Evidence for Top-down Meter Perception in Infancy as Shown by Primed Neural Responses to an Ambiguous Rhythm

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Abstract

From auditory rhythm patterns, listeners extract the underlying steady beat, and perceptually group beats to form meters. While previous studies show infants discriminate different auditory meters, it remains unknown whether they can maintain (imagine) a metrical interpretation of an ambiguous rhythm through top-down processes. We investigated this via electroencephalographic mismatch responses. We primed 6-month-old infants ($N = 24$) to hear a 6-beat ambiguous rhythm either in duple meter ($n = 13$), or in triple meter ($n = 11$) through loudness accents either on every second or every third beat. Periods of priming were inserted before sequences of the ambiguous unaccented rhythm. To elicit mismatch responses, occasional pitch deviants occurred on either beat 4 (strong beat in triple meter; weak in duple) or beat 5 (strong in duple; weak in triple) of the unaccented trials. At frontal left sites, we found a significant interaction between beat and priming group in the predicted direction. Post-hoc analyses showed mismatch response amplitudes were significantly larger for beat 5 in the duple- than triple-primed group ($p = .047$) and were non-significantly larger for beat 4 in the triple- than duple-primed group. Further, amplitudes were generally larger in infants with musically experienced parents. At frontal right sites, mismatch responses were generally larger for those in the duple compared to triple group, which may reflect a processing advantage for duple meter. These results indicate infants can impose a top-down, internally generated meter on ambiguous auditory rhythms, an ability that would aid early language and music learning.

Evidence for Top-down Meter Perception in Infancy: Primed Neural Responses to an Ambiguous Rhythm

Rhythms are common across biological systems, from circadian cycles (Foster & Kreitzman, 2014), to locomotion (Lacquaniti et al., 2012), to the auditory communication signals of music (Brett & Grahn, 2007; Drake et al., 2000; Fitch & Rosenfeld, 2007; Jacoby & McDermott, 2017; Kotz et al., 2018; Large & Palmer, 2002; Merchant et al., 2015; Merchant & Honing, 2014; Nettl, 2000; Ravignani et al., 2014) and speech (Buiatti et al., 2009; Chait et al., 2015; Ding et al., 2016; Giraud & Poeppel, 2012; Lerner et al., 2011; Liberman & Prince, 1977; C. Luo & Ding, 2020; H. Luo et al., 2010; H. Luo & Poeppel, 2007, 2012; Pallier et al., 2011; Poeppel & Assaneo, 2020; Schroeder & Lakatos, 2009). The rhythmic organization of music and speech provides a scaffold for organizing incoming information into patterns, motifs and phrases in music, or syllables, words, and phrases in speech. Furthermore, the regularities inherent in rhythms enable people to move in synchrony to the beat, an activity that enhances social affiliation and cooperation (Hove & Risen, 2009; Tarr et al., 2015; Tunçgenç & Cohen, 2016; Valdesolo et al., 2010; Wiltermuth & Heath, 2009) even in infancy (Cirelli et al., 2018; Cirelli, Einarson, et al., 2014; Trainor & Cirelli, 2015; Tunçgenç et al., 2015). The importance of rhythmic processing is also evident in that major developmental disorders are associated with timing and rhythm deficits (Ladányi et al., 2020; Lense et al., 2021), including dyslexia (Beker et al., 2021; Goswami et al., 2016; Huss et al., 2011; Power et al., 2013; Thomson & Goswami, 2008), autism (Fitzpatrick et al., 2016, 2017; Franich et al., 2021), attention deficit disorder (Carrer, 2015; Hove et al., 2017; Puyjarinet et al., 2017; Zelaznik et al., 2012), and developmental coordination disorder (A. Chang et al., 2021; Puyjarinet et al., 2017; Trainor et al., 2018). Additionally, the regularities in rhythms enable predictive coding, whereby upcoming information can be anticipated, and whereby prediction errors can serve as learning tools to improve prediction in the future (Andreou et al., 2011; Jones et al., 2002; Jones & Boltz, 1989; Large & Jones, 1999; Repp, 2005; Repp & Su, 2013).

Many studies have investigated how the brain encodes auditory rhythms in a stimulus-driven ("bottom-up") manner (Bendixen et al., 2009; Breska & Deouell, 2014; Fujioka et al., 2012; Haenschel et al., 2005; Henry & Obleser, 2012; Herrmann & Johnsrude, 2018; Jones et al., 2002; Näätänen & Winkler, 1999; Schaefer et al., 2011), including in infancy (e.g. Choi et al., 2020; Cirelli et al., 2016; Perani et al., 2010). However, the perception of rhythm involves an interaction between *incoming* sensory information and *intrinsic* ("top-down") factors such as attention (Andreou et al., 2011; Ding et al., 2016; Haegens et al., 2012; Haegens & Zion Golumbic, 2018; Iversen et al., 2009; Nozaradan et al., 2011, 2012; Stefanics et al., 2010) and enculturation (i.e., internal templates sculpted by experience). For example, Western listeners tend to interpret rhythms in groups of two or four beats whereas listeners from Bulgaria can easily interpret rhythmic patterns in groups of seven beats (Hannon & Trehub, 2005a, 2005b). To some extent, adult listeners can voluntarily modify how they perceive a particular rhythm, especially if its grouping structure is ambiguous. This can be done through imagination (Nozaradan et al., 2011), being primed through accents (Bouwer et al., 2014; Ladinig et al., 2009; Repp, 2010; Schaefer et al., 2011), or moving on every second versus every third beat, for example (Chemin et al., 2014; Phillips-Silver & Trainor, 2007, 2008). Yet, it remains unknown whether young infants can engage intrinsic or top-down processes to perceive a rhythmic stimulus in different ways. Here we investigated whether priming infants to hear an ambiguous rhythm in groups of two versus groups of three enables them to maintain that interpretation once priming is removed.

Rhythm, beat, and meter are all terms used to describe the timing structure of music. Rhythm is the surface structure, made up of the timing of event onsets and is therefore inherent to the stimulus. Beat and meter are both derived in the brain, based in part on regularities actually in the rhythm, and in part on the brain's expectations for regularity. The beat is the perceptually constant underlying pulse of the music, and it is what listeners typically tap to. Beats can be hierarchically organized into different grouping patterns, forming a metrical hierarchy. For example, duple meter is a binary grouping of beats, with the first of each pair of beats being perceptually strong, or accented, as in a march (Thomassen, 1982). For Western listeners, this perceptual accenting of duple meter is often automatic, for example, hearing the "*tick, tock, tick, tock"* of a clock, instead of *"tick, tick, tick, tick"*, even though each sound event is identical (Brochard et al., 2003). In triple meter, beats are grouped in threes, as in a waltz (e.g., "ONE two three, ONE two three"). Consequently, a rhythmic stimulus consisting of six beats, can be ambiguous (see Figure 1), as the listener could either perceive three groups of two beats (duple meter), or two groups of three beats (triple meter).

Rhythm perception is evident early in infancy. 39- to 41-week-old fetuses show heart rate changes in response to maternal rocking movements (Lecanuet & Jacquet, 2002). Sucking rate changes in newborns have been used to show that they can use rhythmic cues to discriminate between categories of languages that follow different rhythmic patterns (Mehler et al., 1988; Nazzi et al., 1998). By two months, infants have been shown to discriminate changes in tempo of 15% in a habituation paradigm (Baruch & Drake, 1997). By five months infants will spontaneously move their limbs rhythmically to musical stimuli; although they do not move at the correct tempo, they will move faster to music presented at faster tempos (Zentner & Eerola, 2010). Five-month-olds also have been shown to discriminate between two different groupings of a 6-beat stimulus (H.-W. Chang & Trehub, 1977), and 7-month-olds can categorize rhythms and melodies according to metrical structure (Hannon & Johnson, 2005). Further, 6- to 7-month-old infants can be biased towards perceiving either duple or triple meter, by bouncing them either on every second or every third beat of a 6-beat stimulus (Phillips-Silver & Trainor, 2005), demonstrating the role of body movement on rhythm perception. Together, these behavioural findings show that infants can readily process and distinguish rhythms from the early months after birth.

The early development of rhythm processing is perhaps not surprising given the role of rhythm in enabling synchronous and coordinated social interactions. While behavioural studies indicate infants are sensitive to rhythmic structure in auditory sequences, the neural correlates of rhythm perception in infants have been less studied. One component of the event-related potential (ERP) measured by electroencephalography (EEG) that can be used to examine rhythm perception is the mismatch negativity (MMN). MMN occurs in response to infrequent deviant stimuli inserted into a stream of repeating standard stimuli. Deviants can differ from standards on an acoustic feature, such as pitch or loudness, or on more abstract features such as a difference in the pattern of a sequence (Bendixen et al., 2012; Escera et al., 2000; Näätänen et al., 2007). MMN can be elicited in the absence of attention, peaks between 150 and 250 ms in adults, and manifests at the scalp as a negativity at frontal sites and a positivity at posterior sites, consistent with a main generator in auditory cortex. Younger infants often show a mismatch response (MMR) between 200 and 400 ms after deviant onset that is positive at frontal sites and negative at anterior sites (Basirat et al., 2014; Bristow et al., 2009; Trainor, 2012; Trainor et al., 2003). MMRs have been shown in 3-month-old infants to deviants at both local and global pattern levels (Basirat et al., 2014). Clear adult-like MMN emerges by 3-4 months for simple pitch deviants (He et al., 2007, 2009; Trainor et al., 2001, 2003), but MMR continues in response to complex stimuli or subtle deviants into childhood (Cheng et al., 2015; Cheng & Lee, 2018; Lee et al., 2012; Maurer et al., 2003).

Although MMN occurs in the absence of attention or awareness of stimulus change, its amplitude and/or latency can be affected by attention (Alain & Woods, 1997; Näätänen et al., 1993; Sussman et al., 1998, 2002, 2014) and by intrinsic or top-down processes, such as internalized metrical interpretation of a rhythm. For example, stimulus omissions on metrically strong beats are associated with earlier and larger MMN than omissions on metrically weak beats in adults (Bouwer et al., 2014, 2016; Ladinig et al., 2009) as well as newborns (Winkler et al., 2009), although in the infant case, the deviants were confounded by statistical regularities in the stimulus that co-occurred with the omissions. MMN can also be modulated in adults through active imagery to maintain a primed metrical structure (Schaefer et al., 2011). Specifically, unaccented tones occurring after perceptually accented tones elicit larger, earlier MMN compared to those occurring after perceptually unaccented tones, even though the tones of interest are identical in both contexts. Thus, in adults, both attention and endogenous templates formed by experience can affect the brain’s sensitivity to deviants in rhythms. These studies provide further evidence that rhythmic structures are generated and maintained in the brain through top-down processes and do not only reflect sensory encoding of the stimulus.

The neural correlates of rhythm perception also include neural oscillations, whose frequency and/or phase can align with presented auditory rhythms, a process generally termed neural entrainment (Lakatos et al., 2008; H. Luo & Poeppel, 2007; Obleser & Kayser, 2019; Schroeder & Lakatos, 2009). For the purposes of this study, we use the term neural entrainment to refer to the neural tracking of rhythm. Note, however, that we do not imply that the neurological measures used here are synonymous with other, stricter definitions of neural entrainment (for a critical review, see Haegens & Zion Golumbic, 2018). Neural oscillations in the delta (1-4 Hz) frequency range phase align with auditory rhythmic input, as do fluctuations in the power of oscillations in the beta (~ 20 Hz) frequency range in both auditory and motor regions (Arnal et al., 2015; Cirelli, Bosnyak, et al., 2014; Fujioka et al., 2012, 2015; Henry et al., 2014; Henry & Obleser, 2012; Herrmann et al., 2016; H. Luo et al., 2010; Markova et al., 2019; Power et al., 2013, 2012). For example, delta phase entrainment was found in response to the perceived pulse or beat of simple and syncopated complex drum patterns in attentive adults, even when there was no energy in the stimulus at the perceived pulse (Tal et al., 2017). Thus, low-frequency oscillatory activity can reflect not only entrainment to energy present in the stimulus, but also top-down, neurologically derived representations of the stimulus rhythm. The current study examined whether infants also show top-down effects in their neural tracking of rhythm in the delta band in the form of steady-state evoked potentials (SSEPs).

SSEPs reflect the neural energy at frequencies of interest, rather than the phase alignment between a stimulus and the neural response. In adults, SSEPs can reflect both the rhythmic frequencies actually present in a stimulus as well as participants' interpretation of the metrical structure of an ambiguous rhythm (Celma-Miralles & Toro, 2019; Chemin et al., 2014; Nozaradan et al., 2011). For example, adults who were presented with the same ambiguous rhythm, but instructed to imagine accents either on every second or on every third beat, showed SSEPs with more energy at frequencies corresponding to the imagined metrical interpretations, even though the stimulus was identical in both cases (Nozaradan et al., 2011, 2012). Further, enhancement of SSEPs can occur at spontaneous perceived beat and meter frequencies, even though the actual rhythmic stimuli presented contains little energy at those frequencies (Fujioka et al., 2010; Nozaradan et al., 2012). Thus, when the meter is ambiguous, or there is no energy at the perceived beat of a stimulus, rhythmic structures can be generated intrinsically in the adult brain, modulated by attention to one metrical interpretation or another, and measured in SSEPs.

In a previous study, we presented 7- and 15-month-olds with a 6- or 12-beat repeating ambiguous rhythm, respectively, containing energy at the beat frequency as well as at duple and at either triple or quadruple meter levels (Cirelli et al., 2016). SSEPs showed peaks at all three frequencies in the stimulus: at beat, duple, and triple for 7-month-olds in response to the 6-beat pattern, and at beat, duple and quadruple for 15-month-olds in response to the 12-beat pattern. Further, younger infants who had engaged in music classes showed greater enhancement at the duple meter frequency level, which is consistent with enculturation to the dominant meter in Western music, and larger evoked potentials to the first beat in the 6-beat rhythm. Older infants showed larger evoked potentials in general if they had musically trained parents (Cirelli et al., 2016). Thus, at 7 and 15 months, infants show neural entrainment to frequencies in the stimulus, and their responses may be affected by musical experience. These results cannot tell us, however, whether the infant brain is able to generate intrinsic metrical interpretations in response to an ambiguous rhythmic input. This is explored in the present paper.

Rhythmic entrainment has perceptual benefits. The oscillatory selection hypothesis states that attention applied to more salient or relevant information in an auditory stream (i.e., information occurring at beat onsets) will in turn enhance the neural representation of this information by means of adjusting the excitable phase of neuronal oscillations (Schroeder & Lakatos, 2009). Evidence from audio-visual studies with macaques (Lakatos et al., 2008, 2009) and human epilepsy patients (Besle et al., 2011) supports this hypothesis. Similarly, dynamic attending theory proposes that internal oscillators with different preferred rates entrain to incoming beat rates, thus guiding attention to the expected timing of events. The allocation of attention to beat onsets enables better processing of stimuli presented on beats than off beats (A. Chang et al., 2019; Henry & Herrmann, 2014; Large & Jones, 1999; McAuley & Fromboluti, 2014). Both theories are supported by studies showing neural entrainment is related to behavioural accuracy (Arnal et al., 2015; Bauer et al., 2018; A. Chang et al., 2019; Henry et al., 2014; Henry & Herrmann, 2014; Henry & Obleser, 2012; Herrmann et al., 2016). Further, detection of gaps in rhythmic sequences was found to be best for those that occurred during the rising phase of delta oscillations (Bauer et al., 2018; Henry & Obleser, 2012; Simon & Wallace, 2017).

Despite the rich literature in adults, the extent to which infants use top-down processes to interpret rhythmic stimuli is unclear. MMN and MMR are typically measured in infants under conditions of distracting them to minimize movement artifacts in the EEG recordings by keeping them as still as possible. This distraction typically consists of visual displays or moving toys that are unsynchronized with the auditory stimuli. However, if top-down processing manifests most clearly when attention is engaged with the stimulus, this could be problematic. In the current study, we presented infants with the repeating ambiguous 6-beat rhythm pattern shown in Figure 1, after priming them to hear it either in duple meter or in triple meter via loudness accents either on every second or on every third beat, respectively. Accents were then removed, leaving the meter ambiguous. To attempt to engage infants' attention to the rhythmic pattern, we presented visual displays where a pattern of circle increased and immediately decreased rapidly in size on the first beat of every 6-beat pattern and remained static thereafter for beats 2 to 6. As infants integrate information across auditory and visual modalities (multisensory integration, e.g., Bahrick & Lickliter, 2012; Brandwein et al., 2011; Lewkowicz & Ghazanfar, 2009; Lewkowicz

& Turkewitz, 1980; Molholm et al., 2002; Smith et al., 2017), the visual stimulus would be expected to increase infants' engagement with the auditory rhythm. If 6- to 7-month-old infants can internally derive and maintain the primed auditory meter by means of top-down processes similarly to adults, then we expected (1) small occasional pitch changes (presented only when the visual stimulus was static) to generate larger MMRs on beats perceived as accented (either beat 4 or beat 5) compared to beats perceived as unaccented (either beat 5 or beat 4), according to the primed meter and (2) energy at the primed meter frequency (either duple or triple) to be enhanced.

Materials & Methods

This study on infant rhythm perception is part of a larger collaborative project investigating infant microbiome and joint attention. The following methods and results concern the infant rhythm perception portion of the study only.

Participants

Thirty-one healthy, full-term infants with normal hearing (by parent report) between 6 and 7 months of age (*N* = 16 female, M age = 6.57 months) participated. Infants were randomly assigned to priming group (duple or triple meter; see Stimuli), while counterbalancing infant sex. Seven infants participated but were excluded from analyses: 3 were excluded for completing less than half of the auditory paradigm due to fussiness, and 4 were excluded for having insufficient trial counts after artifact rejection in the ERP analysis (outlined below), leaving the final sample at 24 (*N* = 11 female, M age = 6.56 months), 13 infants in the duple priming group, and 11 in the triple priming group. We aimed for a sample size of 36 infants. Similar studies of rhythm perception using infant EEG measures with comparable sample sizes have yielded moderate effect sizes (e.g., Basirat et al., 2014; Choi et al., 2020; Winkler et al., 2009). A power analysis was conducted using Superpower in R, a package that uses simulated data to estimate power for factorial ANOVAs (Lakens & Caldwell, 2021). Data were simulated for the planned mismatch response analysis using means and standard deviations based on previous studies with infants (Basirat et al., 2014; Cheng et al., 2015; He et al., 2009). For a 3-way within-between effects interaction in a 2x2x2 ANOVA to obtain an effect size equal to 0.24, a sample size of 36 (18 per group) would be needed; this would yield statistical power equal to 0.83. Thus, our sample is short of our intended *N*; however, further recruitment was not possible due to the COVID-19 pandemic. Even though we were officially given permission to test again for a short time between pandemic waves, parents were understandably reluctant to bring in their infants and we were not able to recruit. We are also concerned that infants with limited social interactions due to lockdowns may differ from the infants in the current sample. While comparing pre- and post-pandemic infants would be interesting, it is beyond the scope of the present study.

Infants were recruited from the Developmental Studies Database at McMaster University. The McMaster Research Ethics Board approved all procedures and informed consent was obtained from all parents of infants.

Stimuli

The auditory stimulus was a repeating 1.8-s 6-beat rhythmic pattern (*as per* Cirelli et al., 2016; Phillips-Silver & Trainor, 2005) composed of synthesized tones and silences. The inter-onset-interval between beats was 300 ms, and the pattern had the following structure: tone, silence (rest), tone, tone, tone, silence (see Figure 1A). Tones were in either piano, vibraphone, or guitar timbre (depending on the stimulus condition, described below). All tones were synthesized using the Apple program Garageband. Infants heard the stimulus at a comfortable level [~60 dB SPL over a noise floor of < 30 dB (A)] at the location of the infants' head through an Audio Video Methods speaker (P73) that was approximately 1 m in front of the infant.

Stimuli were played continuously in sets of 20 trials (20 trials lasted 36 s), starting with 4 priming trials, followed by 16 test trials (see Figure 1C). After the 20th trial, another 20-trial set began, again with the 4 initial priming trials. The meter was indicated in the priming trials by loudness accents (increase of 10 dB over unaccented tones) on beats 1, 3, and 5 (duple meter), or beats 1 and 4 (triple meter). We chose to prime between-subjects to ensure there were no carry over effects, such as could occur if the same infant was primed alternatively in both duple and triple meter. In addition, testing infants in both duple and triple conditions would have doubled the length of the experiment, making to too long for infants to complete.

Test trials had no accents so that the meter was ambiguous. An oddball paradigm was used: 25% of test trials were deviant, containing a quartertone (i.e., 50 cents or 1/24th of an octave) increase in the pitch of one tone (12.5% on beat 4, 12.5% on beat 5), while the remaining 75% of test trials contained only standard tones. This proportion of standards and deviants was maintained for each 16 test-trial set. Deviant trials occurred pseudo-randomly in the set, with the limitation that they had to occur after at least one standard trial. We expected to find larger MMR for beat 4 in infants primed to hear triple meter (ONE two three FOUR five six), and on beat 5 for those primed to hear duple meter (ONE two THREE four FIVE six). The whole test consisted of three blocks, each with nine 20-trial sets, making each block 5 min 24 s long. All tones were 300 ms in duration with a 15 ms onset. Since tones were created with piano, vibraphone, and guitar timbres, they decayed naturally; however, to ensure all tones decayed to silence similarly, a 100 ms cosine decay ramp that started 200 ms after tone onset was applied. Thus, there were no pauses between tones (except for beats 1 and 5, since they were followed by a silence), but all tones decayed, approaching silence before the onset of the next tone.

To try to keep infants interested and attentive, in each block either the pitch or timbre of the tones changed from 20-trial set to 20-trial set. In pitch-varying blocks, standard tones were either piano A 440 Hz, C# 554.37 Hz, or E 659.26 Hz. In timbre-varying blocks, standard tones were either piano, vibraphone, or guitar A 440 Hz. The block type alternated for each infant, and infants were counterbalanced on whether they started with a pitch- or timbre-varying block.

The following steps were carried out to confirm the frequencies of interest from the stimulus: First, given that the EEG data were averaged across the different block types, an average signal segment was computed using a random 28.8 s segment of unaccented trials taken from each different type of sound (i.e., piano A, C# and E for the pitch-varying condition, and piano, guitar, or vibraphone A for the timbre-varying condition). Next, a Hilbert transform was performed in MATLAB to yield the instantaneous amplitude of each rhythm. Then a fast Fourier transform (FFT) was applied, yielding an envelope of the acoustic energy for each trial type (see Figure 1B). As expected, clear peaks were found at the triple (1.11 Hz), duple (1.67 Hz), and beat (3.33 Hz) frequencies, as well as their harmonics (2.22, 2.78 Hz), and the sextuple frequency (0.56 Hz). As shown in the spectral envelope, the stimulus contained the most energy at the duple frequency, followed by the beat frequency, then the triple frequency. Identical steps were carried out again for each stimulus type separately, yielding comparable envelopes (see Figure S1).

To obtain analyzable EEG recordings from infants listening to auditory stimuli, it is necessary to keep them as still as possible to reduce noise artifacts. We and others have typically accomplished this with visual stimuli that are randomly timed with respect to the auditory stimulus of interest (e.g., blowing bubbles; watching a silent video; Cheng & Lee, 2018; Choi et al., 2020; Cirelli et al., 2016; He et al., 2007, 2009; Trainor et al., 2001, 2003). However, in the present case of auditory rhythmic patterns, it is possible that the random timing of such concurrent visual stimuli might actually impede infants' processing of the timing of the auditory rhythms. Thus, to keep infants still while also encouraging them to orient to the timing of the auditory rhythm, we created a controlled visual stimulus that was identical across all conditions. At the start of each auditory 6-beat pattern, infants saw an array of 5-9 coloured circles (4.5 cm diameter per circle) on a computer screen 1 meter in front of them (see Figure 1A). The visual angle of each circle was 2.58°, and for a row of three circles was 11.70°. The visual stimulus remained static for the duration of the 6-beat rhythm pattern except during the first beat. At the onset of beat 1, each circle in the array expanded ~ 60% in size (7 cm diameter per circle) during the first 30 ms and then immediately shrunk to the original size before the start of the second beat (300 ms). The visual array then stayed static for the remainder of the auditory rhythm. The visual angle of each expanded circle was 4.01°, and for an expanded row of three circles was 12.84°. The colour of the circles was either yellow, green, pink, blue, or red, and changed pseudo-randomly at the start of each 20-trial set, such that no colour was repeated two sets in a row. Five different videos were created for each block type (pitch- or timbre-varying) that randomly combined the visual with the auditory stimuli, and these were chosen randomly for each participant. Importantly, the visual stimulus was identical across priming conditions and remained static during beats 4 and 5 when pitch changes could occur, and MMR responses would be measured. The aim of the visual stimulus was to act as a visual accent for beat 1 such that infants would be drawn to the timing of the auditory rhythm via audio-visual integration that has been documented in infants (e.g., Bahrick & Lickliter, 2012; Lewkowicz & Ghazanfar, 2009;

Lewkowicz & Turkewitz, 1980; Smith et al., 2017), thus enhancing their attention to/processing of the auditory rhythm as a whole.

Procedure

After receiving a description of the study, the infant's parent signed a consent form, and completed a language and music background questionnaire. Questions included demographics, hearing status (note that universal newborn hearing screening is in place in this jurisdiction), musical exposure in the home, musical experience of the parents, and languages spoken in the home. Responses to questions on musical exposure in the home were low in variability, and thus were not useful for investigating whether musical exposure related to the EEG findings. Musical experience of the parents was, however, suitable for analysis. Specifically, we asked whether the mother (or primary caregiver) and/or father (or secondary caregiver) currently played a musical instrument (including voice). Responses to the question on languages in the home were used to confirm that all infants came from English-speaking families.

Infants were randomly assigned to either the duple or triple prime condition. This factor was between-subjects to avoid carry over effects between the two priming conditions. Each infant sat on their parent's lap (parents were blind as to the study hypotheses) for the duration of the study ~1 m in front of the loudspeaker and screen, which was eye level for the infant. Parents were asked to not speak to their infant and minimize their movements during the recording session. A researcher remained behind the parent, out of the infant's view, to intervene if the infant became fussy. A short break was taken at the end of each block. Sometimes, a research assistant was in the room to help redirect the infant's attention to the screen by pointing to the screen. This was done in the second block only if the infant was not attending and was done in the third block for all participants. A webcam facing the participant recorded their behaviour and a live feed was used to manually code looking. A researcher outside the testing room indicated with a mouse-click when participants were looking or not looking at the visual stimulus on the screen, and this information was directly inserted to the EEG datafile. They also coded whether the researcher was sitting beside the infant in blocks 2 and 3. This enabled us to check if infants attended to the visual stimuli most of the time and whether EEG differed when they looked to the visual stimuli compared to not. However, for the primary analyses, all data were analyzed to maximize power. Infants who completed less than 2 blocks were excluded from the analyses. Following presentation of the auditory stimuli, resting state EEG was collected for 3 minutes while a researcher silently blew bubbles at the infant. Resting state was not analyzed in the present study.

Four of the infants (*N* = 2 for each priming group) completed a slightly different version of the paradigm, but they were included to ensure the largest sample size possible. There were 3 differences for these infants: 1) instead of using just pitch- and timbre-varying blocks of stimuli, infants heard a simpler first block of stimuli that did not vary in timbre or pitch; all tones were A440 Hz and in piano timbre. The second and third blocks were then the same pitch- or timbre-varying conditions (counterbalanced across priming groups) as used for the rest of the infants. 2) Instead of having nine 20-trial sets in each block of stimuli, there were ten 20-trial sets, making each block 6 minutes long. 3) If an infant became inattentive, the researcher still sat beside the infant and pointed to the screen, but we did not record when the researcher was pointing to the screen. To ensure that these differences did not impact overall results, we plotted the boxplots for all infants' MMRs for each condition to identify potential outliers (see Figure S2). Aside from one infant in the beat 4 standard condition, none of these infants showed data outside of the whiskers on the boxplot. Further, the MMR analysis was redone excluding this infant, and results remained the same.

After completing the EEG portion of the study, some infants also participated in a joint attention task as part of the larger, collaborative project; these data are not included in this paper.

Data Acquisition and Analysis

EEG data were collected with a 124-channel Hydrocel GSN net with an Electrical Geodesic NetAmps 200 amplifier and Electrical Geodesics NETSTATION software (v.5.4.2). Signals were recorded online at a sampling rate of 1000 Hz using a Cz reference. Electrode impedance during recording was maintained below 50 kΩ. A researcher marked any bad channels in the session notes. All preprocessing steps were completed in MATLAB, and all statistical analyses were performed in IBM SPSS Statistics, Version 20.

Preprocessing

The data were filtered offline using the fieldtrip toolbox (Oostenveld et al., 2011) for MATLAB, with zero-phase, 3rd order Butterworth high-pass and low-pass filters at 0.5 Hz and 15 Hz, respectively. After filtering, the data were then processed through the Artifact Blocking algorithm in MATLAB (Fujioka et al., 2011; Mourad et al., 2007), which is an effective way to remove artifacts and maximize the signal-to-noise ratio in infant data (Fujioka et al., 2011). Bad channels that had been previously labelled by the researcher were then interpolated using the 6-10 neighbouring channels. Most infants (*N* = 22) had only 0 to 4 bad channels, while the other two infants had 5 to 6 bad channels. Data were then re-referenced to the average of all the electrodes. For MMR analysis, data were segmented into trials from -100 to 1800 ms post-stimulus onset, relative to the onset of the first beat of every 6-beat trial. For SSEP analyses, the data were segmented from -100 to 28,800 ms post-stimulus onset, relative to the first unaccented test trial after each round of priming (i.e., each SSEP segment was made up of the 16 consecutive unaccented trials, thus resulting in 27 segments for infants who completed all three blocks). After segmenting, and for the MMR analysis only, a conventional trial rejection was applied to remove any trials that still exceeded +-100 μV. To check for infants with noisy ERP data, the original data were re-preprocessed without applying the artifact blocking method to see how many trials would have been rejected. Those infants with < 5% trials left using conventional trial rejection with a +-100 μV threshold were excluded (*n* = 1 in the duple priming group; 3 in the triple priming group).

Mismatch Response Analysis

To isolate the brain activity for the beats of interest, the data were segmented between -100 to 600 ms relative to the onsets of each of beats 4 and 5, then averaged separately for the standards and deviants for each participant. The averaged trials were then baselined using the average amplitude from -100 to 0 ms. From here, visual inspection of the deviant-standard difference waves determined the presence of positive MMRs that were strongest at frontal sites (see Figure 3B), at 200 to 325 ms post-stimulus onset, for most participants. Given that infants typically show high variability in ERPs, the latencies for the MMR peaks were found separately for each participant using the deviant-standard difference waves at frontal left (FL) and frontal right (FR) sites. FL included EGI channels 12, 18, 19, 22, 23, 24, 26, and 27, while FR included channels 2, 3, 4, 5, 9, 10, 123 and 124 (see Figure S3 for where these channels are located on the scalp). Once peak latencies were determined from the difference waves, the average amplitudes +/- 20 ms around these peak latencies were calculated for the standards and deviants. For infants who did not show a clear peak in a condition (*n* = 4: in the duple group, 1 infant did not have a clear peak for beat 4 FL; in the triple group, 1 for beat 4 FL, 1 for beat 4 FR, 1 for beat 5 FL), the average amplitudes were taken around the average peak latency of the group. All MMR peaks fell within 201 to 325 ms, post-stimulus onset.

An initial Repeated Measures (RM) ANOVA with within-subjects factors of hemisphere (right, left), stand/dev (standard, deviant), beat position (beat 4 – strong in triple meter, beat 5 – strong in duple meter) and a between-subjects factor of priming group (duple, triple) revealed significant main effects of stand/dev ($F(1,22) = 59.420$, $p < .001$, $\eta_p^2 = .730$), beat position ($F(1,22) = 18.010$, $p < .001$, $\eta_p^2 = .450$), beat position*group ($F(1,22) = 6.139$, $p = .021$, $\eta_p^2 = .218$), and hemisphere*stand/dev*group ($F(1,22) = 5.550$, $p = .028$, $\eta_p^2 = .201$). Given the interaction involving hemisphere and group, all subsequent analyses of MMR amplitudes were based on a priori hypotheses that involved conducting separate RM ANOVAs for FL and FR electrode groupings with factors stand/dev (standard, deviant), beat position (beat 4, beat 5), and priming group (duple, triple). Tones on both beats 4 and 5 follow a tone in the stimulus (i.e., there are tones on beats 3 and 4), so have the same local context. Since each beat was only 300 ms long, peaks in the MMR time interval may have overlapped slightly (up to 25 ms in some cases) with the onset of the next beat. Beat 4 is followed by a tone, but beat 5 is followed by a silence, so beat position effects that were not accompanied by a stand/dev effect were interpreted with caution. A priori analyses of MMR latencies were identical to those used for amplitudes, except that stand/dev was not included as a factor, because latencies used for deviants were the same as their equivalent standards within condition and participant. Thus, separate RM ANOVAs for latency were conducted for FL and FR electrode groupings with a within-subjects factor of beat position (beat 4, beat 5), and a between-subjects factor of priming group (duple, triple). Further, infants who did not show a clear peak were excluded from latency analyses. Any significant interactions were further analyzed using simple main effects analyses corrected for multiple comparisons using Bonferroni correction.

Steady-State Evoked Potentials Analysis

The segmented data were first averaged to get one average 16-trial-long segment for each participant, then baselined using the average amplitude from -100 to 0 ms. An FFT was then applied to the averaged segment at each electrode, to get the signal power (μV^2) for 0 to 4 Hz, at a resolution of 0.035 Hz. To accurately isolate the SSEP signal, the average amplitude in frequency bins on each side of the frequency of interest was subtracted from the amplitude of the frequency of interest. Specifically, the average amplitude of the 3rd, 4th, and 5th neighbouring bins on each side (thus ranging from -0.174 Hz to -0.104 Hz and +0.104 to +0.174 Hz) were subtracted from each of the frequency bins in the spectrum (Cirelli et al., 2016; Nozaradan et al., 2011). Following this, SSEPs were separately averaged across the electrodes in each of the FL and FR electrode groupings. These electrode groupings were chosen because 1) this is where we found the strongest effects for the mismatch response, and 2) SSEP power at the duple and triple frequencies appeared strongly in frontal and central regions (see Figure 5B). Topographically, it appeared that SSEPs were strong in occipital sites as well, so, following previous studies, we ran the analyses again on the average of all electrodes. The results were the same as what we found using only FL sites (see Figure S4).

To determine if peaks at the frequencies of interest observed in the EEG frequency spectra were significantly above the noise floor, paired-sample t-tests were performed for each electrode grouping, using each of the frequencies of interest (1.11 Hz, triple; 1.67 Hz, duple; 3.33 Hz, beat), the sextuple frequency (0.56 Hz), its harmonics (0.56 Hz, 2.22 Hz, 2.78 Hz) and the average noise floor for each participant. The average noise floor amplitude was calculated across frequencies determined not present in the stimulus, specifically, frequencies falling exactly halfway between the frequencies of interest (0.833, 1.389, 1.945, 2.500 Hz, and 3.055 Hz; see Figure 1). To check for outliers in the SSEPs, an average SSEP amplitude score was computed across the frequency bins of interest and their harmonics, and a z-score for each participant was calculated such that $z = (x - \mu)/\sigma$, where μ and σ were the mean and standard deviation of the group's average SSEP amplitudes, respectively. Any participant who exceeded +/- 3 SD from the group mean was excluded. No additional infants were identified as being outliers in the SSEP results after removing those in the MMR analysis. Thus, the final sample was $N = 13$ for the duple group and $N = 11$ for the triple group for all analyses.

Separate RM ANOVAs with the within-subjects factor of meter frequency (1.11; 1.67 Hz), and the between-subjects factor of priming group (duple; triple) were used to investigate effects of metrical priming in FL and FR sites.

Exploratory Analyses of Relations to Parents' Music Experience

To explore the relationship between the musical experience of the parents and EEG results, the same RM ANOVAs outlined above were performed again but instead of using priming group as the between-subjects factor, we collapsed across priming groups and included a between-subjects factor of whether infants had at least one parent who currently played a musical instrument(s) (including voice). Sixteen infants did not have a musically experienced parent whereas 8 had at least one musically experienced parent (6/8 infants' parent(s) had > 4 years of lessons with their instrument). Of those with a musically experienced parent, 4 were primed with duple meter, and 4 were primed with triple meter. Thus, the exploratory MMR analysis was an RM ANOVA with the factors of stand/dev and beat position, and a between-subjects factor of musically experienced parent (none or at least one), and for SSEP, an RM ANOVA with the factor meter frequency (1.11; 1.67 Hz) and a between-subjects factor of musically experienced parent.

Results

Mismatch Response. Results are shown in Figures 2-3. For FL sites, there was a significant main effect of stand/dev ($F(1,22) = 27.696$, $p < .001$, $\eta_p^2 = .557$), where amplitudes for deviants were significantly more positive than for standards, demonstrating an MMR. There was also a main effect of beat position ($F(1,22) = 13.710$, $p = .001$, $\eta_p^2 = .384$), where beat 5 amplitudes were significantly more positive than beat 4 amplitudes. These main effects were qualified by a significant beat position x priming group interaction ($F(1,22) = 7.593$, $p = .012$, $\eta_p^2 = .257$).We also found a 3-way stand/dev x beat position x priming group interaction ($F(1,22) = 4.215$, $p = .052$, $\eta_p^2 = .161$). Though .052 is slightly greater than alpha = .05, this interaction was further investigated because this statistical test is non-directional whereas we had a directional hypothesis. The effect was consistent with our directional, predicted differences between the priming groups; in a directional one-tailed test, p would = .052/2 = .026, rendering the result statistically significant. A Levene's Test of Equality of Error Variances revealed a significant group difference for the deviants on beat 4 ($F(1,22) = 5.776$, $p = .025$), and beat 5 ($F(1,22) = 5.504$, $p = .028$). Thus, for follow-up t tests, we report the t test results for equal variances not assumed, where the df are adjusted using the Satterthwaite approximation for the degrees of freedom.

To analyze these interactions, we collapsed stand/dev by taking the deviant-standard difference as the dependent variable, as is commonly done with oddball paradigm data. An independent samples t test was performed on the deviant-standard difference amplitudes for beats 4 and 5, to see if the MMR was larger for beat 5 in the duple group, and larger for beat 4 in the triple group. Given that these are directional hypotheses, we used one-tailed t tests. MMR amplitudes were significantly larger for the duple group on beat 5 ($t_{(18.7)} = 1.772$, $p = .047$), but groups did not differ on beat 4 ($t_{(14.68)} = -1.089$, $p = .147$), although the direction of the effect was for larger MMR amplitude in the triple group.

At FR sites there was a main effect of stand/dev ($F(1,22) = 49.565$, $p < .001$, $\eta_p^2 = .693$) where, as with FL, amplitudes for deviants were significantly more positive than for standards, signifying an MMR. There was also a significant effect of beat position ($F(1,22) = 16.512$, $p = .001$, $\eta_p^2 = .429$), where beat 5 amplitudes were more positive than beat 4 amplitudes. The main effect of stand/dev was qualified by a significant stand/dev x priming group interaction ($F(1,22) = 11.309$, $p = .003$, $\eta_p^2 = .340$). To investigate this interaction, an independent samples t test comparing priming groups was performed on the deviant-standard difference amplitudes averaged across beat position. Results showed that MMR amplitudes of those in the duple group were significantly larger in general than those in the triple group ($t_{(22)} = 3.363$, $p = .003$). There were no significant interactions involving beat position and group at FR sites.

There were no significant differences in latency in the MMR time window for either FL or FR sites (all p's > .05).

An exploratory analysis was performed to see whether the musical experience of the parents affected infants' MMR results. At FL sites, there was a main effect of musically experienced parent ($F(1,22) = 7.882$, $p = .010$, $\eta_p^2 = .264$), which was qualified by a significant stand/dev x musically experienced parent interaction ($F = 5.217$, $p = .032$, $\eta_p^2 = .192$). Main and interaction effects involving beat position were not significant. Follow-up one-way ANOVAs with the between-subjects factor of musically experienced parent were conducted by taking the deviant-standard difference as the dependent variable, confirming that infants who had at least one musically experienced parent showed larger MMRs in general than those infants without a musically experienced parent (Figure 4; $F = 5.217$, $p = .032$, $\eta_p^2 = .192$). There were no significant effects of musically experienced parent at FR sites.

Looking Behaviour. Because the visual stimulus was identical across priming conditions and because it was static during beats 4 and 5, any effects of duple versus triple priming on MMR should not be a result of the visual stimulus. Nonetheless, it is interesting to determine whether there were general differences depending on the extent to which infants looked directly at the visual stimulus. We calculated the proportion of time infants looked by dividing the time spent looking at the screen during trials (priming and test), by the total duration of trials. As shown in table S1 of the Supplementary Information, infants in both the duple- and triple-priming groups looked for similar amounts of time across the experiment. To further test whether looking behaviour influenced infants' MMR, we conducted a median split to divide the infants into two groups: those who looked during fewer trials than the median (< 61%), and those who looked during more trials (> 61%). We then performed a one-way ANOVA at FL and at FR, comparing the overall MMR for infants between the looking groups. Results were non-significant with low effect sizes in FL ($F(1,22) = 0.280$, $p = .602$, $\eta^2 = .013$) and FR ($F(1,22) = 0.561$, $p = .462$, $\eta^2 = .025$).

Steady-State Evoked Potentials. Results are shown in Figure 5. All peaks at the frequencies of interest (beat, duple, triple) were above the noise floor, as well as the frequency of the entire 6-beat pattern (.56 Hz) and its harmonics (all p's < .002; see Table 1). Contrary to our hypotheses, there were no priming group x frequency interactions (FL; $F(1,22) = 1.050$, $p = .317$, $\eta_p^2 = .046$, FR; $F(1,22) = 0.242$, $p = .628$, $\eta_p^2 = .011$), but there was a main effect of frequency in FL ($F(1,22) = 9.236$, $p = .006$, $\eta_p^2 = .296$), where energy at the triple frequency was significantly greater than for the duple frequency, which is opposite to that of the stimulus. There were no significant meter differences at FR ($F(1,22) = 0.433$, $p = .518$, $\eta_p^2 = .019$) sites.

Given that there were no group differences based on priming effects, an exploratory RM ANOVA with the same within-subjects factors as above was done, but with grouping based on whether infants had a musically experienced parent or not. There were no significant differences between frequency peaks at FL ($F(1,22) = 1.970$, $p = .174$, $\eta_p^2 = .082$) or FR ($F(1,22) = 0.094$, $p = .762$, $\eta_p^2 = .004$) sites based on musically experienced parent(s).

Discussion

In the current study, we measured the effects of metrical priming on rhythm processing in 6- to 7-month-old infants using an ambiguous rhythm that could be interpreted as in either duple or triple meter. We intermittently primed infants with accents on either every second beat (duple meter) or on every third beat (triple meter). We note that our sample size was somewhat underpowered because of interruptions due to the COVID-19 pandemic. Nonetheless, we found a significant interaction indicating that, when presented with the ambiguous rhythm (with no accents) there was enhancement of mismatch response amplitudes for pitch changes that occurred on metrically strong, as opposed to weak, beats, according to their priming. Post-hoc analyses revealed a significant effect of priming group on beat 5 ($p = .047$). While the effect was not significant on beat 4 ($p = .147$), it was in the predicted direction. In any case, the significant interaction provides novel evidence that infants engage in internally driven or top-down interpretations of the rhythmic structure of incoming auditory patterns. It also has implications for our understanding of early language development, specifically, how pre-verbal infants may learn to parse speech structures and develop internal rhythmic templates specialized for the metrical structure of the language in their environment. For example, research indicates that through repeated exposure to new 3-syllable words, over time, infants' brains become more tuned to the word-level structure created by grouping the syllables, and less tuned to the syllable structure, which is necessary to understand words in their native language. (Choi et al., 2020).

Infants showed significant MMR around 250 ms after deviant onset on average, but no adult-like MMN. This is consistent with findings that older infants and even children continue to show MMR to complex stimuli (Lee et al., 2012; Maurer et al., 2003), and to small deviants (Cheng et al., 2013, 2015; Cheng & Lee, 2018; Lee et al., 2012; Maurer et al., 2003), as in the present study. For example, while newborns only showed positive MMR, 6- 12- and 18-month-old infants showed adult-like MMN to large acoustic deviants amongst Mandarin lexical tones but showed MMR to small acoustic changes (Cheng et al., 2015; Cheng & Lee, 2018). Further, 6- to 7-year-olds showed exclusively MMR to deviants with short durations, but there was greater positivity for phonemes (complex) compared to tones (simple), and for small compared to large deviants (Maurer et al., 2003). Similarly, 4- to 6-year-olds showed only MMR to initial consonants, but MMN for relatively simpler lexical tones and vowels (Lee et al., 2012). The current study used a relatively complex rhythmic pattern and deviants were subtle, consisting of quarter-tone pitch changes. Thus, the dominant response in the 6- to 7-month-old infants of the current study would be expected to be a MMR, as was found.

In support for our hypotheses, MMRs at frontal left sites were affected by the priming condition, as evidenced by a beat position x stand/dev x priming group interaction in the predicted direction, with a modest effect size. As can be seen in Figure 3, this interaction was driven by a more positive MMR on beat 5 in the duple-primed group compared to the triple-primed group, than by a group difference on beat 4. Given that both the duple-primed and triple-primed groups heard the identical ambiguous rhythm pattern, our results indicate that infants can interpret metrical structure in rhythms through internal or top-down processes. We note, however, that replication of these effects with a larger sample size will aid in interpretation of the findings.

At frontal right sites, we did not find differences in MMRs across beat position according to whether they were primed in duple or triple meter. However, we did find a group difference in that MMRs were larger in the duple-primed than triple-primed group at both beat 4 and beat 5. Both this finding of generally larger MMRs at frontal right sites in the duple-primed group, and the finding that group differences at frontal left sites emerged more strongly for beat 5, which is a strong beat in the duple interpretation, than for beat 4, which is strong in the triple interpretation, suggest that infants were better able to interpret the ambiguous rhythm in duple than in triple meter. Interestingly, Western music in general is heavily biased towards duple metrical structures. If infants were a priori biased towards hearing the ambiguous rhythm in duple meter, then this could mean that infants primed to hear triple meter would have to work harder to overcome this bias, thus weakening the saliency of deviants on beat 4 compared to beat 5. While it appears behaviourally that infants are not strongly encultured to the meters present in their Western environment until after 6 months (Hannon & Trehub, 2005a, 2005b), 7-month-old Western infants already show a preference for duple meter (Bergeson & Trehub, 2006). Thus, our findings might reflect the beginnings of enculturation to the duple meter dominant in their environment. On the other hand, the duple frequency is more strongly represented in the stimulus, so these effects may simply reflect that.

With respect to steady-state evoked potentials, as expected, we found clear peaks at the frequencies of interest (triple, 1.11 Hz; duple, 1.67 Hz; and beat, 3.33 Hz) that were above the noise floor at both left and right frontal sites. However, we did not find any significant differences related to duple versus triple priming. Unexpectedly, infants' peaks at the triple frequency were higher than at the duple frequency, regardless of priming, at frontal left sites. This is in contrast to the stimulus, which shows greater energy at duple than triple frequencies, and is also in contrast to our previous results with 7-month-olds (Cirelli et al., 2016). There were critical differences, however, between the present study and the previous one: infants in Cirelli et al. (2016) were tested in a context where there was no priming, and where attention was drawn away from the temporal structure of the rhythm. While we do not have a good explanation for the present SSEP results, it is possible that, assuming the infants had a culturally induced bias for duple meter (Bergeson & Trehub, 2006), when their attention was drawn to the meter, as in the present study, the triple meter was more novel than the duple, resulting in further attentional resources being applied to processing it. What is clear is that additional studies need to be done before the steady-state evoked potentials can be definitively interpreted.

Infants with at least one musically experienced parent (currently playing an instrument, including voice) had larger MMRs than infants without a musically experienced parent. This is similar to previous results from our lab: 7-month-old infants who participated in weekly music classes with their parent showed larger evoked responses to the first beat of the 6-beat stimulus and larger responses at meter frequencies compared to infants not attending music classes (Cirelli et al., 2016). It is unclear what role musical experience plays in these neural differences. It is possible that parents with more musical background provide a musical environment at home that nurtures their rhythmic processing; further, it is possible that this could be impacted by interactions with genes that might be associated with musical ability. In addition, it could also be the case that parents who play music are better able to provide their infants with opportunities to learn in enriched environments, which could then influence their rhythm perception. Neither the current nor the previous study (Cirelli et al., 2016) measured socio-economic status (SES), which could at least partially explain these differences. Future studies could address these questions around development of rhythm perception by including genomic sequencing of parents with more and less musical experience from varying SES backgrounds, while carefully measuring the extent of music in the home.

We found hemispheric differences in both the MMR and SSEP results. First, the effect of metrical priming on the MMR was only found in the left hemisphere. Second, the duple group showed larger MMRs in general than the triple group, but only in the right hemisphere. Third, infants with musically experienced parents had larger MMRs than those without, but only in the left hemisphere. Lastly, the amplitudes of SSEPs at the triple frequency were larger than the duple frequency across groups, but only in the left hemisphere. Many studies from children to adults have shown hemispheric differences in processing auditory rhythms and language. It has been proposed that the left hemisphere specializes in rapid temporal changes and the right hemisphere specializes in spectral information (Boemio et al., 2005; Okamoto & Kakigi, 2015; Zatorre & Belin, 2001). While our study did not address effects of spectral information, across our measures, we did find the strongest metrical effects in processing the auditory rhythm in the left hemisphere already at 6 months.

Other functional differences between hemispheres exist beyond simple acoustic features. For example, 10-week-old infants' MMRs for incongruent face-vowel pairs have been found to be left-lateralized while gender processing was right-lateralized (Bristow et al., 2009). The left hemisphere may be more involved with top-down processing, while the right hemisphere may be more involved in bottom-up processing (Park et al., 2015; Shuai & Gong, 2014). For example, one study in infants found that top-down global effects on MMRs were evident only in the left hemisphere, while local effects were found in both hemispheres (Basirat et al., 2014). The current study was consistent with this in that MMR differences between groups reflecting differences in metrical processing were found only in the left hemisphere.

We paired a visual stimulus with our auditory rhythm, such that an array of circles moved on beat 1 and stayed static for beats 2-6. The visual stimulus served both the keep infants still during the EEG recordings and to direct their attention to the auditory pattern. Given that infants engage in multisensory integration (e.g., Brandwein et al., 2011; Lewkowicz & Turkewitz, 1980; Molholm et al., 2002; Smith et al., 2017), is possible that directing infants' attention to the rhythm, as opposed to distracting them as is often done during EEG recordings, is a necessary component for observing the carryover of the primed interpretation to when the ambiguous pattern was presented. Since beat 1 is metrically strong for both the duple- and triple-primed infants, and this beat position was not analyzed in the ERPs, visual activity would not impact the MMR results. As for the SSEPs, the visual stimulus on beat 1 might have impacted the neural response to the sextuple frequency (0.556 Hz), however, we did not analyze differences between or within groups at this frequency. Nonetheless, one could argue that if infants attended to the visual stimulus more or less in certain priming conditions, that this could impact the EEG findings. We showed that this is not the case, however, as infants from both groups looked similarly across the experiments.

The present study had several limitations. First, although we did not find any effects of duple versus triple priming on MMR latency, we did not measure the temporal dynamics of the EEG response across the entire rhythmic pattern or how closely the EEG responses matched the timing of the stimulus. Future studies could use time-frequency analyses to investigate neural entrainment under different metrical interpretations. Second, we found a positive association between MMR amplitude and whether infants had a parent who played a musical instrument, but it remains for future studies to disentangle genetic and experiential contributions to this effect. Third, we chose not to give parents masking headphones, to better be able to communicate with the parent. While parents were instructed to remain perfectly still, and were reminded if any overt movements were observed, it is possible that parents' micro-movements could have impacted some of the findings. However, researchers in the booth and observing from outside through a webcam were trained to recognize and verbally correct parents on any such movements. It should also be noted that parents were blind as to the hypotheses. Additionally, adult EEG data collected with the same stimuli (currently being written up) shows differences between infants' and adults' perceptions of the meter, suggesting that it is unlikely adults were influencing infants' perception of the ambiguous rhythm. Finally, we were forced to end testing earlier than planned due to COVID-19 restrictions, resulting in a somewhat smaller sample size than desired.

Conclusions. We conclude: (1) Priming different metrical interpretations of an ambiguous rhythm leads to different neural representations of the rhythm in 6- to 7-month-old infants, indicating that infants are able to engage intrinsic or top-down processes. (2) These top-down processes are lateralized to the left hemisphere. (3) Metrical priming appears to have more robust effects for duple compared to triple meter priming, suggesting the beginnings of enculturation to the dominant duple meter in Western music. (4) Infants with musically experienced parents show larger neural responses, although we cannot determine the extent to which this reflects genetic versus environmental factors. Together these results show that a short amount of exposure to a particular interpretation of an ambiguous rhythm pattern biases infants to subsequently impose that interpretation when presented with the ambiguous rhythm. Such processes likely underly perceptual narrowing and enculturation to the speech and musical stimuli in infants' environments.

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Abbreviations

EEG: electroencephalography; ERP: event-related potential; FFT: fast Fourier transform; FL: frontal left; FR: frontal right; MMN: mismatch negativity; MMR: mismatch response; RM: repeated-measures; SSEP: steady-state evoked potential

Conflict of Interest Statement

The authors declare that this research was conducted without any relationships that could warrant conflicts of interest.

Author Contributions

LJT and EF designed the project. EF, SM and AD performed the research. EF analyzed the data. EF and LJT wrote the paper. All authors edited the final manuscript.

Data Availability Statement

All data and SPSS outputs for all tables and figures can be found here.

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	FL Sites	
Frequency (Hz)	*t*	*p*
0.556	4.853	<.001
1.111	5.345	<.001
1.667	5.139	<.001
2.222	5.607	<.001
2.778	4.615	<.001
3.333	5.161	<.001
	FR Sites	
0.556	4.215	<.001
1.111	5.125	<.001
1.667	5.245	<.001
2.222	5.039	<.001
2.778	3.530	.002
3.333	6.768	<.001

Table 1. t-test Results for Infant SSRs Comparing Frequencies of Interest and Harmonics Against the Noise floor.

Note. All t-tests reflect the comparison of frequency-noise floor for all participants across groups, with df = 23. All results are significant after Bonferroni correction (all $p < .008$).

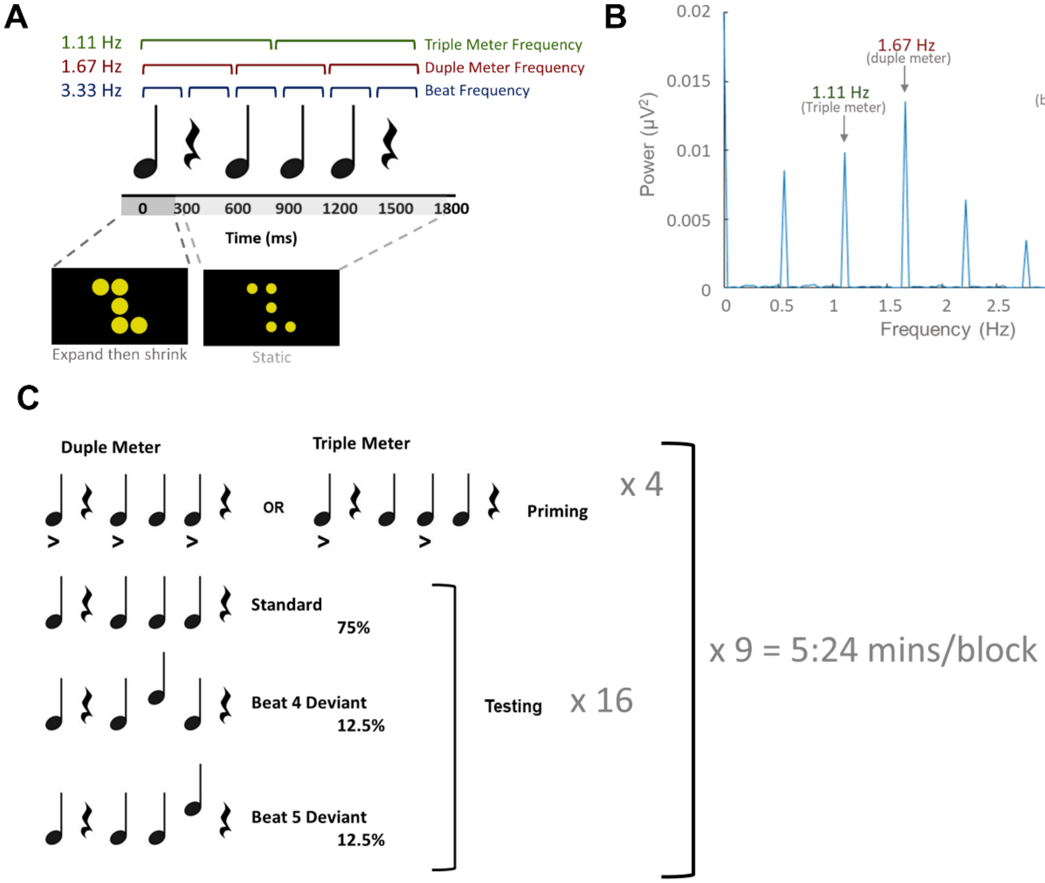

Figure 1. Stimulus. A) Single repetition of the 6-beat ambiguous pattern. Labelled are the beat and meter frequencies in the stimulus used for the steady-state response analysis, as well as the visual stimulus sequence. An array of 5 to 9 circles expanded and shrunk on every beat 1 of the six-beat stimulus, then remained static for beats two to six. The colour and arrangement of the circles changed randomly every 20 trials. **B)** Stimulus power across frequency (based on the average stimulus across the different pitches and timbres used). **C)** Continuous auditory stimulus paradigm. Each set of stimuli always started with 4 priming trials of either duple or triple meter indicated by loudness accents, followed by 16 pseudo-randomly ordered test trials. This 20-trial set repeated 9 times (5 min 24 s) in each block. Infants could complete up to 3 blocks. Each block varied either in timbre (piano, guitar, or vibraphone A440), or pitch (piano A, C#, or E), such that the timbre or pitch changed every 20-trial set.

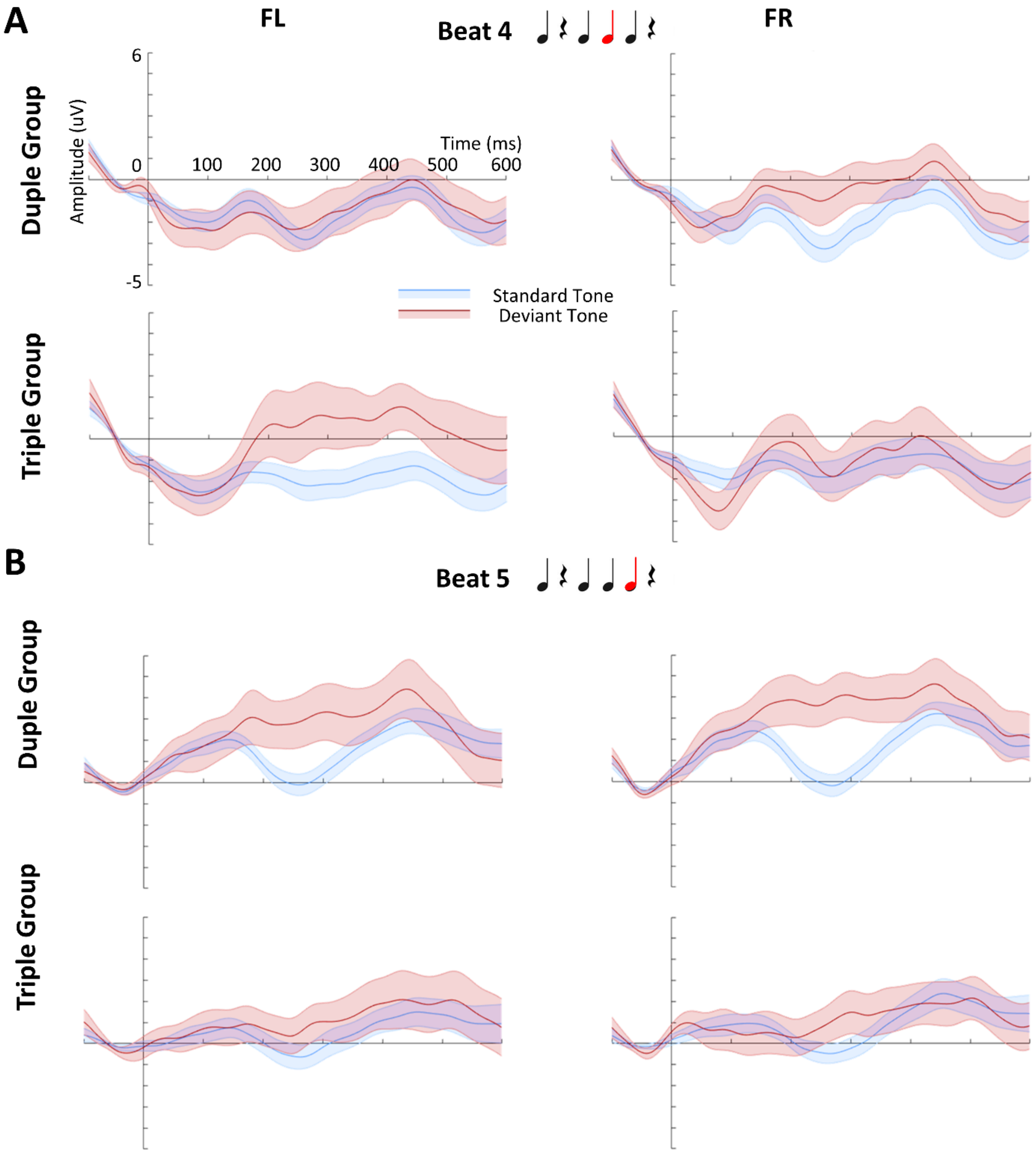

Figure 2. Infant ERPs – Standards and Deviants. ERPs for beat 4 (A) and beat 5 (B) standards and deviants for FL (left column) and FR (right column) electrode site averages for the duple (top row) and triple (bottom row) priming groups. Shaded regions represent the standard error of the mean. Note that in (A) deviants on are beat 4 whereas in (B) deviants are on beat 5.

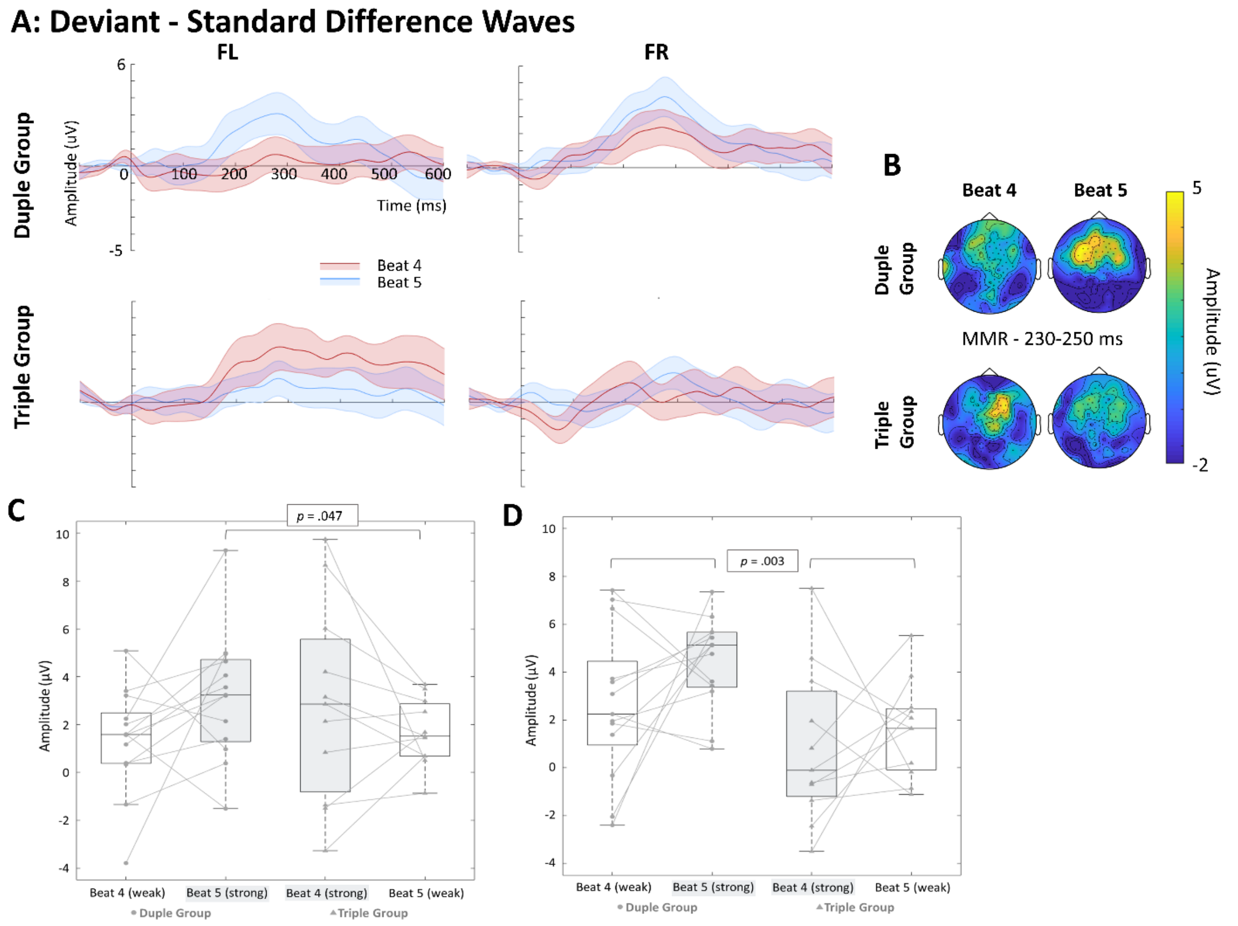

Figure 3. Infant ERPs – Difference Waves. A) Infants' deviant-standard difference waves for beats 4 and 5 separately by duple (top row) and triple (bottom row) priming groups. Shaded regions represent the standard error of the group mean. **B)** The MMR topographies for beat 4 (left) and beat 5 (right) for both priming groups averaged between 230 and 250 ms. **C)** Boxplots with paired scatterplots for the stand/dev x beat position x group interaction in FL showing the MMR amplitudes for beat 4 and beat 5 for each priming group for the deviant-standard differences. **D)** Boxplots with paired scatterplots for the stand/dev x group interaction in FR showing the amplitudes for each priming group for beat 4 and beat 5 for the deviant-standard differences.

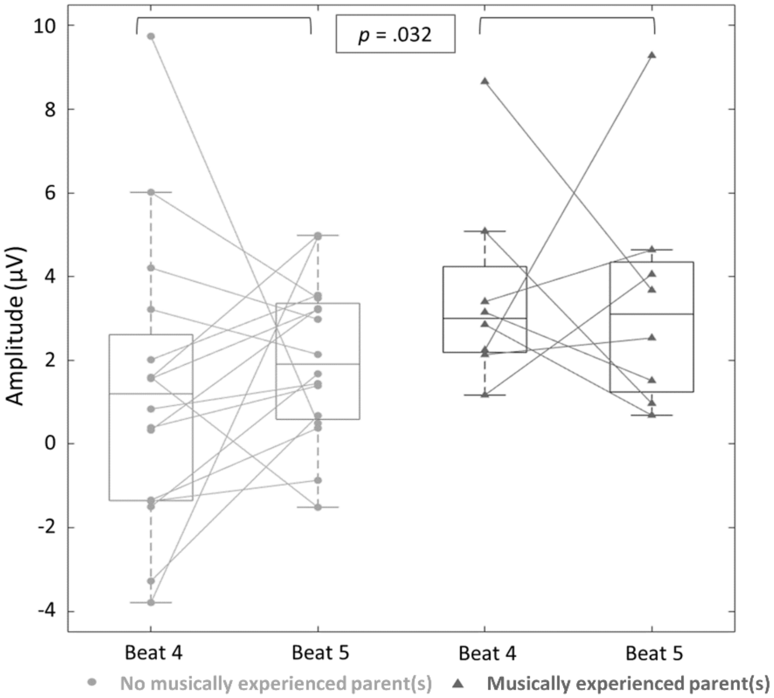

Figure 4. Effect of Musical Experience of the Parent on MMR at Frontal Left Sites. Boxplots with paired scatterplots for MMR (deviant-standard) amplitudes. Amplitudes were more positive for infants with at least one musically experienced parent.

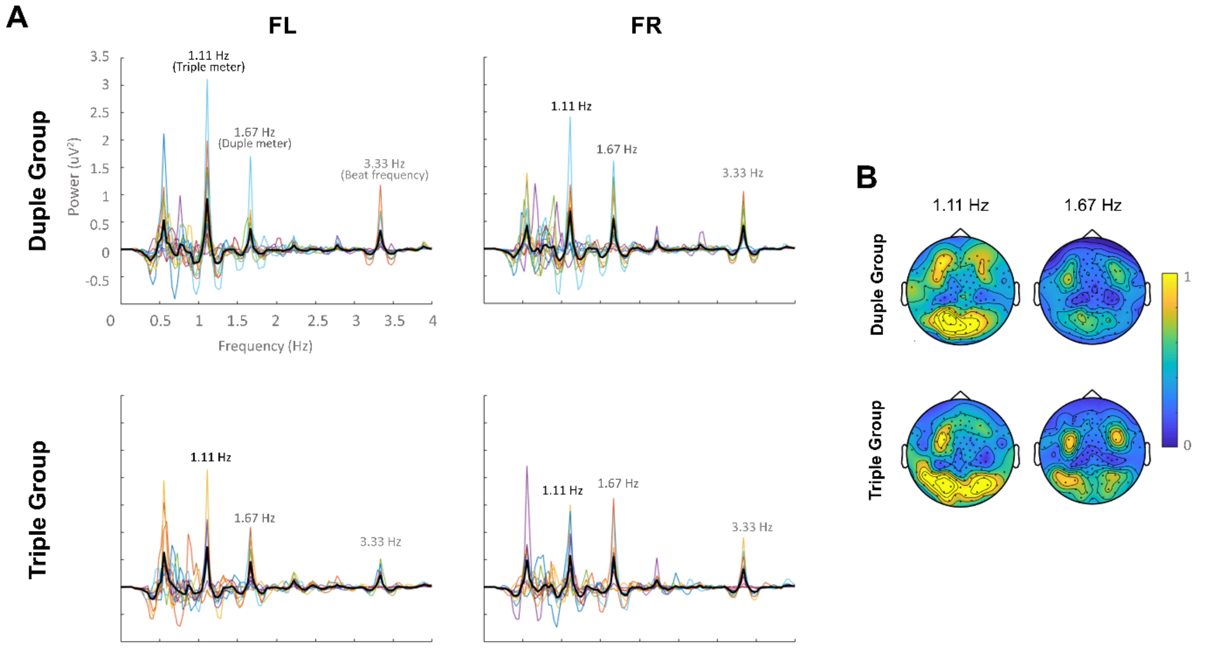

Figure 5. (A) The frequency spectra of individuals' (coloured lines) and the group average (bold black lines) SSEPs for FL (left column) and FR (right column) electrode groupings for the duple (top row) and triple (bottom row) priming groups. **B)** The average topography for the triple (left column; 1.11 Hz) and duple (right column; 1.67 Hz) frequencies in the duple (top) and triple (bottom) priming groups.