., Schulz, I., & Patel, A. D. (2019). Spontaneity and diversity of movement to music are not uniquely human. *Current Biology*, *29*(13), R621–R622. https://doi.org/10.1016/J.CUB.2019.05.035

Joon Kim, Y., Grabowecky, M., Paller, A. K., Muthu, K., & Suzuki, S. (2007). Attention induces synchronization-based response gain in steady-state visual evoked potentials. *Nature Neuroscience*, *10*(1), 117–125. https://doi.org/10.1038/nn1821

Kim, J. C., & Large, E. W. (2019). Mode locking in periodically forced gradient frequency neural networks. *Physical Review E*, *99*, 22421. https://doi.org/10.1103/PhysRevE.99.022421

Kirschner, S., & Tomasello, M. (2009). Joint drumming: Social context facilitates synchronization in preschool children. *Journal of Experimental Child Psychology*, *102*(3), 299–314. https://doi.org/10.1016/j.jecp.2008.07.005

Kotz, S. A., Ravignani, A., & Fitch, W. T. (2018). The evolution of rhythm processing. *Trends in Cognitive Sciences*, *22*(10), 896–910. https://doi.org/10.1016/j.tics.2018.08.002

Lakens, D., & Caldwell, A. R. (2021). Simulation-based power analysis for factorial analysis of variance designs. *Advances in Methods and Practices in Psychological Science*, *4*(1). https://doi.org/10.1177/2515245920951503

Large, E. W., Herrera, J. A., & Velasco, M. J. (2015). Neural networks for beat perception in musical rhythm. *Frontiers in Systems Neuroscience*, *9*, 159. https://doi.org/10.3389/fnsys.2015.00159

Lawrence, M. A. (2016). *ez: Easy Analysis and Visualization of Factorial Experiments*. https://cran.r-project.org/package=ez

Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2018). Neural tracking of the musical beat is enhanced by low-frequency sounds. *Proceedings of the National Academy of Sciences*, *115*(32), 8221–8226. https://doi.org/10.1073/pnas.1801421115

Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2020a). Neural and behavioral evidence for frequency-selective context effects in rhythm processing in humans. *Cerebral Cortex Communications*, *1*(1), 1–15. https://doi.org/10.1093/texcom/tgaa037

Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2020b). Attention affects overall gain but not selective contrast at meter frequencies in the neural processing of rhythm. *bioRxiv*, https://doi.org/10.1101/2020.09.23.309443

Lenc, T., Merchant, H., Keller, P. E., Honing, H., Varlet, M., & Nozaradan, S. (2021). Mapping between sound, brain and behaviour: Four-level framework for understanding rhythm processing in humans and non-human primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1835), 20200325. https://doi.org/10.1098/rstb.2020.0325

Lenc, T., Peter, V., Hooper, C., Keller, P. E., Burnham, D. T., & Nozaradan, S. (2022). Infants show enhanced neural responses to musical meter frequencies beyond low-level features; OSF; https://doi.org/10.17605/OSF.IO/9WF5U

Lense, M. D., Ladányi, E., Rabinowitch, T. C., Trainor, L., & Gordon, R. (2021). Rhythm and timing as vulnerabilities in neurodevelopmental disorders. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1835). https://doi.org/10.1098/rstb.2020.0327

Leroy, F., Glasel, H., Dubois, J., Hertz-Pannier, L., Thirion, B., Mangin, J. F., & Dehaene-Lambertz, G. (2011). Early maturation of the linguistic dorsal pathway in human infants. *Journal of Neuroscience*, *31*(4), 1500–1506. https://doi.org/10.1523/JNEUROSCI.4141-10.2011

Locke, D. (2010). Yewevu in the metric matrix. *Music Theory Online*, *16*(4). https://doi.org/10.30535/mto.16.4.3

London, J. (2004). *Hearing in time*. Oxford University Press.

London, J., Polak, R., & Jacoby, N. (2017). Rhythm histograms and musical meter: A corpus study of Malian percussion music. *Psychonomic Bulletin and Review*, *24*(2), 474–480. https://doi.org/10.3758/s13423-016-1093-7

Longuet Higgins, H. C., & Lee, C. S. (1982). The perception of musical rhythms. *Perception*, *11*(2), 115–128. https://doi.org/10.1068/p110115

Luck, S. J. (2014). *An introduction to the event-related potential technique*. MIT press.

Malloch, S., & Trevarthen, C. (2018). The human nature of music. *Frontiers in Psychology*, *9*, 1680. https://doi.org/10.3389/fpsyg.2018.01680

Margulis, E. H. (2014). *On repeat: How music plays the mind*. Oxford University Press.

Marie, C., & Trainor, L. J. (2013). Development of simultaneous pitch encoding: Infants show a high voice superiority effect. *Cerebral Cortex*, *23*(3), 660–669. https://doi.org/10.1093/cercor/bhs050

Marie, C., & Trainor, L. J. (2014). Early development of polyphonic sound encoding and the high voice superiority effect. *Neuropsychologia*, *57*, 50–58. https://doi.org/10.1016/j.neuropsychologia.2014.02.023

McAuley, J. D., Jones, M. R., Holub, S., Johnston, H. M., & Miller, N. S. (2006). The time of our lives: Life span development of timing and event tracking. *Journal of Experimental Psychology. General*, *135*(3), 348–367. https://doi.org/10.1037/0096-3445.135.3.348

Meddis, R. (1986). Simulation of mechanical to neural transduction in the auditory receptor. *The Journal of the Acoustical Society of America*, *79*(3), 702–711. https://doi.org/10.1121/1.393460

Mehr, S. A., Krasnow, M. M., Bryant, G. A., & Hagen, E. H. (2021). Origins of music in credible signaling. *Behavioral and Brain Sciences*, *44*, e60. https://doi.org/10.1017/S0140525%D7;20000345

Mehr, S. A., Singh, M., Knox, D., Ketter, D. M., Pickens-Jones, D., Atwood, S., Lucas, C., Jacoby, N., Egner, A. A., Hopkins, E. J., Howard, R. M., Hartshorne, J. K., Jennings, M. V., Simson, J., Bainbridge, C. M., Pinker, S., O'Donnell, T. J., Krasnow, M. M., & Glowacki, L. (2019). Universality and diversity in human song. *Science*, *366*(6468). https://doi.org/10.1126/science.aax0868

Moore, B. C. J., Glasberg, B. R., Varathanathan, A., & Schlittenlacher, J. (2016). A loudness model for time-varying sounds incorporating binaural inhibition. *Trends in Hearing*, *20*, 1–16. https://doi.org/10.1177/2331216516682698

Morey, R. D. (2008). Confidence intervals from normalized data: A correction to cousineau (2005). *Tutorials in Quantitative Methods for Psychology*, *4*(2), 61–64. https://doi.org/10.20982/tqmp.04.2.p061

Mourad, N., Reilly, J. P., Bruin, H. D., Hasey, G., Maccrimmon, D., & Joseph, S. (2007). A simple and fast algorithm for automatic suppression of high-amplitude artifacts in EEG data. *ICASSP '79. IEEE International Conference on Acoustics, Speech, and Signal Processing*, 393–396. https://doi.org/10.1109/ICASSP.2007.366699

Mouraux, A., Iannetti, G. D., Colon, E., Nozaradan, S., Legrain, V., & Plaghki, L. (2011). Nociceptive steady-state evoked potentials elicited by rapid periodic thermal stimulation of cutaneous nociceptors. *Journal of Neuroscience*, *31*(16), 6079–6087. https://doi.org/10.1523/JNEUROSCI.3977-10.2011

Nettl, B. (2000). An ethnomusicologist contemplates universals in musical sound and musical culture. In N. L. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (Vol. 3, Issue 2, pp. 463–472). MIT Press.

Norcia, A. M. (2013). Linking hypotheses in visual neuroscience: A tribute to Davida Teller. *Visual Neuroscience*, *30*, 223–227. https://doi.org/10.1017/S0952523813000205

Nozaradan, S. (2014). Exploring how musical rhythm entrains brain activity with electroencephalogram frequency-tagging. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1658), 1–10. https://doi.org/10.1098/rstb.2013.0393

Nozaradan, S., Keller, P. E., Rossion, B., & Mouraux, A. (2017). EEG frequency-tagging and input–output comparison in rhythm perception. *Brain Topography*, *31*(2), 153–160. https://doi.org/10.1007/s10548-017-0605-8

Nozaradan, S., Mouraux, A., Jonas, J., Colnat-Coulbois, S., Rossion, B., & Maillard, L. (2016). Intracerebral evidence of rhythm transform in the human auditory cortex. *Brain Structure and Function*, *222*(5), 2389–2404. https://doi.org/10.1007/s00429-016-1348-0

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Nozaradan, S., Peretz, I., & Keller, P. E. (2016). Individual differences in rhythmic cortical entrainment correlate with predictive behavior in sensorimotor synchronization. *Scientific Reports*, *6*, 20612. https://doi.org/10.1038/srep20612

Nozaradan, S., Peretz, I., Missal, M., & Mouraux, A. (2011). Tagging the neuronal entrainment to beat and meter. *Journal of Neuroscience*, *31*(28), 10234–10240. https://doi.org/10.1523/JNEUROSCI.0411-11.2011

Nozaradan, S., Peretz, I., & Mouraux, A. (2012a). Steady-state evoked potentials as an index of multisensory temporal binding. *Neuroimage*, *60*(1), 21–28. https://doi.org/10.1016/j.neuroimage.2011.11.065

Nozaradan, S., Peretz, I., & Mouraux, A. (2012b). Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *Journal of Neuroscience*, *32*(49), 17572–17581. https://doi.org/10.1523/JNEUROSCI.3203-12.2012

Nozaradan, S., Schönwiesner, M., Keller, P. E., Lenc, T., & Lehmann, A. (2018). Neural bases of rhythmic entrainment in humans: Critical transformation between cortical and lower-level representations of auditory rhythm. *European Journal of Neuroscience*, *47*(4), 321–332. https://doi.org/10.1111/ejn.13826

Nozaradan, S., Schwartze, M., Obermeier, C., & Kotz, S. A. (2017). Specific contributions of basal ganglia and cerebellum to the neural tracking of rhythm. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior*, *95*, 156–168. https://doi.org/10.1016/j.cortex.2017.08.015

Palmer, C., & Krumhansl, C. L. (1990). Mental representations for musical meter. *Journal of Experimental Psychology. Human Perception and Performance*, *16*(4), 728–741. https://doi.org/10.1037/0096-1523.16.4.728

Parncutt, R. (2016). Prenatal development and the phylogeny and ontogeny of music. In S. Hallam, I. Cross, & M. Thaut (Eds.), *The oxford handbook of music psychology* (pp. 371–386). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780199298457.013.0020

Parncutt, R., & Chuckrow, R. (2019). Chuckrow's theory of the prenatal origin of music. *Musicae Scientiae*, *23*(4), 403–425. https://doi.org/10.1177/1029864917738130

Patel, A. D., & Iversen, J. R. (2014). The evolutionary neuroscience of musical beat perception: The action simulation for auditory prediction (ASAP) hypothesis. *Frontiers in Systems Neuroscience*, *8*, 57. https://doi.org/10.3389/fnsys.2014.00057

Patel, A. D., Iversen, J. R., Bregman, M. R., & Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. *Current Biology*, *19*(10), 827–830. https://doi.org/10.1016/j.cub.2009.03.038

Patterson, R. D., & Holdsworth, J. (1996). A functional model of neural activity patterns and auditory images. *Advances in Speech, Hearing, and Language Processing*, *3*, 547–563.

Phillips-Silver, J., & Keller, P. E. (2012). Searching for roots of entrainment and joint action in early musical interactions. *Frontiers in Human Neuroscience*, *6*, 26. https://doi.org/10.3389/fnhum.2012.00026

Phillips-Silver, J., & Trainor, L. J. (2005). Feeling the beat: Movement influences infant rhythm perception. *Science*, *308*(5727), 1430. https://doi.org/10.1126/science.1110922

Povel, D.-J., & Essens, P. J. (1985). Perception of temporal patterns. *Music Perception*, *2*(4), 411–440. https://doi.org/10.2307/40285311

Pressing, J. (2002). Black atlantic rhythm: Its computational and transcultural foundations. *Music Perception*, *19*(3), 285–310. https://doi.org/10.1525/mp.2002.19.3.285

Provasi, J., Anderson, D. I., & Barbu-Roth, M. (2014). Rhythm perception, production, and synchronization during the perinatal period. *Frontiers in Psychology*, *5*, 1048. https://doi.org/10.3389/fpsyg.2014.01048

R Core Team (2022). *R: A Language and Environment for Statistical Computing*. https://www.r-project.org/

Rajendran, V. G., Harper, N. S., Garcia-Lazaro, J. A., Lesica, N. A., & Schnupp, J. W. H. (2017). Midbrain adaptation may set the stage for the perception of musical beat. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171455. https://doi.org/10.1098/rspb.2017.1455

Rajendran, V. G., Harper, N. S., & Schnupp, J. W. H. (2020). Auditory cortical representation of music favours the perceived beat. *Royal Society Open Science*, *7*(3), 191194. https://doi.org/10.1098/rsos.191194

Rekow, D., Baudouin, J. Y., Poncet, F., Damon, F., Durand, K., Schaal, B., Rossion, B., & Leleu, A. (2021). Odor-driven face-like categorization in the human infant brain. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(21), e2014979118. https://doi.org/10.1073/pnas.2014979118

Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, *12*(6), 969–992. https://doi.org/10.3758/BF03206433

Repp, B. H., & Jendoubi, H. (2009). Flexibility of temporal expectations for triple subdivision of a beat. *Advances in Cognitive Psychology*, *5*(1), 27–41. https://doi.org/10.2478/v10053-008-0063-7

Repp, B. H., & Su, Y.-H. (2013). Sensorimotor synchronization: A review of recent research (2006–2012). *Psychonomic Bulletin & Review*, *20*(3), 403–452. https://doi.org/10.3758/s13423-012-0371-2

Retter, T. L., & Rossion, B. (2016). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, *91*, 9–28. https://doi.org/10.1016/j.neuropsychologia.2016.07.028

Rossion, B., Retter, T. L., & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. *European Journal of Neuroscience*, *52*, 4283–4344. https://doi.org/10.1111/ejn.14865

Savage, P. E., Brown, S., Sakai, E., & Currie, T. E. (2015). Statistical universals reveal the structures and functions of human music. *Proceedings of the National Academy of Sciences*, *112*(29), 8987–8992. https://doi.org/10.1073/pnas.1414495112

Savage, P. E., Loui, P., Tarr, B., Schachner, A., Glowacki, L., Mithen, S., & Fitch, W. T. (2021). Music as a coevolved system for social bonding. *Behavioral and Brain Sciences*, *44*, e59. https://doi.org/10.1017/S0140525%D7;20000333

Schachner, A., Brady, T. F., Pepperberg, I. M., & Hauser, M. D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. *Current Biology*, *19*(10), 831–836. https://doi.org/10.1016/j.cub.2009.03.061

Sifuentes-Ortega, R., Lenc, T., Nozaradan, S., & Peigneux, P. (2022). Partially preserved processing of musical rhythms in REM but not in NREM sleep. *Cerebral Cortex*, *32*(7), 1508–1519. https://doi.org/10.1093/cercor/bhab303

Slaney, M. (1998). Auditory toolbox, version 2. *Interval Research Corporation, Technical Report, 1998–010*, 1–52.

Steedman, M. J. (1977). The perception of musical rhythm and metre. *Perception*, *6*(5), 555–569. https://doi.org/10.1068/p060555

Stefanics, G., Háden, G., Huotilainen, M., Balázs, L., Sziller, I., Beke, A., Fellman, V., & Winkler, I. (2007). Auditory temporal grouping in newborn infants. *Psychophysiology*, *44*(5), 697–702. https://doi.org/10.1111/j.1469-8986.2007.00540.x

Stupacher, J., Hove, M. J., & Janata, P. (2016). Audio features underlying perceived groove and sensorimotor synchronization in music. *Music Perception: An Interdisciplinary Journal*, *33*(5), 571–589. https://doi.org/10.1525/mp.2016.33.5.571

Su, Y. H., & Pöppel, E. (2012). Body movement enhances the extraction of temporal structures in auditory sequences. *Psychological Research*, *76*(3), 373–382. https://doi.org/10.1007/s00426-011-0346-3

Suppanen, E., Huotilainen, M., & Ylinen, S. (2019). Rhythmic structure facilitates learning from auditory input in newborn infants. *Infant Behavior and Development*, *57*, 101346. https://doi.org/10.1016/J.INFBEH.2019.101346

Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., & Zion Golumbic, E. (2017). Neural entrainment to the beat: The "missing-pulse" phenomenon. *Journal of Neuroscience*, *37*(26), 6331–6341. https://doi.org/10.1523/JNEUROSCI.2500-16.2017

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Temperley, D., & Bartlette, C. (2002). Parallelism as a factor in metrical analysis. *An Interdisciplinary Journal*, *20*(2), 117–149. https://doi.org/10.1525/mp.2002.20.2.117

Tichko, P., Kim, J. C., & Large, E. W. (2021). Bouncing the network: A dynamical systems model of auditory–vestibular interactions underlying infants' perception of musical rhythm. *Developmental Science*, *24*(5), e13103. https://doi.org/10.1111/desc.13103

Tichko, P., Kim, J. C., & Large, E. W. (2022). A dynamical, radically embodied, and ecological theory of rhythm development. *Frontiers in Psychology*, *13*, 653696. https://doi.org/10.3389/fpsyg.2022.653696

Tichko, P., & Large, E. W. (2019). Modeling infants' perceptual narrowing to musical rhythms: Neural oscillation and Hebbian plasticity. *Annals of the New York Academy of Sciences*, *1453*(1), 125–139. https://doi.org/10.1111/nyas.14050

Todd, N. P. M., Cody, F. W. J., & Banks, J. R. (2000). A saccular origin of frequency tuning in myogenic vestibular evoked potentials?: Implications for human responses to loud sounds. *Hearing Research*, *141*(1), 180–188. https://doi.org/10.1016/S0378-5955(99)00222-1

Todd, N. P. M., & Lee, C. S. (2015a). Source analysis of electrophysiological correlates of beat induction as sensory-guided action. *Frontiers in Psychology*, *6*, 1178. https://doi.org/10.3389/fpsyg.2015.01178

Todd, N. P. M., & Lee, C. S. (2015b). The sensory-motor theory of rhythm and beat induction 20 years on: A new synthesis and future perspectives. *Frontiers in Human Neuroscience*, *9*, 444. https://doi.org/10.3389/fnhum.2015.00444

Toiviainen, P., & Snyder, J. S. (2003). Tapping to Bach: Resonance-based modeling of pulse. *Music Perception*, *21*(1), 43–80. https://doi.org/10.1525/mp.2003.21.1.43

Trainor, L. J., Gao, X., Jing-jiang, L., Lehtovaara, K., & Harris, L. R. (2009). The primal role of the vestibular system in determining musical rhythm. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior*, *45*(1), 35–43. https://doi.org/10.1016/j.cortex.2007.10.014

Trainor, L. J., & Unrau, A. (2009). Extracting the beat: An experience-dependent complex integration of multisensory information involving multiple levels of the nervous system. *Empirical Musicology Review*, *4*(1), 32–36. https://doi.org/10.18061/1811/36606

Trehub, S. E., & Thorpe, L. A. (1989). Infants' perception of rhythm: Categorization of auditory sequences by temporal structure. *Canadian Journal of Psychology*, *43*(2), 217–229. https://doi.org/10.1037/h0084223

van der Weij, B., Pearce, M. T., & Honing, H. (2017). A probabilistic model of meter perception: Simulating enculturation. *Frontiers in Psychology*, *8*, 824. https://doi.org/10.3389/fpsyg.2017.00824

Van Dyck, E., Moelants, D., Demey, M., Deweppe, A., Coussement, P., & Leman, M. (2013). The impact of the bass drum on human dance movement. *Music Perception: An Interdisciplinary Journal*, *30*(4), 349–359. https://doi.org/10.1525/mp.2013.30.4.349

Winkler, I., Háden, G. P., Ladinig, O., Sziller, I., & Honing, H. (2009). Newborn infants detect the beat in music. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(7), 2468–2471. https://doi.org/10.1073/pnas.0809035106

Witek, M. A. G. (2017). Filling in: Syncopation, pleasure and distributed embodiment in groove. *Music Analysis*, *36*(1), 138–160. https://doi.org/10.1111/musa.12082

Witek, M. A. G., Clarke, E. F., Wallentin, M., Kringelbach, M. L., & Vuust, P. (2014). Syncopation, body-movement and pleasure in groove music. *PLoS ONE*, *9*(4), e94446. https://doi.org/10.1371/journal.pone.0094446

Wojtczak, M., Mehta, A. H., & Oxenham, A. J. (2017). Rhythm judgments reveal a frequency asymmetry in the perception and neural coding of sound synchrony. *Proceedings of the National Academy of Sciences*, *114*(5), 1201–1206. https://doi.org/10.1073/pnas.1615669114

Zarco, W., Merchant, H., Prado, L., & Mendez, J. C. (2009). Subsecond timing in primates: Comparison of interval production between human subjects and rhesus monkeys. *Journal of Neurophysiology*, *102*(6), 3191–3202. https://doi.org/10.1152/jn.00066.2009

Zentner, M., & Eerola, T. (2010). Rhythmic engagement with music in infancy. *Proceedings of the National Academy of Sciences*, *107*(13), 5768–5773. https://doi.org/10.1073/pnas.1000121107

Zhao, T. C., & Kuhl, P. K. (2016). Musical intervention enhances infants' neural processing of temporal structure in music and speech. *Proceedings of the National Academy of Sciences*, *113*(19), 5212–5217. https://doi.org/10.1073/pnas.1603984113

Zuk, N. J., Carney, L. H., & Lalor, E. C. (2018). Preferred tempo and low-audio-frequency bias emerge from simulated Sub-cortical processing of sounds with a musical beat. *Frontiers in Neuroscience*, *12*, 349. https://doi.org/10.3389/fnins.2018.00349

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: Lenc, T., Peter, V., Hooper, C., Keller, P. E., Burnham, D., & Nozaradan, S. (2023). Infants show enhanced neural responses to musical meter frequencies beyond low-level features. *Developmental Science*, *26*, e13353. https://doi.org/10.1111/desc.13353

14677687, 2023, 5, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/desc.13353 by University Of The Sunshine Coast, Wiley Online Library on [11/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License