TOP-DOWN NEURAL PROCESSING OF RHYTHM IN INFANTS AND ADULTS

TOP-DOWN INFLUENCES ON NEURAL PROCESSING OF RHYTHM IN INFANTS AND ADULTS

By Erica Flaten, B.Sc. (Honours)

A Thesis Submitted to the School of Graduate Studies in Partial Fulfillment of the

Requirements for the Degree Doctor of Philosophy

McMaster University © Copyright by Erica Flaten, November 2024

McMaster University DOCTOR OF PHILOSOPHY (2024), Hamilton, Ontario (Psychology, Neuroscience & Behaviour)

TITLE: Top-down influences on neural processing of rhythm in infants and adults AUTHOR: Erica Flaten, B.Sc. (Honours, University of Manitoba) SUPERVISOR: Professor Laurel J. Trainor NUMBER OF PAGES: 314, xvii

Lay Abstract

Rhythm perception involves grouping sounds into meaningful units, especially in ambiguous contexts. In music, an unaccented 6-beat rhythm pattern could be interpreted as three groups of 2 beats (e.g., a march), or two groups of 3 beats (e.g., a waltz). Infants are born with some rhythm perception abilities, but whether they can apply their own interpretations of an ambiguous rhythm was not well understood. Here I show for the first time that the infant brain can be influenced to interpret the same ambiguous rhythm either as a march or a waltz, although this may be limited to certain contexts. Comparatively, adults were less flexible to applying different interpretations, likely due to a learned bias to hear the rhythm as a march, although engaging attention reduced this bias. Overall, this work shows how the brain applies interpretations of auditory rhythms in infancy and adulthood, having implications for music and language development.

Abstract

In music, listeners extract the beat and can also group beats, such as duple metre (2-beat groupings) or triple metre (3-beat groupings). This internally derived (top-down) structure can give rise to multiple interpretations of a metrically ambiguous rhythm. Top-down rhythm perception is important for music and language development but has thus far been understudied in infants. In the current thesis, six-month-old infants (Chapters 2 and 4) and adults (Chapter 3) were primed to interpret a metrically ambiguous 6-beat rhythm either in duple or triple metre, by periodically adding loudness accents on beats 1,3 and 5, or on beats 1 and 4, respectively, before hearing the unaccented, ambiguous rhythm. Using electroencephalography (EEG), I examined whether the primed metre influenced participants' predictions of individual beats within the rhythm, indexed by mismatch responses, as well as whether the primed metre improved the brain's overall tracking of the metre frequency, as indexed by neural tracking measures.

Infants' predictions of unexpected pitch changes occurring on beats 4 or 5 were modulated by the primed metre, such that mismatch responses were larger for the strong compared to weak beat position according to the primed metre (Chapter 2), especially in the duple case. Adults (Chapter 3) were comparatively less flexible than infants to being primed, showing a robust bias to the duple metre across EEG measures, although actively attending to the metre improved neural tracking of the primed metre. Further, infants may be limited in their generalizability of a primed metrical structure across different tempos (Chapter 4). Across chapters the results also suggest a duple bias that starts in infancy and is strengthened by musical experience. This thesis provides the first evidence of infants' top-down maintenance of a structure on an ambiguous rhythm while directly comparing to adults. The work has implications for understanding music and language perception development, and developmental disorders.

Acknowledgements

I have many people to thank for supporting me during my PhD journey over the last 6 years. I first need to thank my supervisor, Dr. Laurel Trainor. I will forever be grateful that I got to conduct such interesting and fun research with someone as experienced and supportive as Laurel, and in such a positive lab environment. I have Laurel to thank for encouraging me to be the best researcher I can be, allowing me to achieve more in these last 6 years than I thought I was capable of. I look forward to continuing a collaborative relationship with Laurel as I continue research in developmental neuroscience during my post-doc with Dr. Janet Werker. I also thank my wonderful committee members, Dan B., Louis, and Gabriel, who've provided invaluable mentorship and encouragement over the years.

The positive lab environment that Laurel has fostered would not be the same without her amazing staff. Elaine, thank you so much for being such a joy to work with and for teaching me so much about how to work with infants and families. I could not have completed any of my data collection without you, and the positive energy that you brought into the EEG lab is infectious. Susan, thank you for your unwavering efforts to make sure all our research in the lab had ethics to run, including in adapting everything for COVID measures which is no small feat. I also want to thank Dave, Dan B, Sally, and Hany for their technical support, and although the current thesis does not include some of my work done in the LIVELab, these folks are imperative in helping to keep things running smoothly and have been great colleagues.

vi

Further, I would not have been able to complete this thesis without the support of such amazing lab mates. When I first joined the lab, Andrew and Haley were inspirational senior grad mentors who helped me immensely in getting settled into my research, not to mention both being extremely kind. One of my first friends and fastest bonds when I moved to Hamilton was Sarah L, whose unwavering friendship I am continually grateful for. I also must thank Laura Cirelli, whose incredible work with infants in the Trainor lab has inspired a lot of the work in this thesis, and who has taken time to give me valuable insight while starting her professorship at U of T. Several post-docs in the lab have been amazing mentors, friends, and collaborators, Dobri, Dan C, Sean, March, and Rafa. I also must thank the rest of my lab mates, David, Hector, Debanjan, Chantal, Emily, Rachael, Lucas K, Jesse, Shu, Sara, and Maya. A special thank you goes to David, as I could not have survived these last 6 years without you. It has been an honour to have you not only as my lab mate, but my also my room mate and best friend. I am also grateful for the close friendships I share with Shu and Emily, which have been part of the best parts of living in Hamilton.

Other important Hamilton/McMaster friends who are now near and far, and whom I can't thank enough for their friendship and support are Lucas G, Connie, Brendan M, Jessica O, Dani, Carley, Zoë, Brendan W, Sami, Cathy, Lisa, Konrad, and Alaine. Additionally, my family and friends in Winnipeg have always been there for me, and continued to cheer me on, even from ~2000 km away. I have to thank my parents, Tanis and Don (the original Dr. Flaten), who raised me to be the person I am today, always supporting my academic endeavors, and who love and support me every step of the way.

vii

Finally, I thank my loving partner, Eric, who is the best thing to come into my life while living in Hamilton. He has been my number one rock and supporter the last 4+ years. He's loved me at my best, and worst, always knowing exactly how to best support me without question or judgement. I could not have done this without his unconditional love, friendship, and our adventures. I also have to thank Eric's family for giving me a second family while being far away from my own, and who do more for me than they probably know.

Table of Contents

Abstract	iv
Acknowledgements	vi
Table of Contents	ix
List of Figures	xii
List of Tables	xiv
List of All Abbreviations and Symbols	xv
Declaration of Academic Achievement	xvii
Chapter 1: General Introduction	1
Introduction	1
Neural & Behavioural Evidence of Infants' Rhythm Perception	
Neural Measures of Rhythm Perception in the Current Thesis	
Theories of Rhythm Perception: Dynamic Attending & Predictive Coding	
Thesis Outline	
Thesis Contributions	
Deferences	22
References	
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed	23 d neural
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm.	d neural
Chapter 2: Evidence for top-down metre perception in infancy as shown by prime responses to an ambiguous rhythm. Preface.	d neural
Chapter 2: Evidence for top-down metre perception in infancy as shown by prime responses to an ambiguous rhythm. Preface	d neural 47 47 47
Chapter 2: Evidence for top-down metre perception in infancy as shown by prime responses to an ambiguous rhythm. Preface	d neural 47 47 48 49
Chapter 2: Evidence for top-down metre perception in infancy as shown by prime responses to an ambiguous rhythm. Preface	d neural 47 47 48 48 49 58
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm. Preface	d neural 47 47 48 48 49 58 58
Chapter 2: Evidence for top-down metre perception in infancy as shown by primeoresponses to an ambiguous rhythm. Preface	d neural 47 47 48 48 58 58 60
Chapter 2: Evidence for top-down metre perception in infancy as shown by primeoresponses to an ambiguous rhythm. Preface	d neural 47 47 47 48 49 58 58 58 60 60 64
Chapter 2: Evidence for top-down metre perception in infancy as shown by primeoresponses to an ambiguous rhythm. Preface	d neural 47 47 48 48 58 58
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm. Preface. Abstract. Introduction. Materials & Methods. Participants. Stimuli. Procedure. Data Acquisition and Analysis. Results.	d neural 47 47 47 48 49 58 58 58 58 60 60 64 64 66 71
Keterences Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm. Preface Abstract. Introduction Materials & Methods Participants Stimuli Procedure Data Acquisition and Analysis Mismatch Response.	d neural 47 47 47 47 48 49 58 58 58 58 60 64 64
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm. Preface	d neural 47 47 47 48 49 58 58 58 58 60 64 64 66 71 71 71
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm. Preface. Abstract. Introduction. Materials & Methods Participants. Stimuli Procedure. Data Acquisition and Analysis. Results. Mismatch Response. Looking Behaviour. Steady-State Evoked Potentials	d neural 47 47 48 49 58 60 64 66 71 74
Chapter 2: Evidence for top-down metre perception in infancy as shown by primed responses to an ambiguous rhythm. Preface. Abstract. Introduction. Materials & Methods. Participants. Stimuli. Procedure. Data Acquisition and Analysis. Results. Mismatch Response. Looking Behaviour. Steady-State Evoked Potentials.	a neural 47 47 47 48 49 58 58 60 64 66 71 71 74 74 75

Acknowledgements	83
Abbreviations	83
Conflict of Interest Statement	83
Author Contributions	83
Data Availability Statement	83
References	84
Tables	106
Figures	107
Supplementary Information	112
Chapter 3: Western Adults' Neural Responses to An Ambiguous Rhythm: Effects of Priming with and without Active Imagination	116
Preface	116
Abstract	117
Introduction	118
Experiment 1	127
Materials & Methods	128
Results	138
Interim Discussion	139
Experiment 2	141
Materials & Methods	142
Results	148
Combined Exploratory Analyses of Music/Dance Experience for Experiments 1 & 2	152
General Discussion	154
Data Availability Statement	162
Author Contributions	162
Acknowledgements	162
References	164
Figures	178
Tables	186
Supplementary Information	188
Chapter 4: Investigating generalizability of top-down neural representation of metre infancy	n 195
Preface	195

Abstract	
Introduction	
Methods	
Participants	
Stimuli	
Procedure	
Data Acquisition & Analysis	
Looking Behaviour	
Results	
Tempo Control Analysis	
MMR	
SSEPs	
ITPC	
Exploratory effects of musical background	
Looking Behaviour	
Discussion	
Limitations	
Conclusion	
Data Availability Statement	
Author Contributions	
Acknowledgements	
Funding Information	
References	
Figures	
Tables	
Supplementary Information	
Chapter 5: General Discussion	
Main Findings & Contributions	
Additional Interesting Findings	
Limitations & Future Directions	
Potential Clinical Applications	
Summary	
References	

List of Figures

CHAPTER 2

Figure 1	107
Figure 2	
Figure 3	109
Figure 4	110
Figure 5	111
Figure S1	113
Figure S2	113
Figure S3	114
Figure S4	114
Figure S5	115

CHAPTER 3

Figure 1	178
Figure 2	179
Figure 3	
Figure 4	
Figure 5	
Figure 6	
Figure 7	
Figure 8	
Figure S1	
Figure S2	
Figure S3	
Figure S4	

Figure S5	192
Figure S6	193
Figure S7	194

CHAPTER 4

Figure 1	254
Figure 2	
Figure 3	
Figure 4	
Figure 5	
Figure S1	
Figure S2	
Figure S3	

List of Tables

CHAPTER 2

Table 1	
Table S1	112

CHAPTER 3

Table 1	
Table 2	

CHAPTER 4

ole 1

List of All Abbreviations and Symbols

- η_p^2 : partial eta squared
- μ: sample mean
- μV; microvolts
- σ : sample standard deviation
- ANOVA: analysis of variance
- CL: central left
- cm: centimetre
- CR: central right
- CZ: central midline
- d: Cohen's d
- dB: decibels
- DCD: Developmental Coordination Disorder
- DLD: Developmental Language Disorder
- EEG: electroencephalography
- EGI: Electrical Geodesics, Inc.
- ERP: event-related potential
- *F*: F-test statistic
- FFT: fast Fourier transform
- FL: frontal left
- FR: frontal right
- FZ: frontal midline
- Hz: Hertz
- ICA: independent component analysis
- IBI: inter-beat interval
- ITPC: inter-trial phase coherence

kΩ: kiloohms

M: mean

m: metre

ms: milliseconds

min: minutes

MMN: mismatch negativity

MMR: mismatch response

N/n: sample size

n.s.: non-significant

N1: N1 event-related potential

N2b: N2b event-related potential

p: p-value

P3: P3 event-related potential response

P3a: P3a event-related potential response

R: circular mean vector

r: Pearson's r

RM: repeated measures

s: seconds

sec: seconds

SD: standard deviation

SEM: standard error of the mean

SES: socioeconomic status

SSEP: steady-state evoked potential

t: t-test statistic

U: Mann-Whitney U test

x: individual score

z: *z*-score

Declaration of Academic Achievement

The following thesis contains 5 chapters and follows the format of a sandwich thesis. The first chapter is a general intro, followed by three data chapters, all of which are either published articles or submitted manuscripts, then finally a general discussion of the main findings of the thesis for chapter 5. I, Erica Flaten, am the author of this thesis and the primary author for all data chapters. For all data chapters, I conceptualized the research with supervision from Dr. Laurel Trainor, organized and completed the data collection with help from Elaine Whiskin and undergraduate students, completed all the data preparation and analyses, and wrote the manuscripts. Dr. Laurel Trainor is the last author on all 3 manuscripts, as she supervised and provided funding for the research, and contributed to the manuscript preparation. Technical support was provided for Chapter 2 from Dave Thompson. Two of my previous undergraduate thesis students, Angela Dittrich and Sara Marshall, are coauthors on data Chapter 2, they helped with data collection and editing the manuscript. Analysis of tapping behaviour and editing of the final manuscript drafts were done by Chantal Carrillo in Chapter 3, as such she is the second author. For chapter 4, undergraduate students Virtues Dawn Serrano, Maggie (Meng Jia) Lu, and Selina Bains also aided in data collection and Virtues and Selina helped in the stimulus creation.

Chapters 3 and 4 are both extensions of Chapter 2, so the methodology, stimuli, and research questions overlap somewhat.

xvii

Chapter 2 is a reprint of the published article in the European Journal of Neuroscience and has been reprinted with permission from John Wiley & Sons Ltd ("Wiley").

Flaten, E., Marshall, S. A., Dittrich, A., & Trainor, L. J. (2022). Evidence for topdown 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

Chapter 3 is a submitted manuscript to journal Psychophysiology, which is under review and also been posted to Authorea as a preprint.

Flaten, E., Carrillo, C., Trainor, L. (2024) Western adults' neural responses to an ambiguous rhythm: Effects of priming with and without active attention. *Authorea.* Manuscript Under Review.

https://doi.org/10.22541/au.172814927.73345976/v2

Chapter 4 is a submitted manuscript which is currently under review at the Journal

of Cognitive Neuroscience

Flaten, E., Trainor, L. (2024) Investigating generalizability of top-down neural representation of metre in infancy. *Journal of Cognitive Neuroscience*. Manuscript Under Review.

Chapter 1: General Introduction

Introduction

The auditory system is functioning before the third gestational trimester in humans (Fernald, 2004; Graven & Browne, 2008), and even in the womb, infants are exposed to a plethora of rhythmic stimuli such as music and language (Mendoza & Fausey, 2021). Rhythm and musical experience play an important role in infant development, with greater musical exposure at home predicting positive language outcomes (Franco et al., 2024; Langus et al., 2023; Papadimitriou et al., 2021). Further, research suggests a strong link between developmental disorders and deficits in behavioural and neural correlates of rhythm perception (for reviews, see Falter & Noreika, 2014; Ladányi et al., 2020; Lense et al., 2021; Pranjić et al., 2023; Slater & Tate, 2018). Thus, investigating rhythm perception in infancy and adulthood will inform our understanding of development, including potential clinical applications for diagnosing and treating developmental disorders. Infant research on rhythm processing has primarily focused on bottom-up processing, such as showing how the infant brain encodes the rhythmic features indicated by the sound (e.g., Cirelli et al., 2016; Edalati et al., 2023). However, the ability to organize sounds into meaningful units using internally derived, or top-down processes is important for understanding music and speech. Thus, the current thesis aimed to better understand infants' ability to maintain a rhythmic structure in an ambiguous context requiring top-down processes.

For the current thesis, I broadly define top-down processes as those that influence the perceiver's interpretation of a stimulus, such as ingrained or learned biases, or

attentional processes. This can be illustrated by bistable stimuli (Brascamp et al., 2018; Pitts et al., 2008), in which 2 possible interpretations for the same audio or video can arise, where participants with different perceptual biases will have different interpretations, or where the listener can switch between interpretations by means of attention. In audition, a classic example is of hearing two isochronous auditory streams A and B, which are separated by pitch and are at different tempos such that they can be heard as an integrated 'gallop' percept where the A and B events alternate (ABA), or can be heard as two separate, co-occurring streams (van Noorden, 1975). In this example, listeners may be instructed or primed to employ top-down attentional mechanisms to hear the two streams either as integrated or segregated. Rhythms in music and speech are hierarchically structured such that organizing individual sounds into groupings can help to extract or interpret their meaning. For example, speech input is perceptually segmented into syllables, words, and phrases, with segmentation aided by prosodic rhythm, including changes in syllable stress. Such organization is accomplished in part through top-down mechanisms that begin developing early in infancy (Choi et al., 2020; de la Cruz-Pavía & Gervain, 2023; Gervain et al., 2008, 2012; Gervain & Werker, 2013), and infants' ability to perform such segmentation predicts language outcomes (Kabdebon et al., 2015; Kuhl et al., 2005; Menn et al., 2022).

Music is similarly hierarchically organized, and thus involves similar top-down organization. A regular beat or pulse can be derived in the brain from musical rhythmic input, and beats can be grouped to create metres (e.g., groups of 2 or 3 beats). Rhythm is defined by the temporal pattern of successive sound events, and so is indicated in the

sound itself, whereas the beat is the regular underlying pulse in music that is extracted by the brain, even though there need not be sounds occurring on every beat. Metre is the grouping or dividing of beats such that beats starting each grouping are perceived to be emphasized. Often the metre is indicated explicitly by the music, such as by adding loudness accents, or by the pattern of durations between notes (Povel & Essens, 1985; D. Temperley, 2004). Perceivers can encode these features in a bottom-up manner, but metre perception can also involve top-down interpretation of the metrical structure, especially in ambiguous contexts. For example, a metrically ambiguous 6-beat rhythm could be perceptually grouped as one group of 6 beats (ONE two three four five six), two groups of 3 beats (triple metre), like a waltz (ONE two THREE four FIVE six).

I aimed to better understand how infants and adults use internal (i.e., top-down) processes to apply structure to ambiguous auditory rhythms, a skill that can also aid in linguistic processing. To do so, I used electroencephalography (EEG) since it lends well to studying preverbal infants in a non-invasive way, while also allowing for analyses requiring high temporal precision. First, I asked if infants can be primed to neurally interpret an ambiguous rhythm in duple or triple metre by first presenting the rhythm as accented to indicate the particular metre. Second, I asked how adults compare to infants in their ability to be primed to flexibly hear an ambiguous rhythm in duple or triple metre processing. Third, I asked whether infants could maintain a primed metrical interpretation of an ambiguous rhythm while generalizing the metre across varying tempos. I found that in the context of a single

tempo (Chapter 2), infants can be primed to process an ambiguous rhythm in duple or triple metre, indicative of top-down processes; however, they failed to do so in the face of tempo generalization (Chapter 4). Further, I found that adults were less flexible than infants in the face of metrical priming, likely due in part to a strong bias towards the duple metre; however, they did show evidence of top-down metre processing when actively attending to the metrical structure (Chapter 3). Finally, across all three studies I found a duple bias, which is already emerging in infancy, robust in adulthood, and appears to be enhanced by musical experience.

Neural & Behavioural Evidence of Infants' Rhythm Perception

Young Infants Can Discriminate Rhythmic patterns. Infants readily process auditory rhythms as neonates such as by showing neural sensitivity to sudden tempo changes within rhythms, and to silence occurring after the end of rhythms where a tone would be expected if the rhythm were to continue (Háden et al., 2015). Newborns also show neural responses for tone groupings that match the rhythmic structure of their native language (Abboub et al., 2016). Starting prenatally, infants can also segment rhythmic sequences of phonemes based on learned probabilities of the sequential order (Choi et al., 2020; de la Cruz-Pavía et al., 2023; Kabdebon et al., 2015; Gervain et al., 2008, 2012; Panzani et al., 2023). Young infants therefore can learn to group sound events based on patterns of changes in the physical features of such events, a skill involved in grouping sounds based on a metrical structure.

Infants can also detect changes in the tempo of a rhythm. For rhythmically presented tones, the newborn brain detects changes in tempo of at least as small as 100

ms (Háden et al., 2015), and by 2 months, infants can behaviourally detect a 15% increase in tempo (Baruch & Drake, 1997). They can also adjust somatosensory behaviours to tempo changes in an auditory rhythm. Two-month-olds will match their rhythmic sucking rate to a rhythmic cue at 15% faster than their natural sucking rate, although slowing sucking rate to the 15% slower cue appears to be more difficult (Bobin-Bègue et al., 2006). At 5-24 months infants will rhythmically move to music, and while they cannot synchronize their movements to the beat, they will adjust their tempo accordingly to the tempo of the music (Zentner & Eerola, 2010). Thus, infants can detect and utilize timing information in rhythms from birth, with one salient cue being tempo changes.

Infants Encode Beat and Metre. Infants can discriminate different rhythms and detect changes in tempo, but what about their ability to process metrical structure? Research indicates that the infant brain is equipped to encode beat and metre from before birth. Premature infants neurally track beat and metre, showing clear peaks in EEG activity at the beat and metre frequencies (Edalati et al., 2023, 2024), which has also been shown in older infants (Cirelli et al., 2016). Further, the newborn brain can detect unexpected events in a rhythm better if they occur on the beat compared to off the beat (Winkler et al., 2009; Háden et al., 2024). By 6 to 7 months, infants can behaviourally discriminate between rhythms that are in duple versus triple metre, where the metre is indicated by note durations (Hannon & Johnson, 2005; Phillips-Silver & Trainor, 2005). Together this shows infants can detect the metrical structure in rhythms early on, such as by bottom-up encoding of beat and metre, and later they can discriminate different metres.

Enculturation Influences Metre Perception. Metre perception development is influenced by the music in one's cultural environment, a process called enculturation (Hannon & Trainor, 2007). Bulgarian or Macedonian adults can just as easily process Balkan and Western rhythms (Hannon & Trehub, 2005a), but Western adults are generally better able to process Western rhythms (Hannon & Trehub, 2005a, 2005b). In Western music, the most common metre is duple (D. Cohen & Katz, 2008; Gerry et al., 2010; D. Temperley, 2010) and accordingly, Western adults (Møller et al., 2021; Poudrier, 2020) and children (Drake, 1993) show biases towards duple over non-duple metres. For example, Western adults automatically apply a duple grouping structure to an isochronous rhythm of identical sounds (e.g., hearing 'Tick', 'Tock' instead of 'Tick', 'Tick'; Brochard et al., 2003; Haumann et al., 2018; N. M. Temperley, 1963), whereas bicultural adults with Western and African music exposure seem to not do this (Haumann et al., 2018). Infants seem to be more flexible than adults in perceiving rhythms that are in different metres, and this flexibility fades with age as they gain experience with the music from their culture. For example, 6-month-old Western infants can easily distinguish rhythms with simple Western (e.g., duple) or complex Balkan (e.g., groups of 7) metres (Hannon & Trehub, 2005a), whereas 12-month-olds cannot, although exposure at around 12 months of age to complex rhythms can reinstate this ability (Hannon & Trehub, 2005b). Note that a universal duple or binary bias may be present due to its ubiquity across natural systems (e.g., locomotion; Larsson, 2014; Larsson et al., 2019; Sadeghi et al., 2000), and across music systems (Polak et al., 2018; Savage et al., 2015). Interestingly, infants taking music classes (Cirelli et al., 2016; Gerry et al., 2010, 2012;

Trainor et al., 2012) show enhanced processing of Western over non-Western rhythms, melodies, and/or enhanced neural responses to tones, suggesting accelerated enculturation via experience engaging in Western music-making. A duple bias internal to the listener, whether arising from universal or enculturated biases, represents a top-down influence.

Gaps Addressed by the Current Thesis. To summarize, while the aforementioned studies clearly show a propensity for infants to process auditory rhythm, there is little evidence of their top-down maintenance of an internalized metre. Although, top-down rhythm processing is suggested by neural encoding of beat and metre from a rhythm with little energy at the beat frequency (Lenc et al., 2022), and by their derivation of a beat beyond information from learning statistical regularities in the rhythm (Háden et al., 2024). Seven-month-olds can even be behaviourally influenced to perceive an ambiguous 6-beat rhythm in either duple or triple metre, by first bouncing them on every second or on every third beat, respectively (Phillips-Silver & Trainor, 2005), suggesting some ability to flexibly apply a top-down metrical interpretation. However, whether infants could be influenced (primed) to perceive the same rhythm in different metres without explicit movement had not previously been investigated. Further, the neural underpinnings of top-down cognitive processes involved in infants' metre processing had not been previously explored thoroughly.

Additionally, research on the generalizability of infants' rhythm perception across different examples is limited. We know that at 7 to 9 months, infants can categorize tones that share the same timbre but vary in frequency, loudness, or duration (Trehub et al., 1990) or can group tones within a rhythm based on shared frequency or loudness (Trehub

& Thorpe, 1989). Thus, while there is preliminary evidence that infants can categorize rhythms, the extent to which infants can generalize an internally derived metrical structure across different tempos is unknown. Finally, given that metre perception changes across development, with greater influence of enculturation with age, the thesis directly compared top-down metre processing between infants and adults.

Neural Measures of Rhythm Perception in the Current Thesis

How the brain encodes rhythm and applies a top-down structure can be investigated with EEG measures. Specifically, how metre can influence the way the brain responds to and predicts individual upcoming beats can be measured using event-related potentials (ERPs), which are neural responses to sound events. Additionally, how the brain tracks the frequencies of the different hierarchical levels of an auditory rhythm (e.g., beat, duple metre, triple metre) over longer durations can be measured by neural tracking.

Event-Related Potentials. An ERP is a measure of the brain's response to a particular event, shown by changes in amplitude over time from the onset of the event. Different ERP components are elicited by different types of events. Upon presentation of an auditory rhythm, the brain will automatically predict upcoming events (e.g., Vuust & Witek, 2014), and this process can be probed by inserting unexpected deviant tones amongst a stream of expected standard tones and measuring the brain's response to these expectation violations. Deviants can take the form of any unexpected change in a stimulus feature, such as a change in pitch, loudness, duration, or timbre. In adults, deviants elicit the mismatch negativity (MMN), which is a response with negative amplitude at frontocentral sites, peaking ~ 100-250 ms after the deviant onset (Maurer et al., 2003;

Näätänen et al., 1993, 2004, 2007; Schwade et al., 2017). MMN is often followed by a positive P3a response, peaking ~ 200-350 ms maximally in central channels (Escera et al., 2000; Polich, 2007; Widmann et al., 2018; Wronka et al., 2012). MMN measures the automatic detection of deviant events, although it may be modulated by top-down processes (Sussman et al., 1998, 2002). For example, metrical context can lead to enhanced MMN for unexpected omissions (Bouwer et al., 2014; Ladinig et al., 2009; Winkler et al., 2009), or loudness decrements (Bouwer et al., 2016; Háden et al., 2024; Haumann et al., 2018) in strong, compared to weak beat positions. P3a immediately follows MMN in conscious participants, indexes the initial capture of attention by the deviant (Comerchero & Polich, 1998; Escera et al., 2000; Katayama & Polich, 1998; Polich, 2007; Trainor et al., 1999), and may also be modulated by loudness decrements in strong beat positions (Abecasis et al., 2005; Bouwer et al., 2016; Brochard et al., 2003; Potter et al., 2009), or for a probe tone occurring in-versus out-of-phase with the strong beat position (Jongsma et al., 2004). Auditory MMN is generated primarily by auditory cortex, but also includes contributions from frontal and parietal areas (Giard et al., 1990; Maurer et al., 2003; Rinne et al., 2000; Takasago et al., 2020), and shows right hemisphere dominance (Giard et al., 1990; Levänen et al., 1996; Paavilainen et al., 1991; Rinne et al., 2000). P3a sources are primarily located in frontal cortex and anterior cingulate gyrus (Polich, 2007; Wronka et al., 2012), suggesting a role of top-down attentional mechanisms in P3a generation (Polich, 2007).

Infants show a mismatch response to deviant tones as well, but this often appear as a frontally positive slow response peaking ~ 200-400 ms (Basirat et al., 2014; Bristow

et al., 2009; Chen et al., 2022; Cheng et al., 2015; Trainor, 2012; Trainor et al., 2003). Easier deviant contrasts (Cheng et al., 2015; Cheng & Lee, 2018; Götz et al., 2024), and older infant age (Cheng et al., 2015; Götz et al., 2024; He et al., 2009a, 2009b; Kushnerenko et al., 2001; Morr et al., 2002; Trainor et al., 2003; Werwach et al., 2022) are both associated with elicitation of more adult-like MMN (Govaart et al., 2023). While evidence is preliminary, studies suggest that sources of positive mismatch response (MMR) are somewhat different from those for MMN. As expected, MMR has been localized to auditory cortex (Sambeth et al., 2009), but the main generator appeared to be shifted in orientation, and more left-lateralized compared to adult-like MMN (Hämäläinen et al., 2011; Ruhnau et al., 2013). This suggests that positive MMR and adult-like MMN index similar functions, but distinct neural processes (Govaart et al., 2023; Kushnerenko et al., 2002; Sambeth et al., 2009; Trainor, McFadden, et al., 2003). For the current thesis, I consistently found a frontally positive MMR in infants, which I refer to throughout as MMR. Across Chapters 2, 3 and 4, infant MMR and adult MMN/P3a were measured for pitch deviants on primed strong and weak beat positions, with the prediction that they would be enhanced for strong compared to weak beat positions, according to duple or triple priming.

Neural Tracking Measures. While mismatch responses represent transient predictive processes across beats, I used measures of neural tracking to examine how the brain tracks the hierarchical structure of a repeating rhythm. Note that Chapter 2 loosely uses the term 'neural entrainment' in the introduction, but otherwise the thesis uses the more general term of 'neural tracking' (Obleser & Kayser, 2019). Oscillatory neural

entrainment occurs when pre-existing oscillatory activity synchronizes in time with a rhythmic stimulus, by predictively aligning periods of high excitability with beat onsets, and continues entraining at least a few cycles after the rhythm stops (Haegens & Zion Golumbic, 2018; Obleser & Kayser, 2019). For example, in non-human primates, delta oscillations from primary auditory cortex were recorded and distinguished from evoked responses, showing phase-locking of ongoing activity with a rhythmic stimulus which continued for several seconds (Lakatos et al., 2013). Further suggestive evidence of neural entrainment comes from time-frequency analyses such as phase-locking of delta activity in time to the beat of a presented rhythm (Arnal et al., 2015; Besle et al., 2011; Schroeder & Lakatos, 2009; Stefanics et al., 2010), or power modulation (desynchronization and resynchronization) of high frequency neural oscillations (e.g., beta band, 15-30 Hz) at the tempo of the perceived beat, and in anticipation of the event onsets (Arnal et al., 2015; Fujioka et al., 2012, 2015). The current thesis used two measures to index how low-frequency brain activity tracks the beat and metre frequencies in infants and adults. Specifically, steady-state evoked potentials (SSEPs) and inter-trial phase coherence (ITPC) were used to measure the neural signal power and phase consistency, respectively, at the specific beat, duple metre, and triple metre frequencies of interest. Given that these measures likely index both oscillatory and evoked activity (Damsma et al., 2024), I use *neural tracking* here to generally refer to alignment of regular activity (oscillatory and/or evoked) with the beat and metre.

While ERPs measure the averaged time-locked change in amplitude to individual events, SSEPs measure the energy of specific frequencies in the time-averaged signal for

the full duration of the repetitive stimulus. SSEPs have been used to index rhythm perception in many studies and over different age groups. There is evidence of top-down modulation of SSEPs in adults, such as enhancement of SSEP peaks at metre-related frequencies via active imagination of the metre (Celma-Miralles et al., 2016; Nozaradan et al., 2011; Nave et al., 2019), or via moving to the metre beforehand (Chemin et al., 2014). One study also showed enhanced SSEPs for duple or triple metre for an ambiguous 6-beat rhythm after being primed with a melody that implied a duple or triple context (Nave et al., 2022). Fewer studies have used SSEPs in infants and have thus far only shown bottom-up encoding of the beat and metre frequencies in the stimulus (Cantiani et al., 2022; Cirelli et al., 2016; Edalati et al., 2023), except for one study showing SSEP peaks at metre frequencies even for rhythms with little energy at those frequencies (Lenc et al., 2022). However, there's been some criticism of interpreting beat perception from SSEPs, given that stimulus properties can greatly influence stimulus spectra from the same rhythmic pattern (Obleser et al., 2017). Nonetheless, given topdown effects of metre imagination on SSEPs (Nozaradan et al., 2011; Nave et al., 2019), and evidence of enhancement of SSEPs correlating with perception of the rhythm (Gibbings et al., 2023; Nave et al., 2022; Nozaradan et al., 2016), SSEPs do at least partially index beat and metre perception. There also may be an important role of explicit attention to the metre in facilitating SSEPs to index beat perception in some cases (Celma-Miralles & Toro, 2019; Gibbings et al., 2023).

ITPC is a measure of consistency in phase angles of neural activity in a certain narrow frequency range from trial-to-trial, where each trial is the neural time signal over

the full duration of a repetitive rhythm. ITPC values range from 0, for equally uniform randomness of phase angles, to 1, for perfectly identical phase angles (M. X. Cohen, 2014). Thus, unlike SSEPs which calculate the signal power over the time-averaged signal, ITPC maintains trial variability. Similarly to SSEPs, ITPC can be measured at the beat and metre frequencies in the stimulus as an index of how consistently the brain is processing the rhythmic structure (Cameron et al., 2019; Herrmann & Johnsrude, 2018), and can indicate participants' subjective beat perception (Tal et al., 2017). In language, this measure has similarly been used to show word learning over time in infants and adults. For example, ITPC increased for the triple frequency as participants learned to group syllables into trisyllabic pseudowords (Batterink & Paller, 2019; Choi et al., 2020; Kabdebon et al., 2015). In the current thesis, ITPC was used to explore whether phase consistency would be greater at the primed compared to unprimed metre frequency.

Neural processing of rhythm has been linked to musical experience across age groups. For example, relative to untrained participants, auditory evoked potentials to tones are enhanced in adult musicians (Shahin et al., 2003), and in 4- to 5-year-old children taking music classes (Shahin et al., 2004), including after being randomly assigned to the classes for a year (Fujioka et al., 2006). In adults, metre-specific effects in modulating ERPs for strong compared to weak beat positions were greater in musically experienced, compared to inexperienced participants (Bouwer et al., 2016; Brochard et al., 2003; Jongsma et al., 2004), suggesting that musical experience may benefit participants' ability to utilize metre to make temporal predictions. Further, SSEPs (Celma-Miralles & Toro, 2019) or ITPC (Doelling & Poeppel, 2015) were stronger to

beat-related frequencies in musicians than non-musicians, suggesting music experience may enhance neural tracking of rhythmic structure. Western infants attending regular music classes also show enhanced ERPs to the tones at the onsets of metre groupings (Cirelli et al., 2016; Trainor et al., 2012), and an enhanced SSEP peak at the duple frequency (Cirelli et al., 2016). Although mostly correlational, these results suggest that musical experience may bestow listeners with more efficient or advantaged neural processing of rhythms, at least for those with metres reflective of the culture, which seems to start in infancy.

In summary, neural top-down processing of auditory rhythms can be indexed using EEG. Predictive processing of individual beats can be reliably measured by the MMN and P3a in adults, as well as the complementary MMR in infants, in response to unexpected events. I predicted that listeners would show larger ERP amplitudes (more negative MMN, more positive P3a and MMR) for pitch deviants on perceptually strong compared to weak beat positions. Neural tracking measures can be used to index how low-frequency brain activity tracks the beat and metre overall. I predicted increased power (SSEPs) and phase consistency (ITPC) for perceived beat and metre frequencies. Further, given links between musical experience and neural measures of rhythm perception, the current thesis explored the role of music and/or dance training (in adults) and music class enrollment (in infants), in modulating neural processing of rhythm. Overall, I found effects of musical experience in all three data chapters, which were linked to a bolstered duple bias in Chapters 3 and 4, suggesting effects of enculturation to Western music in both infants and adults.

Theories of Rhythm Perception: Dynamic Attending & Predictive Coding

Two seminal theoretical frameworks of rhythm perception are dynamic attending (Jones & Boltz, 1989; Large & Jones, 1999; Schroeder & Lakatos, 2009) and predictive coding (Friston, 2005; Lumaca et al., 2019; Vuust et al., 2009; Vuust & Witek, 2014). Dynamic attending, and it's more recently adapted neural resonance theory (Large & Snyder, 2009) are based on dynamical systems modelling, suggesting that coupled oscillatory mechanisms will emerge when neural activity and/or attention synchronizes with a rhythmic stimulus. This is proposed to benefit processing of events occurring incompared to out-of-phase with the oscillations, due to increased predictability and thus attention at those places (Large & Jones, 1999; Schroeder & Lakatos, 2009). Consequently, studies have shown that strength of neural tracking to an auditory or audiovisual rhythm is correlated with behavioural performance (e.g., Chang et al., 2019; Henry & Herrmann, 2014; Henry & Obleser, 2012; ten Oever et al., 2017; Townsend et al., 2024). In the context of metre perception, enhanced ERPs for strong compared to weak beat positions has been associated with stronger beat/metre perception (Bouwer et al., 2023; Bouwer & Honing, 2015; Fitzroy & Sanders, 2020; Nozaradan et al., 2011, 2016; Schaefer et al., 2011), consistent with dynamic attending. Many auditory studies, however, have failed to find support for dynamic attending by means of facilitated perception/behaviour for tone duration (Román-caballero et al., 2024) or pitch discrimination (Bauer et al., 2015; Lin et al., 2022; Román-caballero et al., 2024), or for target detection at varying lags compared to beat onsets (Sanabria et al., 2011; Sun et al., 2022). Often if there are effects, they are highly heterogenous across participants (Bouwer et al., 2023; Criscuolo et al., 2023). Thus, more work is needed to elucidate the conditions under which dynamic attending effects are observed, but it is still a relevant framework for the current thesis to consider how a primed metre may facilitate neural processing of events at strong and weak beat positions.

Additionally relevant to the current thesis is predictive coding, which posits that the listener forms a predictive model based on the rhythmic input. Thus, a neural representation of the rhythm is formed along with weighted expectancies, which are modulated based on the rhythmic context. Metre can thus help to reduce prediction error for surprising events occurring at points with higher certainty (Friston, 2005; Koelsch et al., 2019; Vuust & Witek, 2014), which could hypothetically reduce MMN amplitudes depending on the deviant and the expected context (Bouwer & Honing, 2015; Koelsch et al., 2019; Lumaca et al., 2019; Vuust et al., 2009). For example, loudness accents on a weak beat elicited larger magnitude MMN than on the strong beat, in line with a larger prediction error for louder notes occurring in weak beat positions, given that they'd be more unexpected (Bouwer & Honing, 2015). Thus, while MMN and P3a may generally be enhanced for deviants in strong compared to weak beat positions in line with dynamic attending, certain contexts may lead to reductions of prediction error, and thus reduce MMN/P3a amplitudes for strong beat positions.

In sum, dynamic attending and predictive coding models of rhythm perception are both relevant to understanding neural tracking of rhythm and top-down metre processing (Large et al., 2023), but may lead to different interpretations. In the context of metre processing, the processing of surprising or unexpected events may be facilitated by

underlying oscillations that track the interpreted metre frequency, thus facilitating processing of events on strong compared to weak beat positions. Further, a predictive model formed based on a metrical interpretation may help to reduce prediction error for deviants in strong beat positions, but this may depend on the level of surprise of the event, the listener's context, and the stage of processing in the brain.

Thesis Outline

The current thesis investigated whether 6-month-old infants (Chapters 2 and 4) and adults (Chapter 3) could be primed to interpret a metrically ambiguous rhythm in duple or triple metre via top-down processes, as shown by enhanced mismatch responses (MMN/P3a in adults, MMR in infants) to deviants occurring in strong, compared to weak beat positions, as well as by enhanced neural tracking as shown by SSEPs ITPC (Chapters 3 and 4) at the rhythmic frequency of the primed, compared to unprimed metre. Further, I explored whether active attention modulated top-down metre processing in adults (Chapter 3), and whether infants could generalize a primed metrical structure across rhythms of varying tempos (Chapter 4). Finally, connections to musical experience were explored across all three data chapters. While previous work has demonstrated a clear propensity for rhythm perception in infants from birth, very few studies have tested if infants can maintain a top-down metrical interpretation of an auditory rhythm. The current thesis additionally extends previous work by applying identical methods between infants and adults to compare neural processing of rhythm at two different developmental timepoints.
Chapter 2 asked whether infants could neurologically maintain a top-down metrical interpretation of an ambiguous rhythm. Six-month-old infants were primed to hear a 6-beat rhythm either in duple or triple metre, by intermittently presenting the rhythm with loudness accents on beats 1, 3 and 5 to indicate duple metre, or on beats 1 and 4 to indicate triple. Unaccented (ambiguous) test trials were identical between priming groups, and contained rare pitch deviants that could occur on either beat 4 or 5 and which elicited MMR. I predicted larger amplitude MMRs for the strong beat (beat 5 in the duple-primed group, beat 4 in the triple-primed group), compared to the weak beat (beat 4 in duple, beat 5 in triple), even though infants in both priming groups heard the same unaccented trials at test. Neural tracking to all ambiguous trials was measured with SSEPs, for which I predicted enhanced peaks at the primed compared to unprimed frequencies. I found novel evidence of infants' top-down metre perception as indexed by larger MMR for the strong compared to weak beat, although effects were stronger in the duple-primed infants. However, evidence of priming was not present in the SSEPs, suggesting that infants' processing of unexpected events was influenced by top-down processes, whereas their overall neural tracking of the metre was not (at least as measured by SSEPs).

Chapter 3 explored whether Western adults—with much experience with the rhythms common in Western music—primed exactly as infants in chapter 2 would also show neural evidence of a top-down metrical interpretation of an ambiguous rhythm (Experiment 1), and whether explicit attention would modulate effects of priming on neural processing of the rhythm (Experiment 2). In experiment 1, adults underwent an

identical priming paradigm as infants in chapter 2, where they heard a metrically ambiguous 6-beat rhythm after being primed to hear it either in duple or in triple metre. Adults were asked simply to listen attentively to the rhythm but were not explicitly instructed to interpret the rhythm in duple or triple metre. MMN and P3a were measured for pitch deviants occurring on beats 4 and 5. I predicted that, if adults' predictive processing of the rhythm could be influenced by metrical priming similarly to infants, then ERPs should be enhanced for strong compared to weak beat positions. Additionally, given adults' general abilities to engage in sustained attention and top-down processes, I expected them to neurally track the primed metre, as shown by enhanced SSEP peaks at the primed compared to unprimed frequencies. Unlike the infants in Chapter 2, instead of enhanced ERPs to the strong beat compared to the weak beat, a larger P3a was found for the duple strong beat (beat 5), regardless of whether adults were primed with the duple or the triple metre. Similar to the infants in Chapter 2, SSEP spectra were equivalent for the beat and metre frequencies between priming conditions. This suggests that adults were not primed to neurally process the rhythm in duple or triple metre, but instead showed a bias to process the rhythm in duple metre. Thus, in Experiment 2, another sample of adults underwent the same priming paradigm as in experiment 1, with the additional instruction to actively attend to the metre by imagining the accents from priming trials to continue through the unaccented trials. Metre perception was separately confirmed with a drum tapping task, and questions were asked intermittently to probe participants' ratings of their metre perception. Experiment 2 replicated ERP effects from Experiment 1, where the only effect was a larger P3a for beat 5 regardless of priming group. Attention to the

metre did, however, enhance SSEPs at the primed, compared to unprimed frequency, but especially in the duple context. I additionally measured ITPC to the beat and metre frequencies but did not find any differences between priming groups in either experiment. Combined results from both experiments in Chapter 3 revealed that adults' bias towards beat 5 in P3a was driven by the musically experienced participants, thus suggesting that Western adults have an inherent duple bias that is augmented by musical training. Further, while predictive processing of events in strong and weak beats was generally not influenced by priming, neural tracking of the metre was strengthened with active attention.

Chapter 4 aimed to extend the findings of chapter 2 by testing infants on their ability to generalize a primed metrical structure across rhythms of varying tempos. Additionally, the stimulus was changed from the non-isochronous pattern used in Chapters 2 and 3 to an isochronous stimulus, given that the non-isochronous rhythm was slightly biased toward the duple metre. Six-month-old infants were again primed via loudness accents to indicate either duple or triple metre, and rare pitch deviants occurred in the following ambiguous trials on beats 4 or 5. To test tempo generalizability, priming trials occurred at one of four possible tempos (i.e., four different inter-beat-intervals) and test trials all occurred at the same tempo, which was different from any of the priming tempos. Unlike in Chapter 2, MMRs were not enhanced for the strong beat compared to the weak beat under these conditions, suggesting that the dual task of maintaining a primed metre and generalizing across tempo may have been too difficult for 6-month-old infants. However, MMR for beat 5 was larger than for beat 4, but only in infants who

were attending regular music classes. Neural tracking of the rhythm was stronger in the duple-primed group, at the beat frequency for both SSEPs and ITPC, and at the duple frequency for SSEPs. These results suggest that while 6-month-old infants may have some ability to engage in top-down metre processing (Chapter 2), they may not yet be able to additionally generalize this structure across varying tempos. The results additionally suggest that Western infants already have an internal duple bias, as infants primed with duple metre showed better neural tracking, and that this duple bias is enhanced by musical experience, as MMR showed a bias to beat 5 only in musically experienced infants. This latter effect further implies that the duple bias found here is due (at least in part) to enculturation to Western rhythms that is accelerated by music experience.

Thesis Contributions

This thesis greatly advances our knowledge of (Western) infants' and adults' neural processing of rhythms. By utilizing a priming paradigm to investigate neural responses to identical rhythms between two metre priming groups, I was able to measure effects of metre processing in the brain that was internally derived, and thus top-down, compared to stimulus-driven. I provided the first evidence of top-down neural processing of musical rhythm with different metrical interpretations for a metrically ambiguous rhythm in young infants, while demonstrating limitations to the generalizability of such processes. The thesis also builds on previous literature showing effects of enhanced enculturated biases in musically trained, compared to untrained participants. Furthermore, likely partly due to the duple bias, adults are less flexible to primed metrical

interpretations than 6-month-old infants, although unlike the infants, they show enhanced neural tracking of the metre when asked to actively attend to the metre. At a broader level, these results aid in our understanding of neural markers of beat and metre perception. Given the overlap between hierarchical structures in music and language, these findings can thus help in the broader understanding of early child development, with potential implications for studying developmental disorders.

References

- Abboub, N., Nazzi, T., & Gervain, J. (2016). Prosodic grouping at birth. *Brain and Language*, *162*, 46–59. https://doi.org/10.1016/j.bandl.2016.08.002
- Abecasis, D., Brochard, R., Granot, R., & Drake, C. (2005). Differential brain response to metrical accents in isochronous auditory sequences. *Music Perception*, 22(3), 549– 562. https://doi.org/10.1525/mp.2005.22.3.549
- Arnal, L. H., Doelling, K. B., & Poeppel, D. (2015). Delta beta coupled oscillations underlie temporal prediction accuracy. *Cerebral Cortex*, 25(9), 3077–3085. https://doi.org/10.1093/cercor/bhu103
- Bahrick, L. E. (2002). Generalization of learning in three-and-a-half-month-old infants on the basis of amodal relations. *Child Development*, 73(3), 667–681. https://doi.org/10.1111/1467-8624.00431
- Baruch, C., & Drake, C. (1997). Tempo discrimination in infants. *Infant Behavior and Development*, 20(4), 573–577.
- Basirat, A., Dehaene, S., & Dehaene-lambertz, G. (2014). A hierarchy of cortical responses to sequence violations in three-month-old infants. 132, 137–150.
- Batterink, L. J., & Paller, K. A. (2019). Statistical learning of speech regularities can occur outside the focus of attention. *Cortex*, 115, 56–71. https://doi.org/10.1016/j.cortex.2019.01.013
- Bauer, A. K. R., Jaeger, M., Thorne, J. D., Bendixen, A., & Debener, S. (2015). The auditory dynamic attending theory revisited: A closer look at the pitch comparison task. *Brain Research*, *1626*, 198–210. https://doi.org/10.1016/j.brainres.2015.04.032

- Besle, J., Schevon, C. A., Mehta, A. D., Lakatos, P., Goodman, R. R., Mckhann, G. M., Emerson, R. G., & Schroeder, C. E. (2011). Tuning of the human neocortex to the temporal dynamics of attended events. *Journal of Neuroscience*, *31*(9), 3176–3185. https://doi.org/10.1523/JNEUROSCI.4518-10.2011
- Bobin-Bègue, A., Provasi, J., Marks, A., & Pouthas, V. (2006). Influence of auditory tempo on the endogenous rhythm of non-nutritive sucking. *Revue Europeenne de Psychologie Appliquee*, 56(4), 239–245. https://doi.org/10.1016/j.erap.2005.09.006
- Bouwer, F. L., Fahrenfort, J. J., Millard, S. K., Kloosterman, N. A., & Slagter, H. A.
 (2023). A silent disco: Differential effects of beat-based and pattern-based temporal expectations on persistent entrainment of low-frequency neural oscillations. *Journal of Cognitive Neuroscience*, *35*(6), 990–1020. https://doi.org/10.1162/jocn_a_01985
- Bouwer, F. L., & Honing, H. (2015). Temporal attending and prediction influence the perception of metrical rhythm: evidence from reaction times and ERPs. *Frontiers in Psychology*, 6(July), 1–14. https://doi.org/10.3389/fpsyg.2015.01094
- 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), 1–9. 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

Brascamp, J., Sterzer, P., Blake, R., & Knapen, T. (2018). Multistable perception and the

role of the frontoparietal cortex in perceptual inference. *Annual Review of Psychology*, 69, 77–103. https://doi.org/10.1146/annurev-psych-010417-085944

- Bristow, D., Dehaene-Lambertz, G., Mattout, J., Soares, C., Gliga, T., Baillet, S., &
 Mangin, J.-F. F. (2009). Hearing faces: How the infant brain matches the face it sees
 with the speech it hears. *Journal of Cognitive Neuroscience*, *21*(5), 905–921.
 https://doi.org/10.1162/jocn.2009.21076
- Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "ticktock" of our internal clock: Direct brain evidence of subjective accents in isochronous sequences. *Psychological Science*, *14*(4), 362–366. https://doi.org/10.1111/1467-9280.24441
- Cameron, D. J., Zioga, I., Lindsen, J. P., Pearce, M. T., Wiggins, G. A., Potter, K., & Bhattacharya, J. (2019). Neural entrainment is associated with subjective groove and complexity for performed but not mechanical musical rhythms. *Experimental Brain Research*, 237(8), 1981–1991. https://doi.org/10.1007/s00221-019-05557-4
- Cantiani, C., Dondena, C., Molteni, M., Riva, V., & Piazza, C. (2022). Synchronizing with the rhythm: Infant neural entrainment to complex musical and speech stimuli. *Frontiers in Psychology*, 13, 1–13. https://doi.org/10.3389/fpsyg.2022.944670

Celma-Miralles, A., & Toro, J. M. (2019). Ternary meter from spatial sounds:

Celma-Miralles, A., de Menezes, R. F., & Toro, J. M. (2016). Look at the beat, feel the meter: Top–down effects of meter induction on auditory and visual modalities. *Frontiers in Human Neuroscience*, 10, 1–13. https://doi.org/10.3389/fnhum.2016.00108

Differences in neural entrainment between musicians and non-musicians. *Brain and Cognition*, *136*(September 2018), 103594.

https://doi.org/10.1016/j.bandc.2019.103594

- Chang, A., Bosnyak, D. J., & Trainor, L. J. (2019). Rhythmicity facilitates pitch discrimination: Differential roles of low and high frequency neural oscillations. *NeuroImage*, 198, 31–43. https://doi.org/10.1016/j.neuroimage.2019.05.007
- 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
- Chen, A., Peter, V., & Burnham, D. (2022). Development of neural discrimination of pitch across speech and music in the first year of life, a mismatch response study. *Language, Cognition and Neuroscience*, *37*(9), 1153–1168. https://doi.org/10.1080/23273798.2022.2051571
- Cheng, Y. Y., & Lee, C. Y. (2018). The development of mismatch responses to Mandarin lexical Tone in 12-to 24-month-old infants. *Frontiers in Psychology*, 9, 1–11. https://doi.org/10.3389/fpsyg.2018.00448
- Cheng, Y. Y., Wu, H. C., Tzeng, Y. L., Yang, M. T., Zhao, L. L., & Lee, C. Y. (2015).
 Feature-specific transition from positive mismatch response to mismatch negativity in early infancy: Mismatch responses to vowels and initial consonants. *International Journal of Psychophysiology*, 96(2), 84–94.
 https://doi.org/10.1016/j.ijpsycho.2015.03.007

Choi, D., Batterink, L. J., Black, A. K., Paller, K. A., & Werker, J. F. (2020). Preverbal

infants discover statistical word patterns at similar rates as adults: Evidence from neural entrainment. *Psychological Science*, *31*(9), 1161–1173. https://doi.org/10.1177/0956797620933237

- 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, 1–11. https://doi.org/10.3389/fnins.2016.00229
- Cohen, D., & Katz, R. (2008). Rhythmic patterns reflecting cognitive constraints and aesthetic ideals. *Journal of New Music Research*, 37(1), 15–35. https://doi.org/10.1080/09298210802095635
- Cohen, M. X. (2014). Intertrial phase clustering. In *Analyzing neural time series data: Theory and practice* (Issue 1, pp. 241–258).
- Comerchero, M. D., & Polich, J. (1998). P3a, perceptual distinctiveness, and stimulus modality. *Cognitive Brain Research*, 7(1), 41–48. https://doi.org/10.1016/S0926-6410(98)00009-3
- Criscuolo, A., Schwartze, M., Henry, M. J., Obermeier, C., & Kotz, S. A. (2023).
 Individual neurophysiological signatures of spontaneous rhythm processing.
 NeuroImage, 273, 120090. https://doi.org/10.1016/j.neuroimage.2023.120090

de la Cruz-Pavía, I., & Gervain, J. (2023). Six-month-old infants' perception of structural

Damsma, A., de Roo, M., Doelling, K., Bazin, P.-L., & Bouwer, F. L. (2024). Tempodependent selective enhancement of neural responses at the beat frequency can be explained by both an oscillator and an evoked model. https://www.biorxiv.org/content/10.1101/2024.07.11.603023v1

regularities in speech. Cognition, 238(June), 105526.

https://doi.org/10.1016/j.cognition.2023.105526

Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, *112*(45). https://doi.org/10.1073/pnas.1508431112

Drake, C. (1993). Reproduction of musical rhythms by children, adult musicians, and adult nonmusicians. *Perception & Psychophysics*, 53(1), 25–33. https://doi.org/10.3758/BF03211712

Edalati, M., Wallois, F., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi, S. (2024).
Neural oscillations suggest periodicity encoding during auditory beat processing in the premature brain. *Developmental Science*, *August 2023*, 1–12.
https://doi.org/10.1111/desc.13550

Edalati, M., Wallois, F., Safaie, J., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi,
S. (2023). Rhythm in the premature neonate brain: Very early processing of auditory
beat and meter. *The Journal of Neuroscience*, *43*(15), 2794–2802.
https://doi.org/10.1523/JNEUROSCI.1100-22.2023

- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neuro-Otology*, 5, 151–166. https://doi.org/10.1159/000013877
- Falter, C. M., & Noreika, V. (2014). Time processing in developmental disorders: A comparative view. In Subjective Time: The Philosophy, Psychology, and Neuroscience of Temporality (pp. 557–599). The MIT Press.

https://doi.org/10.7551/mitpress/8516.003.0039

- Fernald, A. (2004). Hearing, Listening, and Understanding: Auditory Development in Infancy. In G. Bremner & A. Fogel (Eds.), *Blackwell Handbook of Infant Development* (pp. 35–70). https://doi.org/10.1002/9780470996348.ch2
- Fitzroy, A. B., & Sanders, L. D. (2020). Subjective Metric Organization Directs the Allocation of Attention across Time. *Auditory Perception & Cognition*, 3(4), 212– 237. https://doi.org/10.1080/25742442.2021.1898924
- Franco, F., Chifa, M., & Politimou, N. (2024). Home musical activities boost premature infants' language development. *Children*, 11(5), 1–18. https://doi.org/10.3390/children11050542
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1456), 815–836. https://doi.org/10.1098/rstb.2005.1622
- Fujioka, T., Ross, B., Kakigi, R., Pantev, C., & Trainor, L. J. (2006). One year of musical training affects development of auditory cortical-evoked fields in young children. *Brain*, 129(10), 2593–2608. https://doi.org/10.1093/brain/awl247
- Fujioka, T., Ross, B., & Trainor, L. J. (2015). Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery. *Journal of Neuroscience*, 35(45), 15187–15198. https://doi.org/10.3389/fnins.2016.00389
- Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of Neuroscience*, 32(5), 1791–1802. https://doi.org/10.1523/JNEUROSCI.4107-

11.2012

- Gerry, D. W., Faux, A. L., & Trainor, L. J. (2010). Effects of Kindermusik training on infants' rhythmic enculturation. *Developmental Science*, 13(3), 545–551. https://doi.org/10.1111/j.1467-7687.2009.00912.x
- Gerry, D. W., Unrau, A., & Trainor, L. J. (2012). Active music classes in infancy enhance musical, communicative and social development. *Developmental Science*, 15(3), 398–407. https://doi.org/10.1111/j.1467-7687.2012.01142.x
- Gervain, J., Berent, I., & Werker, J. F. (2012). Binding at birth: The newborn brain detects identity relations and sequential position in speech. *Journal of Cognitive Neuroscience*, 24(3), 564–574. https://doi.org/10.1162/jocn a 00157
- Gervain, J., Macagno, F., Cogoi, S., Peña, M., & Mehler, J. (2008). The neonate brain detects speech structure. *Proceedings of the National Academy of Sciences*, 105(37), 14222–14227. https://doi.org/10.1073/pnas.0806530105
- Gervain, J., & Werker, J. F. (2013). Prosody cues word order in 7-month-old bilingual infants. *Nature Communications*, *4*. https://doi.org/10.1038/ncomms2430
- Giard, M., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain generators implicated in the processing of auditory stimulus deviance: A topographic event-related potential study. *Psychophysiology*, 27(6), 627–640. https://doi.org/10.1111/j.1469-8986.1990.tb03184.x
- Gibbings, A., Henry, M. J., Cruse, D., Stojanoski, B., & Grahn, J. A. (2023). Attention modulates neural measures associated with beat perception. *European Journal of Neuroscience*, *December 2020*, 1–17. https://doi.org/10.1111/ejn.15962

- Götz, A., Männel, C., Schwarzer, G., Krasotkina, A., & Höhle, B. (2024). Neural correlates of lexical-tone and vowel-quality processing in 6- and 9-month-old German-learning infants and adults. *Journal of Child Language*, 1–23. https://doi.org/10.1017/S030500092400014X
- Govaart, G. H., Dvorakova, M., Chladkova, K., & Männel, C. (2023). Infant brain responses in auditory perception: A review of the factors influencing the polarity of the mismatch response. https://doi.org/10.31234/osf.io/bx952 Graven, S. N., & Browne, J. V. (2008). Auditory development in the fetus and infant. *Newborn and Infant Nursing Reviews*, 8(4), 187–193. https://doi.org/10.1053/j.nainr.2008.10.010
- Háden, G. P., Bouwer, F. L., Honing, H., & Winkler, I. (2024). Beat processing in newborn infants cannot be explained by statistical learning based on transition probabilities. *Cognition*, 243(March 2023).

https://doi.org/10.1016/j.cognition.2023.105670

- Háden, G. P., Honing, H., Török, M., & Winkler, I. (2015). Detecting the temporal structure of sound sequences in newborn infants. *International Journal of Psychophysiology*, 96(1), 23–28. https://doi.org/10.1016/j.ijpsycho.2015.02.024
- Haegens, S., & Zion Golumbic, E. (2018). Rhythmic facilitation of sensory processing: A critical review. *Neuroscience and Biobehavioral Reviews*, 86(December 2017), 150– 165. https://doi.org/10.1016/j.neubiorev.2017.12.002
- Hämäläinen, J. A., Ortiz-Mantilla, S., & Benasich, A. A. (2011). Source localization of event-related potentials to pitch change mapped onto age-appropriate MRIs at 6 months of age. *NeuroImage*, 54(3), 1910–1918.

https://doi.org/10.1016/j.neuroimage.2010.10.016

- 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., & Trainor, L. J. (2007). Music acquisition: effects of enculturation and formal training on development. *Trends in Cognitive Sciences*, 11(11), 466–472. https://doi.org/10.1016/j.tics.2007.08.008
- 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*, 102(35), 12639–12643. https://doi.org/10.1073/pnas.0504254102
- Haumann, N. T., Vuust, P., Bertelsen, F., & Garza-Villarreal, E. A. (2018). Influence of musical enculturation on brain responses to metric deviants. *Frontiers in Neuroscience*, 12, 1–15. https://doi.org/10.3389/fnins.2018.00218
- He, C., Hotson, L., & Trainor, L. J. (2009a). Maturation of cortical mismatch responses to occasional pitch change in early infancy: Effects of presentation rate and magnitude of change. *Neuropsychologia*, 47(1), 218–229.
 https://doi.org/10.1016/j.neuropsychologia.2008.07.019
- He, C., Hotson, L., & Trainor, L. J. (2009b). Development of infant mismatch responses to auditory pattern changes between 2 and 4 months old. *European Journal of*

Neuroscience, 29(4), 861-867. https://doi.org/10.1111/j.1460-9568.2009.06625.x

- Henry, M. J., & Herrmann, B. (2014). Low-frequency neural oscillations support dynamic attending in temporal context. *Timing and Time Perception*, 2(1), 62–86. https://doi.org/10.1163/22134468-00002011
- Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proceedings of the National Academy of Sciences of the United States of America*, 109(49), 20095–20100. https://doi.org/10.1073/pnas.1213390109
- Herrmann, B., & Johnsrude, I. S. (2018). Neural signatures of the processing of temporal patterns in sound. *Journal of Neuroscience*, 38(24), 5466–5477. https://doi.org/10.1523/JNEUROSCI.0346-18.2018
- Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, 96(3), 459–491. https://doi.org/10.1037//0033-295x.96.3.459
- Jongsma, M. L. A., Desain, P., & Honing, H. (2004). Rhythmic context influences the auditory evoked potentials of musicians and nonmusicians. *Biological Psychology*, 66(2), 129–152. https://doi.org/10.1016/j.biopsycho.2003.10.002
- Kabdebon, C., Pena, M., Buiatti, M., & Dehaene-Lambertz, G. (2015).
 Electrophysiological evidence of statistical learning of long-distance dependencies in 8-month-old preterm and full-term infants. *Brain and Language*, *148*, 25–36.
 https://doi.org/10.1016/j.bandl.2015.03.005
- Katayama, J., & Polich, J. (1998). Stimulus context determines P3a and P3b. *Psychophysiology*, *35*, 23–33.

Koelsch, S., Vuust, P., & Friston, K. (2019). Predictive Processes and the Peculiar Case of Music. *Trends in Cognitive Sciences*, 23(1), 63–77. https://doi.org/10.1016/j.tics.2018.10.006

Kuhl, P. K., Conboy, B. T., Padden, D., Nelson, T., & Pruitt, J. (2005). Early speech perception and later language development: Implications for the "critical period." *Language Learning and Development*, *1*(3–4), 237–264. https://doi.org/10.1080/15475441.2005.9671948

- Kushnerenko, E., Ceponiene, R., Fellman, V., Huotilainen, M., & Winkler, I. (2001). Event-related potential correlates of sound duration: Similar pattern from birth to adulthood. *NeuroReport*, *12*(17), 3777–3781. https://doi.org/10.1097/00001756-200112040-00035
- Ladányi, E., Persici, V., Fiveash, A., Tillmann, B., & Gordon, R. L. (2020). Is atypical rhythm a risk factor for developmental speech and language disorders? *Wiley Interdisciplinary Reviews: Cognitive Science*, *11*(5), 1–32. https://doi.org/10.1002/wcs.1528

Ladinig, O., Honing, H., Háden, G., & Winkler, I. (2009). Probing attentive and preattentive emergent meter in adult listeners without extensive music training.
 Music Perception, 26(4), 377–386. https://doi.org/10.1525/mp.2009.26.4.377

Lakatos, P., Musacchia, G., O'Connel, M. N., Falchier, A. Y., Javitt, D. C., & Schroeder,
C. E. (2013). The spectrotemporal filter mechanism of auditory selective attention. *Neuron*, 77(4), 750–761. https://doi.org/10.1016/j.neuron.2012.11.034

Langus, A., Boll-Avetisyan, N., van Ommen, S., & Nazzi, T. (2023). Music and language

in the crib: Early cross-domain effects of experience on categorical perception of prominence in spoken language. *Developmental Science*, *May 2022*, 1–12. https://doi.org/10.1111/desc.13383

- Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track timevarying events. *Psychological Review*, *106*(1), 119–159.
- Large, E. W., Roman, I., Kim, J. C., Cannon, J., Pazdera, J. K., Trainor, L. J., Rinzel, J., & Bose, A. (2023). Dynamic models for musical rhythm perception and coordination. *Frontiers in Computational Neuroscience*, *17*(May). https://doi.org/10.3389/fncom.2023.1151895
- Large, E. W., & Snyder, J. S. (2009). Pulse and meter as neural resonance. Annals of the New York Academy of Sciences, 1169, 46–57. https://doi.org/10.1111/j.1749-6632.2009.04550.x
- Larsson, M. (2014). Self-generated sounds of locomotion and ventilation and the evolution of human rhythmic abilities. *Animal Cognition*, *17*(1), 1–14. https://doi.org/10.1007/s10071-013-0678-z
- Larsson, M., Richter, J., & Ravignani, A. (2019). Bipedal steps in the development of rhythmic behavior in humans. *Music & Science*, 2, 205920431989261. https://doi.org/10.1177/2059204319892617
- Lenc, T., Peter, V., Hooper, C., Keller, P. E., Burnham, D., & Nozaradan, S. (2022). Infants show enhanced neural responses to musical meter frequencies beyond lowlevel features. *Developmental Science*, 26(5), 1–15. https://doi.org/10.1111/desc.13353

- 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, 20200327. https://doi.org/10.1098/rstb.2020.0327
- Levänen, S., Ahonen, A., Hari, R., McEvoy, L., & Sams, M. (1996). Deviant auditory stimuli activate human left and right auditory cortex differently. *Cerebral Cortex*, 6(2), 288–296. https://doi.org/10.1093/cercor/6.2.288
- Lin, W. M., Oetringer, D. A., Bakker-Marshall, I., Emmerzaal, J., Wilsch, A., ElShafei,
 H. A., Rassi, E., & Haegens, S. (2022). No behavioural evidence for rhythmic
 facilitation of perceptual discrimination. *European Journal of Neuroscience*, 55(11–12), 3352–3364. https://doi.org/10.1111/ejn.15208
- Lumaca, M., Trusbak Haumann, N., Brattico, E., Grube, M., & Vuust, P. (2019).
 Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity. *European Journal of Neuroscience*, 49(12), 1597–1609. https://doi.org/10.1111/ejn.14329
- Maurer, U., Bucher, K., Brem, S., & Brandeis, D. (2003). Development of the automatic mismatch response: From frontal positivity in kindergarten children to the mismatch negativity. *Clinical Neurophysiology*, *114*(5), 808–817. https://doi.org/10.1016/S1388-2457(03)00032-4
- Mendoza, J. K., & Fausey, C. M. (2021). Everyday music in infancy. *Developmental Science*, 24(6), 1–15. https://doi.org/10.1111/desc.13122

Menn, K. H., Ward, E. K., Braukmann, R., van den Boomen, C., Buitelaar, J., Hunnius,

S., & Snijders, T. M. (2022). Neural tracking in infancy predicts language development in children with and without family history of autism. *Neurobiology of Language*, *3*(3), 495–514. https://doi.org/10.1162/nol_a_00074

Meyer, L., Elsner, A., Turker, S., Kuhnke, P., & Hartwigsen, G. (2018). Perturbation of left posterior prefrontal cortex modulates top-down processing in sentence comprehension. *NeuroImage*, 181, 598–604. https://doi.org/10.1016/j.neuroimage.2018.07.059

- Møller, C., Stupacher, J., Celma-Miralles, A., & Vuust, P. (2021). Beat perception in polyrhythms: Time is structured in binary units. *PLOS ONE*, *16*(8), e0252174. https://doi.org/10.1371/journal.pone.0252174
- Morr, M. L., Shafer, V. L., Kreuzer, J. A., & Kurtzberg, D. (2002). Maturation of mismatch negativity in typically developing infants and preschool children. *Ear and Hearing*, 23(2), 118–136. https://doi.org/10.1097/00003446-200204000-00005

Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*(12), 2544–2590. https://doi.org/10.1016/j.clinph.2007.04.026

- Näätänen, R., Paavilainen, P., Tiitinen, H., Jiang, D., & Alho, K. (1993). Attention and mismatch negativity. *Society for Psychophysiological Research*, *30*, 436–450.
- Näätänen, R., Pakarinen, S., Rinne, T., & Takegata, R. (2004). The mismatch negativity (MMN): Towards the optimal paradigm. *Clinical Neurophysiology*, *115*(1), 140– 144. https://doi.org/10.1016/j.clinph.2003.04.001

Nave, K.M., Hannon, E.E., & Snyder, J.S. (2019). Registered report: Replication and

extension of Nozaradan, Peretz, Missal and Mouraux (2011). *Advances in Methods and Practices in Psychological Science*. Provisionally accepted manuscript. OSF Page: <u>https://osf.io/rpvde/</u>.

- Nave, K. M., Hannon, E. E., & Snyder, J. S. (2022). Steady state-evoked potentials of subjective beat perception in musical rhythms. *Psychophysiology*, 59(2), 1–15. https://doi.org/10.1111/psyp.13963
- Nozaradan, S., Peretz, I., & Keller, P. E. (2016). Individual differences in rhythmic cortical entrainment correlate with predictive behavior in sensorimotor synchronization. *Scientific Reports*, 6(1), 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
- Obleser, J., Henry, M. J., & Lakatos, P. (2017). What do we talk about when we talk about rhythm? *PLOS Biology*, *15*(9), e2002794. https://doi.org/10.1371/journal.pbio.2002794
- Obleser, J., & Kayser, C. (2019). Neural entrainment and attentional selection in the listening brain. *Trends in Cognitive Sciences*, 23(11), 913–926. https://doi.org/10.1016/j.tics.2019.08.004
- Paavilainen, P., Alho, K., Reinikainen, K., Sams, M., & Näätänen, R. (1991). Right hemisphere dominance of different mismatch negativities. *Electroencephalography and Clinical Neurophysiology*, 78(6), 466–479. https://doi.org/10.1016/0013-4694(91)90064-B

- Panzani, M., Mahmoudzadeh, M., Wallois, F., & Dehaene-Lambertz, G. (2023).
 Detection of regularities in auditory sequences before and at term-age in human neonates. *NeuroImage*, 284, 120428.
 https://doi.org/10.1016/j.neuroimage.2023.120428
- Papadimitriou, A., Smyth, C., Politimou, N., Franco, F., & Stewart, L. (2021). The impact

of the home musical environment on infants' language development. *Infant Behavior* and Development, 65, 101651. https://doi.org/10.1016/j.infbeh.2021.101651

- 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
- Pitts, M. A., Gavin, W. J., & Nerger, J. L. (2008). Early top-down influences on bistable perception revealed by event-related potentials. *Brain and Cognition*, 67(1), 11–24. https://doi.org/10.1016/j.bandc.2007.10.004
- Polak, R., Jacoby, N., Fischinger, T., Goldberg, D., Holzapfel, A., & London, J. (2018).
 Rhythmic prototypes across cultures. *Music Perception*, *36*(1), 1–23.
 https://doi.org/10.1525/mp.2018.36.1.1
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019
- Potter, D. D., Fenwick, M., Abecasis, D., & Brochard, R. (2009). Perceiving rhythm where none exists: Event-related potential (ERP) correlates of subjective accenting. *Cortex*, 45(1), 103–109. https://doi.org/10.1016/j.cortex.2008.01.004

Poudrier, E. (2020). The influence of rate and accentuation on subjective rhythmization.

Music Perception, 38(1), 27-45. https://doi.org/10.1525/mp.2020.38.1.27

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

Pranjić, M., Hashemi, N., Arnett, A. B., & Thaut, M. H. (2023). Auditory–perceptual and auditory–motor timing abilities in children with Developmental Coordination
Disorder: A scoping review. *Brain Sciences*, *13*(5), 729.
https://doi.org/10.3390/brainsci13050729

- Rinne, T., Alho, K., Ilmoniemi, R. J., Virtanen, J., & Näätänen, R. (2000). Separate time behaviors of the temporal and frontal mismatch negativity sources. *NeuroImage*, *12*(1), 14–19. https://doi.org/10.1006/nimg.2000.0591
- Román-caballero, R., Martín-arévalo, E., & Martín-sánchez, C. (2024). Influence of rhythmic contexts on perception: No behavioral and eye- tracker evidence for rhythmic entrainment. https://osf.io/preprints/psyarxiv/vt6zy
- Ruhnau, P., Herrmann, B., Maess, B., Brauer, J., Friederici, A. D., & Schröger, E. (2013).
 Processing of complex distracting sounds in school-aged children and adults:
 Evidence from EEG and MEG data. *Frontiers in Psychology*, *4*, 1–15.
 https://doi.org/10.3389/fpsyg.2013.00717
- Sadeghi, H., Allard, P., Prince, F., & Labelle, H. (2000). Symmetry and limb dominance in able-bodied gait: A review. *Gait and Posture*, 12(1), 34–45. https://doi.org/10.1016/S0966-6362(00)00070-9
- Sambeth, A., Pakarinen, S., Ruohio, K., Fellman, V., van Zuijen, T. L., & Huotilainen, M. (2009). Change detection in newborns using a multiple deviant paradigm: A study

using magnetoencephalography. *Clinical Neurophysiology*, *120*(3), 530–538. https://doi.org/10.1016/j.clinph.2008.12.033

- Sanabria, D., Capizzi, M., & Correa, Á. (2011). Rhythms that speed you up. Journal of Experimental Psychology: Human Perception and Performance, 37(1), 236–244. https://doi.org/10.1037/a0019956
- 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 of the United States of America, 112(29), 8987–8992. https://doi.org/10.1073/pnas.1414495112
- Schaefer, R. S., Vlek, R. J., & Desain, P. (2011). Decomposing rhythm processing: electroencephalography of perceived and self-imposed rhythmic patterns. *Psychological Research*, 75, 95–106. https://doi.org/10.1007/s00426-010-0293-4
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*, 32(1), 9–18. https://doi.org/10.1016/j.tins.2008.09.012
- Schwade, L., Didoné, D., & Sleifer, P. (2017). Auditory evoked potential mismatch negativity in normal-hearing adults. *International Archives of Otorhinolaryngology*, 21(03), 232–238. https://doi.org/10.1055/s-0036-1586734
- Shahin, A., Bosnyak, D. J., Trainor, L. J., & Roberts, L. E. (2003). Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. *Journal of Neuroscience*, 23(13), 5545–5552. https://doi.org/10.1523/jneurosci.23-13-05545.2003

- Shahin, A., Roberts, L. E., & Trainor, L. J. (2004). Enhancement of auditory cortical development by musical experience in children. *NeuroReport*, 15(12), 1917–1921. https://doi.org/10.1097/00001756-200408260-00017
- Slater, J. L., & Tate, M. C. (2018). Timing deficits in ADHD: Insights from the neuroscience of musical rhythm. *Frontiers in Computational Neuroscience*, 12, 51. https://doi.org/10.3389/fncom.2018.00051
- Stefanics, G., Hangya, B., Hernádi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. *Journal of Neuroscience*, *30*(41), 13578–13585. https://doi.org/10.1523/JNEUROSCI.0703-10.2010
- Sun, Y., Michalareas, G., & Poeppel, D. (2022). The impact of phase entrainment on auditory detection is highly variable: Revisiting a key finding. *European Journal of Neuroscience*, 55(11–12), 3373–3390. https://doi.org/10.1111/ejn.15367
- Sussman, E., Ritter, W., & Vaughan, H. G. (1998). Attention affects the organization of auditory input associated with the mismatch negativity system. *Brain Research*, 789(1), 130–138. https://doi.org/10.1016/S0006-8993(97)01443-1
- Sussman, E., Winkler, I., Huotilainen, M., Ritter, W., & Näätänen, R. (2002). Top-down effects can modify the initially stimulus-driven auditory organization. *Cognitive Brain Research*, 13(3), 393–405. https://doi.org/10.1016/S0926-6410(01)00131-8
- Takasago, M., Kunii, N., Komatsu, M., Tada, M., Kirihara, K., Uka, T., Ishishita, Y., Shimada, S., Kasai, K., & Saito, N. (2020). Spatiotemporal differentiation of MMN from N1 adaptation: A human ECoG study. *Frontiers in Psychiatry*, 11, 1–8.

https://doi.org/10.3389/fpsyt.2020.00586

- Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., &
 Golumbic, E. Z. (2017). Neural entrainment to the beat: The "missing-pulse"
 phenomenon. *The Journal of Neuroscience*, *37*(26), 6331–6341.
 https://doi.org/10.1523/JNEUROSCI.2500-16.2017
- Temperley, D. (2004). An evaluation system for metrical models. *Computer Music Journal*, 28(3), 28–44. https://doi.org/10.1162/0148926041790621
- Temperley, D. (2010). Modeling common-practice rhythm. *Music Perception*, 27(5), 355–376. https://doi.org/10.1525/mp.2010.27.5.355
- Temperley, N. M. (1963). Personal tempo and subjective accentuation. *The Journal of General Psychology*, 68(2), 267–287.

https://doi.org/10.1080/00221309.1963.9920534

- ten Oever, S., Schroeder, C. E., Poeppel, D., Van Atteveldt, N., Mehta, A. D., Mégevand, P., Groppe, D. M., & Zion-Golumbic, E. (2017). Low-frequency cortical oscillations entrain to subthreshold rhythmic auditory stimuli. *Journal of Neuroscience*, *37*(19), 4903–4912. https://doi.org/10.1523/JNEUROSCI.3658-16.2017
- Townsend, P. H., Jones, A., Patel, A. D., & Race, E. (2024). Rhythmic temporal cues coordinate cross-frequency phase-amplitude coupling during memory encoding. *Journal of Cognitive Neuroscience*, 2008, 1–17.

https://doi.org/10.1162/jocn_a_02217

Trainor, L. J. (2012). Musical experience, plasticity, and maturation: Issues in measuring developmental change using EEG and MEG. *Annals of the New York Academy of*

Sciences, 1252(1), 25-36. https://doi.org/10.1111/j.1749-6632.2012.06444.x

- Trainor, L. J., Desjardins, R. N., & Rockel, C. (1999). A comparison of contour and interval processing in musicians and nonmusicians using event-related potentials. *Australian Journal of Psychology*, *51*(3), 147–153.
 https://doi.org/10.1080/00049539908255352
- Trainor, L. J., Marie, C., Gerry, D. W., Whiskin, E., & Unrau, A. (2012). Becoming musically enculturated: Effects of music classes for infants on brain and behavior. *Annals of the New York Academy of Sciences*, *1252*(1), 129–138. https://doi.org/10.1111/j.1749-6632.2012.06462.x
- Trainor, L. J., Mcfadden, M., Hodgson, L., Darragh, L., Barlow, J., Matsos, L., &
 Sonnadara, R. (2003). Changes in auditory cortex and the development of mismatch negativity between 2 and 6 months of age. *International Journal of Psychophysiology*, *51*(1), 5–15. https://doi.org/10.1016/S0167-8760(03)00148-X
- Trehub, S. E., Endman, M. W., & Thorpe, L. A. (1990). Infants' perception of timbre:
 Classification of complex tones by spectral structure. *Journal of Experimental Child Psychology*, 49(2), 300–313. https://doi.org/10.1016/0022-0965(90)90060-L
- 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.
- Noorden, van, L. P. A. S. (1975). *Temporal coherence in the perception of tone sequences*. [Phd Thesis 1 (Research TU/e / Graduation TU/e), Institute for Perception Research, Eindhoven]. Technische Hogeschool Eindhoven.

- Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music - Brain responses to rhythmic incongruity. *Cortex*, 45(1), 80–92. https://doi.org/10.1016/j.cortex.2008.05.014
- Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, 5, 1–14. https://doi.org/10.3389/fpsyg.2014.01111
- Werwach, A., Männel, C., Obrig, H., Friederici, A. D., & Schaadt, G. (2022).
 Longitudinal trajectories of electrophysiological mismatch responses in infant speech discrimination differ across speech features. *Developmental Cognitive Neuroscience*, 56, 101127. https://doi.org/10.1016/j.dcn.2022.101127
- Widmann, A., Schröger, E., & Wetzel, N. (2018). Emotion lies in the eye of the listener:
 Emotional arousal to novel sounds is reflected in the sympathetic contribution to the
 pupil dilation response and the P3. *Biological Psychology*, *133*(January), 10–17.
 https://doi.org/10.1016/j.biopsycho.2018.01.010
- 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*, 106(7), 2468–2471. https://doi.org/10.1073/pnas.0809035106
- Wronka, E., Kaiser, J., & Coenen, A. M. L. (2012). Neural generators of the auditory evoked potential components P3a and P3b. *Acta Neurobiologiae Experimentalis*, 72(1), 51–64.
- Zentner, M., & Eerola, T. (2010). Rhythmic engagement with music in infancy. *Proceedings of the National Academy of Sciences of the United States of America*,

107(13), 5768–5773. https://doi.org/10.1073/pnas.1000121107

Chapter 2: Evidence for top-down metre perception in infancy as shown by primed neural responses to an ambiguous rhythm.

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. <u>https://doi.org/10.1111/ejn.15671</u>

Copyright © 2022 Federation of European Neuroscience Societies and John Wiley & Sons Ltd. Reprinted with permission. Further reprinting or reproduction is not allowed without written permission from Wiley & Sons Ltd.

Preface

Top-down perception of metre for an ambiguous rhythm is important for music and language development. There is some evidence that adults can induce a subjective neural interpretation of metre, but such abilities are not well understood in infants. In Chapter 2, we primed 6-month-old infants to perceive a metrically ambiguous 6-beat rhythm in either duple or triple metre, by adding loudness accents on beats 1, 3 and 5, or 1 and 4, respectively, then measuring their electroencephalographic responses to the unaccented, ambiguous rhythm. Infants' neural mismatch responses (MMR) were enhanced for rare pitch deviants on strong (beat 5 for duple; beat 4 for triple), compared to weak (beat 4 for duple; beat 5 for triple) beats, according to priming condition, but especially for the duple priming group. However, neural tracking as measured by steady state evoked potentials (SSEPs) was not modulated by priming. These results provide novel evidence of top-down application of subjective metre in infancy, as shown by enhanced neural processing of events on primed strong versus weak beat positions. The lack of priming effects on neural tracking suggests that perhaps a sustained maintenance of the metre was not maintained in infants.

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 6month-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 triplethan 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.

Introduction

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, tock,*

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 & 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 (M age = 6.58 months [SD = (0.19]), and 11 in the triple priming group (M age = 6.54 months [SD = 0.25]). 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 withinbetween 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 timbrevarying 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 6beat 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 $\sim 60\%$ 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 timbrevarying 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 k Ω . 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 μ V. 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 μ V 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 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 $z = (x - \mu)/s$, where μ and s 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 nondirectional 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 deviantstandard 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, η_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-monthold 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.

Acknowledgements

This research was funded by grants to LJT from the Natural Sciences and Engineering Research Council of Canada (RGPIN-2019-05416), the Canadian Institutes of Health Research (MOP 153130), and the Canadian Institute for Advanced Research (CIFAR). We also thank Elaine Whiskin for helping with data collection, and Dave Thompson for technical support.

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.

References

- Alain, C., & Woods, D. L. (1997). Attention modulates auditory pattern memory as indexed by event-related brain potentials. *Psychophysiology*, 34(5), 534–546. https://doi.org/10.1111/j.1469-8986.1997.tb01740.x
- Andreou, L. V., Kashino, M., & Chait, M. (2011). The role of temporal regularity in auditory segregation. *Hearing Research*, 280(1–2), 228–235. https://doi.org/10.1016/j.heares.2011.06.001
- Arnal, L. H., Doelling, K. B., & Poeppel, D. (2015). Delta beta coupled oscillations underlie temporal prediction accuracy. *Cerebral Cortex*, 25(9), 3077–3085. https://doi.org/10.1093/cercor/bhu103
- Bahrick, L. E., & Lickliter, R. (2012). The role of intersensory redundancy in early perceptual, cognitive, and social development. In A. J. Bremner, D. J. Lewkowicz, & C. Spence (Eds.), *Multisensory development* (pp. 183-206). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199586059.003.0008
- Baruch, C., & Drake, C. (1997). Tempo discrimination in infants. *Infant Behavior and Development*, **20**(4), 573–577. https://doi.org/10.1016/S0163-6383(97)90049-7
- Basirat, A., Dehaene, S., & Dehaene-Lambertz, G. (2014). A hierarchy of cortical responses to sequence violations in three-month-old infants. *Cognition*, 132(2), 137– 150. https://doi.org/10.1016/j.cognition.2014.03.013
- Bauer, A. K. R., Bleichner, M. G., Jaeger, M., Thorne, J. D., & Debener, S. (2018).
 Dynamic phase alignment of ongoing auditory cortex oscillations. *NeuroImage*, *167*, 396–407. https://doi.org/10.1016/j.neuroimage.2017.11.037

- Beker, S., Foxe, J. J., & Molholm, S. (2021). Oscillatory entrainment mechanisms and anticipatory predictive processes in children with autism spectrum disorder. *Journal* of Neurophysiology, **126**(5), 1783–1798. https://doi.org/10.1152/jn.00329.2021
- Bendixen, A., SanMiguel, I., & Schröger, E. (2012). Early electrophysiological indicators for predictive processing in audition: A review. *International Journal of Psychophysiology*, 83(2), 120–131. https://doi.org/10.1016/j.ijpsycho.2011.08.003
- Bendixen, A., Schröger, E., & Winkler, I. (2009). I heard that coming: Event-related potential evidence for stimulus-driven prediction in the auditory system. *Journal of Neuroscience*, 29(26), 8447–8451. https://doi.org/10.1523/JNEUROSCI.1493-09.2009
- 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
- Besle, J., Schevon, C. A., Mehta, A. D., Lakatos, P., Goodman, R. R., Mckhann, G. M., Emerson, R. G., & Schroeder, C. E. (2011). Tuning of the human neocortex to the temporal dynamics of attended events. *Journal of Neuroscience*, *31*(9), 3176–3185. https://doi.org/10.1523/JNEUROSCI.4518-10.2011
- Boemio, A., Fromm, S., Braun, A., & Poeppel, D. (2005). Hierarchical and asymmetric temporal sensitivity in human auditory cortices. *Nature Neuroscience*, 8(3), 389–395. https://doi.org/10.1038/nn1409
- 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), 1–9. 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
- Brandwein, A. B., Foxe, J. J., Russo, N. N., Altschuler, T. S., Gomes, H., & Molholm, S. (2011). The development of audiovisual multisensory integration across childhood and early adolescence: A high-density electrical mapping study. *Cerebral Cortex*, *21*(5), 1042–1055. https://doi.org/10.1093/cercor/bhq170
- Breska, A., & Deouell, L. Y. (2014). Automatic bias of temporal expectations following temporally regular input independently of high-level temporal expectation. *Journal* of Cognitive Neuroscience, 26(7), 1555–1571. https://doi.org/10.1162/jocn_a_00564
- Brett, M., & Grahn, J. A. (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
- Bristow, D., Dehaene-Lambertz, G., Mattout, J., Soares, C., Gliga, T., Baillet, S., &
 Mangin, J.-F. (2009). Hearing faces : How the infant brain matches the face it sees
 with the speech it hears. *Journal of Cognitive Neuroscience*, *21*(5), 905–921.
 https://doi.org/10.1162/jocn.2009.21076
- Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "tick tock" of our internal clock: Direct brain evidence of subjective accents in isochronous sequences. *Psychological Science*, *14*(4), 362–366. https://doi.org/10.1111/1467-9280.24441

- Buiatti, M., Peña, M., & Dehaene-Lambertz, G. (2009). Investigating the neural correlates of continuous speech computation with frequency-tagged neuroelectric responses. *NeuroImage*, 44(2), 509–519. https://doi.org/10.1016/j.neuroimage.2008.09.015
- Carrer, L. R. J. (2015). Music and sound in time processing of children with ADHD. *Frontiers in Psychiatry*, *6*, 1–7. https://doi.org/10.3389/fpsyt.2015.00127
- Celma-Miralles, A., & Toro, J. M. (2019). Ternary meter from spatial sounds:
 Differences in neural entrainment between musicians and non-musicians. *Brain and Cognition*, *136*, 1–16. https://doi.org/10.1016/j.bandc.2019.103594
- Chait, M., Greenberg, S., Arai, T., Simon, J. Z., & Poeppel, D. (2015). Multi-time resolution analysis of speech: Evidence from psychophysics. *Frontiers in Neuroscience*, 9, 1–10. https://doi.org/10.3389/fnins.2015.00214
- Chang, A., Bosnyak, D. J., & Trainor, L. J. (2019). Rhythmicity facilitates pitch discrimination: Differential roles of low and high frequency neural oscillations. *NeuroImage*, **198**, 31–43. https://doi.org/10.1016/j.neuroimage.2019.05.007
- Chang, A., Li, Y.-C., Chan, J. F., Dotov, D. G., Cairney, J., & Trainor, L. J. (2021). Inferior auditory time perception in children with motor difficulties. *Child Development*, 92(5), e907-e923. https://doi.org/10.1111/cdev.13537

Chang, H.-W., & Trehub, S. E. (1977). Infants' perception of temporal grouping in auditory patterns. *Child Development*, 48(4), 1666–1670. https://doi.org/10.2307/1128532

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

- Cheng, Y. Y., & Lee, C. Y. (2018). The development of mismatch responses to Mandarin lexical tone in 12-to 24-month-old infants. *Frontiers in Psychology*, 9, 1–11. https://doi.org/10.3389/fpsyg.2018.00448
- Cheng, Y. Y., Wu, H. C., Tzeng, Y. L., Yang, M. T., Zhao, L. L., & Lee, C. Y. (2013).
 The development of mismatch responses to Mandarin lexical tones in early infancy. *Developmental Neuropsychology*, 38(5), 281–300.
 https://doi.org/10.1080/87565641.2013.799672
- Cheng, Y. Y., Wu, H. C., Tzeng, Y. L., Yang, M. T., Zhao, L. L., & Lee, C. Y. (2015).
 Feature-specific transition from positive mismatch response to mismatch negativity in early infancy: Mismatch responses to vowels and initial consonants. *International Journal of Psychophysiology*, 96(2), 84–94.

https://doi.org/10.1016/j.ijpsycho.2015.03.007

- Choi, D., Batterink, L. J., Black, A. K., Paller, K. A., & Werker, J. F. (2020). Preverbal infants discover statistical word patterns at similar rates as adults: Evidence from neural entrainment. *Psychological Science*, *31*(9), 1–13. https://doi.org/10.1177/0956797620933237
- Cirelli, L. K., Bosnyak, D., Manning, F. C., Spinelli, C., Marie, C., Fujioka, T.,
 Ghahremani, A., & Trainor, L. J. (2014). Beat-induced fluctuations in auditory
 cortical beta-band activity: Using EEG to measure age-related changes. *Frontiers in Psychology*, 5, 1–9. https://doi.org/10.3389/fpsyg.2014.00742

Cirelli, L. K., Einarson, K. M., & Trainor, L. J. (2014). Interpersonal synchrony increases

prosocial behavior in infants. *Developmental Science*, **17**(6), 1003–1011. https://doi.org/10.1111/desc.12193

- 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, 1–11. https://doi.org/10.3389/fnins.2016.00229
- Cirelli, L. K., Trehub, S. E., & Trainor, L. J. (2018). Rhythm and melody as social signals for infants. *Annals of the New York Academy of Sciences*, **1423**(1), 66–72. https://doi.org/10.1111/nyas.13580
- Ding, N., Melloni, L., Zhang, H., Tian, X., & Poeppel, D. (2016). Cortical tracking of hierarchical linguistic structures in connected speech. *Nature Neuroscience*, 19(1), 158–164. https://doi.org/10.1038/nn.4186
- Drake, C., Penel, A., & Bigand, E. (2000). Tapping in time with mechanically and expressively performed music. *Music Perception: An Interdisciplinary Journal*, 18(1), 1–23. https://doi.org/10.2307/40285899
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neuro-Otology*, 5, 151–166. https://doi.org/10.1159/000013877
- Fitch, W. T., & Rosenfeld, A. J. (2007). Perception and production of syncopated rhythms. *Music Perception: An Interdisciplinary Journal*, 25(1), 43–58. https://doi.org/10.1525/mp.2007.25.1.43
- Fitzpatrick, P., Frazier, J. A., Cochran, D. M., Mitchell, T., Coleman, C., & Schmidt, R.C. (2016). Impairments of social motor synchrony evident in autism spectrum
disorder. Frontiers in Psychology, 7, 1–13. https://doi.org/10.3389/fpsyg.2016.01323

- Fitzpatrick, P., Romero, V., Amaral, J. L., Duncan, A., Barnard, H., Richardson, M. J., & Schmidt, R. C. (2017). Evaluating the importance of social motor synchronization and motor skill for understanding autism. *Autism Research*, 10(10), 1687–1699. https://doi.org/10.1002/aur.1808
- Foster, R. G., & Kreitzman, L. (2014). The rhythms of life: What your body clock means to you! *Experimental Physiology*, 99(4), 599–606. https://doi.org/10.1113/expphysiol.2012.071118
- Franich, K., Wong, H. Y., Yu, A. C. L., & To, C. K. S. (2021). Temporal coordination and prosodic structure in autism spectrum disorder: Timing across speech and nonspeech motor domains. *Journal of Autism and Developmental Disorders*, 51, 2929-2949. https://doi.org/10.1007/s10803-020-04758-z

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

- Fujioka, T., Ross, B., & Trainor, L. J. (2015). Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery. *Journal of Neuroscience*, 35(45), 15187–15198. https://doi.org/10.1523/JNEUROSCI.2397-15.2015
- Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of Neuroscience*, 32(5), 1791–1802. https://doi.org/10.1523/JNEUROSCI.4107-

11.2012

- Fujioka, T., Zendel, B. R., & Ross, B. (2010). Endogenous neuromagnetic activity for mental hierarchy of timing. *The Journal of Neuroscience*, **30**(9), 3458–3466. https://doi.org/10.1523/JNEUROSCI.3086-09.2010
- Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging computational principles and operations. *Nature Neuroscience*, 15(4), 511–517. https://doi.org/doi:10.1038/nn.3063
- Goswami, U., Cumming, R., Chait, M., Huss, M., Mead, N., Wilson, A. M., Barnes, L., & Fosker, T. (2016). Perception of filtered speech by children with developmental dyslexia and children with specific language impairments. *Frontiers in Psychology*, 7, 1–16. https://doi.org/10.3389/fpsyg.2016.00791
- Haegens, S., Luther, L., & Jensen, O. (2012). Somatosensory anticipatory alpha activity increases to suppress distracting input. *Journal of Cognitive Neuroscience*, 24(3), 677–685. https://doi.org/10.1162/jocn_a_00164
- Haegens, S., & Zion Golumbic, E. (2018). Rhythmic facilitation of sensory processing: A critical review. *Neuroscience and Biobehavioral Reviews*, 86, 150–165. https://doi.org/10.1016/j.neubiorev.2017.12.002

Hannon, E. E., & Johnson, S. P. (2005). Infants use meter to categorize rhythms and

<sup>Haenschel, C., Vernon, D. J., Dwivedi, P., Gruzelier, J. H., & Baldeweg, T. (2005).
Event-related brain potential correlates of human auditory sensory memory-trace formation.</sup> *Journal of Neuroscience*, 25(45), 10494–10501.
https://doi.org/10.1523/JNEUROSCI.1227-05.2005

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., & 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*, **102**(35), 12639–12643. https://doi.org/10.1073/pnas.0504254102
- He, C., Hotson, L., & Trainor, L. J. (2007). Mismatch responses to pitch changes in early infancy. *Journal of Cognitive Neuroscience*, 19(5), 878–892.
 https://doi.org/10.1162/jocn.2007.19.5.878
- He, C., Hotson, L., & Trainor, L. J. (2009). Development of infant mismatch responses to auditory pattern changes between 2 and 4 months old. *European Journal of Neuroscience*, 29(4), 861–867. https://doi.org/10.1111/j.1460-9568.2009.06625.x
- Henry, M. J., & Herrmann, B. (2014). Low-frequency neural oscillations support dynamic attending in temporal context. *Timing and Time Perception*, 2(1), 62–86. https://doi.org/10.1163/22134468-00002011

Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural

^{Henry, M. J., Herrmann, B., & Obleser, J. (2014). Entrained neural oscillations in multiple frequency bands comodulate behavior.} *Proceedings of the National Academy of Sciences of the United States of America*, 111(41), 14935–14940. https://doi.org/10.1073/pnas.1408741111

oscillations and optimizes human listening behavior. *Proceedings of the National Academy of Sciences of the United States of America*, **109**(49), 20095–20100. https://doi.org/10.1073/pnas.1213390109

Herrmann, B., Henry, M. J., Haegens, S., & Obleser, J. (2016). Temporal expectations and neural amplitude fluctuations in auditory cortex interactively influence perception. *NeuroImage*, *124*, 487–497. https://doi.org/10.1016/j.neuroimage.2015.09.019

Herrmann, B., & Johnsrude, I. S. (2018). Neural signatures of the processing of temporal patterns in sound. *Journal of Neuroscience*, *38*(24), 5466–5477.

https://doi.org/10.1523/JNEUROSCI.0346-18.2018

Hove, M. J., Gravel, N., Spencer, R. M. C., & Valera, E. M. (2017). Finger tapping and pre-attentive sensorimotor timing in adults with ADHD. *Experimental Brain Research*, 235(12), 3663–3672. https://doi.org/10.1007/s00221-017-5089-y

Hove, M. J., & Risen, J. L. (2009). It's all in the timing: Interpersonal synchrony increases affiliation. *Social Cognition*, 27(6), 949–960. https://doi.org/10.1521/soco.2009.27.6.949

Huss, M., Verney, J. P., Fosker, T., Mead, N., & Goswami, U. (2011). Music, rhythm, rise time perception and developmental dyslexia: Perception of musical meter predicts reading and phonology. *Cortex*, 47(6), 674–689. https://doi.org/10.1016/j.cortex.2010.07.010

Iversen, J. R., Repp, B. H., & Patel, A. D. (2009). Top-down control of rhythm perception modulates early auditory responses. *Annals of the New York Academy of Sciences*,

1169(1), 58–73. https://doi.org/10.1111/j.1749-6632.2009.04579.x

- 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
- Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, **96**(3), 459–491. https://doi.org/10.1037//0033-295x.96.3.459
- Jones, M. R., Moynihan, H., MacKenzie, N., & Puente, J. (2002). Temporal aspects of stimulus-driven attending in dynamic arrays. *Psychological Science*, 13(4), 313–319. https://doi.org/10.1111/1467-9280.00458
- 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

- Lacquaniti, F., Ivanenko, Y. P., & Zago, M. (2012). Patterned control of human locomotion. *Journal of Physiology*, **590**(10), 2189–2199. https://doi.org/10.1113/jphysiol.2011.215137
- Ladányi, E., Persici, V., Fiveash, A., Tillmann, B., & Gordon, R. L. (2020). Is atypical rhythm a risk factor for developmental speech and language disorders? *Wiley Interdisciplinary Reviews: Cognitive Science*, 11(5), 1–32. https://doi.org/10.1002/wcs.1528
- Ladinig, O., Honing, H., Háden, G. P., & Winkler, I. (2009). Probing attentive and preattentive emergent meter in adult listeners without extensive music training.
 Music Perception, 26(4), 377–386. https://doi.org/10.1525/mp.2009.26.4.377

- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, *320*(5872), 110–113. https://doi.org/10.1126/science.1154735
- Lakatos, P., O'Connell, M. N., Barczak, A., Mills, A., Javitt, D. C., & Schroeder, C. E. (2009). The leading sense: Supramodal control of neurophysiological context by attention. *Neuron*, **64**(3), 419–430. https://doi.org/10.1016/j.neuron.2009.10.014
- 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., & Jones, M. R. (1999). The dynamics of attending: How people track timevarying events. *Psychological Review*, *106*(1), 119–159. https://doi.org/10.1037/0033-295X.106.1.119
- Large, E. W., & Palmer, C. (2002). Perceiving temporal regularity in music. *Cognitive Science*, **26**(1), 1–37. https://doi.org/10.1016/S0364-0213(01)00057-X
- Lecanuet, J. P., & Jacquet, A. Y. (2002). Fetal responsiveness to maternal passive swinging in low heart rate variability state: Effects of stimulation direction and duration. *Developmental Psychobiology*, **40**(1), 57–67. https://doi.org/10.1002/dev.10013
- Lee, C. Y., Yen, H. L., Yeh, P. W., Lin, W. H., Cheng, Y. Y., Tzeng, Y. L., & Wu, H. C. (2012). Mismatch responses to lexical tone, initial consonant, and vowel in Mandarin-speaking preschoolers. *Neuropsychologia*, 50(14), 3228–3239. https://doi.org/10.1016/j.neuropsychologia.2012.08.025

- Lense, M., Ladányi, E., Rabinowitch, T., Trainor, L. J., & Gordon, R. (2021). Rhythm and timing as vulnerabilities in neurodevelopmental disorders. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **376**(1835), 20200327– 20200339. https://doi.org/10.1098/rstb.2020.0327.
- Lerner, Y., Honey, C. J., Silbert, L. J., & Hasson, U. (2011). Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *Journal of Neuroscience*, *31*(8), 2906–2915. https://doi.org/10.1523/JNEUROSCI.3684-10.2011
- Lewkowicz, D. J., & Ghazanfar, A. A. (2009). The emergence of multisensory systems through perceptual narrowing. *Trends in Cognitive Sciences*, **13**(11), 470-478.
- Lewkowicz, D.J., & Turkewitz G. (1980). Cross-modal equivalence in early infancy:
 Auditory-visual intensity matching. *Developmental Psychology*, 16(6), 597–607.
 doi: 10.1037/0012-1649.16.6.597.
- Liberman, M., & Prince, A. (1977). On stress and linguistic rhythm. *Linguistic Inquiry*, 8(2), 249–336.
- Luo, C., & Ding, N. (2020). Cortical encoding of acoustic and linguistic rhythms in spoken narratives. *ELife*, 9, 1–25. https://doi.org/10.7554/ELIFE.60433
- Luo, H., Liu, Z., & Poeppel, D. (2010). Auditory cortex tracks both auditory and visual stimulus dynamics using low-frequency neuronal phase modulation. *PLoS Biology*, 8(8), e1000445. https://doi.org/10.1371/journal.pbio.1000445
- Luo, H., & Poeppel, D. (2007). Phase patterns of neuronal responses reliably discriminate speech in human auditory cortex. *Neuron*, **54**(6), 1001–1010.

https://doi.org/10.1016/j.neuron.2007.06.004

- Luo, H., & Poeppel, D. (2012). Cortical oscillations in auditory perception and speech:
 Evidence for two temporal windows in human auditory cortex. *Frontiers in Psychology*, 3(MAY), 1–10. https://doi.org/10.3389/fpsyg.2012.00170
- Markova, G., Nguyen, T., & Hoehl, S. (2019). Neurobehavioral interpersonal synchrony in early development: The role of interactional rhythms. *Frontiers in Psychology*, 10, 1–6. https://doi.org/10.3389/fpsyg.2019.02078
- Maurer, U., Bucher, K., Brem, S., & Brandeis, D. (2003). Development of the automatic mismatch response: From frontal positivity in kindergarten children to the mismatch negativity. *Clinical Neurophysiology*, *114*(5), 808–817. https://doi.org/10.1016/S1388-2457(03)00032-4
- McAuley, D. J., & Fromboluti, E. K. (2014). Attentional entrainment and perceived event duration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369, 1–10. https://doi.org/10.1098/rstb.2013.0401
- Mehler, J., Jusczyk, P., Lamsertz, G., Halsted, N., Bertoncini, J., & Amiel-Tison, C.
 (1988). A precursor of language acquisition in young infants. *Cognition*, 29(2), 143–178. https://doi.org/10.1016/0010-0277(88)90035-2

Merchant, H., & Honing, H. (2014). Are non-human primates capable of rhythmic

^{Merchant, H., Grahn, J., Trainor, L. J., Rohrmeier, M., & Fitch, W. T. (2015). Finding the beat: A neural perspective across humans and non-human primates.} *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1664), 1–16. https://doi.org/10.1098/rstb.2014.0093

entrainment? Evidence for the gradual audiomotor evolution hypothesis. *Frontiers in Neuroscience*, **7**, 1–8. https://doi.org/10.3389/fnins.2013.00274

- Molholm, S., Ritter, W., Murray, M. M., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). Multisensory auditory-visual interactions during early sensory processing in humans: A high-density electrical mapping study. *Cognitive Brain Research*, 14(1), 115–128. https://doi.org/10.1016/S0926-6410(02)00066-6
- Mourad, N., Reilly, J. P., de Bruin, H., Hasey, G., & MacCrimmon, D. (2007). A simple and fast algorithm for automatic suppression of high-amplitude artifacts in EEG data. *ICASSP, IEEE International Conference on Acoustics, Speech and Signal Processing - Proceedings*, 1, 393–396. https://doi.org/10.1109/ICASSP.2007.366699
- Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*(12), 2544–2590. https://doi.org/10.1016/j.clinph.2007.04.026
- Näätänen, R., Paavilainen, P., Tiitinen, H., Jiang, D., & Alho, K. (1993). Attention and mismatch negativity. *Psychophysiology*, **30**(5), 436–450. https://doi.org/10.1111/j.1469-8986.1993.tb02067.x
- Näätänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. *Psychological Bulletin*, *125*(6), 826–859.
 https://doi.org/10.1037/0033-2909.125.6.826
- Nazzi, T., Bertoncini, J., & Mehler, J. (1998). Language discrimination by newborns: Toward an understanding of the role of rhythm. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(3), 756–766.

https://doi.org/10.1037//0096-1523.24.3.756

- 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* (pp. 463–472). Cambridge, MA:MIT Press. https://doi.org/10.7551/mitpress/5190.003.0032
- 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. (2012). Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *The Journal of Neuroscience*, *32*(49), 17572–17581. https://doi.org/10.1523/JNEUROSCI.3203-12.2012
- Obleser, J., & Kayser, C. (2019). Neural entrainment and attentional selection in the listening brain. *Trends in Cognitive Sciences*, 23(11), 913–926. https://doi.org/10.1016/j.tics.2019.08.004
- Okamoto, H., & Kakigi, R. (2015). Hemispheric asymmetry of auditory mismatch negativity elicited by spectral and temporal deviants: A magnetoencephalographic study. *Brain Topography*, 28(3), 471–478. https://doi.org/10.1007/s10548-013-0347-1
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 1–9. https://doi.org/10.1155/2011/156869

Pallier, C., Devauchelle, A.-D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(6), 2522–2527.
https://doi.org/10.1073/pnas.1018711108

Park, H., Ince, R. A. A., Schyns, P. G., Thut, G., & Gross, J. (2015). Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. *Current Biology*, 25(12), 1649–1653. https://doi.org/10.1016/j.cub.2015.04.049

Perani, D., Saccuman, M. C., Scifo, P., Spada, D., Andreolli, G., Rovelli, R., Baldoli, C., & Koelsch, S. (2010). Functional specializations for music processing in the human newborn brain. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(10), 4758–4763. https://doi.org/10.1073/pnas.0909074107

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

Phillips-Silver, J., & Trainor, L. J. (2007). Hearing what the body feels: Auditory encoding of rhythmic movement. *Cognition*, **105**(3), 533–546. https://doi.org/10.1016/j.cognition.2006.11.006

Phillips-Silver, J., & Trainor, L. J. (2008). Vestibular influence on auditory metrical interpretation. *Brain and Cognition*, 67(1), 94–102. https://doi.org/10.1016/j.bandc.2007.11.007

Poeppel, D., & Assaneo, M. F. (2020). Speech rhythms and their neural foundations.

Nature Reviews Neuroscience, **21**(6), 322–334. https://doi.org/10.1038/s41583-020-0304-4

- Power, A. J., Mead, N., Barnes, L., & Goswami, U. (2012). Neural entrainment to rhythmically presented auditory, visual, and audio-visual speech in children. *Frontiers in Psychology*, 3, 1–13. https://doi.org/10.3389/fpsyg.2012.00216
- Power, A. J., Mead, N., Barnes, L., & Goswami, U. (2013). Neural entrainment to rhythmic speech in children with developmental dyslexia. *Frontiers in Human Neuroscience*, 7, 1–19. https://doi.org/10.3389/fnhum.2013.00777
- Puyjarinet, F., Bégel, V., Lopez, R., Dellacherie, D., & Dalla Bella, S. (2017). Children and adults with attention-deficit/hyperactivity disorder cannot move to the beat. *Scientific Reports*, 7(1), 1–11. https://doi.org/10.1038/s41598-017-11295-w
- Ravignani, A., Bowling, D. L., & Fitch, W. T. (2014). Chorusing, synchrony and the evolutionary functions of rhythm. *Frontiers in Psychology*, 5, 1–15. https://doi.org/10.3389/fpsyg.2014.01118
- Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin and Review*, **12**(6), 969–992. https://doi.org/10.3758/BF03206433

Repp, B. H. (2010). Do metrical accents create illusory phenomenal accents? Attention, Perception & Psychophysics, 72(5), 1390–1403. https://doi.org/10.3758/APP.72.5.1390

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

- Schaefer, R. S., Vlek, R. J., & Desain, P. (2011). Decomposing rhythm processing:
 Electroencephalography of perceived and self-imposed rhythmic patterns. *Psychological Research*, 75, 95–106. https://doi.org/10.1007/s00426-010-0293-4
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neuroscience*, 32(1), 9–18. https://doi.org/10.1016/j.tins.2008.09.012
- Shuai, L., & Gong, T. (2014). Temporal relation between top-down and bottom-up processing in lexical tone perception. *Frontiers in Behavioral Neuroscience*, 8, 1–16. https://doi.org/10.3389/fnbeh.2014.00097
- Simon, D. M., & Wallace, M. T. (2017). Rhythmic modulation of entrained auditory oscillations by visual inputs. *Brain Topography*, 30(5), 565–578. https://doi.org/10.1007/s10548-017-0560-4
- Smith, N. A., Folland, N. A., Martinez, D. M., & Trainor, L. J. (2017). Multisensory object perception in infancy: 4-month-olds perceive a mistuned harmonic as a separate auditory and visual object. *Cognition*, 164, 1–7. https://doi.org/10.1016/j.cognition.2017.01.016

Sussman, E. S., Chen, S., Sussman-Fort, J., & Dinces, E. (2014). The five myths of

Stefanics, G., Hangya, B., Hernádi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. *Journal of Neuroscience*, *30*(41), 13578–13585. https://doi.org/10.1523/JNEUROSCI.0703-10.2010

MMN: Redefining how to use MMN in basic and clinical research. *Brain Topography*, **27**(4), 553–564. https://doi.org/10.1007/s10548-013-0326-6

- Sussman, E. S., Ritter, W., & Vaughan Jr., H. G. (1998). Attention affects the organization of auditory input associated with the mismatch negativity system. *Brain Research*, 789(1), 130–138. https://doi.org/10.1016/S0006-8993(97)01443-1
- Sussman, E. S., Winkler, I., Huotilainen, M., Ritter, W., & Näätänen, R. (2002). Topdown effects can modify the initially stimulus-driven auditory organization. *Cognitive Brain Research*, 13(3), 393–405. https://doi.org/10.1016/S0926-6410(01)00131-8
- Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., &
 Golumbic, E. Z. (2017). Neural entrainment to the beat: The "missing-pulse"
 phenomenon. *The Journal of Neuroscience*, *37*(26), 6331–6341.
 https://doi.org/10.1523/JNEUROSCI.2500-16.2017
- Tarr, B., Launay, J., Cohen, E., & Dunbar, R. (2015). Synchrony and exertion during dance independently raise pain threshold and encourage social bonding. *Biology Letters*, 11(10), 1–4. https://doi.org/10.1098/rsbl.2015.0767
- Thomassen, J. M. (1982). Melodic accent: Experiments and a tentative model. *Journal of the Acoustical Society of America*, **71**(6), 1596–1605. https://doi.org/10.1121/1.387814
- Thomson, J. M., & Goswami, U. (2008). Rhythmic processing in children with developmental dyslexia: Auditory and motor rhythms link to reading and spelling. *Journal of Physiology Paris*, **102**(1–3), 120–129.

https://doi.org/10.1016/j.jphysparis.2008.03.007

- Trainor, L. J. (2012). Musical experience, plasticity, and maturation: Issues in measuring developmental change using EEG and MEG. *Annals of the New York Academy of Sciences*, 1252(1), 25–36. https://doi.org/10.1111/j.1749-6632.2012.06444.x
- Trainor, L. J., Chang, A., Cairney, J., & Li, Y. C. (2018). Is auditory perceptual timing a core deficit of developmental coordination disorder? *Annals of the New York Academy of Sciences*, 1423(1), 30–39. https://doi.org/10.1111/nyas.13701
- Trainor, L. J., & Cirelli, L. K. (2015). Rhythm and interpersonal synchrony in early social development. *Annals of the New York Academy of Sciences*, 1337(1), 45–52. https://doi.org/10.1111/nyas.12649
- Trainor, L. J., Mcfadden, M., Hodgson, L., Darragh, L., Barlow, J., Matsos, L., &
 Sonnadara, R. (2003). Changes in auditory cortex and the development of mismatch negativity between 2 and 6 months of age. *International Journal of Psychophysiology*, *51*(1), 5–15. https://doi.org/10.1016/S0167-8760(03)00148-X
- Trainor, L. J., Samuel, S. S., Desjardins, R., & Sonnadara, R. (2001). Measuring temporal resolution in infants using mismatch negativity. *NeuroReport*, 12(11), 2443–2448. https://doi.org/10.1097/00001756-200108080-00031

Tunçgenç, B., & Cohen, E. (2016). Movement synchrony forges social bonds across group divides. *Frontiers in Psychology*, 7, 1–12. https://doi.org/10.3389/fpsyg.2016.00782

Tunçgenç, B., Cohen, E., & Fawcett, C. (2015). Rock with me: The role of movement synchrony in infants' social and nonsocial choices. *Child Development*, **86**(3), 976–

984. https://doi.org/10.1111/cdev.12354

- Valdesolo, P., Ouyang, J., & DeSteno, D. (2010). The rhythm of joint action: Synchrony promotes cooperative ability. *Journal of Experimental Social Psychology*, 46(4), 693–695. https://doi.org/10.1016/j.jesp.2010.03.004
- Wiltermuth, S. S., & Heath, C. (2009). Synchrony and cooperation. *Psychological Science*, **20**(1), 1–5. https://doi.org/10.1111/j.1467-9280.2008.02253.x
- 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*, **106**(7), 2468–2471. https://doi.org/10.1073/pnas.0809035106
- Zatorre, R. J., & Belin, P. (2001). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, *11*(10), 946–953. https://doi.org/10.1093/cercor/11.10.946
- Zelaznik, H. N., Vaughn, A. J., Green, J. T., Smith, A. L., Hoza, B., & Linnea, K. (2012).
 Motor timing deficits in children with attention-deficit/hyperactivity disorder. *Human Movement Science*, 31(1), 255–265.

https://doi.org/10.1016/j.humov.2011.05.003

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

Tables				
FL Sites				
t	р			
4.853	<.001			
5.345	<.001			
5.139	<.001			
5.607	<.001			
4.615	<.001			
5.161	<.001			
FR Sites				
4.215	<.001			
5.125	<.001			
5.245	<.001			
5.039	<.001			
3.530	.002			
6.768	<.001			
	Tables FL Sites t 4.853 5.345 5.139 5.607 4.615 5.161 FR Sites 4.215 5.125 5.245 5.039 3.530 6.768			

Table 1. t-test Results for Infant SSEPs Comparing Frequencies of Interest andHarmonics 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 group 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.

		Duple Group		
Participant	Looking Time	Experiment Time	Looking time	Group
ID	(mins)	(mins)	(%)	M(SD)
14	8.42	10.8	78	59.8 (14.44)
16	5.36	16.2	33.1	
18	10.76	16.2	66.4	
24	9.01	15.84	56.9	
28	6.75	15.03	44.9	
30	9.18	16.2	56.7	
32	12.54	16.2	77.4	
34	7.88	16.2	48.7	
38	9.84	16.2	60.7	
40	11.59	16.2	71.5	
46	4.63	10.8	42.9	
50	6.75	10.8	62.5	
52	12.55	16.2	77.4	
		Triple Group		
Participant	Looking Time	Experiment Time	Looking time	Group
ID	(mins)	(mins)	(%)	M(SD)
13	7.69	10.8	71.2	54.8 (21.63)
15	4.29	10.8	39.7	
19	10.84	16.2	66.9	
23	n/a	n/a	n/a	
25	5.91	16.2	36.5	
27	6.44	16.2	39.8	
29	14.83	16.2	91.5	
39	7.03	15.06	46.7	
41	2.17	10.8	20.1	
43	8.81	13.92	63.3	
49	11.77	16.2	72.7	

Supplementary Information

Table S1. Infant Looking Times Separated by Priming Group.





Fig S1. Hilbert transforms of the different stimulus types.



Fig. S2. Visual stimulus example. An array of 5 to 9 circles expanded and shrunk on every beat 1 of the six-beat stimulus (shown in green), then remained still for beats two to six (shown in red). The colour and arrangement of the circles changed randomly every 20 trials.



Fig S3. Boxplots for the MMR across the different conditions in frontal left (FL) and frontal right (FR) sites. The four infants (N = 2 in each condition) who completed a slightly different version of the paradigm shown in red.



Fig. S4. Channel groupings for FL and FR outlined in red.



Fig S5. SSEP analysis using the average of all electrodes. A RM ANOVA of the SSEPs over all electrodes with the factors of frequency (duple meter; triple meter) and group (duple primed; triple primed) revealed a main effect of frequency, such that amplitudes at the triple meter frequency were larger than at the duple frequency (F = 5.289, p = .031, $\eta_p^2 = .194$). These results reflect what was found in the original analysis that included FL sites.

Chapter 3: Western Adults' Neural Responses to An Ambiguous Rhythm: Effects of Priming with and without Active Imagination

Flaten, E., Carrillo, C., Trainor, L. (2024) Western adults' neural responses to an ambiguous rhythm: Effects of priming with and without active attention. *Authorea*. Manuscript Under Review.

https://doi.org/10.22541/au.172814927.73345976/v2.

Preface

Chapter 2 demonstrated that infants can be primed to process a metrically ambiguous rhythm either in duple or triple metre, as shown by enhanced MMRs for subjectively strong, compared to weak beat positions. Neural tracking measures, however, were not influenced by priming, perhaps because infants generally did not maintain the subjective metre for sustained periods of time. Remaining questions from this work, and which were addressed in Chapter 3, are how adults undergoing the same priming conditions (Chapter 3 Experiment 1) compare to infants in their top-down metre processing, and whether engagement of sustained attention to the metre enhances topdown effects (Chapter 3 Experiment 2). Further, previous research is limited in testing adults' subjective rhythm perception under different metrical interpretations, and across different neural measures. Thus, in Chapter 3 we measured adults' mismatch negativity [MMN] and P3a for pitch deviants on primed strong, compared to weak beats, as well as

their neural tracking (steady state evoked potentials [SSEPs] and intertrial phase coherence [ITPC]) for the primed compared to unprimed metre frequency. Overall, adults' MMN and P3a were not modulated by priming, but instead P3a was enhanced for the duple strong beat (beat 5), regardless of priming or attention conditions. This was especially the case for participants with music and dance experience. On the other hand, neural tracking for the primed compared to unprimed metre was enhanced, but only when adults actively imagined the metre. These results provide novel evidence of a robust bias towards duple metre in adults' neural processing of rhythm that is enhanced by musical experience, and which can be reduced with active attention.

Abstract

Auditory rhythm perception involves bottom-up encoding of timing information and top-down maintenance of a particular interpretation. Beats in musical rhythms can be grouped to form metres, such as duple (two-beat groupings) or triple (three-beat groupings). Subjective (top-down) metre perception can be measured using electroencephalographic responses like mismatch negativity (MMN), P3a, and Steady-State Evoked Potentials (SSEPs). Previously we showed infants could be primed to perceive an ambiguous 6-beat rhythm as either duple or triple by adding loudness accents to every second, or third beat, respectively. For the subsequently presented unaccented rhythm, infants exhibited larger mismatch responses for pitch deviants on primed strong beats, particularly after duple priming (Flaten et al., 2022). Here we applied the same protocol to adults in two experiments. In Experiment 1, adults were passively primed to perceive the rhythm as duple or triple identically as the infants in the previous study. In Experiment 2, participants actively imagined the accents. Results showed that MMN and P3a were not enhanced for strong beats; however, P3a showed significant enhancement for duple beats regardless of priming or attention, driven mainly by musically experienced participants. SSEPs were enhanced at the primed frequency but only when participants actively imagined the metre. As with infants, effects were stronger in the duple group. These results suggest a strong bias toward duple metre in adults that requires attention to overcome, and which likely relates to enculturation to Western music as it was enhanced by music and dance experience.

Introduction

Auditory rhythm perception involves bottom-up encoding of the onsets and offsets of events, as well as top-down application of hierarchical grouping structures. For example, in music, a rhythm is the structure indicated by the onsets and offsets of events, whereas the beat is perceptually derived as the regular pulse underlying the rhythm and can be felt even in places where there is no event onset. Adult listeners typically group beats to form metres, which can arise by emphasizing certain beats either perceptually or through the stimulus itself (e.g., loudness accents), such as emphasizing every second or third beat to form duple metre (e.g., a march), or triple metre (e.g., a waltz), respectively. The ability to perceive metrical organization in auditory rhythms has been linked to infant language outcomes (Choi et al., 2020; Menn et al., 2022) and is often compromised in developmental disorders (for a review see Lense et al., 2021). Even in adults, rhythmic tapping and discrimination abilities can predict grammar skills (Kim et al., 2024), and

neural encoding of rhythm can remain impaired in adult "recovered" dyslexics (Chang et al., 2021). Thus, it is important to better understand how rhythm processing develops across the lifespan. Previously, we showed novel evidence that infants' brains can maintain an internal (top-down) metrical interpretation of an ambiguous rhythm (duple vs. triple metre) at 6 months of age, a critical time point for language learning, as shown by enhanced neural responses to pitch changes occurring on beat positions primed to be perceived as strong compared to weak (Flaten et al., 2022). Further, enhanced responses were found for more musically experienced infants. Unlike infants, adults are fully enculturated to the rhythmic structures common in the music in their culture (e.g., Hannon & Trehub, 2005a), while at the same time they are able to apply attention to a metrical interpretation. Given that there is limited research on adults' flexibility to metrically interpret an ambiguous rhythm, the current study had three main aims: 1) to investigate whether adults can be primed to perceive an ambiguous rhythm in different metrical interpretations, and how this compares to previous findings in infants, 2) to investigate whether such top-down metre processing is modulated by active attention to the metre in adults, and 3) to explore connections to musical experience.

Top-down influences on metre perception can be studied with multiple neural measures that index different aspects of rhythm perception. For example, event-related potentials (ERPs) show that that identical events can elicit different neural responses depending on whether they are internally interpreted as occurring on strong compared to weak beat positions. More specifically, the amplitude of neural ERPs in response to occasional deviants (e.g., a pitch change) can be larger on perceptually strong compared

to weak beat positions. In particular, mismatch negativity (MMN) and P3a responses are typically measured because they are elicited by unexpected events amongst standard/expected events in an auditory stream. MMN is a frontally negative response (~ 100 to 150 ms post-deviant onset) representing the automatic detection of the deviant, and has been framed as a measure of neural prediction error (Friston, 2005; Lumaca et al., 2019; Prete et al., 2022; Vuust et al., 2009; Vuust & Witek, 2014; but see May, 2021). In older children and adults, P3a often follows the MMN and indexes the orienting of attention to the deviant (Comerchero & Polich, 1998; Escera et al., 2000; Katayama & Polich, 1998; Trainor et al., 1999). Enhanced MMN (Bouwer et al., 2014, 2016; Bouwer & Honing, 2015; Ladinig et al., 2009) and P3/P3a/P3b (Abecasis et al., 2005; Bouwer et al., 2016) amplitudes have been found for deviants occurring on strong, compared to weak beat positions when the metre is implied by the stimulus, and is associated with better detection of the deviants (Ladinig et al., 2009). Similar effects have been found in young infants as well, when the metre is unambiguous (Háden et al., 2024; Winkler et al., 2009). Further, enhanced P3 responses for the strong beats have been shown for adults' automatic application of subjective duple metre to an isochronous rhythm (Brochard et al., 2003; Potter et al., 2009). Thus, here we used MMN and P3a to investigate top-down metre perception in the context of a rhythm with ambiguous metre, when a particular beat was primed to be perceived as strong in one condition and weak in another.

Metrical processing has also been measured by examining neural tracking of the beat and metre of a rhythm over an extended time period. Specifically, the power and phase of the EEG responses at each of the beat and metre frequencies of interest index the

fidelity of the neural representations. Power can be indexed by steady state evoked potentials (SSEPs) at the beat, duple or triple metres in the stimulus (e.g., Nozaradan et al., 2011; 2012; 2016), and phase by inter-trial phase coherence (ITPC; e.g., Cohen, 2014; Doelling & Poeppel, 2015; Herrmann & Johnsrude, 2018). These neural tracking measures can index subjective metre perception. For example, spontaneous enhancement of SSEPs (relative to either the stimulus envelope or a model of stimulus encoding by the cochlea) or ITPC (Tal et al., 2017) at the beat and metre frequencies has been found even for stimuli with little to no energy at those frequencies (Fujioka et al., 2010; Nozaradan et al., 2012; Tal et al., 2017), and even in infants (Lenc et al., 2023). Further, metre-specific SSEP enhancement can continue during silence after presentation of beat-based rhythms (Bouwer et al., 2023). Thus, in the present study, we used SSEPs and ITPC to investigate neural tracking of beat and metre in an ambiguous rhythm after priming to hear it in one metre or another.

Clear evidence of top-down influences on rhythm perception comes from studies in which adults were instructed to imagine a rhythm in either duple or triple metre. Specific SSEP enhancement at the perceived metre was stronger when actively imagining the metre compared to passively listening to the rhythm (Celma-Miralles et al., 2016; Nave et al., 2019; Nozaradan et al., 2011). Similar enhancement of metre representation in SSEPs has been shown after auditory priming (Nave et al., 2022) and after body movement to the metre (Chemin et al., 2014), although this was only the case for duple, but not triple movement priming. SSEP magnitude at metre-related frequencies is

therefore thought to reflect participants' perception of the metre (Nave et al., 2022; Nozaradan et al., 2016).

There is little evidence, however, of how subjective metre may influence the predictive processing of individual beats within the rhythm, as most evidence showing enhanced MMN or P3a to strong beat positions (discussed above) is limited to duple rhythms that clearly indicated the metre. One study showed enhanced P3 for amplitude decrements on strong compared to weak beat positions for both duple and triple metre rhythms (Abecasis et al., 2005), and another found that metrical context modulated P3a for probe tones occurring in- compared to out-of-phase with the preceding metre (Jongsma et al., 2004). However, only one study directly compared results for imagined duple (quaternary) and triple (ternary) rhythms, showing enhanced N1 and a late negativity for imagined strong compared to weak beats for duple and triple metres, although perception of and tapping to the metrical accents were superior in the duple condition (Fitzroy & Sanders, 2020). Note also that given that this study did not include deviant tones, MMN and P3a were not measured, limiting claims about predictive processing.

Recently, we provided the first evidence of subjective duple versus triple metre processing of an ambiguous rhythm in 6-month-old infants (Flaten et al., 2022). Infants primed by loudness accents to hear an ambiguous (unaccented) rhythm in either duple or triple metre showed mismatch responses (an ERP elicited in infants and young children in oddball paradigms, indexing similar processes as adult MMN) to pitch deviants that were larger for the strong beat position (beat 5 for the duple-primed group and for beat 4 in the

triple-primed group), though effects were larger in the duple group in general (Flaten et al., 2022). Furthermore, neural tracking of the beat and metre was shown by peaks in the SSEPs for the duple, triple and beat frequencies, but these did not appear to be modulated by priming, and were similar to SSEPs of unprimed infants (Cirelli et al., 2016). Thus, our goal here was to examine subjective metre processing in adults, and whether priming would influence their predictive processing of individual beats (measured by MMN and P3a to strong or weak beats), and/or their neural tracking of the metrical structure of the rhythm (measured by SSEPs and ITPC to the beat and metre frequencies).

A possible reason for the differential effects of priming on mismatch ERPs and SSEPs in infants is that some top-down effects of metre processing may be independent of, while others may be clearest with, explicit attention. For example, adults' MMN and P3 amplitudes in response to unexpected loudness increments or decrements (Bouwer et al., 2016; Bouwer & Honing, 2015), or omissions (Ladinig et al., 2009) on strong compared to weak beat positions were similarly modulated for attended compared to passive or distracted conditions. In our previous study (Flaten et al., 2022), we aimed to engage infant attention with a visual cue synchronized to beat one of every repetition of the 6-beat pattern but found that mismatch responses were similarly modulated for infants who looked more compared to less at the visual display. Thus, the visual stimulus might not have been very effective in eliciting infants' attention to the metre, and/or as a pre-attentive component, mismatch response might not be highly affected by attention, in line with MMN being automatically elicited in adults (e.g., Näätänen et al., 1993). On the other hand, for measures that index the brain's tracking of the structure over longer

repetitions such as SSEPs and ITPC, explicit attention may facilitate metre-specific effects in adults (Celma-Miralles & Toro, 2019; Gibbings et al., 2023), especially in the case of an ambiguous rhythm with more than one possible interpretation. For example, in one study, adults showed top-down modulation of SSEPs for a spatially signalled metre only in the attended condition, but not when distracted by a visual task (Celma-Miralles & Toro, 2019), although another study found that implicit priming via motor engagement to the duple metre did modulate SSEPs at the duple frequency, but not in the triple case (Chemin et al., 2014). Priming alone may thus not have been strong enough in our previous study to elicit top-down modulation of SSEPs in infants, but adults who can engage in sustained attention to the metre through explicit instruction may be more influenced by priming. Thus, here we investigated the effects of priming and attention on SSEP responses in adults.

Other than Nave et al. (2022), to our knowledge, this is the first study to explore whether adult SSEPs can be implicitly primed (i.e., without explicit instruction; Experiment 1) to reflect processing of an ambiguous rhythm in either duple or triple metre, and the first to directly compare adult responses to a previous sample of infants who were tested under the same implicit priming conditions. In Experiment 1, we primed participants and asked them to listen attentively to the rhythm in general. In Experiment 2 we primed participants identically as in Experiment 1, but included explicit instructions to attend to the metre by imagining the accents during the unaccented test trials. Thus, we predicted that active attention would influence the neural tracking of the rhythmic structure, but given previous null interactions between attention and metre for modulating

MMN and P3a, we did not have strong predictions for how attention would influence processing of unexpected pitch deviants on primed strong and weak beats.

Many of the studies outlined thus far have found links between musical experience and modulated neural responses. Musical training has been associated with the enhancement of P300/P3a (Bouwer et al., 2016; Brochard et al., 2003; Jongsma et al., 2004), or N2b (Bouwer et al., 2016) for events occurring on metrically strong compared to weak positions. Further, SSEP enhancements (Celma-Miralles & Toro, 2019) and ITPC (Doelling & Poeppel, 2015) at beat and metre frequencies were stronger in musicians than non-musicians. In Western infants, participation in music classes may accelerate a cultural bias for duple metre. Compared to those not in music classes. 6- to 7month-old infants who were in active music classes showed SSEP enhancement at the duple metre frequency (Cirelli et al., 2016), and a general bias for enhanced MMRs consistent with a duple over triple metre interpretation (Flaten & Trainor, 2024). Infants in music classes (Cirelli et al., 2016; Trainor et al., 2012) or who had musician parents (Flaten et al., 2022) also showed generally enhanced ERPs to tones presented in a rhythmic context. These studies demonstrate a clear link between music experience and neural tracking of rhythms that may start early in development. Note, however, that in adults, some studies report similar effects of metre on MMN across level of musical experience (Bouwer et al., 2014; 2016), so effects may depend on the developmental stage. There is less research examining effects of dance experience on neural tracking of rhythms, but dancers have been reported to show augmented alpha modulation (Nakano et al., 2021), and early auditory components (Poikonen et al., 2016) for naturalistic music
compared to non-dancers. Here we therefore explored connections between music and/or dance experience and the neural processing of metre in adults.

Finally, top-down influences of rhythm perception include learned biases, such as from enculturation to one's musical environment (Hannon & Trainor, 2007). Although a universal duple bias may be present in part due to the ubiquity of binary rhythms in nature (Larsson, 2014; Larsson et al., 2019), and music (Jacoby & McDermott, 2017; Polak et al., 2018; Savage et al., 2015), clear effects of enculturation have been demonstrated in behavioural studies. Western music is dominated by duple metre (Gerry et al., 2010; Temperley, 2010), but other cultures commonly use more complex metres. Bulgarian & Macedonian adults show equal abilities to process simple Western and more complex Balkan rhythms while Western adults show better processing of simple Western rhythms (Hannon & Trehub, 2005a). Adults also show less flexibility than their infant counterparts. Behavioural studies show that Western 6-month-olds can discriminate Western and non-Western rhythms better than adults (Hannon & Trehub, 2005a) and that this effect diminishes by 12 months, but at this age they can still relearn non-Western rhythms with only two weeks exposure (Hannon & Trehub, 2005b). Western listeners consistently tap to the duple compared to the triple metre in the presence of a 2:3 polyrhythm (Møller et al., 2021), and both adults and children reproduce duple rhythms better than triple rhythms (Drake, 1993). Western listeners also automatically apply duple metre for an isochronous stimulus, as measured by enhanced P3 to every other tone (Abecasis et al., 2005; Brochard et al., 2003; Potter et al., 2009), and earlier MMN for binary versus non-binary integer ratios (Pablos Martin et al., 2007). Top-down effects on

SSEPs also tend to be stronger for induced duple than triple metre (Celma-Miralles et al., 2021; Chemin et al., 2014; Cheng et al., 2022). Thus, here we explored whether Western adults would show the same flexibility for duple or triple priming as infants tested previously under identical conditions, or whether they would maintain a strong duple bias, and whether this was influenced by musical experience.

In sum, the current study investigated how adults undergoing similar conditions as infants tested previously (Flaten et al., 2022) differ in their top-down processing of a metrically ambiguous rhythm. First, we explored whether implicit priming (Experiment 1) would bias adults' processing of the rhythm towards duple or triple metre, as indexed by better processing of pitch deviants on beats 5 and 4, respectively, and by metre-specific enhancement of SSEPs and ITPC to the primed rhythmic frequencies of the stimulus. The former would replicate the previous infant results, and the latter would suggest developmental differences in auditory priming effects on neural tracking. Secondly, we explored the role of active attention to the metre for top-down effects on neural processing of rhythms (Experiment 2). Specifically, we investigated whether attention to the primed metre would enhance top-down effects on MMN and P3a as well as neural tracking as indexed by SSEPs and ITPC. Finally, we explored whether neural processing of the metre was enhanced in participants with musical or dance experience.

Experiment 1

Experiment 1 was a direct comparison to Flaten et al. (2022), investigating whether adults, like infants, could be primed to process a metrically ambiguous rhythm in duple or triple metre, while being asked to listen without explicit instructions. We

predicted that adults would show enhanced MMN and P3a for pitch changes occurring on primed strong compared to weak beat positions. Further, if priming alone without explicit attention induces a robust neural representation of the metre, SSEPs should be amplified at the primed compared to unprimed frequency.

Materials & Methods

Participants

Participants were recruited from McMaster University and the greater Hamilton, Ontario, Canada area via word of mouth and social media. Fifty-four healthy adults with normal-hearing (provided by self-report) participated in this study, but 2 were removed due to data loss (< 65% trials kept after running ICA; see Data Acquisition & Preprocessing), 4 were removed because they fell asleep, and an additional 4 participants were removed for excessive visual alpha activity (> 2 SD above the mean for parietooccipital alpha activity [7 - 13 Hz] see EEG Data Analysis: Visual Alpha). Thus, a total of 10 participants were removed, leaving the final sample size of 44. The planned sample size of at least 18 participants per group was based on a previous power analysis conducted in Flaten et al. (2022) for a significant 2 (between-subjects) x 2 (withinsubjects) interaction with a medium effect size and 80% power, for priming group (duple or triple) and beat position (beat 4 or beat 5) of the deviant for the MMN/P3a (deviantstandard amplitude difference). This study used a between-subjects design for the condition of priming group in order to compare to the previously reported infant sample (Flaten et al., 2022), in which we opted not to prime within-subjects given a concern for carry-over effects between priming conditions. Thus, half the participants were randomly

assigned to each priming condition, while counterbalancing across sex: 23 participants were primed to hear the stimulus in duple metre (duple group; M age = 22.65 years; N = 14 females), and 21 were primed to hear the stimulus in triple metre (triple group; M age = 22.05; N = 15 females). All participants gave their informed consent to participate, and all methods and procedures were approved by the McMaster Research and Ethics Board. *Stimuli*

The auditory stimulus was a repeating, 1.8 s duration six-beat rhythmic pattern (Chemin et al., 2014; Cirelli et al., 2016; Flaten et al., 2022; Phillips-Silver & Trainor, 2005). All tones were piano tones synthesized using the Apple program Garageband, with a 15 ms onset. Tones and silences had an inter-onset-interval of 300 ms and were arranged: tone, silence, tone, tone, silence (see Figure 1). Tone duration was 299 ms, thus without added silence between consecutive tones, but to ensure that tones decayed to silence just before the onset of the next tone, a cosine decay ramp was applied from 200 to 299 ms. The pitch of the standard tones was A 440 Hz, while deviants were increased by a quartertone (i.e., 50 cents) to 452.89 Hz. Stimuli were played in groups of 20 (36 s), starting with 4 priming trials, followed by 16 test trials. After the 20th trial, another 20-trial set immediately started, again with the 4 priming stimuli. Duple or triple metre was indicated in the priming trials with loudness accents (10 dB increase relative to unaccented tones) on beats 1, 3 and 5, or beats 1 and 4, respectively. Test trials had no accents so that the metre would be ambiguous. To elicit MMN and P3a responses, test trials contained a pitch deviant 25% of the time (12.5% on beat 4, 12.5% on beat 5). This proportion of standards and deviants was maintained for each 20-trial group, with

deviants occurring pseudo-randomly, with the constraint that deviants followed at least one standard trial. Given that beat 4 is a strong beat for triple metre, but not duple, and beat 5 is a strong beat for duple, but not triple, we expected that adult MMN/P3a would be larger for beat 4 in the triple-primed group, and for beat 5 in the duple-primed group. The whole session consisted of three 6-minute blocks, each with ten 20-trial groups.

To compare to our previous results in infants, we followed the procedure of Flaten et al. (2022) to implicitly draw general attention to the auditory rhythm by presenting a visual stimulus that emphasized each beat one via intersensory redundancy (e.g., Brandwein et al., 2011; Lewkowicz & Turkewitz, 1980; Molholm et al., 2002; Smith et al., 2017). A coloured circle (10 cm, 5.72° visual angle) centered on a 68.6 cm monitor expanded 30 % in size at the onset of the first tone of every 6-beat pattern, and immediately shrunk before the start of the second beat (See Figure 1A). The colour of the circle was either yellow, green, pink, blue, or red, with the colour changing pseudorandomly at the start of each 20-trial set, such that no colour could be repeated twice in a row. Various videos were created for each block that combined the visual with the auditory stimulus, and these were chosen randomly for each participant. Auditory stimuli were presented via a loudspeaker located above the monitor ~ 1 metre in front of the participant. One channel of the audio file delivered the sound to the speaker, and the other channel delivered a square wave on every beat 1 to a trigger box connected to the Electrical Geodesics Inc. (EGI) EEG recording system to ensure precise synchronization of the auditory stimulus and triggers.

Procedure

After receiving a description of the study, participants signed a consent form, followed by a language and music background questionnaire. The questionnaire included items about demographics, hearing ability, music and dance experience, and languages spoken. All but 1 participant (in the triple-primed group) filled out the questionnaire. The participant then sat on a chair in a sound-attenuated room in front of the loudspeaker. The computer screen for the visual stimuli was just below the loudspeaker and slightly below eye level. Instructions for adults were chosen to make the experience as comparable as possible to that of the infants in Flaten et al. (2022). Thus, participants were instructed to look at the centre of the screen and simply listen to the presented rhythms. They were told to not speak unless needing to stop the experiment, and to minimize their movements during the recording session. A short break was taken at the end of each 6-minute block, so the participant could readjust their position if needed. A webcam was placed above the computer screen, so that a researcher outside the room could monitor the participant and ensure they were looking at the screen, coding through a mouse directly into the EEG recording whether the participant looked away from the screen. One participant closed their eves (without falling asleep) for ~ 2 minutes at the end of the first block, so instructions were clarified that they needed to look at the screen. It was confirmed posthoc that this participant was not an outlier in visual alpha activity during the experiment (see EEG Data Analysis: Visual Alpha). All other participants kept in the final sample looked at the screen for the duration of the experiment.

EEG Data Acquisition & Preprocessing

The EEG data were recorded at 1000 Hz sampling rate using a 128-channel Hydrocel GSN net with an Electrical Geodesic NetAmps 200 amplifier and Electrical Geodesics NETSTATION software (v.5.4.2). At the start of recording, all impedances were maintained below 50 k Ω , and the reference was channel Cz. A researcher kept a record of any bad channels. All data were processed using MATLAB R2022a (v.9.12) and the Fieldtrip Toolbox (v. 20210301; Oostenveld et al., 2011), and statistical analyses were done in SPSS (v. 20).

The data were filtered with two 3rd order zero phase shift Butterworth filters, one a high pass with a 1 Hz cutoff and the other a lowpass filter with a 20 Hz cutoff. The 1 Hz high-pass was used because independent components analysis (ICA) carried out subsequently has a better signal-to-noise ratio when using a 1-2 Hz high pass filter (Winkler et al., 2015). After filtering, Fieldtrip's ft_rejectvisual function was used to identify noisy channels by plotting their variance over time. Any channel that contributed > 10⁴ μ V of variance was removed. In most cases, channels that were marked as bad during testing were above the threshold, but if they were below the threshold, they were double-checked and removed if they visually appeared to be outliers (if close to the 10⁴ μ V variance threshold, or ~ >2 SD from the rest of the channels). Further, given that the 4 face channels (E125 – E128) were often noisy due to mask-wearing protocols, they were removed from all participants. Next, the data were re-referenced to the average of all electrodes and downsampled to 200 Hz, before running ICA to remove eye, muscle, and heart artifacts, as well as line noise.

The ICA was run from within Fieldtrip, using the ft_componentanalysis function to call RUNICA from EEGLAB (Delorme & Makeig, 2004) with the number of components set to the number of channels minus one, to account for using an average reference. The components were plotted over time along with their topographic map, to visually identify and remove stereotypical eye blinks and movements, muscle and heart artifacts, as well as line noise, for each participant. The resulting weighted unmixing matrix with the removed components was saved for each participant, and the identical preprocessing steps up to and including the re-referencing were run again on the raw data, with the exception that the high- and low-pass filter cutoffs were set to 0.25 Hz and 20 Hz, respectively. After re-referencing, the data were multiplied with the unmixing matrix to remove the artifacts. A range of 5 to 16 components (M = 8.65) were removed for each participant. The data were then segmented -100 to 900 ms relative to the onset of beat 4 (i.e., 100 ms before beat 4, to the end of beat 6) in each trial for the ERP analyses. The data were also segmented -100 to 28 800 ms relative to the onset of each 16- trial set of unaccented trials for the frequency analyses. Following segmenting and for the ERPs only, any remaining trials exceeding $\pm 100 \,\mu\text{V}$ at any point in the trial were removed, and the trials were linearly detrended. Finally, the channels removed before preprocessing were replaced using interpolation based on the average of all neighbouring channels. Any participants who maintained < 65% of ERP trials (N = 4; see Participants) were removed from all analyses.

Event-Related Potentials Analysis

To extract the brain activity of interest for the ERPs, the epochs were then segmented separately for each beat position from -100 ms (pre-stimulus period) to 600 ms relative to the beat onset, resulting in separate epochs for beats 4 and 5 during standard trials, and for beat 4 during beat 4 deviant trials, and for beat 5 during beat 5 deviant trials. The epochs were then averaged separately for each participant and condition, resulting in four ERPs per participant, for the beat 4 and 5 standards and deviants. Only standard trials that were followed by a deviant trial were included in an attempt to equate the number of standards and deviants in the average. Epochs were then baseline corrected by subtracting the average of the 100 ms pre-stimulus period.

Channel selection for analyzing MMN and P3a were chosen a priori to be the frontal and central electrodes, as this is where auditory MMN tends to appear maximally negative in amplitude (Näätänen et al., 2007; Prete et al., 2022; Sussman et al., 1998, 2002). The electrodes were grouped into six regions based on frontality (frontal (F) or central (C)), and laterality (left (L), midline (Z) and right (R)) resulting in regions denoted FL FZ FR CL CZ & CR (See Figure 1D). The deviant-standard difference waves were calculated for beats 4 and 5 at each channel and then plotted for each individual for FL FZ and FR regions to investigate the latency of the MMN. The intervals of interest for the MMN and P3a were expected to be 100-250 ms, and 200-350 ms based on previous literature with pitch deviants in auditory oddball paradigms (Bendixen et al., 2012; Maurer et al., 2003; Näätänen et al., 1993, 2007; Schwade et al., 2017; Sussman et al., 1998, 2002; Widmann et al., 2018; Wronka et al., 2012). Upon visual inspection of the

individual waveforms for FZ, all adults' MMN fell within 100-250 ms, with P3a following 200-350 ms, although it appeared participants varied in their latencies. Thus, we used a peak-finding method to determine latencies separately for each participant, using a window of 100-250 ms post-stimulus onset for MMN, and 200-350 post-stimulus onset for P3a. All participants' MMN peaks fell within 101 to 226 ms (M = 135 ms) across frontal and central sites. For P3a, latencies fell within 201 to 338 ms (M = 240 ms). MMN and P3a amplitudes were determined as the average amplitude \pm 20 ms around the latency of the peak. For any participant who did not show a clear peak, the average latency of the group in that condition was used to isolate the peak. Note that except for one participant for the beat 5 deviant in FL, all participants had an MMN peak in all conditions. Only one (a different) participant lacked a P3a peak for beat 5 in FL.

To test the presence of significant MMN and P3a in all 6 regions of interest at both beat positions, a one-tailed t-test tested the deviant-standard amplitude differences against 0, using Bonferroni correction for multiple comparisons. To investigate priming effects on MMN and P3a, separate Mixed ANOVAs were run on the deviant-standard difference waves with the within-subjects' factors of frontality (frontal or central regions), laterality (left, midline, or right regions), and deviant beat position (beat 4 or beat 5), as well as a between-subjects' factor of priming group (duple or triple). Any violations of sphericity (p < .05) were addressed using Greenhouse-Geisser correction, with the corrected df and p values reported. Post-hoc ANOVAs and t-tests all used Bonferroni correction when there were multiple comparisons.

Steady State Evoked Potentials Analysis

Frequency-tagging was used to isolate the power spectra of the SSEPs at the frequencies of interest, using methods established previously (Cirelli et al., 2016; Flaten et al., 2022; Nozaradan et al., 2011). The 30 28.8 s segments per participant made from the unaccented trials (plus a 100 ms pre-stimulus baseline period) were first averaged in the time domain to get one 28.8 s trial for each participant. Then, the segment was baseline corrected by subtracting the average of the 100 ms pre-stimulus period. This 100 ms was then removed before running the Fast Fourier Transform (FFT) to get the power (μV^2) spectra. An FFT using a Hanning multitaper and a frequency resolution of 0.035 Hz was run from 0 to 4 Hz at each channel for each participant. To increase the signal to noise ratio of the SSEP peaks, at each bin, the power from the average of the third, fourth, and fifth neighbouring bins on each side was subtracted. Thus, the power from - 0.174 to -0.104 Hz and + 0.104 to + 0.174 Hz relative to each bin was subtracted (Cirelli et al., 2016; Nozaradan et al., 2011).

The SSEPs were then averaged across all channels similarly to previous studies (Cirelli et al., 2016; Flaten et al., 2022; Nozaradan et al., 2011). First the power peaks in the SSEPs at the frequencies of interest (1.11, 1.67, and 3.33 Hz) were compared against the noise floor to determine whether the peaks were significantly greater than noise. Each participant's noise floor was calculated by averaging the SSEP signal power across frequency bins not in the rhythmic frequencies of interest, namely those equally in between the beat, metre and harmonic frequencies (0.833, 1.389, 1.945, 2.500 Hz and 3.055 Hz). Paired samples t-tests were performed comparing each frequency of interest

against the noise floor. Following this a mixed ANOVA with the factors of frequency (1.11, 1.67, 3.33), and priming group (duple, triple) was conducted, with the hypothesis of a significant group x frequency interaction, which would demonstrate a difference in relative power between the metrical frequencies according to priming group.

Inter-Trial Phase Coherence Analysis

Finally, we explored an additional measure of neural rhythm tracking, inter-trial phase coherence (ITPC), to investigate how consistent the phase of the rhythmic neural activity in the brain was at the frequencies of interest in the stimulus. ITPC is of interest as it provides information about the variability of neural tracking. One benefit to using ITPC to look at low-frequency rhythmic brain activity is that the trial-by-trial variation is maintained, given that phase is estimated from trial to trial for each frequency before averaging, where here the trials are the 28.8 s unaccented segments used in the SSEP analysis. These analyses and results are reported in the Supplementary Information for both experiments 1 and 2 (See Figure S1), as we did not find differences according to priming.

Visual Alpha Analysis

During EEG recordings, the researcher noted the presence of prominent alpha activity, and upon visualizing the data during analysis, some participants' ERPs and ICA components appeared to show strong oscillatory activity. Given that some participants had fallen asleep, we wanted to ensure that none of the remaining sample had EEG recordings dominated by prominent alpha activity due to inattention or sleepiness. Thus, we measured participants' visual alpha activity by running an FFT (with a Hanning

window multitaper) on the preprocessed data for the frequency analyses, for each 28.8 s trial from 5 to 15 Hz, with 0.035 Hz resolution at each electrode. Each participant's alpha activity was taken as the average power for 7-13 Hz across parieto-occipital channels (Gibbings et al., 2023). We plotted boxplots (see Figure S2) and identified and removed the participants (N = 4) whose visual alpha power exceeded 2 SD above the mean.

Results

All statistical analyses were performed in IBM SPSS Statistics (v. 20). Greenhouse-Geisser was used to correct violations of sphericity. All post-hoc multiple comparisons were corrected using Bonferroni and all reported p values have been adjusted using the family-wise error rate.

ERPs

T-test results for the overall presence of MMN and P3a in Experiment 1 are shown in Table 1. MMN and P3a were significantly above chance for both beat positions across all regions of interest (all adjusted p's <.05). The deviant-standard difference waves separated by group are shown in Figure 2; to see examples of the separate deviant and standard waves, see Supplementary Information (Figure S3).

ANOVA results for the MMN are shown in Figure 3A. Contrary to our predictions, there was no priming group x beat position interaction (F(1,42) = .303, p = .585, $\eta_p^2 = .007$), or any other effects involving priming group or beat position (p's > .300). The only effects were those of topography, which are tangential to our hypotheses, and so can be found in the Supplementary Information. Overall, MMN was strongest at FZ and biased to right hemisphere.

ANOVA results for the P3a are shown in Figure 3B. As with the MMN results we did not find the predicted priming group x beat position interaction (F(1,42) = .945, p = .337, $\eta_p^2 = .022$), and instead there was a main effect of beat position (F(1,42) = 4.208, p = .047, $\eta_p^2 = .091$), where overall, P3a was stronger for beat 5 (M = 1.281 µV, 95% CI [0.986, 1.577]) than beat 4 (M = 1.005 µV, 95% CI [0.707, 1.302]). Additionally, there were effects of topography which are summarized in the Supplementary Information. Overall, P3a was strongest in CZ.

Steady State Evoked Potentials and Phase Coherence

SSEP results are shown in Figure 4. All peaks at the frequencies of interest were significantly greater than the noise floor (1.11 Hz: t(43) = 9.202, p < .001, d = 1.387, M = .079 μ V², 95% CI [0.061, 0.096]; 1.67 Hz: t(43) = 10.727, p < .001, d = 1.617, M = 0.083 μ V², 95% CI [0.067, 0.099]; 3.33 Hz: t(43) = 10.343, p < .001, d = 1.562, M = 0.037 μ V², 95% CI [0.030, 0.044]). However, we did not find a frequency x priming group interaction ($F_{GG}(1.71,71.68) = .619$, p = .517, $\eta_p^2 = .015$). There was also no main effect of priming group (F(1,42) = <.001, p = .996, $\eta_p^2 < .001$).

There were no effects of priming on ITPC, (see results in Supplementary Information, Figure S1).

Interim Discussion

In Experiment 1, we primed Western adults identically as we had done in a previous infant study (Flaten et al., 2022) to hear a 6-beat ambiguous rhythm either in duple (groups of 2 beats) or triple metre (groups of 3 beats), and measured their MMN and P3a responses to unexpected pitch changes on strong and weak beat positions, as well

as their SSEPs and ITPC to the beat and metre frequencies in the stimulus. Previously, we found that 6-month-olds' mismatch responses were larger for pitch changes occurring on strong compared to weak beat positions (especially for duple-primed infants), suggesting top-down metre processing, although SSEPs were not enhanced at the primed compared to unprimed frequencies (Flaten et al., 2022). Thus, if adults could be similarly primed to show evidence of top-down effects of metre processing in the brain, then we expected to find larger amplitude MMN & P3a responses for the strong beat. Further, given adults' greater ease in engaging sustained attention compared to infants, we also expected SSEP enhancement at the primed vs. unprimed frequencies. Overall, our hypotheses were not supported in Experiment 1, as adults' MMN and P3a were not modulated by beat position according to priming group and, although SSEPs and ITPC showed peaks at the expected beat and metre frequencies, these were not enhanced for the primed compared to unprimed metre. Further, we found that P3a was larger for beat 5 (strong beat for duple metre, weak for triple) compared to beat 4, regardless of priming group, suggesting an overall bias towards the duple metre.

It is possible that adults require active attention directed to a metrical interpretation to overcome their entrenched duple bias. A few previous studies found ERP modulation for deviants according to metric position was similar across attention conditions (Bouwer et al., 2016; 2020; Bouwer & Honing, 2015; Ladinig et al., 2009), but these studies did not examine metrically ambiguous rhythms. Similarly, previous studies that showed top-down enhancement of SSEPs did so via active imagination of the metre (Nave et al., 2019; Nozaradan et al., 2011), prior body movement to the metre (Chemin et

al., 2014), or auditory priming paired with perceptual questions to engage interest and attention (Nave et al., 2022). Additionally, active attention to the beat or metre has been found to enhance SSEP peaks relative to unattended or distracted conditions (Celma-Miralles & Toro, 2019; Gibbings et al., 2023). Thus, it is possible that the priming in Experiment 1 did not sufficiently engage attention to induce a sustained top-down metrical interpretation. Further, we did not measure their behaviour and/or perception in relation to the metre, so we could not confirm whether they were perceiving the primed metre as expected. Thus, in Experiment 2, we replicated the methods of Experiment 1, but additionally trained adults to actively attend to the primed metre by imagining the accents. We also separately collected tapping and perception data from participants to investigate their motor entrainment and perception of the metre.

Experiment 2

This experiment was carried out identically as experiment 1, while additionally asking participants to actively imagine the accents of the metre, and to answer perceptual questions intermittently to confirm their metre perception. We hypothesized that active attention to the metre would enhance SSEPs at the primed compared to unprimed metre frequencies, as in previous studies where the metre was not ambiguous (Celma-Miralles & Toro, 2019; Gibbings et al., 2023; Nozaradan et al., 2011). Given previous null effects of metrical attention on ERPs (Bouwer et al., 2016; 2020; Bouwer & Honing, 2015; Ladinig et al., 2009), we did not have strong predictions on how MMN and P3a would differ for strong compared to weak beat positions in the context of attention.

Materials & Methods

All methods for Experiment 2 were identical to those in Experiment 1, with the exception of: 1) the addition of an attentional training paradigm added before the EEG data collection, 2) the shortening of stimulus blocks from 6 minutes to 3 minutes, thus resulting in 6 blocks as opposed to 3 blocks, which facilitated 3) the addition of collecting perceptual questions about the metre after each block, and 4) the addition of collecting tapping data after training, half-way through the priming paradigm, and at the end of the experiment. Each of these changes are outlined below. All methods and procedures were approved by the McMaster Research and Ethics Board.

Participants

Participants were recruited via the online student participant recruitment system at McMaster University, where students could sign up to participate to receive course credit. Forty-eight (N = 22 duple; N = 26 triple) healthy adults with normal (provided by self-report) hearing participated. Of these, 13 were excluded: 2 for falling asleep (1 duple, 1 triple); 2 for having too few clean trials after preprocessing (both were in triple group); 2 for exceeding 2 SD from the mean in parieto-occipital alpha activity (1 duple; 1 triple), as determined by an analysis of visual alpha identical to that from Experiment 1 (See Figure S2); and an additional 7 participants for not reaching threshold tapping performance (5 triple; 2 duple; see Tapping Behaviour & Perception Analyses below), leaving a final sample of 35 participants (N = 18 [14 female, 4 male] duple; N = 17 triple [13 female, 4 male]). The mean age in the final sample was 18.5 years for the duple group and 18.4 for the triple group. Note that the sample for Experiment 2 did differ somewhat from that of

Experiment 1 as recruitment through the university online participant pool resulted in a younger and more predominantly female-identifying set of participants.

Stimuli

All auditory and visual stimuli were identical as in Experiment 1, with exception that the number of blocks of stimuli was doubled, and the duration of each block shortened to 3 minutes (from 6 minutes) for the prime-test paradigm to allow for intermittent questions to probe participants' perception of the metre; and the presentation of additional stimuli blocks specific to the training paradigm at the start of the experiment. Training stimuli used the same accented and unaccented pattern as in the rest of the experiment, where 8 accented trials were presented, followed by 8 unaccented standard trials. The training stimuli included the visual stimulus, in this case randomly chosen as the blue colour.

Procedure

The procedure outline for Experiment 2 is shown in Figure 5. Refer to Figure 1 for details on the audiovisual stimuli, and for the prime-test paradigm. After signing a consent form, participants were seated in the sound-attenuated room ~ 1 m in front of the speaker and screen that delivered the stimuli. Participants were then trained on how to imagine the metre.

The researcher played the training stimulus example, while tapping along on their lap to the accents after 2 measures and pointing out to the participant where the accents were, and when they went away, with the unaccented pattern starting at the 9th repetition. After the first training trial ended, the researcher made sure the participant understood the task.

The training trial was then repeated while the researcher and participant tapped the accents together on their laps. If the participant had questions, the researcher avoided telling participants any new instructions and emphasized that the participant should just 'feel' the beat where the accents are. The training trial was then repeated 1-2 times where the participant tapped along to the accents as was just done previously, but this time on their own and on a foam pad with a microphone in it to record their tapping. Taps and triggers for the metrically strong beats were recorded simultaneously to precisely analyze participants' tapping asynchronies relative to the metre. Outside the booth, the researcher (a classically trained pianist for >13 years) observed the tapping recording and if participants failed to tap in synchrony (by visual assessment) to the primed metre for at least 10 out of 12 unaccented trials, they could attempt a second tapping trial. If they still failed to reach this threshold, this was marked down in the recording notes, but EEG was still recorded. Outlier tapping performance was confirmed post-hoc (See Tapping Behaviour & Analyses). If a participant required a second tapping training trial recording, only this second trial was analyzed for the training trial. Participants also had their tapping recorded half-way, and at the end of the experiment. For these post-training tapping trials, we simply instructed participants to tap along to the accents as we had them do previously. Thus, participants had three useable tapping trials total (training, halfway, and end).

After training, participants answered the same music and language background questionnaire as in in Experiment 1. Participants filled the questionnaire online with a tablet, whereas in Experiment 1 this was done on pen and paper. Participants were then

set up with the EEG cap and instructed that while we had them tapping along to the accents previously, we needed them to remain still during the experiment, and just imagine/feel the metre. To ensure they still remembered the metre, we played the training trial one more time, while they tapped the accents on their lap, at which point the researcher asked the participant to stop tapping and simply imagine the accents without moving any part of their body to the rhythm (i.e., finger/foot tapping, blinking, breathing, subvocalizing tongue movements etc.). After the tapping trials for training and halfway through the study, the researcher briefly reminded the participant of how to imagine the metre, by repeating some of the initial instructions from training.

Following training, participants underwent the prime-test paradigm as in Experiment 1. After every 3-minute block, participants rated 1) their perception of how well they imagined the accents (i.e., their confidence ratings) on a sliding scale ("Please use the slider to rate how well (approximately) you think you were imagining the accents in the rhythm in the last 3-minute block from: 0 - I was able to feel it none of the time, to 100 - I was able to feel it all of the time."); 2) how well they thought they were attending to the task in general (from "1 - I was distracted the whole time" to 7 - "I was never distracted"); 3) how tired they currently felt after that block from "1- not tired at all", to "7-extremely tired"; and 4) how relaxed they currently felt after that block from "1- not relaxed at all" to "7-extremeley relaxed". After answering questions for the third block (halfway), and sixth and final block, their tapping to the rhythm was recorded again. Also, at halfway, impedances were checked and bad channels were refilled with saline solution. Questions for the sixth and final block included an additional two questions asking

participants to describe in detail any strategies that they used to maintain the metre with examples given of counting/using words to label beats, using motor imagery, using the visual cue, etc., and finally to give any comments that might inform the researcher of their experiences during the study. Most participants reported using the dot to help anchor their perception of the beat, and many seemed to use some sort of mental verbalizing (i.e., counting numbers, or imagining 'ta' or 'ba'), or motor imagery (i.e., imagining tapping a foot or finger) to aid their perception. Most participants reported multiple strategies. Finally, tapping was recorded one last time.

EEG Data Acquisition, Preprocessing, and Analysis

All preprocessing steps were carried out identically as in Experiment 1. A range of 5 to 12 ICA components (M = 8.7) were removed for each participant. Additionally, all analyses of the MMN, P3a, SSEPs and ITPC were identical to Experiment 1. All MMN peaks fell within the window of 101 to 203 ms, and P3a between 201 to 329 ms.

Tapping Behaviour & Perceptual Questionnaire Analyses

Tapping onsets were recorded using the program Audacity along with square waves (triggers) representing the onset time of the accented notes according to each metre. These were analyzed as per Carrillo et al. (2024). Participants' taps were first identified using an amplitude threshold determined separately for each participant. Then, the trigger closest in time to each tap was used as the reference for where participants were expected to tap if synchronized to the metre. Only taps for the unaccented trials were analyzed. Thus, the distance (asynchrony) from the reference beat and the tap were used to calculate a circular mean vector, R, which was used to calculate tapping accuracy

and consistency for the training, middle, and end tapping trials (Figure S5). Mean tapping accuracy was calculated as the mean phase angle of *R* relative to the beat (where 0 radians would be perfectly synchronized). Positive angles indicate tapping after the beat, whereas negative angles indicate tapping ahead of or before the beat. Tapping consistency was calculated as the mean length of *R*, which is the opposite of the variability in tapping phase over the trial. Note that given that the two groups tapped to different metrical levels, this meant that they tapped at different rates (duple = 1.67 Hz, faster than triple = 1.11 Hz). Thus, comparing tapping outcomes between the groups is not entirely valid.

Tapping results were used to identify participants who likely failed to learn the metre, and we removed N = 7 (5 triple, 2 duple) participants for being outliers (> M ± 2 SD) in tapping accuracy and/or consistency in either the training, middle, or final tapping recording (See Figure S5). Note that one participant's (duple group) tapping data during the training trial was not properly recorded, but they passed the tapping threshold based on experimenter's judgement during training and were not outliers in either their middle or final tapping measures. One potential issue is that the triple metre was more difficult to tap than the duple metre, which is demonstrated by more participants in the triple group being removed for being tapping outliers compared to the duple group. To investigate whether removing these participants changed the results, all main analyses were repeated while including these 7 participants, and the findings did not differ (see Results).

For the questions taken after each 3-minute block, we ran independent samples ttests to compare the priming groups on their mean perception, relaxation, and tiredness ratings. Even though the groups tapped at different rates, we additionally ran a t-test on

their mean tapping accuracy and consistency. To explore potential connections between participants' perception and their EEG results, we ran a median split analysis, comparing the participants who rated their metre perception the highest to those who rated their perception the lowest (median = 76.33%, M = 74.8%), using mixed ANOVAs with grouping factors of low versus high perception ratings, priming group (duple or triple), and a within-subjects' factor of beat position (beat 4 or 5), separately for MMN, and for P3a. We also ran a mixed ANOVA for SSEPs with the factors of perception group, priming group, and frequency (triple, duple, or beat).

Results

As in Experiment 1, all statistical analyses were performed in IBM SPSS Statistics, Version 20. Greenhouse-Geisser was used to correct violations of sphericity. All post-hoc multiple comparisons were corrected using Bonferroni and all reported p values have been adjusted using the family-wise error rate.

ERPs

T-test results for the overall presence of MMN and P3a in Experiment 2 are shown in Table 2. MMN and P3a were significantly above chance for both beat positions across all regions of interest (all adjusted p's <.05). The deviant-standard difference waves separated by group are shown in Figure 6. To see examples of the separate deviant and standard waves, see Supplementary Information (Figure S3).

Results for the analyses of the MMN are shown in Figure 7A. Results from the ANOVA revealed a main effect of priming group (F(1,33) = 4.586, p = .040, $\eta_p^2 = .122$), where adults in the triple group had more negative amplitude MMNs (M = -1.609, 95%)

CI [-1.909, -1.310]) than those in the duple group (M = -1.170, 95% CI [-1.461, -0.878]) overall. However, as with Experiment 1, there was no beat position x priming group interaction (F(1,33) = 0.038, p = .847, $\eta_p^2 = .001$). Additionally, as in Experiment 1, MMN was strongest in FZ and biased to right hemisphere (described in Supplementary Information; see Figure S4). Note that these results do not differ if we include the outlier tappers; the main effect of group was still present, but marginally less significant (F(1,40) = 4.100, p = .050, $\eta_p^2 = .093$).

Results for the analyses of the P3a are shown in Figure 7B. Like in Experiment 1, we did not find the predicted priming group x beat position interaction (F(1,33) = 0.028, p = .867, $\eta_p^2 = .001$), and again found a main effect of beat position (F(1,33) = 4.772, p = .036, $\eta_p^2 = .126$), where beat 5 P3a (M = 1.197 μ V, 95% CI [0.848, 1.547]) was more positive than beat 4 (M = 0.862 μ V, 95% CI [0.503, 1.221]), in general. Note that the main effect of beat position still holds if we re-run the analyses to include the outlier tappers (F(1,40) = 4.622, p = .038, $\eta_p^2 = .104$). P3a was strongest at midline sites and diffuse across frontal and central sites (described in Supplementary Information; See Figure S4).

Low-Frequency Responses

SSEP results for Experiment 2 are shown in Figure 8. Paired samples t-tests showed that all peaks at the frequencies of interest were significantly greater than the noise floor (1.11 Hz: t(34) = 4.973, p < .001, d = 0.891, M = 0.091 μ V², 95% CI [0.054, 0.128]; 1.67 Hz: t(34) = 5.338, p < .001, d = 0.902, M = 0.103 μ V², 95% CI [0.064, 0.143]; 3.33 Hz: t(34) = 8.741, p < .001, d = 1.475, M = 0.030 μ V², 95% CI [0.023,

0.037]). We analyzed the SSEPs with a mixed ANOVA with factors of frequency and priming group, which revealed a frequency x group interaction (F(2, 66) = 2.986, p) = .029, η_{p}^{2} = .083; Note that because we had a directional hypothesis, we used a onetailed p-value here). Post-hoc analyses comparing frequency within priming groups showed that for the duple group, the duple peak was enhanced relative to the triple peak, as predicted (t(17) = 2.407, p = .042, d = 0.566, M = 0.030 μ V², 95% CI [0.004, 0.055]). The duple peak was also larger than that of the beat frequency (t(17) = 4.542, p < .001, d)= 1.071, M = 0.052 μ V², 95% CI [0.028, 0.076]), and the triple peak was numerically larger than that of the beat frequency, but this did not survive Bonferroni correction (t(17))= 2.374, p = .090, d = 0.428, M = 0.022 μ V², 95% CI [0.002, 0.042]). In contrast, for the triple group, the triple peak was not significantly different from the duple peak (t(16) = $0.224, p = .826, d = 0.054, M = 0.005 \,\mu V^2, 95\%$ CI [-0.044, 0.055]), but unlike for the duple group, SSEP power at the triple frequency was greater than at the beat frequency $(t(16) = 3.084, p = .021, d = 0.748, M = 0.102 \mu V^2, 95\% CI [0.032, 0.172])$, and power at the duple frequency was numerically, but not significantly larger than at the beat frequency $(t(16) = 2.622, p = .054, d = 0.636, M = 0.100 \mu V^2, 95\%$ CI [0.019, 0.175]). If we break down frequency x group interaction instead by comparing groups at each frequency separately, then we find that as predicted, the triple group (M = $0.132 \mu V^2$, 95% CI [0.081, 0.182]) shows larger SSEP power compared to the duple group (M = $0.052 \ \mu V^2$, 95% CI [0.003, 0.101]) at the triple frequency (F(1, 33) = 5.247, p = .015, η_p^2 = .137). Groups did not differ at the duple (F(1, 33) = 1.353, p = .253, $\eta_p^2 = .039$), or beat $(F(1, 33) = 0.002, p = .968, \eta_p^2 < .001)$ frequencies. In the Mixed ANOVA, the main

effect of group was trending, suggesting that the triple group may have had moderately stronger SSEP power overall (F(1, 33) = 3.101, p = .087, $\eta_p^2 = .086$). Note that the SSEP results still hold if the outlier tappers are included, with a significant frequency x group interaction ($F_{GG}(1.75,69.94) = 3.000$, p = .032, $\eta_p^2 = .070$).

We additionally ran analyses of ITPC, which are reported in the Supplementary Information (See Figure S1), but there were no effects of priming on ITPC.

Tapping Behaviour and Perceptual Analyses

T-tests comparing the duple and triple groups revealed no significant differences in ratings of perception (t(33) = .237, p = .814, d = 0.014), relaxation (t(33) = .282, p = .780, d = 0.095) or tiredness (t(33) = 1.060, p = .297, d = 0.358), or in their tapping performance (averaged over the first, middle and end trials) consistency (t(33) = .008, p = .994, d = < .001), and accuracy (t(33) = 1.881, p = .345, d = 0.639; See Figure S5).

The mixed ANOVA exploring differences in MMN for the high and low raters on perception revealed a significant perception x priming group interaction (F(1,31) = 5.789, p = .022, $\eta_p^2 = .157$; See Figure S6A), where within the low perception group, those primed with triple metre (M = -1.816 µV, 95% CI [-2.285, -1.331]) had more negative MMN than those primed in duple metre (M = -0.892 µV, 95% CI [-1.183, -0.609]; F(1,16) = 10.080, p = .006). In contrast, participants with high perceptual ratings showed equivalent MMN regardless of priming (F(1,17) = .003, p = .955). Thus, the main effect of priming group for the MMN in the overall analysis seems to be driven by participants with lower perceptual ratings of their performance.

For P3a, there was a significant perception group x beat position interaction $(F(1,31) = 4.412, p = .044, \eta_p^2 = .125;$ See Figure S6B). Specifically, those with low perception ratings had larger P3a on beat 5 compared to beat 4 ($t(16) = 2.935, p = .010, d = 0.712, M = 0.634 \mu V, 95\%$ CI [0.176, 1.092]), but those with high perceptual ratings showed equivalent P3a on beats 4 and 5 ($t(17) = 0.267, p = .792, d = 0.063, M = 0.052 \mu V, 95\%$ CI [-0.358, 0.462]). Thus, although P3a was larger on beat 5 than beat 4 overall, this bias seems to have been driven by participants with lower ratings of their metre perception. For SSEPs, there were no effects of perception ratings (all p's > .200).

Combined Exploratory Analyses of Music/Dance Experience for Experiments 1 & 2

Given that in Flaten et al. (2022) we found that infants with more musically experienced parents showed larger mismatch responses, as well as other links of musical experience with EEG measures (e.g., Bouwer et al., 2016; Brochard et al., 2003; Cirelli et al., 2016; Celma-Miralles & Toro, 2019; Doelling & Poeppel, 2015), we explored whether adults with or without musical training differed across the combined samples of Experiments 1 and 2 (including experiment group as a factor). Some participants had substantial dance experience, so we included dance training in the musically experienced group. The experienced group (N = 53) included current musicians with a minimum of 6 years of training on any instrument (M = 13.24 years, SD = 4.41), as well as current dancers with a minimum of 1 year training in any style (M = 6.7 years, SD = 5.86), where N = 16 were musicians, 16 were dancers, and 21 were both. Participants in the inexperienced group (N = 25) were neither current musicians nor dancers, but most participants (20/25) had played at least one instrument in previous years (M years

experience = 4.96 years). One participant did not fill out the questionnaire and was excluded from this analysis. We re-ran a priori mixed ANOVAs separately for MMN and P3a with factors frontality (frontal or central), laterality (left, midline or right), beat position (beat 4 or 5), experiment group (1- priming only, or 2- priming and attention), and music/dance experience group (experienced or inexperienced). For SSEPs the factors were frequency (triple, duple or beat), experiment group, and music/dance experience group. All post-hoc t-tests used Bonferroni correction for multiple comparisons when appropriate.

Results are shown in Figure S7. For the MMN there was a music/dance group x laterality interaction ($F_{GG}(1.684, 124.60) = 3.585, p = .038, \eta_p^2 = .046$), where the experienced group showed the expected MMN topography based on results from the separate experiments (more negative amplitudes in midline and right; L-Z: t(52) = 6.021, $p = <.001, d = 0.827, M = 0.508 \mu$ V, 95% CI [0.339, 0.677]; L-R: $t(52) = 3.219, p = .006, d = 0.442, M = 0.314 \mu$ V, 95% CI [0.118, 0.510]; Z-R: t(52) = -2.579, p = .039, d = -0.354, M = -0.194 μ V, 95% CI [-0.344, -0.043]), but the MMN for the inexperienced group did not differ across laterality (L-Z: $t(24) = .922, p = .366, d = 0.184, M = 0.115 \mu$ V, 95% CI [-0.142, 0.372]; L-R: $t(24) = .839, p = .410, d = 0.168, M = 0.153 \mu$ V, 95% CI [-0.211, 0.287]). There was also a music/dance group x beat position interaction ($F(1, 74) = 4.553, p = .036, \eta_p^2 = .058$), but this was not significant when broken down, as there was no significant effect of beat position in either the experienced ($F(1, 52) = 2.195, p = .145, \eta_p^2 = .040$), or inexperienced ($F(1, 24) = 2.760, p = .110, \eta_p^2 = .103$) groups. Neither were

the post-hoc analyses significant when the interaction was broken down to compare groups separately for beat 4 (F(1, 76) = 0.661, p = .419, $\eta_p^2 = .009$) and 5 (F(1, 76) = 1.737, p = .191, $\eta_p^2 = .022$). Nonetheless, the interaction is plotted in Figure S7.

For P3a, there was a frontality x music/dance group x beat position interaction $(F(1, 74) = 5.440, p = .022, \eta_p^2 = .068)$, where the experienced group showed the 2-way frontality x beat position interaction $(F(1, 52) = 6.275, p = .015, \eta_p^2 = .108)$, such that at frontal sites there was a stronger P3a on beat 5 than beat 4 $(t(52) = 3.335, p = .002, d = 0.458, M = 0.614 \mu V, 95\%$ CI [0.245, 0.983]), but beat 5 P3a was non-significantly larger than for beat 4 in central sites $(t(52) = 1.916, p = .061, d = 0.263, M = 0.222 \mu V, 95\%$ CI [-0.010, 0.454]). In contrast, the inexperienced group did not show a frontality x beat position interaction $(F(1, 24) = .802, p = .379, \eta_p^2 = .032)$, so the beat 5 bias for P3a seems to be absent in less experienced participants. Given that in Experiment 2 we found that the effect of beat position for P3a was driven by the participants with lower ratings of perceiving the metre, a follow-up t-test was conducted comparing perceptual ratings for the musically experienced (N = 24) and inexperienced (N = 11) participants just for Experiment 2, which revealed no differences (F(1, 33) = .706, p = .407).

There were no effects of musical experience on the SSEPs or ITPC results (all p's > .15).

General Discussion

The current study investigated whether adults could maintain one of two primed metrical interpretations (duple or triple metre) of a metrically ambiguous rhythm, comparing conditions of listening without instruction (Experiment 1) and active attention (via imagining the accents; Experiment 2). Further, adults' metre processing without instruction was qualitatively compared to that of a previous infant sample (Flaten et al., 2022) to explore developmental changes in the flexibility of metre processing, as well as the roles of attention and enculturation. Adults only showed evidence of internally maintaining a primed metrical interpretation when actively attending to the metre, and only for the measure of neural tracking (SSEPs). As far as enhanced processing for beats primed to be strong, adults' MMN and P3a amplitudes to occasional pitch changes on beats 4 (strong in triple metre) and 5 (strong in duple metre) were not different across duple and triple priming conditions, and this was the case for both passive and active attention conditions. Instead, we found evidence of a robust bias towards the duple metre as shown by larger P3a amplitude for beat 5 compared to beat 4, regardless of priming or attention condition, which was driven by the musically experienced participants. This is consistent with other studies showing larger enhancements for strong beats when adults were presented with metrically unambiguous rhythms in duple metre than in triple metre (Abecasis et al., 2005; Jongsma et al., 2004). Overall, we showed that how adults apply an internally derived metrical structure on an ambiguous rhythm is influenced by attention, and a robust (likely enculturated) duple bias.

These results contrast those of infants tested under the identical uninstructed conditions (Flaten et al., 2022) as adults in Experiment 1 of the present paper. Specifically, infants' mismatch responses were modulated by metrical priming, with enhanced amplitudes for pitch changes on beat positions that were strong in accordance with how they were primed, whereas adults showed no evidence of metrical priming on

MMN or P3a responses. However, infants and adults were similar in showing a duple metre bias, with overall larger P3a amplitudes to pitch changes on beat 5 than beat 4 in adults, and larger priming effects and more robust mismatch response in general for infants primed with duple than triple metre. Previous studies in adults showing larger ERPs on perceived strong than weak beats contrast with the present study in that they did not use metrically ambiguous stimuli in which the strong and weak beats were in opposite beat positions for the different metrical interpretations (Abecasis et al., 2005; Bouwer et al., 2014; 2016; 2020; Bouwer & Honing, 2015; Brochard et al., 2003; Ladinig et al., 2009; Potter et al., 2009). Rather, metre was not manipulated (most often the stimuli gave rise to a duple metre percept) and they simply contrasted responses to deviants in strong versus weak beats within the unambiguous metre. The only previous evidence of enhanced ERPs according to subjective duple versus triple metre used an isochronous rhythm and reported differences for N1 and a late negative response to standard tones, which differed according to the metre imagined by the participants (Fitzroy & Sanders, 2020). We cannot compare our results directly to this study as participants in Fitzroy and Sanders were not primed, and MMN and P3a responses could not be measured as it did not include pitch deviants. Thus, the current study was novel in testing adults' top-down modulation of MMN and P3a under metrically ambiguous conditions.

Interestingly, our SSEP results revealed that neural tracking was modulated by attention directed to imagining the primed metre. Those primed with duple metre had greater SSEP power at the duple compared to triple frequency, while those primed with triple metre did not show a significant power difference between duple and triple

frequencies but had greater power at the triple frequency than those primed with duple metre. This suggests two influences at play, one of the imagined/primed metre, and one of a general bias for duple metre that thus facilitated and limited enhancement in the duple and triple groups, respectively. Interestingly, without attention to the metre, there was no evidence that priming had any effect on adults' neural tracking as measured by SSEPs, similarly to uninstructed infants (Flaten, et al., 2022). This is in line with previous studies in adults showing greater metre-specific enhancement when participants were asked to actively imagine or attend to the intended metre, compared to passive or distracted conditions (Celma-Miralles & Toro, 2019; Gibbings et al., 2023). Further, that the present neural tracking effects under explicit attention were clearest in the duple group is in line with a previous study using the same 6-beat stimulus, which showed explicit movement to the metre enhanced subsequent SSEPs for the duple, but not triple frequency (Chemin et al., 2014), thus again suggesting a duple bias. Also consistent with a duple bias in the present results is the trend for larger overall SSEP power and larger MMN amplitude in the triple compared to duple group, suggesting greater neural resources were required to actively attend to and maintain a triple metrical structure. Together, these results indicate that, at least in Western listeners, active imagination of the metre may be required, or at least greatly facilitates, modulation of neural representation of metre in SSEPs when more than one possible interpretation is present, especially in the context of a duple bias.

While adults have the advantage of being able to engage active attention to modulate neural tracking of metre, the results suggest infants are more flexible to being primed to perceive different metres, by enhancing automatic predictions (as measured by

mismatch responses) of unexpected pitch changes on strong beats. There is, in fact, much evidence to suggest that infants generally show more flexible learning than adults. For example, young infants readily perceive phoneme contrasts that could occur in any language but become specialized for those in their native language within the first year (Werker et al., 1981; Werker & Tees, 1983, 2002). Similar trends are seen for increasing specialization over the first year for own-species and own-race faces (Kelly et al., 2007; Liu et al., 2011; Pascalis et al., 2002; Xiao et al., 2018), own-species voices (Friendly et al., 2013, 2014), and own-culture musical structures (Hannon & Trainor, 2007; Hannon & Trehub 2005a; 2005b). Thus, the limited flexibility in adults for metrical priming is likely related to a strongly enculturated Western duple bias (Gerry et al., 2010; Temperley, 2010), in line with a number of previous behavioural (Drake, 1993; Møller et al., 2021) and neural (Abecasis et al., 2005; Brochard et al., 2003; Chemin et al., 2014; Cheng et al., 2022; Celma-Miralles et al., 2021; Pablos Martin et al., 2007; Potter et al., 2009) studies of metre perception. In a predictive coding framework, this duple bias acts as a strong prior that influences rhythmic expectations and predictions and requires explicit top-down attention to overcome, consistent with the results of the present study, where adults' SSEP enhancement for the primed metre was found only when attending and especially in the duple group.

Unlike for neural tracking, we did not have strong predictions about how active attention to the metre would impact MMN and P3a, given previous null effects of attention in modulating the processing of deviants on strong and weak beats (Bouwer et al., 2016; 2020; Bouwer & Honing, 2015; Ladinig et al., 2009). In fact, attention to the

metre did not induce metre-specific effects on ERPs, but notably, adults actively attending to the triple metre showed an overall more negative (enhanced) MMN than those attending to the duple metre, and this was especially the case for the participants who had had lower confidence in their ability to perceive the triple metre. Within a predictive coding framework (Bouwer et al., 2020; Bouwer & Honing, 2015; Vuust et al., 2009; Vuust & Witek, 2014), larger MMN may indicate greater uncertainty, and thus greater prediction error, for the deviants in general. Thus, given a duple bias, those in the more difficult condition of imagining a triple metre, and especially those with low confidence, would be expected to have a larger MMN. Duple-primed participants, on the other hand, would have less uncertainty in imagining the duple metre, given that priming would be consistent with their duple bias. In sum, while the SSEP results indicate that attention led to stronger neural tracking of the primed metre, attention did not generally influence the processing of unexpected events (measured by MMN and P3a) according metre (i.e., events on beat 4 or beat 5) other than to mitigate the duple bias by reducing the prediction error (MMN) through better perception of the metre in the triple group.

It is important to note that the stimulus itself was also biased slightly towards duple metre (See Figure 1C), so it is hard to disentangle how much of the duple bias was stimulus-driven, or a result of preexisting biases in the listeners. However, given that across both experiments the duple bias was driven by the musicians and dancers, we argue that Western music engagement likely increased the duple bias, which is consistent with studies showing accelerated enculturation in Western infants who've attended music classes (Cirelli et al., 2016, Gerry et al., 2010; 2012; Trainor et al., 2012). We have

recently found further evidence for this in 6-month-olds, where infants attending regular music classes showed larger mismatch response for beat 5 compared to beat 4 of an isochronous 6-beat pattern (Flaten & Trainor, 2024). Importantly, the results of the present study were not entirely driven by the duple bias in the stimulus as shown by attention to the metre reducing a duple bias in the SSEPs, and by those who gave stronger ratings in their metre perception showing a reduced beat 5 bias in P3a responses. Thus, while there was a contribution from the stimulus toward a duple interpretation, adults could overcome this with active attention and strong metre perception.

The study has some limitations. One limitation is that, while both beats 4 and 5 were preceded by a tone, the local context did differ. Beat 4 was always followed by a tone whereas beat 5 was always followed by a rest, so subjective accenting could have occurred for beat 5 due to its position in the non-isochronous rhythm (Povel & Essens, 1985). However, potential absolute differences between responses for events on beats 4 and 5 would not be expected to affect interactions with priming, or differ for deviants and standards, and thus should be addressed when the standard amplitudes are subtracted. And indeed, infants did show a significant interaction between priming and beat 4 versus beat 5 responses (Flaten et al., 2022). One reason for using this stimulus is that it has been used many times previously, allowing for comparisons between studies (Chemin et al., 2014; Cirelli et al., 2016; Edalati et al., 2023; Flaten et al., 2022; Hannon & Johnson, 2005; Phillips-Silver & Trainor, 2005). Still, future studies might use isochronous stimuli or various rhythms that are balanced in implying duple versus triple metre. Finally, this study compared adult responses to those of infants in our previous study, making it a

cross-sectional comparison with two widely separate age groups. Future studies could examine a variety of ages and/or employ longitudinal designs to understand more fully how rhythm tracking in the brain changes over development.

In conclusion, this was the first study to test whether adults could be primed to process an ambiguous rhythm either in duple or triple metre, as indexed by MMN, P3a, and neural tracking (SSEPs, ITPC) measures. Further, this was the first study to directly compare adults to a previously tested sample of infants. Unlike infants, adults could apply a sustained interpretation of an ambiguous rhythm by actively attending to the metre. This was shown by enhanced neural tracking of the primed metre frequency in SSEPs in Experiment 2, although this was clearest in the duple group. On the other hand, infants could be primed to better process unexpected pitch changes on subjectively strong compared to weak beat positions (Flaten et al., 2022), while adults were less flexible in responding to such priming, likely due to a robust duple bias. This duple bias was shown by consistently stronger attentional capture (P3a) to unexpected events on beat 5 than beat 4, as well as better neural tracking of the metrical structure when attending to the duple than triple metre. Interestingly, the duple bias likely starts early in infancy, as priming effects on mismatch responses were stronger for duple- than triple-primed infants. While likely partially stimulus-driven, the duple bias also likely reflects enculturated Western biases, given that it was augmented by music and dance experience. Together these findings show that adults' automatic predictions of rhythmic events seem to be greatly influenced by their learned priors, whereas young infants who are less enculturated are more flexible to being influenced by a primed metrical structure. Adults, however, can
better engage attention to induce a sustained metrical interpretation to overcome their duple bias as measured by neural tracking of the metre.

Data Availability Statement

Any data or code can be made available upon request from the corresponding author, LJT at <u>lit@mcmaster.ca</u>.

Author Contributions

EF and LJT conceptualized the research, EF carried out the research including developing the methods, collecting, preparing and analyzing the data, and drafting the manuscript. CC conducted the tapping analysis. LJT supervised the research and acquired the funding. EF and LJT edited and wrote the manuscript, and CC reviewed the final draft.

Acknowledgements

This research was funded by grants acquired by last author LJT from the Natural Sciences and Engineering Research Council of Canada (NSERC; RGPIN-2019-05416), the Social Sciences and Humanities Research Council of Canada (SSHRC; 435-2020-0442), the Canadian Institutes of Health Research (MOP 153130), and the Fondation pour l'Audition (RD-2021-11). Additionally, first author EF acquired graduate funding whilst completing the research from a SSHRC Canadian Graduate Scholarship – Master's grant, an Ontario Graduate Scholarship grant, an NSERC Create grant in Complex Dynamics as well as a SSHRC doctoral fellowship grant. Finally, we thank Elaine Whiskin for assisting with the data collection.

References

Abecasis, D., Brochard, R., Granot, R., & Drake, C. (2005). Differential brain response to metrical accents in isochronous auditory sequences. *Music Perception*, 22(3), 549– 562. https://doi.org/10.1525/mp.2005.22.3.549

Bendixen, A., SanMiguel, I., & Schröger, E. (2012). Early electrophysiological indicators for predictive processing in audition: A review. *International Journal of Psychophysiology*, 83(2), 120–131. https://doi.org/10.1016/j.ijpsycho.2011.08.003

- Bouwer, F. L., Fahrenfort, J. J., Millard, S. K., Kloosterman, N. A., & Slagter, H. A.
 (2023). A silent disco: Differential effects of beat-based and pattern-based temporal expectations on persistent entrainment of low-frequency neural oscillations. *Journal of Cognitive Neuroscience*, *35*(6), 990–1020. https://doi.org/10.1162/jocn_a_01985
- Bouwer, F. L., & Honing, H. (2015). Temporal attending and prediction influence the perception of metrical rhythm: evidence from reaction times and ERPs. *Frontiers in Psychology*, 6, 1–14. https://doi.org/10.3389/fpsyg.2015.01094
- 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), 1–9. 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

Brandwein, A. B., Foxe, J. J., Russo, N. N., Altschuler, T. S., Gomes, H., & Molholm, S.

(2011). The development of audiovisual multisensory integration across childhood and early adolescence: A high-density electrical mapping study. *Cerebral Cortex*, *21*(5), 1042–1055. https://doi.org/10.1093/cercor/bhq170

- Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "ticktock" of our internal clock: Direct brain evidence of subjective accents in isochronous sequences. *Psychological Science*, *14*(4), 362–366. https://doi.org/10.1111/1467-9280.24441
- Celma-Miralles, A. ., Kleber, B. A. ., Toro, J. M. ., & Vuust, P. (2021). Neural entrainment facilitates duplets: Frequency-tagging differentiates musicians and nonmusicians when they tap to the beat. *BioRxiv*. https://doi.org/10.1101/2021.02.15.431304
- Celma-Miralles, A., de Menezes, R. F., & Toro, J. M. (2016). Look at the beat, feel the meter: Top–down effects of meter induction on auditory and visual modalities. *Frontiers in Human Neuroscience*, 10, 1–13.

https://doi.org/10.3389/fnhum.2016.00108

- Chang, A., Bedoin, N., Canette, L. H., Nozaradan, S., Thompson, D., Corneyllie, A., Tillmann, B., & Trainor, L. J. (2021). Atypical beta power fluctuation while listening to an isochronous sequence in dyslexia. *Clinical Neurophysiology*, *132*(10), 2384–2390. https://doi.org/10.1016/j.clinph.2021.05.037
- 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

- Cheng, T.-H. Z., Creel, S. C., & Iversen, J. R. (2022). How do you feel the rhythm:
 Dynamic motor-auditory interactions are involved in the imagination of hierarchical timing. *The Journal of Neuroscience*, *42*(3), 500–512.
 https://doi.org/10.1523/JNEUROSCI.1121-21.2021
- Choi, D., Batterink, L. J., Black, A. K., Paller, K. A., & Werker, J. F. (2020). Preverbal infants discover statistical word patterns at similar rates as adults: Evidence from neural entrainment. *Psychological Science*, *31*(9), 1161–1173. https://doi.org/10.1177/0956797620933237
- 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, 1–11. https://doi.org/10.3389/fnins.2016.00229
- Cohen, M. X. (2014). Intertrial phase clustering. In *Analyzing neural time series data: Theory and practice* (Issue 1, pp. 241–258). The MIT Press.
- Comerchero, M. D., & Polich, J. (1998). P3a, perceptual distinctiveness, and stimulus modality. *Cognitive Brain Research*, 7(1), 41–48. https://doi.org/10.1016/S0926-6410(98)00009-3

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21.

https://doi.org/10.1016/j.jneumeth.2003.10.009

Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, *112*(45). https://doi.org/10.1073/pnas.1508431112

- Drake, C. (1993). Reproduction of musical rhythms by children, adult musicians, and adult nonmusicians. *Perception & Psychophysics*, 53(1), 25–33. https://doi.org/10.3758/BF03211712
- Edalati, M., Wallois, F., Safaie, J., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi,
 S. (2023). Rhythm in the premature neonate brain: Very early processing of auditory
 beat and meter. *The Journal of Neuroscience*, 43(15), 2794–2802.
 https://doi.org/10.1523/JNEUROSCI.1100-22.2023
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neuro-Otology*, 5, 151–166. https://doi.org/10.1159/000013877
- Fitzroy, A. B., & Sanders, L. D. (2020). Subjective metric organization directs the allocation of attention across time. *Auditory Perception & Cognition*, 3(4), 212–237. https://doi.org/10.1080/25742442.2021.1898924
- 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
- Flaten, E., Trainor, L. (2024). Investigating generalizability of top-down neural representation of metre in infancy. Manuscript submitted for publication.
- Friendly, R. H., Rendall, D., & Trainor, L. J. (2013). Plasticity after perceptual narrowing for voice perception: Reinstating the ability to discriminate monkeys by their voices

at 12 months of age. *Frontiers in Psychology*, *4*, 1–8. https://doi.org/10.3389/fpsyg.2013.00718

Friendly, R. H., Rendall, D., & Trainor, L. J. (2014). Learning to differentiate individuals by their voices: Infants' individuation of native- and foreign-species voices. *Developmental Psychobiology*, 56(2), 228–237. https://doi.org/10.1002/dev.21164

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 815–836. https://doi.org/10.1098/rstb.2005.1622

- Fujioka, T., Zendel, B. R., & Ross, B. (2010). Endogenous neuromagnetic activity for mental hierarchy of timing. *The Journal of Neuroscience*, 30(9), 3458–3466. https://doi.org/10.1523/JNEUROSCI.3086-09.2010
- Gerry, D. W., Faux, A. L., & Trainor, L. J. (2010). Effects of Kindermusik training on infants' rhythmic enculturation. *Developmental Science*, 13(3), 545–551. https://doi.org/10.1111/j.1467-7687.2009.00912.x
- Háden, G. P., Bouwer, F. L., Honing, H., & Winkler, I. (2024). Beat processing in newborn infants cannot be explained by statistical learning based on transition probabilities. *Cognition*, 243, 105670.

https://doi.org/10.1016/j.cognition.2023.105670

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., & Trainor, L. J. (2007). Music acquisition: Effects of enculturation and

formal training on development. *Trends in Cognitive Sciences*, *11*(11), 466–472. https://doi.org/10.1016/j.tics.2007.08.008

- 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*, 102(35), 12639–12643. https://doi.org/10.1073/pnas.0504254102
- Herrmann, B., & Johnsrude, I. S. (2018). Neural signatures of the processing of temporal patterns in sound. *Journal of Neuroscience*, 38(24), 5466–5477. https://doi.org/10.1523/JNEUROSCI.0346-18.2018
- 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
- Jongsma, M. L. A., Desain, P., & Honing, H. (2004). Rhythmic context influences the auditory evoked potentials of musicians and nonmusicians. *Biological Psychology*, 66(2), 129–152. https://doi.org/10.1016/j.biopsycho.2003.10.002
- Katayama, J., & Polich, J. (1998). Stimulus context determines P3a and P3b. *Psychophysiology*, *35*, 23–33.
- Kayhan, E., Hunnius, S., O'Reilly, J. X., & Bekkering, H. (2019). Infants differentially update their internal models of a dynamic environment. *Cognition*, 186, 139–146. https://doi.org/10.1016/j.cognition.2019.02.004

- Kelly, D. J., Quinn, P. C., Slater, A. M., Lee, K., Ge, L., & Pascalis, O. (2007). The otherrace effect develops during infancy: Evidence of perceptual narrowing. *Psychological Science*, *18*(12), 1084–1089. https://doi.org/10.1111/j.1467-9280.2007.02029.x
- Kim, H. W., Kovar, J., Bajwa, J. S., Mian, Y., Ahmad, A., Mancilla Moreno, M., Price, T. J., & Lee, Y. S. (2024). Rhythmic motor behavior explains individual differences in grammar skills in adults. *Scientific Reports*, *14*(1), 1–10. https://doi.org/10.1038/s41598-024-53382-9
- Ladinig, O., Honing, H., Háden, G., & Winkler, I. (2009). Probing attentive and preattentive emergent meter in adult listeners without extensive music training.
 Music Perception, 26(4), 377–386. https://doi.org/10.1525/mp.2009.26.4.377
- Larsson, M. (2014). Self-generated sounds of locomotion and ventilation and the evolution of human rhythmic abilities. *Animal Cognition*, *17*(1), 1–14. https://doi.org/10.1007/s10071-013-0678-z
- Larsson, M., Richter, J., & Ravignani, A. (2019). Bipedal steps in the development of rhythmic behavior in humans. *Music & Science*, 2. https://doi.org/10.1177/2059204319892617

Lense, M. D., Ladányi, E., Rabinowitch, T.-C., Trainor, L., & Gordon, R. (2021). Rhythm

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

and timing as vulnerabilities in neurodevelopmental disorders. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*, 20200327. https://doi.org/10.1098/rstb.2020.0327

- Lewkowicz, D. J., & Turkewitz, G. (1980). Cross-modal equivalence in early infancy: Auditory–visual intensity matching. *Developmental Psychology*, 16(6), 597–607. https://doi.org/10.1037/0012-1649.16.6.597
- Liu, S., Quinn, P. C., Wheeler, A., Xiao, N., Ge, L., & Lee, K. (2011). Similarity and difference in the processing of same- and other-race faces as revealed by eye tracking in 4- to 9-month-olds. *Journal of Experimental Child Psychology*, *108*(1), 180–189. https://doi.org/10.1016/j.jecp.2010.06.008
- Lumaca, M., Trusbak Haumann, N., Brattico, E., Grube, M., & Vuust, P. (2019).
 Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity. *European Journal of Neuroscience*, 49(12), 1597–1609. https://doi.org/10.1111/ejn.14329
- Maurer, U., Bucher, K., Brem, S., & Brandeis, D. (2003). Development of the automatic mismatch response: From frontal positivity in kindergarten children to the mismatch negativity. *Clinical Neurophysiology*, *114*(5), 808–817. https://doi.org/10.1016/S1388-2457(03)00032-4
- May, P. J. C. (2021). The adaptation model offers a challenge for the predictive coding account of mismatch negativity. *Frontiers in Human Neuroscience*, 15, 1–10. https://doi.org/10.3389/fnhum.2021.721574
- Menn, K. H., Ward, E. K., Braukmann, R., van den Boomen, C., Buitelaar, J., Hunnius,

S., & Snijders, T. M. (2022). Neural tracking in infancy predicts language development in children with and without family history of autism. *Neurobiology of Language*, *3*(3), 495–514. https://doi.org/10.1162/nol_a_00074

- Molholm, S., Ritter, W., Murray, M. M., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). Multisensory auditory-visual interactions during early sensory processing in humans: A high-density electrical mapping study. *Cognitive Brain Research*, 14(1), 115–128. https://doi.org/10.1016/S0926-6410(02)00066-6
- Møller, C., Stupacher, J., Celma-Miralles, A., & Vuust, P. (2021). Beat perception in polyrhythms: Time is structured in binary units. *PLOS ONE*, *16*(8), e0252174. https://doi.org/10.1371/journal.pone.0252174
- Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*(12), 2544–2590. https://doi.org/10.1016/j.clinph.2007.04.026
- Näätänen, R., Paavilainen, P., Tiitinen, H., Jiang, D., & Alho, K. (1993). Attention and mismatch negativity. *Society for Psychophysiological Research*, *30*, 436–450.
- Nakano, H., Rosario, M.-A. M., & de Dios, C. (2021). Experience affects EEG eventrelated synchronization in dancers and non-dancers while listening to preferred music. *Frontiers in Psychology*, *12*. https://doi.org/10.3389/fpsyg.2021.611355
- Nave, K.M., Hannon, E.E., & Snyder, J.S. (2019). Registered report: Replication and extension of Nozaradan, Peretz, Missal and Mouraux (2011). Advances in Methods and Practices in Psychological Science. Provisionally accepted manuscript. OSF Page: https://osf.io/rpvde/.

- Nave, K. M., Hannon, E. E., & Snyder, J. S. (2022). Steady state-evoked potentials of subjective beat perception in musical rhythms. *Psychophysiology*, 59(2), 1–15. https://doi.org/10.1111/psyp.13963
- Nozaradan, S., Peretz, I., & Keller, P. E. (2016). Individual differences in rhythmic cortical entrainment correlate with predictive behavior in sensorimotor synchronization. *Scientific Reports*, 6(1), 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. (2012). Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *The Journal of Neuroscience*, *32*(49), 17572–17581. https://doi.org/10.1523/JNEUROSCI.3203-12.2012

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 1–9. https://doi.org/10.1155/2011/156869

- Pablos Martin, X., Deltenre, P., Hoonhorst, I., Markessis, E., Rossion, B., & Colin, C. (2007). Perceptual biases for rhythm: The Mismatch Negativity latency indexes the privileged status of binary vs non-binary interval ratios. *Clinical Neurophysiology*, *118*(12), 2709–2715. https://doi.org/10.1016/j.clinph.2007.08.019
- Pascalis, O., De Haan, M., & Nelson, C. A. (2002). Is face processing species-specific during the first year of life? *Science*, 296(5571), 1321–1323.

https://doi.org/10.1126/science.1070223

- 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
- Poikonen, H., Toiviainen, P., & Tervaniemi, M. (2016). Early auditory processing in musicians and dancers during a contemporary dance piece. *Scientific Reports*, 6(1), 33056. https://doi.org/10.1038/srep33056
- Polak, R., Jacoby, N., Fischinger, T., Goldberg, D., Holzapfel, A., & London, J. (2018). Rhythmic prototypes across cultures. *Music Perception*, 36(1), 1–23. https://doi.org/10.1525/mp.2018.36.1.1
- Potter, D. D., Fenwick, M., Abecasis, D., & Brochard, R. (2009). Perceiving rhythm where none exists: Event-related potential (ERP) correlates of subjective accenting. *Cortex*, 45(1), 103–109. https://doi.org/10.1016/j.cortex.2008.01.004
- Povel, D., & Essens, P. (1985). Perception of temporal patterns. *Music Perception*, 2(4), 411–440. https://doi.org/10.2307/40285311
- Prete, D. A., Heikoop, D., McGillivray, J. E., Reilly, J. P., & Trainor, L. J. (2022). The sound of silence: Predictive error responses to unexpected sound omission in adults. *European Journal of Neuroscience*, 55(8), 1972–1985. https://doi.org/10.1111/ejn.15660
- 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 of the United States of America*, *112*(29), 8987–8992.

https://doi.org/10.1073/pnas.1414495112

- Schwade, L., Didoné, D., & Sleifer, P. (2017). Auditory evoked potential mismatch negativity in normal-hearing adults. *International Archives of Otorhinolaryngology*, 21(03), 232–238. https://doi.org/10.1055/s-0036-1586734
- Smith, N. A., Folland, N. A., Martinez, D. M., & Trainor, L. J. (2017). Multisensory object perception in infancy : 4-month-olds perceive a mistuned harmonic as a separate auditory and visual object. *Cognition*, 164, 1–7. https://doi.org/10.1016/j.cognition.2017.01.016
- Sussman, E., Ritter, W., & Vaughan, H. G. (1998). Attention affects the organization of auditory input associated with the mismatch negativity system. *Brain Research*, 789(1), 130–138. https://doi.org/10.1016/S0006-8993(97)01443-1
- Sussman, E., Winkler, I., Huotilainen, M., Ritter, W., & Näätänen, R. (2002). Top-down effects can modify the initially stimulus-driven auditory organization. *Cognitive Brain Research*, 13(3), 393–405. https://doi.org/10.1016/S0926-6410(01)00131-8
- Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., &
 Golumbic, E. Z. (2017). Neural entrainment to the beat: The "missing-pulse"
 phenomenon. *The Journal of Neuroscience*, *37*(26), 6331–6341.
 https://doi.org/10.1523/JNEUROSCI.2500-16.2017
- Temperley, D. (2010). Modeling common-practice rhythm. *Music Perception*, 27(5), 355–376. https://doi.org/10.1525/mp.2010.27.5.355
- Trainor, L. J., Desjardins, R. N., & Rockel, C. (1999). A comparison of contour and interval processing in musicians and nonmusicians using event-related potentials.

Australian Journal of Psychology, *51*(3), 147–153. https://doi.org/10.1080/00049539908255352

Trainor, L. J., Marie, C., Gerry, D. W., Whiskin, E., & Unrau, A. (2012). Becoming musically enculturated: Effects of music classes for infants on brain and behavior. *Annals of the New York Academy of Sciences*, *1252*(1), 129–138. https://doi.org/10.1111/j.1749-6632.2012.06462.x

- Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music - Brain responses to rhythmic incongruity. *Cortex*, 45(1), 80–92. https://doi.org/10.1016/j.cortex.2008.05.014
- Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, 5, 1–14. https://doi.org/10.3389/fpsyg.2014.01111
- Werker, J. F., Gilbert, J. H. V, Humphrey, K., & Tees, R. C. (1981). Developmental aspects of cross-language speech perception. *Child Development*, 52(1), 349. https://doi.org/10.2307/1129249
- Werker, J. F., & Tees, R. C. (1983). Developmental changes across childhood in the perception of non-native speech sounds. *Canadian Journal of Psychology*, 37(2), 278–286. https://doi.org/10.1037/h0080725
- Werker, J. F., & Tees, R. C. (2002). Cross-language speech perception: Evidence for perceptual reorganization during the first year of life. *Infant Behavior and Development*, 25(1), 121–133. https://doi.org/10.1016/S0163-6383(02)00093-0

Widmann, A., Schröger, E., & Wetzel, N. (2018). Emotion lies in the eye of the listener:

Emotional arousal to novel sounds is reflected in the sympathetic contribution to the pupil dilation response and the P3. *Biological Psychology*, *133*, 10–17. https://doi.org/10.1016/j.biopsycho.2018.01.010

Winkler, I., Debener, S., Muller, K. R., & Tangermann, M. (2015). On the influence of high-pass filtering on ICA-based artifact reduction in EEG-ERP. *Proceedings of the Annual International Conference of the IEEE Engineering in Medicine and Biology Society, EMBS, 2015-Novem*, 4101–4105. https://doi.org/10.1109/EMBC.2015.7319296

- 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*, 106(7), 2468–2471. https://doi.org/10.1073/pnas.0809035106
- Wronka, E., Kaiser, J., & Coenen, A. M. L. (2012). Neural generators of the auditory evoked potential components P3a and P3b. *Acta Neurobiologiae Experimentalis*, 72(1), 51–64.
- Xiao, N. G., Mukaida, M., Quinn, P. C., Pascalis, O., Lee, K., & Itakura, S. (2018).
 Narrowing in face and speech perception in infancy: Developmental change in the relations between domains. *Journal of Experimental Child Psychology*, *176*, 113–127. https://doi.org/10.1016/j.jecp.2018.06.007



Figure 1. Audio-visual Stimulus. A) Timing of the stimulus. B) Stimulus presentation protocol. A total of 3 6-minute blocks were presented. C) Stimulus envelope for the unaccented test trials (left), and priming trials (right). D) Electrode groupings chosen for all analyses using the Geodesic 128-channel mapping. F = Frontal; C = Central; L = Left; Z = Midline; R = Right. (Adapted from Flaten et al., 2022).



Figure 2. Event-related potentials for the deviant-standard difference waves for Experiment 1. Duple group is in purple, triple group in teal. Beat 4 is the solid line, beat 5 is the dashed line. MMN was analyzed between 100-150 ms, P3a between 200-350 ms. Shaded area represents the standard error of the mean. F = frontal; C = central; L = Left; Z = midline; R = right.



Figure 3. Boxplots and topographies for ERP amplitudes for Experiment 1. A) MMN effects revealed null effects of priming and beat position (left). Topographies shown on the right. B) For P3a the main finding was an effect of beat position (bottom left), also separated by priming group. Topographies shown on the right. Boxplots for topography effects can be found in the Supplementary Information. Each coloured line/dot on all boxplots represents a participant. *Note.* * p < .05; *n.s. non-significant*



Figure 4. SSEP results for Experiment 1. Spectra averaged across all channels separated by priming group (left), and the topographies (right) for the frequencies of interest (1.11 Hz, 1.67 Hz, & 3.33 Hz). Shaded area in the spectra represents the standard error of the mean. No significant differences were found according to priming group.



Figure 5. Experiment 2 Procedure. A) Experiment 2 protocol. Tapping to the metre was collected at 3 times throughout the experiment, during training, halfway and at the end. After tapping the metre, the participants were reminded by the experimenter of how to imagine the accents for whichever priming group they were in. **B**) Experiment 2 training/tapping protocol. Tapping stimuli included 8 accented trials followed by 12 unaccented trials, and participants were expected to tap the metre. Only unaccented trials were analyzed for tapping. See Figure 1 for details on the audiovisual stimulus and the prime-test paradigm.



Figure 6. Event-related potentials for the deviant-standard difference waves for Experiment 2. Duple group is in purple, triple group in teal. Beat 4 is the solid line, beat 5 is the dashed line. MMN was analyzed between 100-150 ms, P3a between 200-350 ms. Shaded area represents the standard error of the mean. F = frontal; C = central; L = Left; Z = midline; R = right.



Figure 7. Boxplots and topographies for ERP amplitudes for Experiment 2 for MMN (A), and P3a (B). A) The main MMN finding was a main effect of priming group (left). Topographies shown on the right. B) The main finding for P3a was a main effect of beat position (left). Topographies shown on the right. Boxplots for topography effects can be found in the Supplementary Information. Each coloured line/dot on all boxplots represents a participant. *Note.* * p < .05.



Figure 8. SSEP results for experiment 2. A) SSEP frequency spectra and topographies for each group. Shaded area represents the standard error of the mean. **B**) Boxplots for the frequency x priming group interaction, displayed both as the within (left) and between (right) group differences. *Note.* * p < .05; ** p < .01; *** p < .001

Tables										
MMN										
Region	Beat Position	Mean Amplitude	95% Cl [lower, upper]	t	р	d				
FL	4	-1.188	-1.648, -0.728	-5.210	<.001	-0.7856				
FL	5	-1.059	-1.473, -0.644	-5.153	<.001	-0.7767				
FZ	4	-1.867	-2.259, -1.475	-9.609	<.001	-1.4486				
FZ	5	-1.653	-2.037, -1.269	-8.688	<.001	-1.3098				
FR	4	-1.419	-1.810, -1.028	-7.326	<.001	-1.1044				
FR	5	-1.326	-1.715, -0.936	-6.868	<.001	-1.0354				
CL	4	-1.124	-1.396, -0.852	-8.352	<.001	-1.2592				
CL	5	-1.016	-1.290, -0.742	-7.484	<.001	-1.1283				
CZ	4	-1.284	-1.623 <i>,</i> -0.945	-7.639	<.001	-1.1515				
CZ	5	-1.261	-1.587 <i>,</i> -0.936	-7.819	<.001	-1.1789				
CR	4	-1.275	-1.561, -0.989	-8.986	<.001	-1.3547				
CR	5	-1.352	-1.668, -1.037	-8.648	<.001	-1.3037				
			РЗа	_						
FL	4	0.510	0.144, 0.876	2.807	.042	0.4232				
FL	5	0.851	0.520, 1.183	5.177	<.001	0.7805				
FZ	4	1.189	0.782, 1.588	6.001	<.001	0.9047				
FZ	5	1.541	1.124, 1.958	7.449	<.001	1.1230				
FR	4	0.855	0.437, 1.273	4.123	.001	0.6216				
FR	5	1.185	0.778, 1.593	5.869	<.001	0.8849				
CL	4	0.704	0.466, 0.942	5.960	<.001	0.8985				
CL	5	0.995	0.754, 1.237	8.305	<.001	1.2521				
CZ	4	1.600	1.154, 2.040	7.275	<.001	1.0970				
CZ	5	1.864	1.420, 2.309	8.460	<.001	1.2750				
CR	4	1.153	0.772, 1.534	6.109	<.001	0.9210				
CR	5	1.195	0.822, 1.568	6.456	<.001	0.9733				

Table 1. t-test results for the presence of MMN & P3a across all regions of interest for Experiment 1. All t-tests were one-tailed and reflect the comparison of amplitude to 0, with df = 43 for all participants across groups. All results are significant after Bonferroni correction, with corrected p values shown. F = frontal; C = central; L = Left; Z = midline; R = right; d = Cohen's d.; CI = Confidence Interval

			MMN			
Region	Beat Position	Mean Amplitude	95% Cl [lower, upper]	t	p	d
FL	4	-1.236	-1.584, -0.889	-7.230	<.001	-1.222
FL	5	-1.254	-1.685, -0.823	-5.916	<.001	-1.000
FZ	4	-1.812	-2.232, -1.391	-8.760	<.001	-1.482
FZ	5	-1.813	-2.249, -1.377	-8.449	<.001	-1.428
FR	4	-1.522	-1.940, -1.105	-7.409	<.001	-1.253
FR	5	-1.488	-1.917, -1.058	-7.037	<.001	-1.189
CL	4	-1.149	-1.492, -0.806	-6.806	<.001	-1.150
CL	5	-1.028	-1.359, -0.698	-6.319	<.001	-1.068
CZ	4	-1.148	-1.521, -0.774	-6.247	<.001	-1.056
CZ	5	-1.283	-1.546, -1.020	-9.927	<.001	-1.677
CR	4	-1.413	-1.698, -1.127	-10.046	<.001	-1.699
CR	5	-1.452	-1.741, -1.163	-10.199	<.001	-1.724
			РЗа			
FL	4	0.814	0.297, 1.331	3.200	.018	0.541
FL	5	1.299	0.770, 1.828	4.989	<.001	0.844
FZ	4	1.219	0.654, 1.784	4.387	<.001	0.742
FZ	5	1.649	1.109, 2.189	6.208	<.001	1.049
FR	4	0.754	0.250, 1.258	3.042	.030	0.514
FR	5	1.190	0.702, 1.678	4.958	<.001	0.838
CL	4	0.577	0.244, 0.911	3.518	.006	0.595
CL	5	1.000	0.621, 1.378	5.372	<.001	0.908
CZ	4	1.068	0.694, 1.443	5.799	<.001	0.980
CZ	5	1.276	0.849, 1.702	6.082	<.001	1.028
CR	4	0.730	0.417, 1.043	4.741	<.001	0.801
CR	5	0.757	0.443. 1.072	4.895	<.001	0.828

Table 2. t-test results for the presence of MMN & P3a across all regions of interest for Experiment 2. All t-tests were one-tailed and reflect the comparison of amplitude to 0, with df = 35 for all participants across groups. All results are significant after Bonferroni correction, with corrected p values shown. F = frontal; C = central; L = Left; Z = midline; R = right; d = Cohen's d.

Supplementary Information

Inter-trial phase coherence analyses for Experiments 1 and 2

The analyses for ITPC were carried out separately for Experiments 1 and 2, but the steps were identical. First an FFT with a Hanning window multi-taper was run on each 28.8 s trial at each channel for each participant for frequencies 0 to 4 Hz at 0.035 Hz resolution, to get the complex part of the frequency spectra. Complex values were then normalized by dividing them by their amplitude. These were summed across trials and the absolute value was taken then divided by the number of trials (30), resulting in an ITPC value at each frequency and channel (Herrmann & Johnsrude, 2018).

ITPC spectra were then averaged across channels for each of the 6 regions of interest used for the ERP and SSEP analyses, as ITPC has been established to strongly occur in frontocentral sites in other auditory studies (e.g., Batterink & Paller, 2019; Choi et al., 2020; Herrmann & Johnsrude, 2018). The critical ITPC value to be significant using a = .05 was calculated using the following formula: $ITPC_{crit} = \sqrt{\frac{-ln(p)}{n}}$, where p is the critical p value cutoff (set to .05), and n is the number of trials (as per Cohen, 2014). Thus, with 30 trials the critical ITPC value is 0.316. We were most interested in how groups differed at each frequency of interest and given that ITPC is not equivalently estimated for lower vs. higher frequencies (Cohen, 2014), or for frequencies with more vs. less energy (i.e., the SSEP results revealed not all frequencies were equivalent) (Van Diepen & Mazaheri, 2018), we analyzed the group difference separately at each frequency bin. Thus, we ran separate one-way ANOVAs to compare duple and triple groups at each frequency of interest (triple [1.11 Hz], duple [1.67 Hz], beat [3.33 Hz]). The ITPC results are shown below in Figure S1. All peaks at the frequencies of interest were above the significance level threshold of ITPC = 0.316. However, we did not find group differences based on priming, at the duple, triple, or beat frequencies (All p's > .05).



Figure S1. ITPC across frequency for frontocentral sites for Experiment 1 (A) and 2 (B). separated by priming group (left column), with the critical ITPC value for significance shown as a red dotted line, and the topographies (right column) for the frequencies of interest. Note we found no effects of priming group at any frequency of interest.



Figure S2. Visual alpha outlier analysis. Participants' (N = 48) average visual alpha (7-13 Hz) activity for A) Experiment 1, and B) Experiment 2. Highlighted in red on the boxplots are the participants removed whose alpha activity was >2 SD above the mean. C) shows the electrodes averaged over across parietal (PL, PZ, PR) and occipital (OL, OZ, OR) areas.



Figure S3. Standard and deviant waves for FZ and CZ sites in Experiment 1 (A), and Experiment 2 (B).

Effects of Frontality and Laterality on ERPs in Experiments 1 and 2

Experiment 1

For MMN amplitudes, there was a main effect of laterality ($F_{GG}(1.75,73.35) = 10.682$, p < .001, $\eta_p^2 = .203$), which was qualified by a significant frontality x laterality interaction (F(2,84) = 10.073, p < .001, $\eta_p^2 = .329$). To break down the interaction, we compared laterality separately at frontal and central sites. For frontals, MMN was significantly more negative (larger) in FZ than FL (t(43) = -5.647, p < .001, d = -0.851) and FR sites (t(43) = -4.818, p < .001, d = -0.726). There was also a trend for MMN in FR sites to be more negative than in left sites (t(43) = -2.327, p = .075, d = -0.351), but this effect did not survive Bonferroni correction. For centrals, there were no differences in laterality (CZ – CL: t(43) = -1.861, p = .210, d = 0.281; CZ – CR: t(43) = 0.433, p = .667, d = 0.065; CR –

CL: t(43) = -2.024, p = .147, d = 0.305). Thus, in frontal sites, the MMN is strongest in the midline, and in right hemisphere, whereas in central sites, the MMN was more diffuse across laterality.

For P3a amplitudes, we found main effects of frontality (F(1,42) = 4.313, p = .044, $\eta_p^2 = .093$), laterality ($F_{GG}(1.60, 67.18) = 19.539$, p < .001, $\eta_p^2 = .478$), There was also a frontality x laterality interaction (F(2,84) = 3.472, p = .040, $\eta_p^2 = .145$). For frontality, amplitudes were more positive in central, compared to frontal sites. To investigate the frontality x laterality interaction, we compared laterality separately for frontals and centrals. For frontal sites, P3a was more positive in midline compared to both left sites (t(43) = 4.791, p < .001, d = 0.722) and right sites (t(43) = 3.423, p = .003, d = 0.516), and there was a trend for P3a to be stronger in right compared to left sites (t(43) = 2.469, p = .054, d = 0.372), but this didn't survive Bonferroni correction. In central sites, the same pattern emerges: P3a in CZ was more positive than in CL (t(43) = 5.516, p < .001, d = -0.832), and CR (t(43) = 5.468, p < .001, d = 0.824) sites, and there was nonsignificantly more positive P3a in right compared to left sites (t(43) = 2.176, p = .105, d = .328). Thus, P3a was more localized to central sites, and biased slightly to the right hemisphere.

Experiment 2

As in Experiment 1, for MMN, there were main effects of frontality (F(1,33) = 4.517, p = .041, $\eta_p^2 = .120$), and laterality (F(2,66) = 4.262, p = .018, $\eta_p^2 = .114$), which were qualified by a frontality x laterality interaction (F(2,66) = 13.160, p < .001, $\eta_p^2 = .285$) where in frontal sites, MMN was more negative in the midline (FZ) than in left sites (t(34) = -4.790, p < .001, d = -0.809), and less so in midline compared to right sites (t(34) = -2.568, p = .045, d = -0.435). Left and right MMN were comparable in frontal sites (t(34) = -1.821, p = .077, d = -0.308). Central MMN was equivalent across laterality (Main effect: $F_{GG}(1.68, 56.98) = 2.687$, p = .086, $\eta_p^2 = .073$). Note that these results do not differ if we include the outlier tappers; the main effects of frontality (F(1,40) = 4.801, p = .034, $\eta_p^2 = .107$), laterality ($F_{GG}(1.66, 66.23) = 5.335$, p = .011, $\eta_p^2 = .118$), and the frontality x laterality interaction (F(2,80) = 10.255, p < .001, $\eta_p^2 = .204$) remain.

For P3a, we found a main effect of laterality (F(2,66) = 6.768, p = .002, $\eta_p^2 = .170$), where P3a amplitudes were more positive in midline (Z) than in left (t(34) = 2.956, p = .018, d = 0.500), or right sites (t(34) = 3.591, p = .003, d = 0.607), but left and right P3a were equivalent (t(34) = .456, p = .651, d = 0.077). Note that the effect of laterality still



holds if we re-run the analyses to include the outlier tappers (F(2,80) = 6.079, p = .003, $\eta_p^2 = .132$).

Figure S4. Laterality effects of ERPs across Experiments 1 (A) and 2 (B). F = frontal; C = central; L = Left; Z = midline; R = right.



Figure S5. Tapping consistency (i.e., vector length; left column) and accuracy (i.e., tapping phase angle; right column), for the duple and triple groups. Results before (A, top row; N = 42) and after (B, bottom row; N = 35) removing tapping outlier (> mean ± 2 SD) participants. Note that tapping consistency ranges from 0 (totally inconsistent) to 1 (perfectly consistent), and accuracy here is the average phase angle of the tap, which here falls between $-\pi/2$ to $+\pi/2$, where 0 = perfect accuracy in relation to the phase of the accents, negative values = anticipation (early taps) of the accent onset, and positive values = lagged (late taps) response to the accented beat onsets. Also note that one participant in the duple group for the final sample did not have tapping data recorded for the training



High

High

Low Confidence Rater Group

Low

0.05

0 -0.05

trials, but their mid and end training are plotted. Note the different scales for the figures before vs. after removing outliers.

Figure S6. Relations between participants' metre perception confidence ratings and EEG measures based on median split (higher (> median) vs. lower (< median) of confidence ratings. A) Participants' MMN amplitudes were especially more negative in the triple group compared to the duple group, if participants had lower confidence ratings. **B**) Participants' bias in P3a amplitudes to beat 5 compared to beat 4 was particularly strong in adults who had low confidence ratings. C) There were no effects of confidence ratings on SSEPs. * *p* < .05; ** *p* <.01.

-1

High

Low



Figure S7. Effects of musical experience on ERPs. A) Shows MMN laterality x Music/Dance Group interaction. Participants with music/dance experience show expected topographies for MMN with stronger amplitudes in Z and R sites, whereas those with less experience don't show significant lateralization of MMN. B) Shows MMN beat position x Music/Dance group interaction, which was not significant after breaking down into post-hoc comparisons. C) Shows the frontality x beat position x Music/Dance group interaction, participants in the experienced group showed an enhanced P3a for beat 5 compared to beat 4, whereas inexperienced participants did not show a difference in P3a for beat position.

References

- Batterink, L. J., & Paller, K. A. (2019). Statistical learning of speech regularities can occur outside the focus of attention. *Cortex*, 115, 56–71.
- Choi, D., Batterink, L. J., Black, A. K., Paller, K. A., & Werker, J. F. (2020). Preverbal infants discover statistical word patterns at similar rates as adults: Evidence from neural entrainment. *Psychological Science*, 31(9), 1161–1173.
- Cohen, M. X. (2014). Intertrial phase clustering. In *Analyzing neural time series data: Theory and practice* (Issue 1, pp. 241–258). The MIT Press.
- Herrmann, B., & Johnsrude, I. S. (2018). Neural signatures of the processing of temporal patterns in sound. *Journal of Neuroscience*, *38*(24), 5466–5477.
- Van Diepen, R. M., & Mazaheri, A. (2018). The caveats of observing inter-trial phasecoherence in cognitive neuroscience. *Scientific Reports*, 8(1), 1–9.

Chapter 4: Investigating generalizability of top-down neural representation of metre in infancy

Flaten, E., Trainor, L. (2024) Investigating generalizability of top-down neural representation of metre in infancy. *Journal of Cognitive Neuroscience*. Manuscript Under Review.

Preface

Perception of rhythm in the context of music and language is often not limited to a single repetitive rhythm (as was tested in Chapters 2 and 3), and requires recognizing patterns across different timbres (e.g., instruments or speakers), tempos, or other features. Previous studies are limited in showing infants' abilities to generalize a learned rhythmic structure across varying exemplars, but we know that infants are highly sensitive to changes in tempo. Thus, Chapter 4 extends results from Chapter 2 by testing infants' ability to maintain a primed metrical interpretation of an ambiguous rhythm while generalizing it across varying tempos. Further, Chapter 4 addressed the limitation of a moderately duple-biased stimulus in Chapters 2 and 3, by using an isochronous ambiguous rhythm. This allowed us to explore whether we would again find a duple bias in the neural results, which would reflect a top-down bias that starts in infancy, and is not stimulus-driven.

195

Infants were primed to hear an ambiguous 6-beat rhythm in duple or triple metre, where priming tempo varied across 4 possible inter-beat-intervals, and infants had to generalize the primed metre to the ambiguous rhythm which was a single different tempo. Overall, we did not find evidence that infants were able to generalize the primed metre across varying tempos, as MMRs were not enhanced for the strong, compared to weak beat, and neural tracking was not enhanced for the primed, compared to unprimed metre. However, similar to the adults in Chapter 3, MMR was enhanced for the duple strong beat (beat 5) in infants who attended regular music classes. These results suggest that although infants can maintain a primed metrical structure on an ambiguous rhythm (Chapter 2), this may be limited to a single tempo context. Further, a duple bias that is enhanced by musical experience seems to be emerging already at 6 months.

Abstract

Musical speech rhythms are hierarchically organized, including grouping beats to create metrical structures. Previously, we showed that infants can be primed via loudness accents to interpret a metrically ambiguous (unaccented) rhythm either in duple metre (groupings of 2 beats), or in triple metre (groupings of 3 beats), as measured by larger mismatch responses (MMR) in EEG recordings for the perceptual strong compared to weak beat in the unaccented rhythm (Flaten et al., 2022). Given that infants primed with a duple or triple metrical interpretation heard the same ambiguous stimulus at test, this indicated top-down metre perception. The effects were stronger in the duple-primed infants, although this may have reflected that the stimulus was also slightly biased

196

towards the duple metre. Here, we investigated the generalizability of infants' top-down metre processing by varying the tempo of the rhythm from priming to test. We also used an isochronous test rhythm to ensure there was no duple or triple bias in the stimulus. Results showed that infants' MMR did not differ for deviants on primed strong versus weak beat positions, however, infants taking regular music classes showed a larger MMR for beat 5 (the strong beat for duple), regardless of priming. Further, duple-primed infants tracked the rhythm more strongly than triple-primed infants, as shown by steady-state evoked potentials. These results suggest that, although infants did not show evidence of generalizing metrical priming across varying tempo, a bias for duple metrical interpretation develops early and may be accelerated by participation in music classes.

Introduction

Auditory rhythms in music and language are hierarchically organized, enabling listeners to group incoming sounds into meaningful units in real time. For musical rhythms, one aspect of this involves grouping beats (the quasi-regular pulse we extract from rhythms; what we tap along to) to form metres, such as duple metre (two-beat groupings as in a march), or triple metre (three-beat groupings as in a waltz). For example, a listener hearing a 6-beat isochronous rhythm in triple metre would hear it as ONE two three FOUR five six, in duple metre as ONE two THREE four FIVE six. Metre can be indicated directly by acoustic features such as loudness accents on every second or third beat, or by the relative durations between adjacent notes in a rhythm (Povel & Essens, 1985; D. Temperley, 2004). However, the perception of metre is also affected by top-down processes such as attention or imagination, whereby an internally hypothesized

197
grouping structure is applied, especially in cases where the metre is ambiguous. The presence of internally generated (top-down) metre processing can be measured with electroencephalography (EEG). For example, uninstructed Western adults will typically automatically apply a binary (duple) grouping to an incoming isochronous rhythm consisting of identical sounds (N. M. Temperley, 1963; e.g., the "tick tick" of a clock is heard as "tick tock"), which is evident in larger amplitude event-related potentials (ERPs) to tones on every other beat (Brochard et al., 2003). Given that many developmental disorders are associated with rhythm deficits (for reviews, see Falter & Noreika, 2014; Ladányi et al., 2020; Lense et al., 2021; Pranjić et al., 2023; Slater & Tate, 2018), it is important to better understand how top-down aspects of rhythm perception develop, starting in infancy.

There is evidence that infants extract the metre from rhythms in a bottom-up way. For example, 6- to 9-month-olds utilize metrical regularity to process pitch and timing information in a melody, showing better change detection with metric than non-metric rhythms (Bergeson & Trehub, 2006; Trehub & Hannon, 2009). Six-month-olds also differentiate duple from triple metre based on the implied metrical structure via note durations, even in the presence of contradictory evidence from loudness accents (Hannon & Johnson, 2005). There is also some evidence infants can maintain a metrical interpretation of an ambiguous rhythm using top-down processes. For instance, our lab showed that bouncing infants on every second or third beat of an ambiguous 6-beat rhythm biases them to subsequently perceive the rhythm (without bouncing) as in duple or triple metre, respectively (Phillips-Silver & Trainor, 2005). In addition, we recently

showed that infants can be primed to process a metrically ambiguous rhythm in either duple or triple metre through loudness accents. Specifically, infants maintained the induced metrical interpretation after accents were removed, as indicated by larger ERP responses for strong compared to weak beat positions (Flaten et al., 2022). Thus, infants do have at least some ability to apply an internally constructed metrical interpretation to ambiguous rhythms via top-down processes.

Metre perception is also impacted by enculturation to musical norms in the environment, creating learned internal expectations that exert top-down influence (Hannon & Trainor, 2007). For example, at 6-months, Western infants can easily process non-Western rhythms with complex grouping structures (e.g., Balkan rhythms grouped in 7; Hannon & Trehub, 2005a), but by the end of the first year, they are less flexible and had acquired a bias to more readily process rhythms in duple metre (Hannon & Trehub, 2005a), which is the most common metre in Western music (D. Cohen & Katz, 2008; Gerry et al., 2010; D. Temperley, 2010). A duple bias is also found in Western adults (Brochard et al., 2003; Møller et al., 2021; Poudrier, 2020; but see Criscuolo et al., 2023) and children (Drake, 1993). Note, however, that the perception of duple versus triple metre may depend on tempo, where faster tempos are associated with longer (i.e., triple), and slower tempos with shorter (i.e., duple) grouping structures (Bååth, 2015; Poudrier, 2020). Interestingly, Western infants taking music classes show specific behavioural or neural benefits for duple compared to non-duple metres (Cirelli et al., 2016; Gerry et al., 2010, 2012; Trainor et al., 2012). Thus, it appears that enculturation to the metrical biases in the music in one's environment is accelerated by musical experience in infancy.

While it is clear that infants perceive rhythmic structure early in development, with neural responses to beat and metre frequencies present even in premature infants (Edalati et al., 2023), infants' ability to recognize rhythms across changes in tempo and other features is less studied. However, understanding speech and music in the real world requires recognizing a rhythmic pattern across changing tempos, as people speak at different rates, and songs can be sung at different tempos. Newborns and 2-month-olds can detect tempo changes at least as small as 15% (Baruch & Drake, 1997; Bobin-Bègue et al., 2006; Háden et al., 2015). Further, infants 5-24 months of age will move rhythmically to music, and while they cannot precisely synchronize their movements to the beat, they will adjust their tempo accordingly to the tempo of the music (Zentner & Eerola, 2010). Thus, infants can detect and react to tempo changes from early on. Some early work indicates that 7- to 9-month-old infants can identify musical rhythms across variations in tempo, timbre, and frequency (pitch) (Trehub et al., 1990; Trehub & Thorpe, 1989), but little work has addressed this question in younger infants.

In the current study, we aimed to explore whether infants would transfer a primed metrical interpretation of an ambiguous rhythm across varying tempos, following the EEG methods of our previous study (Flaten, et al., 2022). EEG has been used to show that newborns (Háden et al., 2024; Winkler et al., 2009) and even premature infants at 30-33 weeks gestation (Edalati et al., 2023) show clear neural tracking of beat and metre, and statistical learning of rhythmic phoneme sequences (Panzani et al., 2023). One measure of interest is the infant mismatch response (MMR), which is elicited when an unexpected (deviant) event occurs amongst a stream of expected (standard) events and is thought to

index the brain's prediction error (Vuust & Witek, 2014). In adults, the auditory mismatch response is reliably elicited as a frontally negative peak ~ 100-250 ms poststimulus onset, and is thus called the mismatch negativity (MMN; Bendixen et al., 2012; Escera et al., 2000; Näätänen et al., 2007). The infant MMR to acoustic changes typically appears as a slow, frontally positive response, with peak latencies in auditory studies often being ~ 200-400 ms (Basirat et al., 2014; Bristow et al., 2009; Chen et al., 2022; Cheng et al., 2015; Flaten et al., 2022; Trainor, 2012; Trainor, McFadden, et al., 2003), although a negative MMN can be found for some discriminations, particularly for easier speech contrasts (Cheng et al., 2015; Cheng & Lee, 2018; Götz et al., 2024). Infants are also more likely to show an adult-like MMN as they age (Cheng et al., 2015; Götz et al., 2024; He et al., 2009a, 2009b; Kushnerenko et al., 2002; Morr et al., 2002; Trainor, McFadden, et al., 2003; Werwach et al., 2022). Even within the same infants and latencies, both types of MMR have been found (Kushnerenko et al., 2002; Sambeth et al., 2009; Trainor, McFadden, et al., 2003), suggesting that positive MMR and adult-like MMN reflect related but distinct underlying neural processes (Govaart et al., preprint). In the current study, we used a quarter-tone pitch deviant with 6-month-olds as in Flaten et al. (2022), and thus expected to find a positive MMR peaking ~200-400 ms post-stimulus onset.

Mismatch responses have been defined as pre-attentive, but adult studies show top-down modulation of MMN and P3a based on metre. For example, ERP amplitudes are enhanced for deviants occurring on strong versus weak beat positions (Abecasis et al., 2005; Bouwer et al., 2014, 2016; Bouwer & Honing, 2015; Brochard et al., 2003; Flaten

et al., 2022; Ladinig et al., 2009; Potter et al., 2009; Schaefer et al., 2011), and this enhancement relates to behavioural performance (Bouwer & Honing, 2015; Ladinig et al., 2009). These results are in line with dynamic attending theory (Jones & Boltz, 1989; Large & Jones, 1999), which postulates that for rhythmic input, attention is modulated by the beat structure in an oscillatory fashion, thus benefitting the processing of events occurring in-phase versus out-of-phase with attention. Larger MMR for strong compared to weak beat positions has been found in newborns when the metre is clearly indicated in the stimulus (Háden et al., 2024; Winkler et al., 2009). Flaten et al. (2022) was the first to show top-down effects of metre on mismatch responses in infants for an ambiguous rhythm, finding larger MMR for pitch deviants on strong compared to weak beat positions according to priming, thus in line with the dynamic attending hypothesis.

Another EEG index of interest is steady-state evoked potentials (SSEPs), which measure the neural energy in low-frequency brain activity. SSEPs can be measured by the frequency-tagging approach (Nozaradan, 2014; Nozaradan et al., 2011), where the frequency content of the average EEG time signal in response to a rhythmic stimulus is compared to the frequency content of the presented rhythmic stimulus (e.g., beat, duple, triple metre frequencies). SSEPs reflect the bottom-up encoding of the rhythmic stimulus but can also be influenced by top-down processes (Celma-Miralles et al., 2016; Celma-Miralles & Toro, 2019; Chemin et al., 2014; Gibbings et al., 2023; Nozaradan et al., 2011). For example, adults asked to imagine the beat of an ambiguous amplitudemodulated sound in either groupings of two beats or three beats show an enhancement of the SSEP peaks specifically at the duple or triple frequencies (and their harmonics),

respectively, compared to when they don't imagine a metre, in which case they show a peak only at the beat frequency (Nozaradan et al., 2011). Further, SSEP spectra to rhythms with little to no energy at the beat frequency still show clear peaks at the beat frequency (Nozaradan et al., 2012; Tal et al., 2017), even in infants (Lenc et al., 2023). A recent multi-lab project replicated Nozaradan et al. (2011), although the estimated effect size was much smaller than that in the original publication (Nave et al., 2019, provisionally accepted). Premature and 7-month-old infants who passively listen to an ambiguous 6-beat stimulus show significant SSEP peaks at all three frequencies of interest (beat, duple and triple metre; Cirelli et al., 2016; Edalati et al., 2023), and for the 7-month-olds who attended regular music classes, SSEPs were enhanced at the duple frequency specifically (Cirelli et al., 2016). In Flaten et al. (2022), we hypothesized that infants primed with loudness accents would perceive this same ambiguous 6-beat rhythm in either duple or triple metre. Although we found ERP (MMR) indicators of metrical priming as discussed above, we did not find metre-specific enhancement of infants' SSEPs according to priming (Flaten et al., 2022), suggesting that more robust top-down attentional mechanisms may be required to reveal such effects. We thus explored here whether, in addition to ERP indictors, SSEPs would be impacted by metrical priming in infants, but we did not have strong predictions given previous weak or null effects.

Note that SSEP frequency spectra can be impacted by stimulus features, and thus may not always reflect beat perception (Henry et al., 2017). However, in rhythms with a clear indication of the beat, attentional processes enhance metre-related frequencies (Celma-Miralles & Toro, 2019; Gibbings et al., 2023). Further, adults presented with a

clearly duple or triple rhythm followed by an ambiguous rhythm were more likely to report the ambiguous rhythm as matching the primed metre than the unprimed metre, and this effect was associated with enhancement of SSEPs at the matching metre frequency (Nave et al., 2022). Thus, while we did not explicitly measure perception, as a behavioral task would have made the experiment too long for infants, it is reasonable to believe that the neural measures would reflect infants' perceptual experience, given that we used a strongly periodic rhythm. Lastly, SSEPs can also be a useful measure for examining individual differences, such as in predictive timing abilities (Nozaradan et al., 2016), cognitive and social development (Cantiani et al., 2022), or even health outcomes related to infant microbiome characteristics (Hunter et al., 2023), as well as effects of musical experience (Cirelli et al., 2016, Celma-Miralles & Toro, 2019).

One final EEG measure of interest for indexing rhythm perception is inter-trial phase coherence (ITPC). ITPC measures phase angle consistency of oscillatory activity across trials, and typically is measured in the delta or theta range. Like SSEPs, specific rhythmic frequencies can be targeted (e.g., Herrmann & Johnsrude, 2018) to investigate whether top-down processes impact the extent of clustering of phase angles at frequencies of interest. In adults, strong phase locking was found in delta activity to the beat frequency of syncopated rhythms that had no energy at that frequency, demonstrating an internally driven (top-down) neural representation of the beat (Tal et al., 2017). Similarly, stronger ITPC was found for more complex than less complex rhythms, and ITPC was correlated with subjective ratings of desire to move to performed rhythms (Cameron et al., 2019). Six and 8-month-old infants exposed to trisyllabic pseudowords, where the

syllables were presented rhythmically at a constant rate, show an increase in ITPC for the word-level compared to the syllable-level frequency, suggesting word learning via statistical learning (Choi et al., 2020; Kabdebon et al., 2015). Stronger ITPC has also been found for adult musicians compared to non-musicians (Doelling & Poeppel, 2015). Thus, we explored whether ITPC would be stronger for primed than unprimed metre frequencies in infants.

To summarize, infants are equipped with rhythmic timing abilities from birth (including sensitivity to tempo), with enculturation to their rhythmic environment accelerating between 6 and 12 months of age. Metre perception abilities also start early in infancy, though behavioural and neural evidence for the top-down maintenance of an auditory rhythmic interpretation has predominantly been shown in adults to date. Our previous study was the first to show neural evidence of top-down influence on metre processing in infants, as infants primed to process an ambiguous 6-beat rhythm either in duple or triple metre had larger MMR for pitch changes on primed strong beats. At the same time, effects were larger for the duple metre in general, and we did not find effects of priming on SSEPs (Flaten et al., 2022). One question remaining after this study is the extent to which infants can generalize a primed metric structure across varying tempos. Secondly, given that we used a non-isochronous 6-beat rhythm that was slightly biased towards duple metre, this previous study could not definitively discern whether the duple bias was due to early enculturation to Western metre, or to the stimulus itself. Thus, the current study had two main aims: 1) to investigate whether infants' maintenance of a metrical interpretation generalizes across varying tempos by comparing MMRs to beats

primed to be strong versus weak, and 2) to investigate whether the duple bias we found previously occurs for isochronous stimuli, which would suggest an early emergence of a duple bias. We additionally explored whether infants' SSEPs and ITPC at the duple, triple, and beat frequencies were enhanced by priming, as well as explored connections between EEG measures and musical experience.

If 6-month-old infants can generalize a primed metre across different tempos, then MMRs to pitch deviants should be larger on the metrically strong (beat 5 for duple; beat 4 for triple), compared to weak (beat 4 for duple; beat 5 for triple) beat position in the ambiguous stimuli. Additionally, if the duple bias we found in 6-month-olds in Flaten et al (2022) was due to learned biases, then we should replicate the effect of generally stronger encoding of duple than triple metre. Finally, given previous associations between EEG measures of rhythm perception and musical experience (Bouwer et al., 2016; Brochard et al., 2003; Cirelli et al., 2016; Doelling & Poeppel, 2015; Flaten et al., 2022; Shahin et al., 2010; Trainor et al., 2012), we explored whether infants with more, compared to less, experience would have larger magnitude EEG responses to the rhythm.

Methods

Participants

Forty-seven full-term (\geq 37 weeks gestation at birth) 6-month-old infants were recruited for the study via social media and through our Developmental Studies Database at McMaster University. Nine infants were removed from analyses due to insufficient useable EEG data (N = 7; see *preprocessing*), partial hearing loss (N = 1), or being over 6 months and 30 days old (N = 1), leaving a final sample of 38 infants. The study employed

a between-subjects' design where half (N = 19) of the infants were primed to hear the stimulus in duple metre (mean age = 6 mo 8 days [SD = 8 days], N = 11 females), and the other half (N = 19) were primed to hear it in triple metre (mean age = 6 mo 15 days [SD = 9 days]), N = 10 females). Priming group was randomly assigned, while aiming to counterbalance infant sex. Based on a power analysis conducted in the previous study which was calculated for a significant beat position x priming group interaction for the MMR (deviant-standard difference) and a medium effect size, we aimed to have 36 infants in total (Flaten et al., 2022). Infants in the final sample were predominantly white (86% white, 14% were Black, Hispanic, East Asian, or Middle Eastern) and mid- to upper-class (most common response {N = 18} for household yearly income = > \$150 000 CAD). The McMaster Research Ethics board approved all procedures for the study, and informed consent was obtained from all parents on behalf of their infants.

Stimuli

The audiovisual stimulus was similar in design to that of Flaten et al. (2022), consisting of a repeating auditory 6-beat rhythm that was paired with a visual stimulus that cued every beat 1 (See Figure 1B). The auditory stimulus alternated between priming (accented) trials, and test (unaccented) trials (Figure 1A). To ensure that the test stimulus was not biased toward duple or triple metre, it consisted of 6 isochronous tones with a loudness accent only on beat 1, which would be perceived as strong for both duple and triple metre, while always implying a 6-beat grouping. The sounds were presented from an Audio Video Methods loudspeaker (P73) that was approximately 1 m in front of the infant. Loudness was maintained at a comfortable level for the infant (~50- to 60-dB(C)

sound pressure level for all unaccented tones, and ~60 to 70-dB(C) for all accented tones over a noise floor of < 30 dB). Videos combining the visual stimulus with the audio were premade in VSDC Video Editor to ensure precise synchrony between the two modes and presented on a 27-inch monitor directly below the speaker.

Tones were created from piano sounds synthesized in Garageband and were 150 ms in length, with a 15-ms onset, as well as a 100-ms cosine decay ramp from 50 to 150 ms. The tones were either piano A (440 Hz), C# (554.37 Hz), or E (659.26 Hz). The stimuli were organized into sets containing 4 priming trials, 2 transition trials, 1 sec of silence, and 16 test trials (also followed by 1 sec of silence), for a total of 22 trials per set. The pitch remained constant within a set, but changed between A, C#, and E randomly from set to set. For duple priming trials, loudness accents (~10 dB increase) were added on beats 1, 3 and 5, and for triple priming trials on beats 1 and 4.

Each set began with 4 priming trials. To make them more interesting to the infants, and to draw their attention to the metre, priming trials included 1 repetition (trial) of the 6 isochronous tones, followed by 1 6-beat trial of a rhythm pattern (both trials with loudness accents on either beats 1, 3 and 5, or on 1 and 4). These two trials repeated for a total of 4 accented priming trials. These 4 trials were followed by 2 transition trials to ease the transition from priming to test, with the transition trials consisting of the 6-beat isochronous pattern with accents only on beat 1 (as in the following 16 test trials). To investigate whether infants could generalize the primed metrical structure to a new tempo, the 4 priming trials and 2 transition trials of each set were presented at one of 4 tempos (231, 278, 400, or 480 ms inter-beat interval; IBI; See Figure 1B). These tempos were

chosen because they were distinct enough to be perceived as different by 6-month-old infants (e.g., Bobin-Bègue et al., 2006; Háden et al., 2015), while still balancing the length of the study and trial count based on the longest tempo. The inter-onset interval between the tones for the 16 test trials of each set was always 333 ms IBI, which is the mean of all possible stimulus tempos, so that we could analyze neural responses to the same ambiguous stimulus across priming conditions. To ensure that infants were generalizing to a distinct tempo, and not just converging to the mean for the unaccented stimuli, each infant heard 3 out of 4 possible priming tempos across sets in a counterbalanced manner. In other words, each infant heard all tempos except one of 231, 278, 400 or 480 ms IBI. We chose to prime infants in a between-subjects manner by randomly assigning them to either the duple or triple priming group, as priming infants with both would make the experiment too long, and potentially lead to carryover effects between the two primed metres.

Test trials occasionally contained a quartertone (50 cents) pitch deviant on beat 4 (strong beat for triple metre only; 12.5% of trials) or beat 5 (strong beat for duple metre only; 12.5% of trials), to elicit mismatch responses. EEG for beats 4 and 5 were thus analyzed for infant MMR, while the 32 s 16-trial test segments were used for SSEP and ITPC analyses. The stimulus envelope frequencies for the average 16-test-trial segment across Piano A, C# and E was calculated by first applying a Hilbert transform to get the time envelope in MATLAB (as per Cirelli et al., 2016; Flaten et al., 2022). Then, a fast Fourier transform (FFT) was applied, and the absolute value of the spectra taken and normalized by the length of the signal. As shown in Figure 1B, the energy peaks for the

duple (1.5 Hz) and triple (1 Hz) frequencies were equivalent for all test stimuli, with an enhanced peak at the beat frequency (3 Hz).

In most previous infant EEG studies, researchers actively distract the infant visually with dolls, bubbles, and/or a silent movie to keep them still while minimizing movement artifacts. However, these actions are temporally unrelated to the auditory rhythm, and thus may interrupt the infant's ability to attend to (and thus neurally track) the metre. There is evidence that attention to the rhythm may be important for finding effects in EEG of adults listening to rhythms that include a strong sense of beat (e.g., Celma-Miralles & Toro, 2019; Gibbings et al., 2023). Thus, in Flaten et al. (2022) and here as well, we tried to engage infant attention to the sound by means of audiovisual facilitation, as there is evidence of benefits for infants' processing of sensory information when accompanied by redundancies across multiple sensory modes (Bahrick et al., 2002; Lewkowicz & Marcovitch, 2006; Pickens & Bahrick, 1997; Smith et al., 2006). The visual stimulus was comprised of an array of 5 coloured circles in an X or T orientation that was either green or pink in colour (see Figure 1B), with colour and/or orientation changing every 22-trial set. At minimum size, on the screen, the circles were each 5.7 cm $(3.27^{\circ} \text{ visual angle})$, and each row of 3 circles was 20.6 cm (11.76°) . The circles grew to a maximum size (9 cm, 5.15° each; or 24 cm, 13.69° per row) by the midpoint of the first of every 6 beats (e.g., for test stimuli the midpoint was 166 ms), then shrunk back to original size by the end of the first beat, remaining static for beats 2 to 6. Thus, the visual stimulus did not bias perception to either duple or triple meter, while engaging infants' attention.

Procedure

Upon arrival, parents filled out the consent form as well as a questionnaire on language and music background (questions around parent and infant age, ethnicity, infants' musical activities and exposure, parents' musical background such as current and past musical training, languages spoken in the home, parent handedness, questions around socioeconomic status and history of hearing difficulties in the infant and family). This questionnaire confirmed that all infants came from English-speaking families, although one participant came from a family who predominantly spoke languages other than English (Spanish spoken 70% of the time, Italian 20%, and English 10% of the time). This infant was within 2 SD of all analyzed neural measures except for the MMR for beat 4 in 2/3 channel groupings, although these were still within 2.5 SD. Another infant was identified by the parent as having partial hearing loss in one ear and was removed from the analyses (see Participants). Questions around whether infants were attending regular music classes, amount of music listening, book reading, as well as questions around parents' musical training (specifically whether they were currently playing an instrument and for how many years of training on that instrument) were all used in exploratory analyses of musical experience (see Exploratory Analyses of Relations with Musical Background).

Parents were then brought into a sound-attenuated room and sat on a chair ~ 1 m in front of the screen and audio speaker which delivered the stimuli. Parents were asked to keep their child seated in their lap while facing them forward towards the screen, which was at about eye level for the infant. Additionally, parents were asked to minimize

movements other than to readjust their infant's position if necessary. A researcher who stayed in the room with the parent then moved out of view behind the parent and infant, while the experiment started. To ensure that neither the researcher nor the parent could influence the infant's perception of the stimuli, both wore sound-attenuating over-ear headphones with pop, classical and Caribbean music loud enough to mask the sound of the rhythm from the speaker; additionally, they were asked not to move to the headphone music or the rhythm in any way. When the infant got bored of looking at the screen on their own, the researcher in the recording room would move to sit in front of the infant and beside the screen and point to the screen while using puppets and toys to try to keep the infant still and looking forward. All infants lost interest in the screen at some point during the first block, so the researcher was beside the screen for most of the recording for all the infants. A researcher outside the booth recorded infant looking directly into the EEG recording via webcam feed, coding with a mouse click the onset of when infants looked forward toward the screen, versus looking away, and codes differed whether the researcher in the room was behind or in front of the infant. Based on Flaten et al., 2022 we did not expect that looking time would influence our EEG results, but nonetheless, it was recorded to enable comparisons of results for infants who looked at the screen more versus less. A short break was taken after every block. All infants kept in the final analyses completed at least 2 of the 3 blocks.

Data Acquisition & Analysis

EEG data were recorded using the Electrical Geodesics Inc. (EGI) system, using the 124-channel Hydrocel GSN infant nets, a NetAmps 200 amplifier, and the

NETSTATION software (v.5.4.2). Data were recorded with an online sampling rate of 1000 Hz and Cz reference. Impedances for electrodes were maintained below 50 k Ω at the start of recording, and any noisy channels seen during recording were documented by the researcher outside of the recording booth. All the preprocessing steps were conducted using the Fieldtrip EEG toolbox (v. 20220228; Oostenveld et al., 2011) for MATLAB (v. R2022a), and statistical analyses were performed in IBM SPSS Statistics (v. 20).

Preprocessing

The data were filtered 0.5 to 20 Hz for the frequency-based analyses (SSEPs and ITPC), and 1 to 20 Hz for the ERP analyses, using separate zero phase (i.e., 2-pass) 3rd order Butterworth high-pass and low-pass filters, respectively. Note that we chose a more aggressive high-pass filter for the MMR analyses to remove baseline drift due to using the same baseline period for both beats 4 and 5 in the MMR analysis (see *Mismatch Response* Analysis). Next, bad channels were removed based on the amount the amplitude variance contributed to the dataset when plotted visually using the Fieldtrip ft_rejectvisual function, such that channels contributing $> 10^5 \,\mu\text{V}$ variance were removed. This threshold was chosen as it consistently removed any channels that appeared visibly to be outliers. Additionally, channels that were marked during recording were investigated further. In most cases these were confirmed to be removed via the threshold method just described, but otherwise were kept in the analysis if they appeared by visual check to be within ~ 2 SD of the range of the rest of the channels. Overall, an average of 5 channels (range = 1-17) were removed per infant. The continuous data then underwent the artifact-blocking algorithm, which interpolates high amplitude artifacts within a specified window size

using neighbouring time points, and is effective for infant EEG data cleaning (Fujioka et al., 2011; Mourad et al., 2007). The threshold was set to $\pm 75 \,\mu$ V and the window size was set to the function default of 5 seconds. The data were then re-referenced to the average of all kept electrodes before segmenting into trials, based on -100 ms to 999 ms relative to beat 4 (i.e., beats 4 to 6) for the MMR analysis, and -100 to 32,000 ms relative to beat 1 of the first test trial (i.e., 16 unaccented test trial set) for the frequency-based analyses. Following this, and for the MMR analysis only, a conventional trial rejection was applied, removing any remaining trials that had amplitudes exceeding $\pm 100 \,\mu$ V at any time point, in any channel. Given that the artifact blocking was generally effective, this last step removed few trials, ranging from 0 to 17 (mean = 2.6 trials) per participant. Finally, the surrounding neighbouring channels were used to repair the removed bad channels via interpolation (as per Flaten et al., 2022).

To identify outliers, we re-ran the preprocessing for the MMR analysis while omitting the Artifact Blocking algorithm and thus only using the conventional trial rejection ($\pm 100 \mu$ V) and based only on the frontocentral (FC) channels (See Supplementary Information, Figure S1), given that all analyses were planned to be conducted on these channels a priori (though upon visualizing the data, only frontal channels were used for analysis of MMR). This outlier analysis identified 7 participants who lost > 50% of their data. An additional 2 participants were removed because one was older than our age cutoff, and one had partial hearing loss. The remaining sample (N = 19per priming group) would have lost on average 15% MMR trials if only running the conventional trial rejection based on the frontal channels, ranging from 1 to 46% of trials.

All infants in the final sample except for one had all 27 trials for the SSEP and ITPC analyses, and the other infant had 25 trials.

Mismatch Response Analysis

The trials were then averaged within each condition (beat 4 standard, beat 4 deviant, beat 5 standard, and beat 5 deviant) for each participant. For beat 4, the time window was -100 ms to 600 ms around the beat onset. We initially used the same window around beat 5 (-100 to 600 ms), but visual inspection of the deviant and standard waveforms showed that the beat 5 baseline was not flat, while beat 4 was. This may be because of context effects where beat 4 contains a pitch deviant some of the time, whereas beat 3 (containing the baseline period for beat 4) is never a deviant. Thus, for beat 5 we instead used the same pre-stimulus period as we did beat 4, so trials were averaged -433 ms to 600 ms around the onset of beat 5 where -433 to -333 ms was used as the baseline period, and -333 to 0 ms (beat 4) was removed. Thus, the average amplitude for the 100 ms prior to beat 4 was subtracted to baseline each waveform, within each condition. Visual inspection confirmed that this improved the baseline for beat 5, and to deal with the resulting baseline drift, we set the high pass filter to 1 Hz, as described in *preprocessing*. Next, difference waves were calculated by subtracting the amplitudes at each time point in the standard wave from those in the deviant wave, for each beat position for each participant. We then averaged the waveforms across channels according to three channel groupings chosen a priori (See Supplementary Information Figure S1) and confirmed to be appropriate upon visualizing the ERPs, which were frontal left (FL), frontal midline (FZ), and frontal right (FR). We maintained laterality (L,

Z, or R) as a factor in our channel groupings due to finding regional differences in effects for MMR in our previous study (Flaten et al., 2022).

Given that infants showed high variability in their MMR peak latencies, we chose to find individual infants' peaks within the a priori window of 200-400 ms post-stimulus onset, as previous infant auditory studies have found significant MMR in comparable windows (Basirat et al., 2014; Bristow et al., 2009; Chen et al., 2022; Flaten et al., 2022; Trainor, 2012; Trainor, Mcfadden, et al., 2003; Werwach et al., 2022). We first found the latency of the maximum peak in the difference wave for each beat position within 200-400 ms, then used that latency to isolate the response in the deviant and standard waves separately for that beat position. Given that MMR is a slow wave, we averaged the amplitude \pm 50 ms around the peak latency, resulting in a single value for the beat 4 standard and deviant, and for the beat 5 standard and deviant, as well as a latency for the beat 4 MMR was then calculated by subtracting the extracted amplitudes for the deviant – standard. These average amplitudes and the associated latencies were used for the statistical analyses.

SSEP Analysis

The SSEPs were analyzed using the frequency-tagging approach (Nozaradan et al., 2011) using the same steps as in our previous studies (Cirelli et al., 2016; Flaten et al., 2022). First the 32-second trials were averaged in the time domain, then baseline corrected using the average amplitude -100 to 0 ms relative to the first beat. This baseline period was then removed prior to running a FFT from 0 to 4 Hz with a resolution of

0.03125 Hz, and a Hanning multi-taper method on the single trial data for each participant. Next, to increase the signal-to-noise ratio of the SSEPs, the power (μV^2) in the 3rd, 4th, and 5th neighbouring bins on either side of each frequency bin was subtracted from that bin. Given previous studies showing strong SSEP power in frontal and central regions (e.g., Cirelli et al., 2016; Flaten et al., 2022; Lenc et al., 2023), and to be consistent with the ITPC analysis, we averaged the SSEPs across all frontocentral channels (See Supplementary Information, Figure S1), including the FL, FZ and FR groupings, as well as the central channel equivalents (CL, CZ, CR). These regions were confirmed upon visualization of the topographies for the SSEPs and ITPC for the beat frequency, where the signal was strongest (See Figures 3-4),

ITPC Analysis

We also explored the phase consistency of low-frequency brain activity, at the frequencies of interest in the stimulus. First an FFT with a Hanning window multi-taper was run on each 32 s trial separately at each channel for frequencies 0 to 4 Hz at 0.03125 Hz resolution, outputting the real and complex values. Complex values were then normalized by dividing them by their amplitude. These were summed across trials, and the absolute value was divided by the number of trials (27), resulting in an ITPC value at each frequency and channel (Herrmann & Johnsrude, 2018). ITPC values range from 0 (completely random phase), to 1 (perfectly consistent phase). ITPC spectra were then averaged across frontocentral channels, as was done for the SSEPs, given that ITPC has been established to strongly occur in frontocentral sites in other auditory studies (e.g., Herrmann & Johnsrude, 2018; Batterink & Paller, 2017; Choi et al., 2020). The ITPC

critical threshold was calculated to be 0.3331 by the following formula (M. X. Cohen,

2014), $ITPC_{crit} = \sqrt{\frac{-ln(p)}{n}}$, with p being the critical p value cutoff (set to .05), and n is

the number of trials, so 27 in this case.

Statistical Analyses

Tempo Control Analysis. To first ensure that the priming tempo counterbalancing had no effect on the EEG measures, we ran mixed ANOVAs for each measure with the grouping factor of tempo condition. Infants heard 3 out of 4 possible priming tempos, meaning that they were grouped by which tempo they did not hear (i.e., missing 231, 278, 400, or 480 ms IBI condition). Thus, we had 4 tempo-missing groups, with small *N* per group, and unfortunately more infants were removed from the 278 ms IBI group (N = 6 remaining) than the others (231 ms N = 10; 400 ms N = 12; 480 ms N = 10). For MMR, we included within-subjects factors of laterality (Left [L], Midline [Z], Right [R]) and beat position (beat 4, beat 5). For SSEPs and ITPC, we included the within-subjects factor frequency. We investigated main effects and interactions with priming tempo group.

MMR. To first establish the presence of a significant MMR, the deviant-standard difference amplitudes at each electrode grouping and beat position were tested against 0 using multiple one-sample, one-directional t tests. Following this was a mixed repeated measures ANOVA with the within-subjects' factors of laterality (L, Z, R), beat position (beat 4, beat 5), and between-subjects factor of priming group (duple or triple). Identical ANOVAs were performed to examine effects of MMR latency, but no significant effects were found with latency, so they are not reported here.

Frequency-Based Measures (SSEPs/ITPC). First, we first ran a mixed ANOVA with the factors of frequency (triple - 1 Hz, duple - 1.5 Hz, beat - 3 Hz), and group (duple or triple priming), and only considered effects that included group. Given that 1/f noise in the EEG signal enhances power at lower frequencies more than higher frequencies, it is best to only interpret effects of frequency that interact with group to investigate the relative power between the different frequency peaks between groups, or to analyze effects within each frequency bin separately. Therefore, to explore effects of priming further, separate one-way ANOVAs were conducted comparing the effect of priming group on SSEP power/ITPC, separately for the triple frequency (one-tailed, as we had a directional hypothesis), duple frequency (one-tailed, directional hypothesis), and beat frequency (two-tailed, no directional hypothesis).

Secondly, to see whether the SSEP peaks were significantly above the noise floor, the average noise was calculated for each infant by averaging the SSEP power at frequency bins across the spectra that were unrelated to the metrical frequencies (0.75, 1.25, 1.75, 2.25, 2.75 Hz). Then, paired samples t tests comparing each SSEP peak against the noise floor were conducted. To investigate whether ITPC peaks were significantly above the critical ITPC threshold (see *ITPC Analysis*) at the group level, we ran tests comparing each peak against 0.3331.

Exploratory Analyses of Relations with Musical Background. Previous studies have repeatedly shown links between infants' musical experiences and their EEG responses to rhythm (e.g., Cirelli et al., 2016; Flaten et al., 2022; Langus et al., 2023). Thus, we explored here effects of musical experience by re-running analyses of MMR,

SSEPs, and ITPC, but now grouping based on whether they had a musician parent (N = 11; 5 Duple. 6 Triple) or not (N = 27; 14 Duple, 13 Triple), as well as whether infants were regularly attending music classes with their parent (N = 15; 7 Duple, 8 Triple) or not (N = 23; 12 Duple, 11 Triple). Musician parent was defined as one or both parents who currently played a musical instrument, for which they had at least 6 years of musical training. Thus, for MMR, the factors were laterality, beat position, and group (musician parent/non-musician parent; in music classes/not in music classes), and for SSEPs/ITPC the factors were frequency and group.

Looking Behaviour

The visual stimulus in this study was carefully curated to only move on beat 1, and to be identical for both priming groups. Thus, we would not expect visual processes to differ between groups; however, to investigate whether EEG results were related to infants' visual attention to the screen, we correlated infant looking time with their MMR amplitudes, as well as SSEP power and ITPC across the frequencies of interest. Looking time was defined as a percentage, based on the proportion of time spent looking at the screen, compared to the total time for all test trials.

Results

All post-hoc tests used one-way ANOVAs or t tests, corrected for multiple comparisons with Bonferroni correction when appropriate, where reported p values have been corrected using false discovery rate (FDR) adjustment. Corrections for violations of sphericity were done using Greenhouse-Geisser Correction; results are reported with the corrected *df*.

Tempo Control Analysis

Tempo-missing group had no effect on any of the EEG measures (See Supplementary Information, Figure S2): For MMR, neither the main effect of tempo group (F(3,34) = 2.57, p = .070, $\eta_p^2 = .19$), nor the interactions with beat position (F(3,34) = 0.40, p = .76, $\eta_p^2 = .034$), laterality ($F_{GG}(4.48, 50.73) = 0.68$, p = .62, η_p^2 = .057) nor the 3-way laterality x group x beat position interaction ($F_{GG}(4.88, 55.34) =$ 0.32, p = .90, $\eta_p^2 = .027$) were significant. For SSEPs, neither the main effect of tempo group (F(3,34) = 0.46, p = .72, $\eta_p^2 = .039$), nor the frequency x tempo group interaction ($F_{GG}(3.48, 39.47) = 0.18$, p = .93, $\eta_p^2 = .016$) reached significance. Similar results were found for ITPC (main effect of tempo group: F(3,34) = 1.08, p = .37, $\eta_p^2 = .087$; frequency x group interaction: $F_{GG}(4.23, 47.94) = 0.69$, p = .61, $\eta_p^2 = .057$). Thus, tempo group was not included in any further analyses.

MMR

Grand-average ERPs to the deviants are shown in Figure 2A and B. MMR amplitudes were significantly greater than 0 in all regions for both beat positions (all *p* 's < .001), except for beat 4 in FZ, which was trending (p = .060). T-test results are shown in Table 1. The only significant effect from the mixed repeated measures ANOVA was a nearly significant effect of laterality ($F_{GG}(1.54, 55.25) = 3.34, p = .055, \eta_p^2 = .085$). This was the result of a trend for MMR amplitudes to be less positive in FZ compared to FL (t(37) = -2.63, p = .036, d = .43) and FR (t(37) = -2.52, p = .048, d = .41) sites. MMR in FL and FR were equivalent in amplitude (FL; t(37) = .42, p = .68, d = .07). Of most importance, the predicted beat position x priming group interaction was not significant $(F(1, 36) = .99, p = .33, \eta_p^2 = .027;$ Figure 2D), demonstrating that MMR did not differ for beat position according to infants' priming.

SSEPs

SSEP spectra for frontocentral channels are shown in Figure 3. The mixed ANOVA with factors frequency and priming group revealed a main effect of group, with the duple group showing stronger beat- and metre-related frequency tracking overall compared to the triple group (F(1, 36) = 5.06, p = .031, $\eta_p^2 = .12$), but no frequency x group interaction ($F_{GG}(1.18, 42.51) = 2.40$, p = .12, $\eta_p^2 = .062$). Given our hypotheses, we conducted exploratory analyses comparing priming groups at each frequency separately, which revealed that the duple group showed more positive SSEP power than the triple group at the duple frequency (F(1, 36) = 3.27, p = .040, $\eta_p^2 = .083$, one-tailed, as we had a directional hypothesis) and numerically but not significantly at the beat (F(1, 36) = 3.69, p = .063, $\eta_p^2 = .093$, two-tailed) frequency, but groups were equivalent at the triple frequency (F(1, 36) = 1.24, p = .27, $\eta_p^2 = .033$). All beat and metre peaks were confirmed to be significantly above the noise floor (1 Hz: t(37) = 5.70, p < .001, d = .93; 1.5 Hz: t(37) = 4.67, p < .001, d = .76; 3 Hz: t(37) = 8.20, p < .001, d = 1.33).

ITPC

ITPC spectra are shown in Figure 4. Results from the mixed ANOVA showed no main effect of group (F(1, 36) = 2.83, p = .10, $\eta_p^2 = .073$), nor a frequency x group interaction ($F_{GG}(1.44, 51.72) = 2.02$, p = .15, $\eta_p^2 = .053$). Exploratory results from comparing priming groups at each frequency revealed that, like for SSEPs, there was a trend for the duple group to show stronger ITPC at the beat frequency compare to the

triple group (F(1, 36) = 3.26, p = .079, $\eta_p^2 = .083$), but groups did not differ at the triple (F(1, 36) = 0.56, p = .46, $\eta_p^2 = .015$) or duple frequencies (F(1, 36) = 0.25, p = .62, $\eta_p^2 = .007$). Note that even though the ITPC values are comparable to or larger than reported in previous infant studies (Choi et al., 2020; Kabdebon et al., 2015), values at 1 and 1.5 Hz frequencies did not pass the ITPC critical threshold of 0.333. In fact, one sample t-tests at each frequency comparing against 0.333, revealed that only the beat frequency was significantly greater than this threshold at the group level (3 Hz: t(37) = 12.86, p < .001), while the triple (1 Hz: t(37) = -8.80, *n.s.*) and duple (1.5 Hz: t(37) = -13.25, *n.s.*) frequencies were not significant.

Exploratory effects of musical background

We first grouped infants based on whether they had a musician parent (≥ 6 years training) or not, and ran an ANOVA with MMR as the dependent variable and beat position and laterality as factors. Unlike in Flaten et al., 2022, we found no significant effects (all *p*'s > .300).

The current sample included many infants regularly attending music classes with their parent(s), so we explored whether MMR differed depending on if infants were in music classes (N = 15) or not (N = 23). There was a significant laterality x beat position x music class group interaction (F(2, 72) = 8.11, p = .001, $\eta_p^2 = .18$; Figure 5). To break down the interaction, we first ran separate mixed ANOVAs to investigate effects of beat position and music class group separately at each level of laterality. A significant beat position x music class group interaction was found at FL (F(1, 36) = 6.77, p = .013, $\eta_p^2 = .16$), but not at FZ (F(1, 36) = 1.50, p = .23, $\eta_p^2 = .040$) or FR (F(1, 36) = 0.67, p = .42,

 $\eta_p^2 = .018$). Thus, at FL, the infants who were in music classes showed larger MMR for beat 5 compared to beat 4 (t(14) = 2.29, p = .038, d = .59), whereas the infants not in music class showed no such beat position effect (t(22) = 1.14, p = .27, d = .24).

To investigate the extent to which this effect was related to music classes vs. other extraneous variables, we ran additional control analyses, comparing the two groups on music listening behaviour and years of musical experience of the parents with one-way ANOVAs, showing that infants who did or did not attend music classes did not differ in the amount of hours listening to music (F(1, 36) = 1.17, p = .29, $\eta_p^2 = .032$), nor in how many years of musical training the parents had (F(1, 36) = 1.74, p = .20, $\eta_p^2 = .046$). Infants in or not in music classes also did not differ in their yearly household income (U = 151.5, p = .50) or the amount their parents read to them (U = 141.0, p = .29), as shown by Mann-Whitney U tests given that these were rank-ordered variables.

Given previous associations reported between music class attendance and infants' SSEPs (Cirelli et al., 2016), we investigated whether infants attending music classes showed higher SSEP power than those not attending, at any of the frequencies of interest. We did not find any significant effects of music class group whether analyzed as the mixed ANOVA or separately for each frequency bin (all p's > 0.35). We similarly did not find effects of music class attendance on ITPCs (all p's > 0.46).

Looking Behaviour

As expected, proportion of looking time to the visual stimulus did not correlate with either beat 4 (r(38) = .23, p = .17) or 5 (r(38) = -.07, p = .69) MMR amplitude, or with overall SSEP (r(38) = .11, p = .52) or ITPC (r(38) = .25, p = .13). See Supplementary Information, Figure S3.

Discussion

The current study aimed to replicate and extend Flaten et al. (2022), where we showed that infants can be primed to encode a metrically ambiguous rhythm in one of two possible metres (duple or triple metre), as indicated by larger MMRs for pitch changes on subjectively strong, compared to subjectively weak, beat positions, especially for the duple metre. In the present study, we explored whether we would find comparable results when infants were challenged by hearing the metrical priming at varying tempos and then having to generalize the primed metre to a novel tempo. We additionally addressed a limitation in the previous study by using an isochronous ambiguous rhythm, to ensure the stimuli was not biased to duple or triple metre. In addition to analyzing MMR, we explored infants' neural tracking of the rhythm by investigating SSEP and ITPC peaks at the frequencies of interest, and whether these differed according to priming. Finally, connections to musical experience were explored. Overall, results were mixed: infants' MMRs were not modulated by priming, suggesting a lack of generalization of the metre priming across tempo. However, across measures, the results suggested an emerging bias for the duple metre interpretation, facilitating moderate priming effects in the duple group, as shown by enhanced SSEPs for the duple and beat frequencies in comparison to the triple group. Further, the duple bias appeared to be enhanced by musical experience, as MMRs were stronger for deviants occurring on beat 5

(strong for duple metre) in infants taking music classes compared to those not taking music classes. We discuss and interpret these findings in detail below.

We did not find direct evidence that infants could generalize a primed metre across varying tempos. We found significant MMRs for small pitch changes in both metre positions (i.e., for beats 4 and 5) across frontal regions that were similar to our previous study (Flaten et al., 2022) in amplitude (positive), latency (peaking ~200-400 ms), and topography (more lateralized left and right vs. midline). However, in contrast to our prediction, we did not find evidence of priming on MMR under conditions of tempo generalization, as the interaction between beat positions (4 vs. 5) and priming group (duple, triple) was not significant. Thus, even though infants around 6 months are already equipped with some top-down metre processing abilities (Basirat et al., 2014; Choi et al., 2020; Flaten et al., 2022), and can categorize rhythms across varying tempos (Trehub & Thorpe, 1989) or categorize tones sharing timbre across varying frequencies, intensities, or durations (Trehub et al., 1990), the dual task of maintaining a metrical interpretation of an ambiguous rhythm and generalizing to a new tempo may require higher-level cognitive processes, such as better sustained attention, which may not be yet sufficiently functional at 6 months. There may be other contexts, however, under which infants this age can generalize metrical structures across different tempos.

Infants around 6 months of age are well able to perceive tempo changes similar in magnitude to those in the current study (Bobin-Bègue et al., 2006; Háden et al., 2015), and behavioural studies suggest infants can categorize rhythms that vary in tempo by 7 months or earlier (Trehub & Thorpe, 1989), so the question remains as to why infants do

not automatically maintain a metrical interpretation across tempo changes. One possibility is that it is already difficult to maintain a metrical interpretation of an ambiguous rhythm once the metre-defining accents are removed, and more consciously directed attention is needed to do this across tempo changes. Indeed, a role for sustained attention in maintaining metre is evident from adult studies that show metre-specific topdown modulation of SSEPs when participants are instructed to actively imagine the accents for duple or triple metre (Celma-Miralles et al., 2016; Nave et al., 2019, provisionally accepted; Nozaradan et al., 2011), when actively attending (vs. being distracted) to the rhythms (Celma-Miralles & Toro, 2019; Gibbings et al., 2023), or when the rhythm is preceded by tapping (Chemin et al., 2014; although only found for the duple, not triple metre condition). The current study differs in that we tested infants via priming, as it is not possible to instruct infants the way we can instruct adults, but priming is a more passive task than actively engaging attention to the accent structure. Nave et al. (2022) did find enhancement in SSEPs for the metre via a similar priming paradigm in adults, but they included behavioural responses after each trial to engage attention.

In the current study, we did find potential evidence of a top-down effect even in the face of tempo changes, in that infants primed with duple metre showed enhancement of SSEP power at the duple frequency relative to the triple group. However, we should treat this interpretation with caution as there was no frequency by group interaction in the mixed ANOVA. We suspect that a more likely interpretation is that infants have an earlyemerging duple bias, in which case infants primed in triple metre had two competing topdown biases, namely, their enculturated duple bias, and the triple priming bias, resulting

in no difference between the strength of their duple and triple metre tracking. This is also consistent in the results for the infants primed in duple meter; in this case, the duple priming would enhance infants' preexisting duple bias, enabling them to better process the rhythmic frequencies in the stimulus in general, consistent with our finding of a main effect of priming group for SSEPs across the beat and metre frequencies.

There is reason to think that comparing metres across tempos for unfamiliar patterns might be a particularly complex generalization. Specifically, tracking the metrical structure after a change in tempo would require low-frequency neural oscillations entrained to the initial tempo to phase reset and oscillate at the new tempo (Henry & Herrmann, 2014; Lakatos et al., 2008; Luo et al., 2010; Schroeder & Lakatos, 2009). This might be a difficult task for the infant brain. Nonetheless, evidence for some ability to do this was present in the SSEP results, in that infants in the duple group showed higher SSEP power at the duple frequency, compared to the triple group, suggesting that the neural representation of the duple metre was stronger after priming with duple. However, the ITPC results showed weak phase consistency (though comparable values to other infant studies (Choi et al., 2020; Kabdebon et al., 2015) at the triple and duple frequencies in both groups, suggesting that the infant brain has difficulty phase-aligning at slower tempi (i.e., at the metre frequencies of 1 and 1.5 Hz). Thus, it is hard to tease apart whether duple-primed infants' underlying oscillatory activity to the duple metre successfully phase-reset amongst tempo changes, and/or if their evoked responses to the duple metre were enhanced. Future studies could adapt the task to specifically include time-frequency measures of low-frequency neural phase in response

to the tempo changes in infants to investigate phase-resetting. Nonetheless, the trend of stronger ITPC at the beat frequency for infants primed with duple metre mirrors the SSEP results and suggests that priming with duple compared to triple metre strengthens both power and phase alignment to the beat, further supporting the hypothesis of an emerging duple bias in Western infants at 6 months.

If generalizing is particularly difficult across tempo, perhaps generalizing across other acoustic features such as pitch or timbre might be easier as this would not disrupt the slow neural oscillations that track the temporal organization of the sequences. For example, when the tempo remains constant, there is some evidence that infants at 6-8 months can generalize a particular rhythmic structure of syllables that form "words" to new syllables (that, by definition, differ in timbre) that follow the same rhythmic structure. Six- to 8-month-old infants can learn words using statistical transitional probabilities in streams of syllables presented at a consistent tempo, as shown by an increase in the ratio of ITPC at the lower frequency (higher metrical grouping; wordlevel) to that at the higher frequency (lower metrical grouping; syllable level) over the familiarization period (Choi et al., 2020; Kabdebon et al., 2015). Critically, Kabdebon et al. (2015) showed that 8-month-olds could generalize the learned structure across different syllable examples, as indexed by significantly different ITPC and ERPs for examples that were congruent versus incongruent to the learned word structure. Given that the current study used intermittent priming as well as an oddball paradigm, we could not do a comparable analysis by looking at the effect of exposure to the grouping structure (i.e., metre) over time. Future studies could examine how exposure to the duple

or triple metre might lead to a change in ITPC for the primed metre/beat frequency ratio as an index of metre learning, and investigate whether this holds for rhythms that vary in spectral content (i.e., pitch, timbre).

Metre perception can also be tempo-dependent (Bååth, 2015; Poudrier, 2020), such that at our fastest priming tempo (231 ms IBI), it might be easiest to group beats in triple metre, and at our slowest priming tempo (480 ms IBI), it might be easiest to group in duple. However, tempo only varied for priming trials where the metre was unambiguous, and the test tempo was comparatively moderate (333 ms IBI). Nonetheless, it might be harder to transfer the duple metre from faster priming tempos, and to transfer the triple metre from slower tempos. We do not have the statistical power here to test if there was an effect of priming tempo, but we did not find an effect of tempo group on MMR (See Tempo Control Analysis, above).

Finally, the null effects of priming on MMR could be because our sample was underpowered if the real effect size is smaller than what we estimated. As outlined in the Participants section above, we based our sample size on the previous study (Flaten et al., 2022), for which we ran a power analysis that revealed we would need 18 participants per group. It is possible that the present task was more difficult, so the effects of priming were reduced and thus undetectable at the group level with the current sample size. However, if we were simply underpowered, we would likely still expect to see at least a trend in the predicted direction with the current sample size, but Figure 2 shows no evidence of a trend. Thus, it is a reasonable conclusion that infants' MMRs do not reflect

metrical priming that generalizes across tempo under the conditions of the present experiment.

Although MMR was not enhanced according to priming, we did find evidence of a duple bias in MMR that was enhanced by musical experience. Infants who were enrolled in regular music lessons showed MMR that was biased to beat 5 (strong beat for duple metre) compared to beat 4, at least in FL sites, whereas MMR for infants not in music classes did not differ by beat position. This effect could not be explained by stimulus properties since we used an isochronous (unbiased) stimulus, nor could it be explained by household income, hours spent listening to music, amount parents read to their infants, nor years of parental musical training. Given that the dominant metre in Western music is duple (D. Cohen & Katz, 2008; Gerry et al., 2010; D. Temperley, 2010), this suggests that, in line with previous evidence (Cirelli et al., 2016; Gerry et al., 2010; 2012; Trainor et al., 2012), music-making in Western music classes may accelerate early enculturation. In general, infants with greater musical experience show enhanced neural, physiological and behavioural responses to rhythmic stimuli (e.g., Cirelli et al., 2016; Flaten et al., 2022; Langus et al., 2023), such as enhanced SSEPs at the duple frequency, as well as larger ERPs to each first beat of a repeating rhythm (Cirelli et al., 2016). Thus, musical experience may bring infants closer to adult-like biases in terms of Western metrical norms. These results also suggest that the stronger effects of the duple priming we found previously (Flaten et al., 2022) may have at least been in part due to a duple bias. Future studies should further investigate the causal role of different kinds of musical experience on the neural processing of rhythms and accelerated enculturation.

An alternative or additional explanation for the duple bias, aside from Western enculturation, is an innate bias for binary groupings/subdivisions in general (Savage et al., 2015). Groupings of two are often the simplest integer ratio available for organizing input (Jacoby & McDermott, 2017; Møller et al., 2021; Polak et al., 2018), although triple groupings are still common, globally (Polak et al., 2018; Savage et al., 2015). Some also suggest that a universal duple/binary bias is inevitable due to the ubiquity of binary rhythms in the human motor system, including bipedal locomotion (Larsson, 2014; Larsson et al., 2019; Sadeghi et al., 2000). One might thus hypothesize that infants become biased toward duple metre as they learn to locomote via crawling and walking, after 6 months. However, even in the womb fetuses are exposed to sensory input which can shape auditory development (Ullal-Gupta et al., 2013; Webb et al., 2015), such as external sounds, or internal sensations (e.g., Lecanuet & Jacquet, 2002) that are often binary in nature, such as the mother walking or breathing (inhalation vs exhalation). While there is an early exposure to binary rhythms, 6- to 12-month-old Western infants are still flexible in learning metrical structures from other cultures (Hannon & Trehub, 2005b), although they prefer metres from their own culture (Soley & Hannon, 2010). Infants exposed to both Western and non-western music, however, tend not to show preferences for one over the other (Ko & McDonald, 2023; Soley & Hannon, 2010), and may show a preference for the novel culture in their second year (Ko & McDonald, 2023). The present study adds to the evidence for an early bias for duple metre in Western infants, whether due to innate factors, early exposure to duple input, or musical enculturation.

Limitations

One limitation of the present study is that it did not include a behavioural measure to explicitly examine infants' rhythm perception and how this relates to their brain responses, which is typically done in adult studies. However, given the length of EEG measurement and infants' attentional limitations, this is not practical and essentially all infant paradigms are privy to this limitation (e.g., Houston-Price & Nakai, 2004).

A second limitation is that including deviants in the stimulus on beats 4 and 5 to measure MMR could have interrupted entrainment to the frequencies of interest, as these pitch changes could themselves induce perceptual accents (Povel & Essens, 1985; Thomassen, 1982). In other words, when maintaining a triple metre, a pitch deviant on beat 5 could have drawn attention/tracking to the duple metre (or at least away from the triple), and vice versa for when primed with duple metre. It is therefore possible that the perception of the metrical structure could have been weakened over the trials used for measuring SSEPs and ITPC, and future studies could investigate SSEPs and ITPC when there are no pitch changes.

Conclusion

Our previous study showed that infants can internally maintain a primed metrical interpretation of an ambiguous rhythm and apply it in a top-down manner (Flaten et al., 2022). In the present study, event-related analyses failed to show that 6-month-olds transferred metrical predictions across tempo changes, as MMR responses to pitch changes were similar on what should have been perceived as metrically strong versus weak beats of the rhythm at a new tempo. At the same time, the results suggest a bias for
the dominant metre in Western music (duple metre) is already present at 6 months in Western infants, and that it is amplified by musical experience. Specifically, only infants primed with duple metre showed stronger neural tracking of the rhythm at the duple and beat frequencies as shown by the SSEP and ITPC results, whereas those primed with triple metre did not show enhancements at any frequencies of interest. Further, infants attending music classes showed larger MMR on beat 5 (strong for duple) than beat 4 (strong for triple), regardless of priming. We conclude that 6-month-old infants have some capacity for maintaining top-down internal representations of ambiguous patterns (Flaten et al., 2022), but that it does not robustly generalize across varying tempos. Further, evidence for an early-emerging bias for a duple metre interpretation of an ambiguous rhythm complicates the interpretation of the results. Thus, further work is needed to understand the conditions under which infants' internal representation of metre may generalize across tempo variation.

Data Availability Statement

All data may be made available at the request of the corresponding author (email ljt@mcmaster.ca).

Author Contributions

EF and LJT conceptualized the research questions and methodology, EF conducted the research investigation, as well as collected and analyzed the data, EF wrote the original draft of the manuscript, EF and LJT reviewed and edited the manuscript, LJT acquired the funding for the project and supervised the research.

Acknowledgements

The authors would like to thank Elaine Whiskin for helping organize the lab, and for assisting in the data collection. We thank the babies and families for their participation. We also thank our undergraduate research assistants Virtues Dawn Serrano, Maggie (Meng Jia) Lu, and Selina Bains for aiding in data collection and Virtues and Selina for aiding in the stimulus creation.

Funding Information

This research was funded by grants to LJT from the Natural Sciences and Engineering Research Council of Canada (NSERC; RGPIN-2019-05416), the Social Sciences and Humanities Research Council of Canada (SSHRC; 435-2020-0442), the Canadian Institutes of Health Research (MOP 153130), Canadian Institutes for Advanced Research, as well as the Fondation pour l'Audition BabyMusic Grant. During completion of the research, EF received graduate funding from an NSERC Create grant in Complex Dynamics, as well as a SSHRC doctoral fellowship grant.

References

- Abecasis, D., Brochard, R., Granot, R., & Drake, C. (2005). Differential brain response to metrical accents in isochronous auditory sequences. *Music Perception*, 22(3), 549–562. https://doi.org/10.1525/mp.2005.22.3.549
- Bååth, R. (2015). Subjective Rhythmization. *Music Perception*, *33*(2), 244–254. https://doi.org/10.1525/mp.2015.33.2.244
- Bahrick, L. E., Flom, R., & Lickliter, R. (2002). Intersensory redundancy facilitates discrimination of tempo in 3-month-old infants. *Developmental Psychobiology*, 41(4), 352–363. https://doi.org/10.1002/dev.10049
- Baruch, C., & Drake, C. (1997). Tempo discrimination in infants. *Infant Behavior and Development*, 20(4), 573–577. https://doi.org/10.1016/S0163-6383(97)90049-7
- Basirat, A., Dehaene, S., & Dehaene-Lambertz, G. (2014). A hierarchy of cortical responses to sequence violations in three-month-old infants. *Cognition*, 132(2), 137– 150. https://doi.org/10.1016/j.cognition.2014.03.013
- Batterink, L. J., & Paller, K. A. (2017). Sleep-based memory processing facilitates grammatical generalization: Evidence from targeted memory reactivation. *Brain and Language*, 167, 83–93. https://doi.org/10.1016/j.bandl.2015.09.003
- Bendixen, A., SanMiguel, I., & Schröger, E. (2012). Early electrophysiological indicators for predictive processing in audition: A review. *International Journal of Psychophysiology*, 83(2), 120–131. https://doi.org/10.1016/j.ijpsycho.2011.08.003
- 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

- Bobin-Bègue, A., Provasi, J., Marks, A., & Pouthas, V. (2006). Influence of auditory tempo on the endogenous rhythm of non-nutritive sucking. *Revue Europeenne de Psychologie Appliquee*, 56(4), 239–245. https://doi.org/10.1016/j.erap.2005.09.006
- Bouwer, F. L., & Honing, H. (2015). Temporal attending and prediction influence the perception of metrical rhythm: Evidence from reaction times and ERPs. *Frontiers in Psychology*, 6, 1–14. https://doi.org/10.3389/fpsyg.2015.01094
- 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), 1–9. 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
- Bristow, D., Dehaene-Lambertz, G., Mattout, J., Soares, C., Gliga, T., Baillet, S., &
 Mangin, J. F. (2009). Hearing faces: How the infant brain matches the face it sees
 with the speech it hears. *Journal of Cognitive Neuroscience*, *21*(5), 905–921.
 https://doi.org/10.1162/jocn.2009.21076
- Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "ticktock" of our internal clock: Direct brain evidence of subjective accents in isochronous sequences. *Psychological Science*, *14*(4), 362–366. https://doi.org/10.1111/1467-9280.24441

Cameron, D. J., Zioga, I., Lindsen, J. P., Pearce, M. T., Wiggins, G. A., Potter, K., &

Bhattacharya, J. (2019). Neural entrainment is associated with subjective groove and complexity for performed but not mechanical musical rhythms. *Experimental Brain Research*, *237*(8), 1981–1991. https://doi.org/10.1007/s00221-019-05557-4

- Cantiani, C., Dondena, C., Molteni, M., Riva, V., & Piazza, C. (2022). Synchronizing with the rhythm: Infant neural entrainment to complex musical and speech stimuli. *Frontiers in Psychology*, *13*, 1–13. https://doi.org/10.3389/fpsyg.2022.944670
- Celma-Miralles, A., de Menezes, R. F., & Toro, J. M. (2016). Look at the beat, feel the meter: Top–down effects of meter induction on auditory and visual modalities. *Frontiers in Human Neuroscience*, 10, 1–13.

https://doi.org/10.3389/fnhum.2016.00108

- Celma-Miralles, A., & Toro, J. M. (2019). Ternary meter from spatial sounds:
 Differences in neural entrainment between musicians and non-musicians. *Brain and Cognition*, *136*, 103594. https://doi.org/10.1016/j.bandc.2019.103594
- 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
- Chen, A., Peter, V., & Burnham, D. (2022). Development of neural discrimination of pitch across speech and music in the first year of life, a mismatch response study. *Language, Cognition and Neuroscience*, *37*(9), 1153–1168. https://doi.org/10.1080/23273798.2022.2051571
- Cheng, Y. Y., & Lee, C. Y. (2018). The development of mismatch responses to Mandarin lexical Tone in 12-to 24-month-old infants. *Frontiers in Psychology*, *9*, 1–11.

https://doi.org/10.3389/fpsyg.2018.00448

Cheng, Y. Y., Wu, H. C., Tzeng, Y. L., Yang, M. T., Zhao, L. L., & Lee, C. Y. (2015).
Feature-specific transition from positive mismatch response to mismatch negativity in early infancy: Mismatch responses to vowels and initial consonants. *International Journal of Psychophysiology*, 96(2), 84–94.

https://doi.org/10.1016/j.ijpsycho.2015.03.007

- Choi, D., Batterink, L. J., Black, A. K., Paller, K. A., & Werker, J. F. (2020). Preverbal infants discover statistical word patterns at similar rates as adults: Evidence from neural entrainment. *Psychological Science*, *31*(9), 1161–1173. https://doi.org/10.1177/0956797620933237
- 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, 1–11. https://doi.org/10.3389/fnins.2016.00229
- Cohen, D., & Katz, R. (2008). Rhythmic patterns reflecting cognitive constraints and aesthetic ideals. *Journal of New Music Research*, 37(1), 15–35. https://doi.org/10.1080/09298210802095635
- Cohen, M. X. (2014). Intertrial phase clustering. In *Analyzing neural time series data: Theory and practice* (Issue 1, pp. 241–258). http://www.amazon.com/Analyzing-Neural-Time-Series-Data/dp/0262019876/
- Criscuolo, A., Schwartze, M., Henry, M. J., Obermeier, C., & Kotz, S. A. (2023).
 Individual neurophysiological signatures of spontaneous rhythm processing.
 NeuroImage, 273, 120090. https://doi.org/10.1016/j.neuroimage.2023.120090

Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, *112*(45), E6233– E6242. https://doi.org/10.1073/pnas.1508431112

Drake, C. (1993). Reproduction of musical rhythms by children, adult musicians, and adult nonmusicians. *Perception & Psychophysics*, 53(1), 25–33. https://doi.org/10.3758/BF03211712

- Edalati, M., Wallois, F., Safaie, J., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi,
 S. (2023). Rhythm in the premature neonate brain: Very early processing of auditory
 beat and meter. *The Journal of Neuroscience*, *43*(15), 2794–2802.
 https://doi.org/10.1523/JNEUROSCI.1100-22.2023
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology and Neuro-Otology*, 5, 151–166. https://doi.org/10.1159/000013877
- Falter, C. M., & Noreika, V. (2014). Time processing in developmental disorders: A comparative view. In *Subjective Time: The Philosophy, Psychology, and Neuroscience of Temporality* (pp. 557–599). The MIT Press. https://doi.org/10.7551/mitpress/8516.003.0039
- 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

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

- Gerry, D. W., Faux, A. L., & Trainor, L. J. (2010). Effects of Kindermusik training on infants' rhythmic enculturation. *Developmental Science*, 13(3), 545–551. https://doi.org/10.1111/j.1467-7687.2009.00912.x
- Gerry, D. W., Unrau, A., & Trainor, L. J. (2012). Active music classes in infancy enhance musical, communicative and social development. *Developmental Science*, 15(3), 398–407. https://doi.org/10.1111/j.1467-7687.2012.01142.x
- Gibbings, A., Henry, M. J., Cruse, D., Stojanoski, B., & Grahn, J. A. (2023). Attention modulates neural measures associated with beat perception. *European Journal of Neuroscience*, 57(9), 1529–1545. https://doi.org/10.1111/ejn.15962
- Götz, A., Männel, C., Schwarzer, G., Krasotkina, A., & Höhle, B. (2024). Neural correlates of lexical-tone and vowel-quality processing in 6- and 9-month-old German-learning infants and adults. *Journal of Child Language*, 1–23. https://doi.org/10.1017/S030500092400014X
- Govaart, G. H., Dvořáková, M., Chládková, K., & Männel, C. (preprint). Infant brain responses in auditory perception: A Review of the factors influencing the polarity of the mismatch response. https://doi.org/10.31234/osf.io/bx952
- Háden, G. P., Bouwer, F. L., Honing, H., & Winkler, I. (2024). Beat processing in newborn infants cannot be explained by statistical learning based on transition probabilities. *Cognition*, 243, 105670.

https://doi.org/10.1016/j.cognition.2023.105670

- Háden, G. P., Honing, H., Török, M., & Winkler, I. (2015). Detecting the temporal structure of sound sequences in newborn infants. *International Journal of Psychophysiology*, 96(1), 23–28. https://doi.org/10.1016/j.ijpsycho.2015.02.024
- 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., & Trainor, L. J. (2007). Music acquisition: effects of enculturation and formal training on development. *Trends in Cognitive Sciences*, 11(11), 466–472. https://doi.org/10.1016/j.tics.2007.08.008
- Hannon, E. E., & Trehub, S. E. (2005a). Tuning in to musical rhythms: Infants learn more readily than adults. *Proceedings of the National Academy of Sciences*, 102(35), 12639–12643. https://doi.org/10.1073/pnas.0504254102
- Hannon, E. E., & Trehub, S. E. (2005b). Metrical categories in infancy and adulthood. *Psychological Science*, *16*(1), 48–55. https://doi.org/10.1111/j.0956-7976.2005.00779.x

He, C., Hotson, L., & Trainor, L. J. (2009a). Maturation of cortical mismatch responses to occasional pitch change in early infancy: Effects of presentation rate and magnitude of change. *Neuropsychologia*, 47(1), 218–229.
https://doi.org/10.1016/j.neuropsychologia.2008.07.019

He, C., Hotson, L., & Trainor, L. J. (2009b). Development of infant mismatch responses to auditory pattern changes between 2 and 4 months old. *European Journal of* Neuroscience, 29(4), 861-867. https://doi.org/10.1111/j.1460-9568.2009.06625.x

- Henry, M. J., & Herrmann, B. (2014). Low-frequency neural oscillations support dynamic attending in temporal context. *Timing and Time Perception*, 2(1), 62–86. https://doi.org/10.1163/22134468-00002011
- Henry, M. J., Herrmann, B., & Grahn, J. A. (2017). What can we learn about beat perception by comparing brain signals and stimulus envelopes? *PLoS ONE*, *12*(2), 1–17. https://doi.org/10.1371/journal.pone.0172454
- Herrmann, B., & Johnsrude, I. S. (2018). Neural signatures of the processing of temporal patterns in sound. *Journal of Neuroscience*, 38(24), 5466–5477. https://doi.org/10.1523/JNEUROSCI.0346-18.2018
- Houston-Price, C., & Nakai, S. (2004). Distinguishing novelty and familiarity effects in infant preference procedures. *Infant and Child Development*, 13(4), 341–348. https://doi.org/10.1002/icd.364
- Hunter, S., Flaten, E., Petersen, C., Gervain, J., Werker, J. F., Trainor, L. J., & Finlay, B.
 B. (2023). Babies, bugs and brains: How the early microbiome associates with infant brain and behavior development. *PLoS ONE*, *18*, 1–22. https://doi.org/10.1371/journal.pone.0288689
- 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
- Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, 96(3), 459–491. https://doi.org/10.1037//0033-295x.96.3.459

Kabdebon, C., Pena, M., Buiatti, M., & Dehaene-Lambertz, G. (2015).
Electrophysiological evidence of statistical learning of long-distance dependencies in 8-month-old preterm and full-term infants. *Brain and Language*, *148*, 25–36.
https://doi.org/10.1016/j.bandl.2015.03.005

- Ko, E. S., & McDonald, M. (2023). Korean infants' perceptual responses to Korean and Western music based on musical experience. *Developmental Science*, 26(5), 1–14. https://doi.org/10.1111/desc.13378
- Kushnerenko, E., Eponiene, R., Balan, P., Fellman, V., Huotilainen, M., & Näätänen, R. (2002). Maturation of the auditory event-related potentials during the first year of life. *NeuroReport*, *13*(1), 47–51. https://doi.org/10.1097/00001756-200201210-00014
- Ladányi, E., Persici, V., Fiveash, A., Tillmann, B., & Gordon, R. L. (2020). Is atypical rhythm a risk factor for developmental speech and language disorders? *Wiley Interdisciplinary Reviews: Cognitive Science*, *11*(5), 1–32. https://doi.org/10.1002/wcs.1528
- Ladinig, O., Honing, H., Háden, G., & Winkler, I. (2009). Probing attentive and preattentive emergent meter in adult listeners without extensive music training.
 Music Perception, 26(4), 377–386. https://doi.org/10.1525/mp.2009.26.4.377
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I. I., Charles, E., & Schroeder, C. E.
 (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, 320(5872), 110–113. https://doi.org/10.1126/science.1154735

Langus, A., Boll-Avetisyan, N., van Ommen, S., & Nazzi, T. (2023). Music and language

in the crib: Early cross-domain effects of experience on categorical perception of prominence in spoken language. *Developmental Science*, *May 2022*, 1–12. https://doi.org/10.1111/desc.13383

- Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track timevarying events. *Psychological Review*, *106*(1), 119–159.
- Larsson, M. (2014). Self-generated sounds of locomotion and ventilation and the evolution of human rhythmic abilities. *Animal Cognition*, *17*(1), 1–14. https://doi.org/10.1007/s10071-013-0678-z
- Larsson, M., Richter, J., & Ravignani, A. (2019). Bipedal steps in the development of rhythmic behavior in humans. *Music & Science*, 2, 205920431989261. https://doi.org/10.1177/2059204319892617
- Lecanuet, J. P., & Jacquet, A. Y. (2002). Fetal responsiveness to maternal passive swinging in low heart rate variability state: Effects of stimulation direction and duration. *Developmental Psychobiology*, 40(1), 57–67. https://doi.org/10.1002/dev.10013
- 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
- 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*, 20200327.

https://doi.org/10.1098/rstb.2020.0327

- Lewkowicz, D. J., & Marcovitch, S. (2006). Perception of audiovisual rhythm and its invariance in 4- to 10-month-old infants. *Developmental Psychobiology*, 48(4), 288– 300. https://doi.org/10.1002/dev.20140
- Luo, H., Liu, Z., & Poeppel, D. (2010). Auditory cortex tracks both auditory and visual stimulus dynamics using low-frequency neuronal phase modulation. *PLoS Biology*, 8(8), e1000445. https://doi.org/10.1371/journal.pbio.1000445
- Møller, C., Stupacher, J., Celma-Miralles, A., & Vuust, P. (2021). Beat perception in polyrhythms: Time is structured in binary units. *PLOS ONE*, *16*(8), e0252174. https://doi.org/10.1371/journal.pone.0252174
- Morr, M. L., Shafer, V. L., Kreuzer, J. A., & Kurtzberg, D. (2002). Maturation of mismatch negativity in typically developing infants and preschool children. *Ear and Hearing*, 23(2), 118–136. https://doi.org/10.1097/00003446-200204000-00005
- Mourad, N., Reilly, J. P., Bruin, H. De, Haseyt, G., Maccrimmon, D., & Joseph, S. (2007). A simple and fast algorithm for automatic suppression of high-amplitude artifacts in EEG data. *ICASSP*, 393–396.
- Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, *118*(12), 2544–2590. https://doi.org/10.1016/j.clinph.2007.04.026
- Nave, K.M., Hannon, E.E., & Snyder, J.S. (2019, provisionally accepted manuscript).
 Registered report: Replication and extension of Nozaradan, Peretz, Missal and
 Mouraux (2011). Advances in Methods and Practices in Psychological Science. OSF

Page: <u>https://osf.io/rpvde/</u>.

- Nave, K. M., Hannon, E. E., & Snyder, J. S. (2022). Steady state-evoked potentials of subjective beat perception in musical rhythms. *Psychophysiology*, 59(2), 1–15. https://doi.org/10.1111/psyp.13963
- 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), 20130393. https://doi.org/10.1098/rstb.2013.0393
- Nozaradan, S., Peretz, I., & Keller, P. E. (2016). Individual differences in rhythmic cortical entrainment correlate with predictive behavior in sensorimotor synchronization. *Scientific Reports*, *6*(1), 20612. https://doi.org/10.1038/srep20612
- Nozaradan, S., Peretz, I., & Missal, M. (2011). *Tagging the Neuronal Entrainment to Beat and Meter. 31*(28), 10234–10240. https://doi.org/10.1523/JNEUROSCI.0411-11.2011
- Nozaradan, S., Peretz, I., & Mouraux, A. (2012). Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *The Journal of Neuroscience*, *32*(49), 17572–17581. https://doi.org/10.1523/JNEUROSCI.3203-12.2012
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 1–9. https://doi.org/10.1155/2011/156869

Panzani, M., Mahmoudzadeh, M., Wallois, F., & Dehaene-Lambertz, G. (2023).

Detection of regularities in auditory sequences before and at term-age in human neonates. *NeuroImage*, 284, 120428.

https://doi.org/10.1016/j.neuroimage.2023.120428

- 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
- Pickens, J., & Bahrick, L. E. (1997). Do infants perceive invariant tempo and rhythm in auditory-visual events? *Infant Behavior and Development*, 20(3), 349–357. https://doi.org/10.1016/S0163-6383(97)90006-0
- Polak, R., Jacoby, N., Fischinger, T., Goldberg, D., Holzapfel, A., & London, J. (2018). Rhythmic prototypes across cultures. *Music Perception*, 36(1), 1–23. https://doi.org/10.1525/mp.2018.36.1.1
- Potter, D. D., Fenwick, M., Abecasis, D., & Brochard, R. (2009). Perceiving rhythm where none exists: Event-related potential (ERP) correlates of subjective accenting. *Cortex*, 45(1), 103–109. https://doi.org/10.1016/j.cortex.2008.01.004
- Poudrier, È. (2020). The influence of rate and accentuation on subjective rhythmization. *Music Perception*, *38*(1), 27–45. https://doi.org/10.1525/mp.2020.38.1.27
- Povel, D., & Essens, P. (1985). Perception of Temporal Patterns. *Music Perception*, 2(4), 411–440. https://doi.org/10.2307/40285311
- Pranjić, M., Hashemi, N., Arnett, A. B., & Thaut, M. H. (2023). Auditory–perceptual and auditory–motor timing abilities in children with Developmental Coordination Disorder: A scoping review. *Brain Sciences*, 13(5), 729.

https://doi.org/10.3390/brainsci13050729

- Sadeghi, H., Allard, P., Prince, F., & Labelle, H. (2000). Symmetry and limb dominance in able-bodied gait: A review. *Gait and Posture*, 12(1), 34–45. https://doi.org/10.1016/S0966-6362(00)00070-9
- Sambeth, A., Pakarinen, S., Ruohio, K., Fellman, V., van Zuijen, T. L., & Huotilainen, M. (2009). Change detection in newborns using a multiple deviant paradigm: A study using magnetoencephalography. *Clinical Neurophysiology*, *120*(3), 530–538. https://doi.org/10.1016/j.clinph.2008.12.033
- 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 of the United States of America, 112(29), 8987–8992. https://doi.org/10.1073/pnas.1414495112
- Schaefer, R. S., Vlek, R. J., & Desain, P. (2011). Decomposing rhythm processing: electroencephalography of perceived and self-imposed rhythmic patterns. *Psychological Research*, 75, 95–106. https://doi.org/10.1007/s00426-010-0293-4
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*, 32(1), 9–18. https://doi.org/10.1016/j.tins.2008.09.012
- Shahin, A. J., Trainor, L. J., Roberts, L. E., Backer, K. C., & Miller, L. M. (2010). Development of auditory phase-locked activity for music sounds. *Journal of Neurophysiology*, 103(1), 218–229. https://doi.org/10.1152/jn.00402.2009

Slater, J. L., & Tate, M. C. (2018). Timing deficits in ADHD: Insights from the

neuroscience of musical rhythm. *Frontiers in Computational Neuroscience*, *12*, 51. https://doi.org/10.3389/fncom.2018.00051

- Smith, N. A., Trainor, L. J., & Shore, D. I. (2006). The development of temporal resolution: Between-channel gap detection in infants and adults. *Journal of Speech, Language, and Hearing Research*, 49(5), 1104–1113. https://doi.org/10.1044/1092-4388(2006/079)
- Soley, G., & Hannon, E. E. (2010). Infants prefer the musical meter of their own culture: A cross-cultural comparison. *Developmental Psychology*, 46(1), 286–292. https://doi.org/10.1037/a0017555
- Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., &
 Golumbic, E. Z. (2017). Neural entrainment to the beat: The "missing-pulse"
 phenomenon. *The Journal of Neuroscience*, *37*(26), 6331–6341.
 https://doi.org/10.1523/JNEUROSCI.2500-16.2017
- Temperley, D. (2004). An evaluation system for metrical models. *Computer Music Journal*, 28(3), 28–44. https://doi.org/10.1162/0148926041790621
- Temperley, D. (2010). Modeling common-practice rhythm. *Music Perception*, 27(5), 355–376. https://doi.org/10.1525/mp.2010.27.5.355

Temperley, N. M. (1963). Personal tempo and subjective accentuation. *The Journal of General Psychology*, 68(2), 267–287.

https://doi.org/10.1080/00221309.1963.9920534

Thomassen, J. M. (1982). Melodic accent: Experiments and a tentative model. *Journal of the Acoustical Society of America*, *71*(6), 1596–1605.

https://doi.org/10.1121/1.387814

- Trainor, L. J. (2012). Musical experience, plasticity, and maturation: Issues in measuring developmental change using EEG and MEG. *Annals of the New York Academy of Sciences*, 1252(1), 25–36. https://doi.org/10.1111/j.1749-6632.2012.06444.x
- Trainor, L. J., Marie, C., Gerry, D. W., Whiskin, E., & Unrau, A. (2012). Becoming musically enculturated: Effects of music classes for infants on brain and behavior. *Annals of the New York Academy of Sciences*, *1252*(1), 129–138. https://doi.org/10.1111/j.1749-6632.2012.06462.x
- Trainor, L. J., Mcfadden, M., Hodgson, L., Darragh, L., Barlow, J., Matsos, L., &
 Sonnadara, R. (2003). Changes in auditory cortex and the development of mismatch negativity between 2 and 6 months of age. *International Journal of Psychophysiology*, *51*(1), 5–15. https://doi.org/10.1016/S0167-8760(03)00148-X
- Trainor, L. J., McFadden, M., Hodgson, L., Darragh, L., Barlow, J., Matsos, L., &
 Sonnadara, R. (2003). Changes in auditory cortex and the development of mismatch negativity between 2 and 6 months of age. *International Journal of Psychophysiology*, *51*(1), 5–15. https://doi.org/10.1016/S0167-8760(03)00148-X
- Trehub, S. E., Endman, M. W., & Thorpe, L. A. (1990). Infants' perception of timbre:
 Classification of complex tones by spectral structure. *Journal of Experimental Child Psychology*, 49(2), 300–313. https://doi.org/10.1016/0022-0965(90)90060-L
- Trehub, S. E., & Hannon, E. E. (2009). Conventional rhythms enhance infants' and adults' perception of musical patterns. *Cortex*, 45(1), 110–118. https://doi.org/10.1016/j.cortex.2008.05.012

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.

Ullal-Gupta, S., Vanden Bosch der Nederlanden, C. M., Tichko, P., Lahav, A., &
Hannon, E. E. (2013). Linking prenatal experience to the emerging musical mind. *Frontiers in Systems Neuroscience*, 7(SEP), 1–7.
https://doi.org/10.3389/fnsys.2013.00048

- Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, 5(SEP), 1–14. https://doi.org/10.3389/fpsyg.2014.01111
- Webb, A. R., Heller, H. T., Benson, C. B., & Lahav, A. (2015). Mother's voice and heartbeat sounds elicit auditory plasticity in the human brain before full gestation. *Proceedings of the National Academy of Sciences of the United States of America*, 112(10), 3152–3157. https://doi.org/10.1073/pnas.1414924112
- Werwach, A., Männel, C., Obrig, H., Friederici, A. D., & Schaadt, G. (2022).
 Longitudinal trajectories of electrophysiological mismatch responses in infant speech discrimination differ across speech features. *Developmental Cognitive Neuroscience*, 56, 101127. https://doi.org/10.1016/j.dcn.2022.101127
- 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*, 106(7), 2468–2471. https://doi.org/10.1073/pnas.0809035106

Ph.D. Thesis – E. Flaten; McMaster University – Psychology, Neuroscience & Behaviour

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



Figure 1. Stimulus. A) Trials comprising a set. Each set included priming (duple or triple metre), transition, and test trials. Sets repeated 9 times per block, for up to 3 blocks (27 total). Priming and transition trials varied across 4 different priming tempos as indicated by Inter-beat interval (IBI) in B. Tempo of priming and transition and the pitch of the tones (A, C#, or E) changed randomly after every 22-trial set. **B**) Timing of the audiovisual stimulus (333 ms IBI for all test trials, or 231, 278, 400 or 480 ms IBI for priming/transition), with the three metrical levels (beat, duple, and triple) shown above. The visual stimulus is shown, as it grew and shrank on beat one, and remained static for beats 2-6. The colour (pink or green) and/or orientation (X shape or T shape) of the circles in the visual stimulus changed every 22-trial set. **C**) Stimulus envelope for the test trials with the frequency peaks for the triple, duple and beat metre frequencies labelled.



Figure 2. Infant mismatch response ERPs. A) Example grand-average ERPs for standard (dashed line) and deviant (solid line) tones on beat 4 (red) and 5 (blue) for the duple (top) and triple (bottom) groups. The coloured music notes show where the deviant occurred in time, followed by the next tone in grey. Note the two positive peaks to the auditory tones, with a sustained positivity (MMR) from ~200-400 ms (shown by the grey line). B) The grand-average ERPs for the deviant-standard difference waves for frontal left (FL), frontal midline (FZ) and frontal right (FR) sites. C) MMR topographies. D) Boxplots for the extracted MMR for the predicted beat position x group interaction (non-significant).



Figure 3. SSEP results from frontocentral sites. A) Frequency spectra of SSEPs (left) demonstrating power peaks at the triple (1 Hz), duple (1.5 Hz) and beat (3 Hz) frequencies, as well as the boxplots showing greater overall SSEP power in the duple group compared to the triple group (right). B) Boxplots for the exploratory one-way ANOVAs comparing groups at each frequency of interest separately, along with their topographies.







Figure 5. Boxplots for effects of attending music classes on infant mismatch responses. Each coloured dot/line represents one infant. Infants who attended regular music classes had larger MMR amplitudes on beat 5 than beat 4 in frontal left (FL) sites (beat position x laterality x music class group interaction p = .003; post-hoc p = .038), whereas those not in music classes showed no differences for the different beat positions. Results were not significant in frontal midline (FZ) or right (FR) sites.

Tables				
Channel Grouping	Beat Position	t	р	d
FL	4	4.234	<.001	0.69
FL	5	5.426	<.001	0.88
FZ	4	2.428	.060	0.39
FZ	5	5.157	<.001	0.84
FR	4	4.532	<.001	0.74
FR	5	6.620	<.001	1.07

Table 1. t-test Results for Infant MMRs.

Note. df = 37; d = Cohen's d; all one-directional p values corrected using family-wise error rate.







Figure S2. Tempo Control Analysis Results. A) Average MMR for each tempo group (based on which tempo missing) separate B) Average SSEP power across frequencies of



interest (triple, duple, beat frequencies); C) Average ITPC across the frequencies of interest. No group differences were found (all p's >.05).

Figure S3. Looking behaviour Correlations. X axis in all figures is the proportion of time infants spent looking at the screen for all test trials.

Chapter 5: General Discussion

It is well established that infants are sensitive to rhythm from birth, such as being able to detect and encode a rhythmic beat (Háden et al., 2024; Winkler et al., 2009), as well as track the hierarchical structure of a rhythm from before full term (Edalati et al., 2023, 2024). They can detect changes in tempo (Bahrick, 2002; Baruch & Drake, 1997; Bobin-Bègue et al., 2006; Háden et al., 2015), encode regularities in repeating rhythm patterns (Cirelli et al., 2016; Edalati et al., 2023, 2024; Lenc et al., 2022), and detect a regular structure in a speech stream (Gervain et al., 2008, 2012). At least as young as 6-7 months, infants can also discriminate different metres (Hannon & Johnson, 2005; Hannon & Trehub, 2005a, 2005b). Infants can even be behaviourally biased to perceive a metrically ambiguous rhythm in duple or triple metre by previously bouncing them on every 2nd or 3rd beat, respectively (Phillips-Silver & Trainor, 2005). However, the extent to which infants can be primed to neurally apply different top-down interpretations of an ambiguous rhythm had not been tested previously. The current thesis thus employed a metrical priming paradigm to test if 6-month-old infants could be biased to interpret a metrically ambiguous rhythm either in duple or triple metre, in the context of a single tempo (Chapter 2), or varying tempos (Chapter 4). Further, Chapter 3 tested adults who underwent identical conditions as the infants (Chapter 2), while addressing questions about the role of attention in flexibly interpreting an ambiguous rhythm in different metres (Experiment 2). Thus, the current thesis made the novel discoveries that infants can conceive different metrical interpretations of a rhythm, and that adults and infants differ in how they process metre and the role of attention. Additionally, a strength in this

work is that it used multiple neural measures to concurrently index different aspects of rhythm perception; namely, predictive processing of individual beats using mismatch responses, and neural representation of the rhythmic structure using neural tracking.

Overall, the combined main findings provide evidence of top-down metre processing in infants' predictions of events that may not generalize across tempi, whereas adults are less flexible to primed metre but can engage sustained attention to neurally track different metrical interpretations. This lack of flexibility in adults reflects a strong duple bias, one that also appears to be emerging in infants, and which is enhanced by musical experience. Further discussion of these main findings is provided below.

Main Findings & Contributions

The first main finding of this thesis is novel neural evidence that infants can apply a top-down metrical interpretation of an ambiguous rhythm (Chapter 2), as demonstrated by enhanced MMRs to pitch deviants on subjectively strong compared to weak beats after being primed to hear it in duple or triple metre. While prior research has provided ample evidence of infants' bottom-up encoding of rhythmic stimuli, this was the first study to directly show infants' internal neural representation of duple or triple metre for a single ambiguous stimulus under different priming conditions. Some previous studies have shown suggestive evidence of top-down rhythm processing, such as larger ERPs for omissions in strong versus weak beat positions when the metre was clearly indicated (Háden et al., 2024; Winkler et al., 2009), or larger SSEP peaks at the beat frequency in a stimulus with little energy at the beat (Lenc et al., 2022). Chapter 2 builds on these results, as infants in this study had to maintain the metre for a stimulus with multiple

possible interpretations for 16 repetitions before being primed again. Under these conditions, infants were able to maintain the metre, as shown by the enhanced prediction of events occurring on strong beat positions in the primed metre. These top-down effects are in line with dynamic attending theories of rhythm perception (Jones & Boltz, 1989; Large & Jones, 1999; Schroeder & Lakatos, 2009). SSEP measures of beat tracking, however, did not differentiate infants' primed versus unprimed metres, perhaps in part because they were not able to maintain the internal representation for the full 16 measures.

Importantly, although infants clearly have some ability to engage in top-down metre processing, Chapter 4 found no evidence that they are able to maintain metre in the context of generalizing across changing tempos. Infants are highly sensitive to tempo changes from soon after birth (Bahrick, 2002; Baruch & Drake, 1997; Bobin-Bègue et al., 2006; Háden et al., 2015; Trehub & Thorpe, 1989), but as discussed in Chapter 4, perhaps the dual task of maintaining a primed metre while generalizing across tempos from priming to test trials was too difficult. This was the first study to test infants' abilities to learn a top-down metrical structure across varying tempos and, in general, little research has looked at infants' abilities to generalize a learned rule across musical stimuli. Some studies have shown that infants can categorize varying rhythms based on tempo (Trehub & Thorpe, 1989), timbre (Trehub et al., 1990), or metre (Hannon & Johnson, 2005), but none of these required top-down processing. Thus, at least at 6-months, it appears that infants can only engage in top-down metre processing in certain conditions. Future studies could aim to better define which conditions may allow for top-down metre

processing. For example, one could test infants' top-down metre processing while generalizing across different rhythm patterns or timbres instead of across tempos, and could test infants at different ages. As discussed in Chapter 4, I would expect that generalizing a top-down interpretation across these various features may be easier than across tempo changes given that oscillatory mechanisms for neurally tracking the rhythms only need to phase-reset upon a tempo change.

The second main finding of the thesis, which influenced interpretation of the priming effects, was the presence of a bias towards duple over triple metre that was found across infants and adults, and was enhanced by musical experience. Specifically, in Chapter 2, the effect of primed MMR for the strong beat was magnified in the duplecompared to triple-primed infants, and there was also larger MMR overall for the dupleprimed infants. Further, in Chapter 3, enhanced neural tracking according to primed metre (as measure by SSEPs) with active attention was stronger for duple-than triple-primed adults, and in Chapter 4 stronger neural tracking of the stimulus in general was found for infants primed with duple metre (for SSEPs and ITPC). In Chapter 3, the presence of a strong duple bias in adults likely contributed to them being less flexible to priming than infants. Specifically, infants' predictions of unexpected events (MMRs) were enhanced for the primed strong beat in Chapter 2, but adults instead showed evidence of a robust bias in their attentional capture (P3a) to beat 5 over beat 4, regardless of priming or attention condition. This effect was driven by the music- and dance-trained participants, as well as (for the attention group) the participants who had lower confidence ratings for their metre perception. Similarly, in Chapter 4, MMR was generally enhanced for pitch

deviants on beat 5 compared to beat 4 for the infants taking music classes. Unfortunately, Chapters 2 and 3 cannot rule out that the duple bias was at least partially stimulus driven, but the isochronous stimulus used in Chapter 4 was unbiased. Further, given that the duple bias in Chapters 3 and 4 was driven by greater exposure to Western music via music/dance training or infant music classes, I interpret the results to indicate that Western 6-month-old infants already have a duple bias that is enhanced by musical engagement, and that this bias is robust by adulthood. This provides novel evidence of a duple bias that is enhanced by music experience in both infants and adults under similar conditions.

These results are in line with previous studies with infants and children showing enhanced Western enculturation in Western 6- to 12-month-olds participating in music classes (Cirelli et al., 2016; Gerry et al., 2012; Trainor et al., 2012), but few studies have directly compared musicians and non-musicians in subjective metre contexts. In line with the current findings, Brochard et al. (2003) showed automatic duple accenting in response to an isochronous rhythm, which was enhanced in musicians compared to non-musicians, as measured by P3 to deviants in odd beat positions. However, in other studies, musicians also showed better processing of a triple metre than non-musicians, as measured by modulation of P3a for probe tones occurring in- or out-of-phase with a duple or triple metre (Jongsma et al., 2004), as well as measured by SSEPs for the triple frequency (Celma-Miralles & Toro, 2019). In these two latter studies, however, the metre was not ambiguous, being clearly indicated in the immediately preceding context (Jongsma et al., 2004), or by the spatial presentation of the tones (Celma-Miralles & Toro, 2019). Thus,

further work is needed to determine which contexts might trigger an enhanced, compared to reduced, duple bias in musicians.

In sum, my results suggest an early emerging duple bias, that is cemented by adulthood, which reduced adults' flexibility to metrical priming as indicated by nonsignificant effects of duple versus triple priming on their predictive processing. This was reflected in highly consistent MMN for pitch changes across beat positions regardless of priming, suggesting similar automatic detection of the pitch changes on beats primed to be strong or weak, although actively attending to the metre under triple priming enhanced ERP amplitudes in those with poorer perception of the metre. Overall, the MMN and P3a results seem to contrast with previous studies showing enhanced ERPs for strong beat positions (Abecasis et al., 2005; Bouwer et al., 2014, 2016, 2020; Bouwer & Honing, 2015; Brochard et al., 2003; Fitzrov & Sanders, 2015, 2020; Ladinig et al., 2009; Potter et al., 2009), but there is an important difference between these studies and the present studies. In particular, the present study was this was the first to measure MMN and P3a under two different metrical interpretations of a single ambiguous rhythm. In line with previous literature, attention appeared to have little effect on adults' top-down modulation of MMN and P3a other than two main effects: better perception of both metres was associated with a reduced P3a bias to beat 5 over beat 4, while poorer perception of the triple metre was associated with an enhanced MMN. As discussed in Chapter 3, these MMN effects are in line with a predictive coding framework (Friston, 2005; Lumaca et al., 2019; Vuust et al., 2009; Vuust & Witek, 2014), given that poorer attention to the triple-primed metre could be associated with greater uncertainty and thus larger

prediction error for the pitch deviants compared to the case of duple-primed metre, especially in the context of a duple bias. Similarly, for P3a, the greater uncertainty that comes with struggling to maintain the triple-primed metre may have resulted in the default duple bias dominating, whereas better perception of the triple metre could equate the prediction error weights between beats 4 and 5. It is interesting that even for a slightly duple-biased stimulus, infants showed an enhanced MMR for the strong beat in both priming conditions, whereas adults did not and, further, that some adults were more prone to the duple bias than others.

Finally, the third main finding is that while adults are less flexible than infants in applying a primed metre to influence predictive processing, priming modulates adults' neural tracking of the primed metre when they are actively attending to the metre (Chapter 3), as shown by a larger SSEP peak at the primed frequency, although this was stronger in the duple-priming condition. These results are in line with previous studies in adults showing enhanced SSEPs for the imagined or attended to duple or triple frequency (Celma-Miralles et al., 2016; 2021; Gibbings et al., 2023; Nave et al., 2022; Nozaradan et al., 2011; Nave et al., 2019). However, this is the first study to directly compare a sample of adults and a sample of infants, allowing us to make inferences about differences at two developmental time points. That the infants (who have limited attention) and non-attending adults showed a similar lack of priming effects on SSEPs, suggests that primed neural tracking as indexed by SSEPs may require, or at least be greatly facilitated by, sustained attention to the metre. This is likely especially the case for maintaining the triple metre in the duple-biased 6-beat pattern used here. The results are also in line with

Chemin et al. (2014) who used this same stimulus and found that adults' SSEPs were enhanced at the metre frequency after having participants move along to the duple metre, but not after moving to the triple metre.

In sum, the current thesis provides novel evidence that both infants and adults can neurally impose a primed metrical interpretation on an ambiguous rhythm, but in different ways. Infants can more flexibly enhance predictions of pitch events on subjectively strong compared to weak beat positions than adults (at least at a single tempo context), likely due to a duple bias that is only emerging in infancy but is solidified by adulthood. Adults, on the other hand, can actively engage attention to enhance their neural tracking of the metre and reduce their duple bias. Finally, music exposure across age groups enhances the bias towards the duple metre, which suggests a role of enculturation in infants' and adults' subjective metre perception.

Additional Interesting Findings

In addition to the findings that an enhanced duple bias was associated with musical experience, there were other interesting effects of music background. For example, in Chapter 2, infants with musical parents showed generally larger amplitude MMR across beat positions compared to those without musical parents, at least at left hemisphere recording sites. In Chapter 4, the relations were a little different, with music experience defined by engagement in music classes, but not the musicality of the parent, relating to MMR amplitude. Unfortunately, there were not enough infant participants in Chapter 2 who were enrolled in music classes to examine associations with this factor. In the adults in Chapter 3, MMN differed in topography for the musically experienced
(current musicians and dancers) compared to inexperienced participants, where the experienced group showed the expected right hemispheric lateralization (Giard et al., 1990; Levänen et al., 1996; Paavilainen et al., 1991; Rinne et al., 2000), but there was no lateralization of MMN in the inexperienced participants, at least at the group level. So, in addition to musical experience associating with an enhanced duple bias in these Western participants, it appears that it is also associated with a general enhancement of neural rhythm processing, which is in line with previous infant (Cirelli et al., 2016; Trainor et al., 2012), and adult (Bouwer et al., 2016; Brochard et al., 2003; Jongsma et al., 2004) studies. However, unlike some previous studies relating musical experience to neural tracking (Celma-Miralles & Toro, 2019; Cirelli et al., 2016; Doelling & Poeppel, 2015), the current thesis did not find associations between musical experience and either SSEPs or ITPC, perhaps due to testing neural tracking in subjective metre contexts, or due to the definitions of musical experience used.

Notably, although not pertinent to the main research questions, there were hemispheric differences: for both infant datasets, the strongest MMR effects were in the left hemisphere. Specifically, in Chapter 2, top-down priming effects on MMR were significant only in frontal left, not frontal right, sites, and in both infant chapters, effects of musical experience were only found in frontal left sites. These results are in line with previous evidence showing greater left hemisphere involvement in top-down effects on MMR for linguistic stimuli in 3-month-olds (Basirat et al., 2014), similarly to adults (Park et al., 2015; Shuai & Gong, 2014). Furthermore, another study found that passively listening to music involved lateralization to the right hemisphere in newborns, whereas

listening to altered versions (e.g., key changes within the piece) involved predominantly left hemisphere activation (Perani et al., 2010). Listening to altered music might involve auditory change detection, and thus perhaps similar neural processes as MMR. Accordingly, neuroimaging evidence suggests greater left hemispheric dominance in generating positive MMR, such as in premature infants (specifically in left *planum* temporale) for phonetic distinctions, 'ba' and 'ga' (Mahmoudzadeh et al., 2013), in 9- to 10-year-old children for distractor environmental sounds in an audiovisual task (Ruhnau et al., 2013), and in infants tested at 7 and 11 months for native but not non-native speech stimuli (Zhao & Kuhl, 2022). Note that in adults, the auditory MMN is typically right hemispheric dominant (Giard et al., 1990; Levanen et al., 1996; Paavilainen et al., 1991; Rinne et al., 2000), which is also what was found in Chapter 3. For pitch deviants, positive MMR found at 2 and 4 months was left lateralized, while older infants showed right-lateralized adult-like MMN (He et al., 2007). Thus, the current results extend previous findings suggesting left lateralization for top-down influences on positive MMR for musical stimuli at 6 months, that develops into a right-lateralized MMN in adulthood.

Limitations & Future Directions

The current thesis had several limitations that raise interesting questions for future studies. First, the main novel finding of the thesis of enhanced MMR for the primed strong, compared to weak, beat position in Chapter 2 was found in a relatively small sample of infants. Unfortunately, more data could not be collected due to interruptions from the COVID-19 pandemic. Additionally in Chapter 2, we did not include soundcancelling headphones for the parent or the experimenter, and while we took measures to

ensure that the experimenter and parent did not move the infant in any way, it is arguably possible that they could have subconsciously moved to the rhythm and influenced the infants' perception. Although not confirmed experimentally, anecdotally, parents followed instructions to sit still, and researcher inspection of the video during recording confirmed this. Chapter 4 took extra precautions to mask the rhythm audio for the parent and researcher in the room by playing distracting music over headphones, and still found effects of a duple bias; however, in this task involving generalization across tempo, no primed MMR was found, likely due to the task being too difficult for the infants. Thus, further studies should replicate the primed metre effects without tempo generalization (i.e., the study from Chapter 2) on infant MMR with a larger sample size and sound-cancelling headphones for the parent to confirm the original results.

Second, as outlined in Chapters 2 and 3, I also could not rule out the possibility of the duple bias being at least partly stimulus-driven, although this was addressed in Chapter 4 by using an unbiased stimulus. Despite the slight duple stimulus bias in Chapter 2, infants primed with triple metre still showed larger MMR for the strong beat in triple meter, although it was not highly significant. This limitation was addressed in Chapter 4 by using an unbiased isochronous stimulus, and I still observed a duple bias. This, along with enhanced duple biases in participants with more music experience in both chapters 3 (adults) and 4 (infants) suggest an internal bias to perceive ambiguous rhythms in duple metre. Nonetheless, it would be beneficial to test the adults with the isochronous stimulus of Chapter 4 as well, and/or to test infants and adults from non-

Western cultures, to better to tease apart how much of the duple bias is due to enculturation.

Third, the infant participants were all from mid to upper socioeconomic status families from the Hamilton, Ontario, Canada area, and were predominantly White, making it difficult to generalize the findings across diverse groups. The adult sample in Chapter 3, Experiment 2 was somewhat more ethnically diverse, as they were recruited from the undergraduate participant pool at McMaster University, whose student population is quite diverse. However, this sample was not gender diverse, being predominantly female identifying. Given the suggested effects of Western enculturation found in the current thesis, it would be prudent to conduct similar studies in non-Western cultures, especially given concerns about research being dominated by samples that are Western, educated, industrialized, rich and democratic (or WEIRD; Henrich et al., 2010; Rad et al., 2018). However, note that almost all studied cultures across the globe now have been exposed to Western music due to access to the internet and Globalization (Hilton, 2024; Lee et al., 2021; Yurdum et al., 2023), and so separating enculturation effects with multicultural studies would be difficult. Nonetheless, in one previous study, 4- to 8-month-old Turkish infants showed no preference for Western or Balkan metres, due to exposure to both types of music, whereas Western infants preferred Western metres (Soley & Hannon, 2010). Similarly, Western adults showed automatic enhancement of MMN for decrements on strong compared to weak beats according to duple metre, whereas those exposed to both African and Western music had equivalent MMN on all beat positions (Haumann et al., 2018). Future studies could compare infants'

ability to maintain various primed metres in infants exposed only to Western music, which contains primarily duple metre, to those exposed to a musical culture containing different metrical structures as well as to Western music.

Fourth, while I showed compelling effects of top-down metre processing on mismatch responses and neural tracking measures, the current thesis is limited in making conclusions about oscillatory neural entrainment, and whether the effects are primarily occurring in evoked (reactive) versus oscillatory (predictive) activity (Haegens & Zion Golumbic, 2018; Obleser & Kayser, 2019). Future studies could employ time-frequency analyses to investigate how modulations in oscillatory activity synchronize and predict beat positions and whether this is modulated by metrical priming. For example, in adults, Beta power fluctuations will synchronize predictively to the beat (e.g., Fujioka et al., 2012). One recent study showed that even premature infants' alpha power will synchronize with the beat of the same 6-beat rhythm used here, including in the silences (Edalati et al., 2024). Further, enhanced SSEPs to the perceived beat (Bouwer et al., 2023) or speech (Kösem et al., 2018) rate can continue for several cycles after stimulation ceases. Thus, future studies could prime infants to hear the ambiguous rhythm as was done here, then investigate synchrony of alpha power to primed strong compared to weak beat positions, while including silent periods to investigate sustained entrainment.

Another interesting remaining question is how top-down metre perception develops across infancy. Given the cross-sectional nature of the thesis, it is hard to make conclusions about developmental effects outside of simple age or cohort differences. Thus, it would be interesting to test infants starting younger and at different time points

(e.g., newborns, 2 months, 6 months, 12 months), in a longitudinal design to investigate developmental trajectories. I would predict that as infants age that they would show a strengthened priming effect on MMR for strong compared to weak beat positions. However, an isochronous stimulus or otherwise unbiased stimulus should be used, as I'd also predict greater enculturation to a duple bias with age in Western infants. Further, I'd predict that infants would show more adult-like MMN with age. Given the variability in top-down effects on SSEPs in adults for an ambiguous stimulus (Nave et al., 2019), as well as my results from Chapter 3, I'd expect that there may still not be effects of enhanced neural tracking as measured by SSEPs at the primed compared to unprimed frequency, until children are able to actively attend to the metre. It would also be interesting to examine correlations between early neural metre processing and later developmental outcomes, such as vocabulary size (e.g., measured with the MacArthur Bates Communication Index; Fenson et al., 2006), or temperament (e.g., Infant Behaviour Questionnaire; Gartstein & Rothbart, 2003) at 12 months.

Fifth, additional questions remain concerning how these neural responses relate to infants' attention to, and/or behavioural interaction with the metre. I was only able to collect behavioural and perceptual measures directly related to metre perception in adults in Chapter 3 Experiment 2. It is difficult to control or even measure infants' attention in a typical EEG study as movement creates artifacts in the EEG signal. Indeed, most previous infant auditory EEG studies have infants watch an unrelated silent movie, and/or had a researcher actively distracting the infants with toys or other stimuli that are temporally unrelated to the auditory rhythm. Hence, these are conditions under which infants' active

attention is attracted away from the auditory stimulus, and automatic or bottom-up processes presumably dominate the EEG responses. My attempt at engaging infants' attention in Chapters 2 and 4 with an audio-visual stimulus temporally aligned with the beginning of stimulus repetitions is a novel approach. In future studies, this approach could be taken further using audiovisual stimuli in which the visual stimulus serves to direct infants' attention to auditory features. In terms of behaviour, experiments typically involve trying to keep the infant still to limit movement artifacts, making it difficult to get simultaneous EEG and behavioural responses. Nonetheless, given that infants can be behaviourally biased to perceive an ambiguous rhythm in duple or triple metre through bouncing to one metre versus another (Phillips-Silver & Trainor, 2005), even though we might not be able to measure EEG and behaviour simultaneously, it would be interesting to correlate infants' MMR amplitudes or SSEP power with their metre perception, as measured subsequently by their looking-time preference for rhythms matching the primed metre.

Finally, connections between neural measures and music experience in the current thesis were correlational and thus cannot determine directionality of how music experience or other correlated experiences may have contributed towards the effects. In Chapter 4, follow-up control analyses revealed that the enhanced MMR bias to beat 5 was not due to differences in socioeconomic status, amount of music listening or book reading at home, or years of musical training of the parents. Still, random assignment of infants to groups, while matching on demographic and socioeconomic factors, could be used to experimentally test the role of music experience. For example, infants at 6 months could

undergo the priming paradigm as done in Chapter 2, and then could be assigned to weekly music classes, or passive music listening, as was done previously (Gerry et al., 2012; Trainor et al., 2012), and then be tested again at 12 months after 6 months of classes. Previously, enhanced enculturation to Western musical norms and overall enhanced neural responses to tones were found only in infants who experienced the active music classes, suggesting the importance of music making and not just passive exposure to music alone (Gerry et al., 2012; Trainor et al., 2012). Thus, I would predict that all infants would show top-down modulation of MMR as in Chapter 2, but infants in active music classes would show enhanced responses to the rhythm in general, as well as a greater bias towards the duple metre than infants in the passive condition.

Potential Clinical Applications

Given that almost all studied developmental disorders are associated with rhythm timing deficits (e.g., Lense et al., 2021), it is important to better understand the development of rhythm perception and investigate neural markers of top-down rhythm processing. For example, children with probable developmental coordination disorder (DCD) show rhythm and timing perception deficits, as well as slower and smaller MMN and P3a for timing and rhythm deviants, compared to typically developing children (Chang et al., 2021). Thus, testing infants at risk for DCD and other disorders at different time points, can aid in better mapping of neural predictors of disorder diagnosis. Interestingly, both children with and without probable DCD can similarly benefit from a rhythmic cue to increase their motor tapping consistency, although those with probable

DCD perform worse overall, so auditory rhythmic interventions can potentially aid motor skills in this population (Carrillo et al., 2024).

The most research has probably been done relating rhythm deficits to language disorders, such as deficits in sensitivity to prosodic rhythm in speech (Caccia & Lorusso, 2021; Goswami et al., 2013; Weinert, 1992) or in synchronizing rhythmic movements to an auditory cue (e.g., Kreidler et al., 2023; Thomson & Goswami, 2008; but see Colling et al., 2017) in populations with developmental language disorder (DLD) or reading disability. Recent work on the neural mechanisms underlying dyslexia showed altered phase alignment of delta and/or theta phase to rhythmically presented syllables (Power et al., 2013) or an auditory metronome (Colling et al., 2017). Six- to 12-month-old infants at risk for developmental dyslexia had altered neural responses to simple auditory sounds (Mittag et al., 2021) and reduced neural tracking of theta to amplitude modulated white noise (Mittag et al., 2022). In contrast, neurotypical infants at 6- and 9- months (but not 2 months) showed consistent alignment of delta activity to a 2 Hz audiovisual rhythm, and the preferred phase angle of this activity predicted language outcomes at 12-24 months (Ní Choisdealbha et al., 2023). Infant neural delta and theta also track the envelope of natural infant-directed nursery rhymes (Attaheri et al., 2022; Di Liberto et al., 2023), where the tracking of phonetic features increases with age, and neural categorization of phonetic cues (e.g., /ba/ vs /pa/) appears by 7 months (Di Liberto et al., 2023). Such neural tracking seems to be facilitated by the increased rhythmicity of infant-directed speech compared to adult-directed speech (Kalashnikova et al., 2018; Menn et al., 2022), thus drawing infants' attention (Fernald et al., 1989; Trainor, 1996), and facilitating

learning (Nencheva & Lew-Williams, 2022; Singh et al., 2009; Thiessen et al., 2005). Further, priming children with and without DLD with a regular rhythm facilitated grammaticality judgements compared to no priming or priming with an irregular rhythm (Ladányi et al., 2021). Thus, musical rhythm and the rhythm inherent to infant-directed communication can facilitate language development via entrainment of low-frequency neural activity, with children and infants at risk for developmental disorders showing altered entrainment. However, whether these children can flexibly apply rhythmic structures to interpret music or speech has not been studied.

An extension of this research could be to test whether these children similarly benefit from applying a top-down rhythmic structure. For example, in DLD, one could use rhythmic speech stimuli with a metre that matches the prosodic rhythm of the native language (e.g., Abboub et al., 2016; Cason & Schön, 2012). In studies with DCD, a researcher could have them focus on 'marching' to a duple rhythm to increase coordination, given that there was a duple bias across studies. Further, in general for the current thesis, neural responses to the rhythm were enhanced for infants and adults who had more musical experience. This suggests that perhaps music therapies that encourage music making and active engagement to the metre for infants at risk for developmental disorders may aid subsequent language and/or motor development.

Additionally, even premature infants at birth neurally encode the rhythmic structure (beat and metre) of music (Edalati et al., 2023; 2024). However, the consequences of rhythmic deprivation from leaving the rhythmically rich environment of their mother's womb too soon and being exposed to the chaotic auditory environment of

the NICU, are not fully known. Rhythmic treatments could thus be developed to specifically increase exposure to rhythmic regularity in the NICU, to stimulate the rhythm and metre processing important for language development. There is already much work underway that is employing music therapies in the NICU for premature infants (see Bieleninik et al., 2016 for a meta-analysis), but top-down processing of rhythms has not been specifically targeted. Interestingly, recent work shows that infants who experienced multisensory rhythmic stimulation through the mothers' movements in the prenatal period showed enhanced visual attention to and discrimination of rhythms at birth and again at 2 months, compared to infants from mothers who participated in a relaxation control trial (Arioli, 2024). Thus, similar rhythm perception benefits might be seen in neural tracking measures, and perhaps adapting this multisensory rhythmic stimulation to include exposure to different metres could facilitate flexible metre perception at birth and onward, with consequences for language development.

Summary

The current thesis employed a priming paradigm to investigate top-down metrical processing of an ambiguous rhythm in six-month-old infants and adults. I showed that six-month-old Western infants can engage in flexible top-down metre perception, specifically for transient predictive processing of events in individual beats as measured by MMR, but this may be limited to contexts where tempo of the rhythm is constant. Adults, however, are less flexible to a primed metrical interpretation in their predictive processing and neural tracking, as measured by MMN/P3a, and SSEPs/ITPC, respectively, likely due in part to a robust bias toward the duple metre. On the other hand,

if adults engage explicit attentional mechanisms to sustain a metrical interpretation, this can influence the neural tracking/representation of the structure, as indexed by enhanced SSEPs for the perceived metre. Moreover, starting at 6 months, and ingrained in adulthood, Western listeners show a duple bias when processing an ambiguous 6-beat rhythm, which is enhanced by musical experience, suggesting a role of enculturation. These results provide novel evidence of infants' and adults' neural processing of rhythm, with important implications for understanding developmental disorders.

References

- Abboub, N., Nazzi, T., & Gervain, J. (2016). Prosodic grouping at birth. *Brain and Language*, *162*, 46–59. https://doi.org/10.1016/j.bandl.2016.08.002
- Abecasis, D., Brochard, R., Granot, R., & Drake, C. (2005). Differential brain response to metrical accents in isochronous auditory sequences. *Music Perception*, 22(3), 549– 562. https://doi.org/10.1525/mp.2005.22.3.549
- Attaheri, A., Choisdealbha, Á. N., Di Liberto, G. M., Rocha, S., Brusini, P., Mead, N., Olawole-Scott, H., Boutris, P., Gibbon, S., Williams, I., Grey, C., Flanagan, S., & Goswami, U. (2022). Delta- and theta-band cortical tracking and phase-amplitude coupling to sung speech by infants. *NeuroImage*, 247, 118698. https://doi.org/10.1016/j.neuroimage.2021.118698
- Bahrick, L. E. (2002). Generalization of learning in three-and-a-half-month-old infants on the basis of amodal relations. *Child Development*, *73*(3), 667–681.
 https://doi.org/10.1111/1467-8624.00431
- Baruch, C., & Drake, C. (1997). Tempo discrimination in infants. *Infant Behavior and Development*, 20(4), 573–577. https://doi.org/10.1016/S0163-6383(97)90049-7
- Basirat, A., Dehaene, S., & Dehaene-Lambertz, G. (2014). A hierarchy of cortical responses to sequence violations in three-month-old infants. *Cognition*, 132(2), 137– 150. https://doi.org/10.1016/j.cognition.2014.03.013
- Bieleninik, Ł., Ghetti, C., & Gold, C. (2016). Music therapy for preterm infants and their parents: A meta-analysis. *Pediatrics*, 138(3). https://doi.org/10.1542/peds.2016-0971

Bobin-Bègue, A., Provasi, J., Marks, A., & Pouthas, V. (2006). Influence of auditory

tempo on the endogenous rhythm of non-nutritive sucking. *Revue Europeenne de Psychologie Appliquee*, *56*(4), 239–245. https://doi.org/10.1016/j.erap.2005.09.006

- Bouwer, F. L., Fahrenfort, J. J., Millard, S. K., Kloosterman, N. A., & Slagter, H. A. (2023). A silent disco: Differential effects of beat-based and pattern-based temporal expectations on persistent entrainment of low-frequency neural oscillations. *Journal* of Cognitive Neuroscience, 35(6), 990–1020. https://doi.org/10.1162/jocn_a_01985
- Bouwer, F. L., & Honing, H. (2015). Temporal attending and prediction influence the perception of metrical rhythm: evidence from reaction times and ERPs. *Frontiers in Psychology*, 6, 1–14. https://doi.org/10.3389/fpsyg.2015.01094
- Bouwer, F. L., Honing, H., & Slagter, H. A. (2020). Beat-based and memory-based temporal expectations in rhythm: Similar perceptual effects, different underlying mechanisms. *Journal of Cognitive Neuroscience*, *32*(7), 1221–1241. https://doi.org/10.1162/jocn_a_01529
- 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), 1–9. 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
- Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "ticktock" of our internal clock: Direct brain evidence of subjective accents in isochronous

sequences. *Psychological Science*, *14*(4), 362–366. https://doi.org/10.1111/1467-9280.24441

- Caccia, M., & Lorusso, M. L. (2021). The processing of rhythmic structures in music and prosody by children with developmental dyslexia and developmental language disorder. *Developmental Science*, *24*(1), 1–19. https://doi.org/10.1111/desc.12981
- Carrillo, C., Chang, A., Armstrong, H., Cairney, J., McAuley, J. D., & Trainor, L. J. (2024). Auditory rhythm facilitates perception and action in children at risk for developmental coordination disorder. *Scientific Reports*, *14*(1), 1–13. https://doi.org/10.1038/s41598-024-62322-6
- Cason, N., & Schön, D. (2012). Rhythmic priming enhances the phonological processing of speech. *Neuropsychologia*, 50(11), 2652–2658.
 https://doi.org/10.1016/j.neuropsychologia.2012.07.018

Celma-Miralles, A., de Menezes, R. F., & Toro, J. M. (2016). Look at the beat, feel the meter: Top–down effects of meter induction on auditory and visual modalities. *Frontiers in Human Neuroscience*, 10, 1–13. https://doi.org/10.3389/fnhum.2016.00108

- Celma-Miralles, A., Kleber, B. A., Toro, J. M., & Vuust, P. (2021). Neural entrainment facilitates duplets: Frequency-tagging differentiates musicians and non-musicians when they tap to the beat. *bioRxiv*. https://doi.org/10.1101/2021.02.15.431304
- Celma-Miralles, A., & Toro, J. M. (2019). Ternary meter from spatial sounds:
 Differences in neural entrainment between musicians and non-musicians. *Brain and Cognition*, *136*, 103594. https://doi.org/10.1016/j.bandc.2019.103594

- Chang, A., Li, Y.-C., Chan, J. F., Dotov, D. G., Cairney, J., & Trainor, L. J. (2021). Inferior auditory time perception in children with motor difficulties. *Child Development*, 1–17. https://doi.org/10.1111/cdev.13537
- 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
- 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, 1–11. https://doi.org/10.3389/fnins.2016.00229
- Colling, L. J., Noble, H. L., & Goswami, U. (2017). Neural entrainment and sensorimotor synchronization to the beat in children with developmental dyslexia: An EEG study. *Frontiers in Neuroscience*, 11. https://doi.org/10.3389/fnins.2017.00360
- Di Liberto, G. M., Attaheri, A., Cantisani, G., Reilly, R. B., Ní Choisdealbha, Á., Rocha, S., Brusini, P., & Goswami, U. (2023). Emergence of the cortical encoding of phonetic features in the first year of life. *Nature Communications*, *14*(1), 7789. https://doi.org/10.1038/s41467-023-43490-x
- Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, *112*(45). E6233-E6242. https://doi.org/10.1073/pnas.1508431112
- Edalati, M., Wallois, F., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi, S. (2024).
 Neural oscillations suggest periodicity encoding during auditory beat processing in the premature brain. *Developmental Science*, *August 2023*, 1–12.

https://doi.org/10.1111/desc.13550

- Edalati, M., Wallois, F., Safaie, J., Ghostine, G., Kongolo, G., Trainor, L. J., & Moghimi,
 S. (2023). Rhythm in the premature neonate brain: Very early processing of auditory
 beat and meter. *The Journal of Neuroscience*, *43*(15), 2794–2802.
 https://doi.org/10.1523/JNEUROSCI.1100-22.2023
- Fenson, L., Marchman, V. A., Thal, D. J., Dale, P. S., Reznick, J. S., & Bates, E.
 (2006). *MacArthur-Bates Communicative Development Inventories, Second Edition*(*CDIs*) [Database record]. APA PsycTests. https://doi.org/10.1037/t11538-000
- Fernald, A., Taeschner, T., Dunn, J., Papousek, M., De Boysson-Bardies, B., & Fukui, I. (1989). A cross-language study of prosodic modifications in mothers' and fathers' speech to preverbal infants. *Journal of Child Language*, *16*(3), 477–501. https://doi.org/10.1017/S0305000900010679
- Fitzroy, A. B., & Sanders, L. D. (2015). Musical meter modulates the allocation of attention across time. *Journal of Cognitive Neuroscience*, 27(12), 2339–2351. https://doi.org/10.1162/jocn_a_00862
- Fitzroy, A. B., & Sanders, L. D. (2020). Subjective metric organization directs the allocation of attention across time. *Auditory Perception & Cognition*, 3(4), 212–237. https://doi.org/10.1080/25742442.2021.1898924
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 815–836. https://doi.org/10.1098/rstb.2005.1622

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of

isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of Neuroscience*, *32*(5), 1791–1802. https://doi.org/10.1523/JNEUROSCI.4107-11.2012

- Gartstein, M. A., & Rothbart, M. K. (2003). Studying infant temperament via the Revised Infant Behavior Questionnaire. *Infant Behavior and Development*, 26(1), 64–86. https://doi.org/10.1016/S0163-6383(02)00169-8
- Gerry, D. W., Unrau, A., & Trainor, L. J. (2012). Active music classes in infancy enhance musical, communicative and social development. *Developmental Science*, 15(3), 398–407. https://doi.org/10.1111/j.1467-7687.2012.01142.x
- Gervain, J., Berent, I., & Werker, J. F. (2012). Binding at birth: The newborn brain detects identity relations and sequential position in speech. *Journal of Cognitive Neuroscience*, 24(3), 564–574. https://doi.org/10.1162/jocn_a_00157
- Gervain, J., Macagno, F., Cogoi, S., Peña, M., & Mehler, J. (2008). The neonate brain detects speech structure. *Proceedings of the National Academy of Sciences*, 105(37), 14222–14227. https://doi.org/10.1073/pnas.0806530105
- Giard, M., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain generators implicated in the processing of auditory stimulus deviance: A topographic event-related potential study. *Psychophysiology*, 27(6), 627–640. https://doi.org/10.1111/j.1469-8986.1990.tb03184.x
- Gibbings, A., Henry, M. J., Cruse, D., Stojanoski, B., & Grahn, J. A. (2023). Attention modulates neural measures associated with beat perception. *European Journal of Neuroscience*, *December 2020*, 1–17. https://doi.org/10.1111/ejn.15962

Goswami, U., Mead, N., Fosker, T., Huss, M., Barnes, L., & Leong, V. (2013). Impaired perception of syllable stress in children with dyslexia: A longitudinal study. *Journal of Memory and Language*, *69*(1), 1–17. https://doi.org/10.1016/j.jml.2013.03.001

Háden, G. P., Bouwer, F. L., Honing, H., & Winkler, I. (2024). Beat processing in newborn infants cannot be explained by statistical learning based on transition probabilities. *Cognition*, 243, 105670.

https://doi.org/10.1016/j.cognition.2023.105670

- Háden, G. P., Honing, H., Török, M., & Winkler, I. (2015). Detecting the temporal structure of sound sequences in newborn infants. *International Journal of Psychophysiology*, 96(1), 23–28. https://doi.org/10.1016/j.ijpsycho.2015.02.024
- Haegens, S., & Zion Golumbic, E. (2018). Rhythmic facilitation of sensory processing: A critical review. *Neuroscience and Biobehavioral Reviews*, 86(December 2017), 150–165. https://doi.org/10.1016/j.neubiorev.2017.12.002
- 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., & 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*, 102(35), 12639–12643. https://doi.org/10.1073/pnas.0504254102

- Haumann, N. T., Vuust, P., Bertelsen, F., & Garza-Villarreal, E. A. (2018). Influence of musical enculturation on brain responses to metric deviants. *Frontiers in Neuroscience*, 12, 1–15. https://doi.org/10.3389/fnins.2018.00218
- He, C., Hotson, L., & Trainor, L. J. (2007). Mismatch responses to pitch changes in early infancy. *Journal of Cognitive Neuroscience*, *19*(5), 878–892.
 https://doi.org/10.1162/jocn.2007.19.5.878
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, 33(2–3), 61–83. https://doi.org/10.1017/S0140525X0999152X
- Hilton, C. B. (2024). Why music psychology needs larger and more diverse datasets and how citizen science can help. 1–16. https://osf.io/preprints/psyarxiv/zv6w8

Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, 96(3), 459–491. https://doi.org/10.1037//0033-295x.96.3.459

- Kalashnikova, M., Peter, V., Di Liberto, G. M., Lalor, E. C., & Burnham, D. (2018).
 Infant-directed speech facilitates seven-month-old infants' cortical tracking of speech. *Scientific Reports*, 8(1), 1–8. https://doi.org/10.1038/s41598-018-32150-6
- Kösem, A., Bosker, H. R., Takashima, A., Meyer, A., Jensen, O., & Hagoort, P. (2018). Neural entrainment determines the words we hear. *Current Biology*, 28(18), 2867-2875.e3. https://doi.org/10.1016/j.cub.2018.07.023
- Kreidler, K., Vuolo, J., & Goffman, L. (2023). Children with Developmental Language Disorder show deficits in the production of musical rhythmic groupings. *Journal of Speech, Language, and Hearing Research*, 66(11), 4481–4496.

https://doi.org/10.1044/2023_JSLHR-23-00197

- Ladányi, E., Lukács, Á., & Gervain, J. (2021). Does rhythmic priming improve grammatical processing in Hungarian-speaking children with and without developmental language disorder? *Developmental Science*, 24(6), 1–12. https://doi.org/10.1111/desc.13112
- Ladinig, O., Honing, H., Háden, G., & Winkler, I. (2009). Probing attentive and preattentive emergent meter in adult listeners without extensive music training. *Music Perception*, 26(4), 377–386. https://doi.org/10.1525/mp.2009.26.4.377
- Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track timevarying events. *Psychological Review*, *106*(1), 119–159.
- Lee, H., Höger, F., Schönwiesner, M., Park, M., & Jacoby, N. (2021). Cross-cultural mood perception in pop songs and its alignment with mood detection algorithms. *Proceedings of the 22nd International Conference on Music Information Retrieval, ISMIR 2021*, 366–373. https://doi.org/10.5281/zenodo.5625680
- Lenc, T., Peter, V., Hooper, C., Keller, P. E., Burnham, D., & Nozaradan, S. (2022).
 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
- 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*, 20200327. https://doi.org/10.1098/rstb.2020.0327

- Levänen, S., Ahonen, A., Hari, R., McEvoy, L., & Sams, M. (1996). Deviant auditory stimuli activate human left and right auditory cortex differently. *Cerebral Cortex*, 6(2), 288–296. https://doi.org/10.1093/cercor/6.2.288
- Lumaca, M., Trusbak Haumann, N., Brattico, E., Grube, M., & Vuust, P. (2019).
 Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity. *European Journal of Neuroscience*, 49(12), 1597–1609. https://doi.org/10.1111/ejn.14329
- Mahmoudzadeh, M., Dehaene-Lambertz, G., Fournier, M., Kongolo, G., Goudjil, S.,
 Dubois, J., Grebe, R., & Wallois, F. (2013). Syllabic discrimination in premature
 human infants prior to complete formation of cortical layers. *Proceedings of the National Academy of Sciences of the United States of America*, 110(12), 4846–4851.
 https://doi.org/10.1073/pnas.1212220110
- Menn, K. H., Michel, C., Meyer, L., Hoehl, S., & Männel, C. (2022). Natural infantdirected speech facilitates neural tracking of prosody. *NeuroImage*, 251, 118991. https://doi.org/10.1016/j.neuroimage.2022.118991
- Mittag, M., Larson, E., Clarke, M., Taulu, S., & Kuhl, P. K. (2021). Auditory deficits in infants at risk for dyslexia during a linguistic sensitive period predict future language. *NeuroImage: Clinical*, 30, 102578. https://doi.org/10.1016/j.nicl.2021.102578
- Mittag, M., Larson, E., Taulu, S., Clarke, M., & Kuhl, P. K. (2022). Reduced theta sampling in infants at risk for dyslexia across the sensitive period of native phoneme learning. *International Journal of Environmental Research and Public Health*, 19(3).

1180. https://doi.org/10.3390/ijerph19031180

- Nave, K.M., Hannon, E.E., & Snyder, J.S. (2019). Registered report: Replication and extension of Nozaradan, Peretz, Missal and Mouraux (2011). Advances in Methods and Practices in Psychological Science. Provisionally accepted manuscript. OSF Page: https://osf.io/rpvde/.
- Nave, K. M., Hannon, E. E., & Snyder, J. S. (2022). Steady state-evoked potentials of subjective beat perception in musical rhythms. *Psychophysiology*, 59(2), 1–15. https://doi.org/10.1111/psyp.13963
- Nencheva, M. L., & Lew-Williams, C. (2022). Understanding why infant-directed speech supports learning: A dynamic attention perspective. *Developmental Review*, 66, 101047. https://doi.org/10.1016/j.dr.2022.101047
- Ní Choisdealbha, Á., Attaheri, A., Rocha, S., Mead, N., Olawole-Scott, H., Brusini, P.,
 Gibbon, S., Boutris, P., Grey, C., Hines, D., Williams, I., Flanagan, S. A., &
 Goswami, U. (2023). Neural phase angle from two months when tracking speech
 and non-speech rhythm linked to language performance from 12 to 24 months. *Brain and Language*, 243, 105301. https://doi.org/10.1016/j.bandl.2023.105301
- Nozaradan, S., Peretz, I., & Missal, M. (2011). *Tagging the Neuronal Entrainment to Beat and Meter. 31*(28), 10234–10240. https://doi.org/10.1523/JNEUROSCI.0411-11.2011
- Obleser, J., & Kayser, C. (2019). Neural entrainment and attentional selection in the listening brain. *Trends in Cognitive Sciences*, 23(11), 913–926. https://doi.org/10.1016/j.tics.2019.08.004

- Paavilainen, P., Alho, K., Reinikainen, K., Sams, M., & Näätänen, R. (1991). Right hemisphere dominance of different mismatch negativities. *Electroencephalography* and Clinical Neurophysiology, 78(6), 466–479. https://doi.org/10.1016/0013-4694(91)90064-B
- Park, H., Ince, R. A. A., Schyns, P. G., Thut, G., & Gross, J. (2015). Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. *Current Biology*, 25(12), 1649–1653. https://doi.org/10.1016/j.cub.2015.04.049
- Perani, D., Saccuman, M. C., Scifo, P., Spada, D., Andreolli, G., Rovelli, R., Baldoli, C., & Koelsch, S. (2010). Functional specializations for music processing in the human newborn brain. *Proceedings of the National Academy of Sciences of the United States of America*, 107(10), 4758–4763. https://doi.org/10.1073/pnas.0909074107
- 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
- Potter, D. D., Fenwick, M., Abecasis, D., & Brochard, R. (2009). Perceiving rhythm where none exists: Event-related potential (ERP) correlates of subjective accenting. *Cortex*, 45(1), 103–109. https://doi.org/10.1016/j.cortex.2008.01.004
- Power, A. J., Mead, N., Barnes, L., & Goswami, U. (2013). Neural entrainment to rhythmic speech in children with developmental dyslexia. *Frontiers in Human Neuroscience*, 7(NOV), 1–19. https://doi.org/10.3389/fnhum.2013.00777

Rad, M. S., Martingano, A. J., & Ginges, J. (2018). Toward a psychology of Homo

sapiens: Making psychological science more representative of the human population. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(45), 11401–11405. https://doi.org/10.1073/pnas.1721165115

- Rinne, T., Alho, K., Ilmoniemi, R. J., Virtanen, J., & Näätänen, R. (2000). Separate time behaviors of the temporal and frontal mismatch negativity sources. *NeuroImage*, *12*(1), 14–19. https://doi.org/10.1006/nimg.2000.0591
- Ruhnau, P., Herrmann, B., Maess, B., Brauer, J., Friederici, A. D., & Schröger, E. (2013).
 Processing of complex distracting sounds in school-aged children and adults:
 Evidence from EEG and MEG data. *Frontiers in Psychology*, *4*, 1–15.
 https://doi.org/10.3389/fpsyg.2013.00717
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*, 32(1), 9–18. https://doi.org/10.1016/j.tins.2008.09.012
- Shuai, L., & Gong, T. (2014). Temporal relation between top-down and bottom-up processing in lexical tone perception. *Frontiers in Behavioral Neuroscience*, 8, 1–16. https://doi.org/10.3389/fnbeh.2014.00097
- Singh, L., Nestor, S., Parikh, C., & Yull, A. (2009). Influences of infant-directed speech on early word recognition. *Infancy*, 14(6), 654–666. https://doi.org/10.1080/15250000903263973
- Soley, G., & Hannon, E. E. (2010). Infants prefer the musical meter of their own culture: A cross-cultural comparison. *Developmental Psychology*, 46(1), 286–292. https://doi.org/10.1037/a0017555

Thiessen, E. D., Hill, E. A., & Saffran, J. R. (2005). Infant-directed speech facilitates word segmentation. *Infancy*, 7(1), 53–71. https://doi.org/10.1207/s15327078in0701_5

Thomson, J. M., & Goswami, U. (2008). Rhythmic processing in children with developmental dyslexia: Auditory and motor rhythms link to reading and spelling. *Journal of Physiology Paris*, 102(1–3), 120–129. https://doi.org/10.1016/j.jphysparis.2008.03.007

- Trainor, L. J. (1996). Infant preferences for infant-directed versus noninfant-directed playsongs and lullabies. *Infant Behavior and Development*, 19(1), 83–92. https://doi.org/10.1016/S0163-6383(96)90046-6
- Trainor, L. J., Marie, C., Gerry, D. W., Whiskin, E., & Unrau, A. (2012). Becoming musically enculturated: Effects of music classes for infants on brain and behavior. *Annals of the New York Academy of Sciences*, *1252*(1), 129–138. https://doi.org/10.1111/j.1749-6632.2012.06462.x
- Trehub, S. E., Endman, M. W., & Thorpe, L. A. (1990). Infants' perception of timbre:
 Classification of complex tones by spectral structure. *Journal of Experimental Child Psychology*, 49(2), 300–313. https://doi.org/10.1016/0022-0965(90)90060-L
- 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.
- Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music - Brain responses to rhythmic incongruity. *Cortex*, 45(1), 80–92.

https://doi.org/10.1016/j.cortex.2008.05.014

- Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, 5, 1–14. https://doi.org/10.3389/fpsyg.2014.01111
- Weinert, S. (1992). Deficits in acquiring language structure: The importance of using prosodic cues. *Applied Cognitive Psychology*, 6(6), 545–571. https://doi.org/https://doi.org/10.1002/acp.2350060607
- 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*, 106(7), 2468–2471. https://doi.org/10.1073/pnas.0809035106
- Yurdum, L., Singh, M., Glowacki, L., Vardy, T., Atkinson, Q. D., Hilton, C. B., Sauter,
 D., Krasnow, M. M., & Mehr, S. A. (2023). Universal interpretations of vocal music. *Proceedings of the National Academy of Sciences*, *120*(37), 2017.
 https://doi.org/10.1073/pnas.2218593120
- Zhao, T. C., & Kuhl, P. K. (2022). Development of infants' neural speech processing and its relation to later language skills: A MEG study. *NeuroImage*, 256. 119242. https://doi.org/10.1016/j.neuroimage.2022.119242