7-10-2019 2:00 PM

Investigating how neural entrainment relates to beat perception by disentangling the stimulus-driven response

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A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Psychology

Recommended Citation

Gibbings, Aaron WC, "Investigating how neural entrainment relates to beat perception by disentangling the stimulus-driven response" (2019). *Electronic Thesis and Dissertation Repository*. 6281.
https://ir.lib.uwo.ca/etd/6281

Abstract

Beat perception – the ability to perceive a steady pulse in music – is nearly ubiquitous in humans, but the neural mechanisms underlying this ability are unknown. A growing number of electroencephalography (EEG) studies suggest that beat perception is related to neural entrainment, a phenomenon in which cyclic changes in the excitability of populations of neurons synchronize with a rhythmic stimulus. However, the relationship between acoustically-driven and entrainment-driven neural activity is unclear. This thesis presents EEG research that extends our understanding of how neural entrainment is related to beat perception by characterizing, equating, and finally removing the stimulus-driven response in the neural signal isolating the entrainment-driven responses.

Chapter 1 presents a general overview of how neural entrainment may relate to beat perception, the common methods of measuring neural entrainment, and current debates in the literature about how best to account for the stimulus-driven response in the neural signal and also what the neural power spectrum reflects.

Chapter 2 presents research on how perceptual and acoustic factors in auditory stimuli influence neural spectral power in a series of experiments in which beat strength, tone duration, and onset/offset ramp duration were manipulated. The results suggest that both perceptual and acoustic factors influence neural spectral power, and that accounting for the stimulus-driven response in the neural spectrum is more complicated than previously assumed.

Chapter 3 presents research on how power and phase of the neural signal relates to beat strength and beat location, while controlling the stimulus-driven response. The results indicate a relationship between neural entrainment and beat strength, and also, between oscillatory phase and beat location.

Chapter 4 presents research on the potential neural mechanisms of beat perception by examining neural activity during a silent period immediately after rhythm perception for testing for ongoing, oscillatory activity. The results, although not statistically robust, suggest that entrained activity continues into silence, indicating a relationship between neural entrainment and beat perception.

Chapter 5 presents a general discussion of Chapters 2-4 in the context of the existing literature, limitations, and broader interpretations of how these results relate to future directions in the field.

Keywords

electroencephalography (EEG), beat perception, rhythm, neural entrainment, neural oscillations, neural resonance, time-frequency analysis, Fast Fourier Transform (FFT), Morelet Wavelets

Summary for Lay Audience

Beat perception – the ability to perceive a steady pulse in music – is nearly ubiquitous in humans, but the neural mechanisms underlying this ability are unknown. A growing body of literature suggests that beat perception is related to neural entrainment: a phenomenon in which cyclic changes in the excitability of populations of neurons synchronize with a rhythmic stimulus. However, the relationship between acoustically-driven and entrainment-driven neural activity is unclear. This thesis presents research designed to characterize, equate, and finally remove the stimulus-driven response in the neural signal to isolate the entrainment-driven responses to extend our understanding of the relationship between neural entrainment and beat perception.

Co-Authorship Statement

The work presented in this doctoral thesis was designed and written in collaboration with my supervisor, Dr. Jessica Grahn. For each of the studies in this thesis Dr. Grahn contributed to the experimental design, data analysis, interpretation of the findings, as well as revising and editing each of the chapters.

For the studies presented in Chapter 2, Dr. Molly Henry contributed to the experimental design, and data analysis.

Acknowledgments

I am now, and will forever be, grateful for the mentorship and guidance I received from my supervisor, Dr. Jessica Grahn. Thank you for all of the opportunities, advice, and mostly time you have given me over the years. I am grateful to have a mentor that is so committed to the success and well-being of her students. Thank you for helping me keep perspective when I was overwhelmed, and for challenging me when I was content to be comfortable. I have learned so much from you over years; Thank you for making me the scientist I am today.

Molly, if academic lineage is like a family tree, then I consider you my big sister. You've shown me that great scientists can be cool people too. Thank you for sharing with me countless hours of your wisdom and expertise. Truly, without you, the thesis that follows would be very different. You are role model, both as a scientist, and as a human.

I am also very grateful former and current members of the "Music and Neuroscience" Lab: Dr. Molly Henry, Dr. Christina vanden Bosch der Nederlande, Dr. Eric Taylor, Dr. Dan Cameron, Dr. Tram Nguyen, Emily Ready, Avital Sternin, Abdullah Al Jaja, Josh Hoddinott, Brendon Samuels, Kristi Van Hordorf, Syed Raza, Justin Hopper. Thank you all for all the friendship, support, time, thought, feedback, guidance, and distraction you have all given me. It has been an absolute pleasure to work with so many brilliant, positive, and inspiring people.

To the small army of volunteers that are now, and have previously been part of the lab, thank you for all the data you have either collected or provided, and all the studies you have helped pilot over the years. Of special note are Celina Everling, Shaily Brahmbhatt, Ashmita Singh, and Tim (Sangmin) Lee, without whom I would still be collecting data for Chapters 2 & 4.

To my family, who have never wavered in their generosity, support, patience, and love: Thank You. Thank you to my parents, who have supported me through every misstep and misadventure I've had along the way. You have always known what I was capable of, even when I didn't. To my intelligent, curious, hilarious, thoughtful, and beautiful daughters, Hayden and Parker: You light my life. Thank you for reminding me every day what pure curiosity is. Most of all, thank you to my wife Kate, whose love, support, sacrifice, and willingness to live in abject poverty for so many years is the reason I had the opportunity to do something I love every day. I could not have asked for a better partner in life. Thank you for your infinite patience and understanding; this belongs to you as much as it does to me.

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Chapter 1

1 General Introduction

1.1 Beat Perception and Neural Entrainment

Frequently, when listening to music, we find ourselves moving along with the song without even meaning to. Our movements are in time with the music, but do not reflect the timing of every note. But if we're not moving along with every note, then what are we synchronizing our movements to? Rather than moving in time with the rhythm – the temporal pattern of notes – we are usually moving in time with the beat. The beat is the regular, isochronous pulse in musical rhythm – to which the timing of other rhythmic events can be measured (Large & Palmer, 2002; Parncutt, 1994). The ability to perceive the beat in musical rhythm develops early in life (Cirelli, Spinelli, Nozaradan, & Trainor, 2016; Honing, Ladinig, Háden, & Winkler, 2009; Ladinig, Honing, Haden, & Winkler, 2009; Phillips-Silver & Trainor, 2005; Winkler, Háden, Ladinig, Sziller, & Honing, 2009), and seems to be a universal ability in all cultures (McDermott & Hauser, 2005).

Although beat perception is ubiquitous in humans, we seem to be the only species who can reliably detect and synchronize with the beat of a musical rhythm (Bispham, 2006; Hoeschele, Merchant, Kikuchi, Hattori, & ten Cate, 2015). There have been select cases where animals, like Snowball the cockatoo (Patel, Iversen, Bregman, & Schulz, 2009) or Ronan the sea lion (Cook, Rouse, Wilson, & Reichmuth, 2013), have produced evidence of appearing to be able to synchronize with a musical beat. However, even in these exceptional cases, there are still a number of differences between beat perception in humans and animals. One major difference is the spontaneity of the behaviour. From a very young age, humans spontaneously start moving along with music when played (Phillips-Silver & Trainor, 2005; Trainor, 2009; Trehub, Weiss, & Cirelli, 2018; Zentner & Eerola, 2010), however, animals require a great deal of training to learn to move along with musical rhythms (Cook et al., 2013; Hattori, Tomonaga, & Matsuzawa, 2013) with some animals never learning (Hoeschele et al., 2015; Honing, Bouwer, Prado, & Merchant, 2018; Merchant & Honing, 2013; Zarco, Merchant, Prado, & Mendez, 2009). Even when animals can be trained to move along with a musical rhythm, much of the time their actions are rarely predictive, as they are in humans. That is, animals generally react to a stimulus after it as been presented. In contrast, human movement is anticipatory, in that they initiate a movement in advance of the stimulus, such that their movement and the stimulus are synchronized. Lastly, the range of tempi that humans can synchronize to (300 – 1200 ms inter-beat intervals) (Demany & Semal, 2002; Large & Snyder, 2009; Repp, 2005a) is larger than that observed in animal cases (see Cook et al., 2013; Hattori et al., 2013; Merchant & Honing, 2013; Patel et al., 2009).

What makes humans special when it comes to beat perception? Perhaps it is the way our auditory systems respond to regular, rhythmic inputs. One possibility, which is gaining popularity amongst researchers, is that our superior ability to perceive the beat arises from a phenomenon called neural entrainment (Henry & Herrmann, 2014; Henry & Obleser, 2012; Lakatos et al., 2005; Large & Jones, 1999; Large & Palmer, 2002; Lenc, Keller, Varlet, & Nozaradan, 2018a; Nozaradan, Peretz, & Mouraux, 2012a; Nozaradan, Schönwiesner, Keller, Lenc, & Lehmann, 2018; Schroeder & Lakatos, 2009; Tierney & Kraus, 2014). In general, entrainment occurs when one system entrains to, or synchronizes with, another system. For example, we exhibit entrained motor behaviour by tapping in time with the beat in music (Repp, 2005b; Repp & Su, 2013). The key element of entrainment is that we can anticipate/predict when upcoming beats will occur, rather than reacting to the beat after the fact. This distinction between anticipatory and reactionary responses will become important in the discussion to follow. In neural entrainment, the regular cyclic changes in excitability (i.e., oscillations between periods of greater or lesser excitability) of a population of neurons entrain to a rhythmic, external stimulus (Lakatos et al., 2005; Large, 2008; ten Oever et al., 2017). In other words, when a rhythmic auditory stimulus is present, the period and phase of the endogenous oscillations entrain to (i.e., synchronize with) the external stimulus, such that the most excitable phase of the oscillation occurs during the time when a stimulus onset is most likely to occur (Henry & Obleser, 2012; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Lakatos et al., 2013, 2005; Large & Snyder, 2009; Schroeder & Lakatos, 2009; Stefanics et al., 2010).

Although the advantage of entraining the higher excitability phases of neural oscillations to points in time when stimuli are more likely to occur (such as in a rhythmically predictable stimulus like music) is relatively unknown, recent studies suggest that entrainment might increase the efficiency of sampling sensory information from our environment (Baltus & Herrmann, 2016). The suggestion is that consistently maintaining high neural excitability requires more energy than maintaining lower excitability. So, having periods of lower excitability, especially if they coincide with periods when stimuli are less likely to occur, could save energy without sacrificing perception of anticipated events. Evidence that the whisking behaviour in mice (the act of moving their whiskers to get information about their environment) is also rhythmic (Crapse & Sommer, 2008;

Sofroniew & Svoboda, 2015), supports the theory that there may be some advantage to rhythmic sampling of the environment.

A growing number of studies have proposed that beat perception may arise from entrainment of neural oscillations (Large & Jones, 1999; Large & Palmer, 2002; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan et al., 2012a). Previous efforts to measure neural entrainment to musical rhythms have traditionally involved frequency domain transformations, mostly using a Fast Fourier Transformation (FFT), of EEG data collected while participants were listening to auditory stimuli (Cirelli et al., 2016; Fujioka, Trainor, Large, & Ross, 2009; Henry & Herrmann, 2014; Henry, Herrmann, & Obleser, 2016; Henry & Obleser, 2012; B. Herrmann, Henry, Haegens, & Obleser, 2016; Lakatos et al., 2008; Large, 2008; Lenc et al., 2018a; Nozaradan et al., 2011; Nozaradan, Peretz, & Mouraux, 2012b; Nozaradan et al., 2018; Nozaradan, Keller, Rossion, & Mouraux, 2017; Snyder, 2015). The resultant frequency spectrum of the EEG data is then compared to frequency spectra of the stimulus envelope (Cirelli et al., 2016; Nozaradan, 2014; Nozaradan et al., 2012a, 2018) or EEG spectra are compared from different listening conditions (Cirelli et al., 2014; Fujioka, Large, Trainor, & Ross, 2008b; Lakatos et al., 2008; Schroeder & Lakatos, 2009). More power at beat frequencies (i.e., harmonics and sub-harmonics of the beat frequency) when comparing the spectra is interpreted as greater entrainment that, in turn, is thought to reflect a stronger beat percept.

However, depending on the paper, or the lab, the term entrainment can be used differently, and to mean different things. Generally, previous work has used the terms “neural response” and “entrainment” interchangeably. However, for the purposes of this thesis, I will use “entrainment” to refer to neural activity associated with perceptual differences, independent of the stimulus-driven response (i.e., the base level, primary sensory response). Therefore, the neural response represents a combination of the stimulus-driven response as well as the entrained response. It is important to make the distinction because the basis for how we interpret our results depends on how we define entrainment. For the most part, the stimulus-driven response has been ignored when investigating how neural entrainment contributes to beat perception. This becomes apparent as we look at the methods that previous studies have employed to measure entrainment.

Although previous studies have produced convincing evidence of neural entrainment as a mechanism for beat perception (i.e., greater power in the neural spectra for conditions with a stronger beat percept), there are a few issues with the previous approaches that need to be addressed before we can make strong interpretations of previous findings. For example, previous studies have provided evidence of neural entrainment playing a role in beat perception by comparing the power spectrum of the neural signal to the power spectrum of the stimulus amplitude envelope (Nozaradan et al., 2012a). To determine which frequencies in the neural signal (EEG) were enhanced relative to the stimulus envelope, values in both spectra were transformed into z-scores, and then the z-scores of the two spectra were compared. Enhancements in the neural spectra, compared to the stimulus spectrum, were interpreted as an indication of neural entrainment. However, interpreting differences in relative peak height (e.g., z-scored power) as differences in entrainment when comparing the neural spectrum to the stimulus envelope spectrum assumes that in the absence of beat perception, the cortical representation of the stimulus only reflects the envelope of the sound. In other words, it assumes that if no beat is perceived, the fidelity of the auditory stimulus is perfectly preserved, with relative peak heights in the stimulus exactly matching relative peak heights in the EEG, and that no transformations occur between the ear and the brain apart from those related to perceptual processes. However, the stimulus-driven neural response is not a perfect mirror of the auditory signal in either the time or frequency domain. This means that some of the differences between the spectra of the neural response and the spectra of the stimulus envelope, which are being interpreted as changes in entrainment, could simply be transformations of the stimulus-driven response independent of perceptual differences.

One way to attempt to control for the transformation of the auditory stimulus into the stimulus-driven response is to compare the frequency spectra of EEG data from different listening conditions. The transformation of the auditory stimulus between the source and the neural response should be the same in both listening conditions. However, even when comparing spectral differences of neural responses from different listening conditions, a difference in entrainment is not the only reason there might be differences in the observed frequency spectrum. Because the frequency spectrum of the neural response reflects both the stimulus-driven and entrained response, it is also sensitive to changes in evoked brain responses generated by each note in the rhythm, independent of changes to beat percept. This is important because evoked brain responses are sensitive to acoustic characteristics of the stimulus, such as pitch, note duration, onset/onset ramp duration, note rate, etc. (Alain, Woods, & Covarrubias, 1997; Hillyard & Picton, 1978; Kushnerenko, Ceponiene, Fellman, Huotilainen, & Winkler, 2001; Muller, 1973; Onishi & Davis, 1968; Picton, Woods, & Proulx, 1978a, 1978b; Schweitzer, 1977; Schweitzer & Tepas, 1974). Moreover, altering a rhythm's acoustic characteristics affects the rhythm's spectrum, including altering power at the beat frequency, even when it does not alter how strongly a beat is perceived in the rhythm (Henry, Herrmann, & Grahn, 2017). This means that changing the acoustic characteristics of the stimulus can affect the stimulus-driven response both by altering the evoked response and by changing the spectral characteristics of the auditory stimulus. However, because the effect of acoustic manipulations has traditionally been studied by comparing evoked responses (Alain et al., 1997; Hillyard & Picton, 1978; Kushnerenko et al., 2001; Muller, 1973; Onishi & Davis, 1968; Picton et al., 1978a, 1978b; Schweitzer, 1977), and neural entrainment has been studied by comparing power spectra (Cirelli et al., 2014, 2016; Fujioka, Ross, & Trainor, 2015a; Fujioka et al., 2009; Henry, Herrmann, & Obleser, 2014; Henry & Obleser, 2012; Lakatos et al., 2008; Nozaradan, Peretz, & Keller, 2016; Nozaradan et al., 2011, 2012a; Schroeder & Lakatos, 2009; Tierney & Kraus, 2014), the effects of altering acoustic characteristics on the neural response in the frequency domain has not been well characterized. Understanding how the evoked response contributes to the neural power spectrum is important, because it is unclear if, or how, altering acoustic characteristics, which don't affect beat perception, affects power at frequencies traditionally used to make inferences about beat perception.

Understanding how acoustic characteristics affect the spectral characteristics of the neural response is particularly important when trying to make inferences about entrainment by comparing findings across studies. Although acoustic characteristics are generally consistent across conditions within a study, they are less likely to be the same across studies. If changing the acoustic characteristics affects power in the neural response at the beat frequency independently of entrainment, then stimuli with different acoustic characteristics could affect the consistency of findings across studies as a result of factors independent of entrainment. This again, underscores the importance of characterizing how altering the acoustic characteristics of a rhythm affects the stimulus-driven response.

Another potential issue with making comparisons between listening conditions is that although acoustic characteristics (e.g., tone and onset ramp duration) of a stimulus set are consistent within a study, most studies manipulate beat strength by manipulating the rhythms' temporal pattern. That is, beat strength manipulations are made by changing the timing of the note onsets so that rhythms have fewer onsets that coincide with beat positions (Grahn & Brett, 2007; Povel & Essens, 1985). However, changing the temporal pattern of the rhythm also affects the frequency spectrum of the stimulus (Henry et al., 2017). Differences between listening conditions in the stimulus spectrum, whether as a result of changes to either the acoustic or temporal characteristics of a rhythm, suggests differences between conditions may arise from differences in the stimulus-driven response. If the stimulus-driven response differs between listening conditions, it is difficult to make inferences about differences in the neural response being driven by perception. In order to conclude that neural differences between listening conditions are due to differences in entrainment, it is crucial that the stimulus-driven response is identical between listening conditions. Only once the stimulus-driven response is identical in different listening conditions can we conclude that differences in the neural response are the result of entrained response differences.

Observing differences in power at beat-related frequencies when the stimulus-driven response is identical provides evidence that neural entrainment drives these observed neural differences, however one still cannot conclude that beat perception itself arises from entrained neural oscillations. The last major issue with the methodology employed to investigate neural oscillations is how we interpret power in neural frequency spectra. Indeed, there is currently a debate in the literature about what power in neural spectra reflects (Henry et al., 2017; Novembre & Iannetti, 2018; Obleser, Henry, & Lakatos, 2017; Zoefel, ten Oever, & Sack, 2018). The issue is that brain responses evoked by rhythmic stimuli will also be rhythmic (Novembre & Iannetti, 2018; van Ede, Quinn, Woolrich, & Nobre, 2018). The spectral characteristics of a rhythmic evoked response chain, when transformed to the frequency domain using an FFT, are potentially indistinguishable from the spectral characteristics of an entrained, oscillatory response (Novembre & Iannetti, 2018). Therefore, it is possible that the neural power spectra could simply reflect a series of externally-driven evoked responses (Novembre & Iannetti, 2018; van Ede et al., 2018), rather than an internally-driven, entrained response (Fujioka et al., 2009; Lakatos et al., 2008; Large, 2008; Large & Snyder, 2009; Nozaradan et al., 2011; Schroeder & Lakatos, 2009).

Separating the evoked, stimulus-driven response from the entrained, oscillatory response is difficult because the majority of previous work done on understanding how neural oscillations are related to perception has examined neural responses during the presence of external auditory or visual stimuli (Calderone, Lakatos, Butler, & Castellanos, 2014; Fujioka et al., 2009; Henry et al., 2016; Henry & Obleser, 2012; Herbst, Obleser, Joliot, Cognitive, & Unit, 2018; Lakatos, Chen, O’Connell, Mills, & Schroeder, 2007; Snyder, Alain, & Picton, 2006; Wilsch, Henry, Herrmann, Maess, & Obleser, 2015). Because there is a stimulus, stimulus-driven responses have always been present, making it difficult to know how much of the overall neural response is stimulus-driven and how much is perceptually based entrainment. To solve this problem, we can take advantage of the fact that one of the properties of an entrained oscillator is that the oscillations will continue for some time at the entrained rate after external stimulation has ceased (Baltus & Herrmann, 2015; Large, 2008; Large, Herrera, & Velasco, 2015; Large & Snyder, 2009; van Noorden & Moelants, 1999; Velasco & Large, 2011). Evidence of this has recently been shown in the primary auditory cortices of monkeys (Lakatos et al., 2013). When stimulated with an isochronous tone sequence, neural activity in the primary auditory cortices of monkeys continued to oscillate at the stimulation frequency of the tone sequence for many cycles after the tone sequence stopped. We can use the same property to investigate how beat perception may arise from populations of entrained neurons in humans.

The issues discussed so far have all been related to interpreting power in the frequency spectra, however, the key prediction of neural entrainment theories is that that entrained oscillations are phase-locked to the onset of predictable rhythmic stimuli. While most studies have examined the power of the entrained oscillations, the phase of that oscillation relative to the beat is a factor that remains mostly unexplored. This may be due, in part, to the methods typically used to perform the frequency domain transforms of neural signals in previous investigations of how neural oscillations are related to beat perception. Previous studies have generally computed the frequency transformations using FFTs. Although using an FFT is advantageous when one requires fine grained frequency resolution (i.e., the specificity of the frequency response) in the resultant power spectrum, the trade-off of this technique is that the power and phase values are averaged over the entire length of the signal. To investigate the specific relationship between phase of neural oscillations, and the specific beat location in a rhythm one needs to retain some temporal information from the signal, which does not happen when submitting the entire neural signal to an FFT. Before we can confidently make strong claims about neural oscillations as a mechanistic explanation of beat perception, the relationship between the phase of neural oscillations and specific beat location needs to be explored further, and in a way that retains some temporal information.

1.2 Overview of the Current Thesis

The studies reported here will not only tackle the issues discussed previously but will also expand on our current knowledge about the role of neural oscillations in beat perception. In this thesis I describe a series of studies which seek to understand the how neural oscillations contribute to beat perception by characterizing, controlling, and finally removing the stimulus driven response, to better understand how differences in the entrained response are related to differences in beat perception.

In the first study (chapter 2), I characterize how changes in the acoustic characteristics of an auditory rhythm affect the spectral characteristics of the neural response, by altering beat strength, tone duration, and onset ramp duration of auditory rhythms while recording EEG data. Findings from this study will begin to bridge the gap in our understanding of how acoustic characteristics of an auditory stimulus affect the spectral characteristics of the neural response and will inform us about the importance of acoustic characteristics of the stimuli to better interpret findings across studies. Although altering the acoustic characteristics of the stimulus changes the evoked response, which will necessarily alter the spectral characteristics of the neural response, it is possible that altering the acoustic characteristics affects power in the neural response at frequencies not related to the beat.

Figuring out whether changing stimulus characteristics affects power at frequencies related to the beat is important because some studies have interpreted power of the neural response at frequencies related to the beat relative to frequencies unrelated to the beat, or relative to power in the stimulus envelope, as evidence of entrainment. Therefore, if choices about the acoustic characteristics of the stimulus affect power at beat-related frequencies, it could serve to caution about comparing findings across studies when the stimulus characteristics are not consistent.

In the second study (chapter 3), I examine the neural response to the same short rhythmic sequence when it is embedded in a rhythmic context that induces either a strong beat or a weak beat. By analyzing the neural response to identical embedded rhythmic sequences between different perceptual contexts, the stimulus-driven response is identical across listening conditions while beat percept (and presumably entrainment) differs. Therefore, any differences in the spectral power between conditions must be the result of differences in entrainment, caused by the beat percept induced by the rhythmic context. As a complementary measure, I examined oscillatory phase by embedding the common sequences either to begin on the beat induced by the surrounding context (in-phase), or half-way between the beat (anti-phase). Not only will the findings of this study determine how differences in neural entrainment relate to perceived beat strength when the stimulus-driven response is identical, it will also let us explore how the phase of neural oscillations is related to the beat.

The third study (chapter 4) will eliminate the stimulus-driven response altogether by analyzing the neural response to strong and weak beat stimuli in the silence directly after a rhythm stops. Because I analyze the neural response during silence, there is no stimulus, and therefore no stimulus-driven response. Findings of this study provide definitive evidence related to the debate of whether beat perception is truly arises from populations of entrained neural oscillators. Furthermore, by analyzing neural response in the absence of stimulus, it also allows us to investigate the relationship between phase and beat in the absence of evoked, potentially phase-resetting, responses.

Overall, the aim of this thesis is to test predictions about how beat perception arises from populations of entrained neural oscillators, first by characterizing how acoustic factors alter observed neural spectra, then by controlling and ultimately removing the stimulus driven response entirely, characterizing differences in power at beat-related frequencies, as well as differences in phase.

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Chapter 2

2 Characterizing entrained and stimulus driven responses to musical rhythm

2.1 Introduction

Being able to track dynamic, complex auditory stimuli, especially rhythmic stimuli such as speech and music, is an important part of everyday life. Of particular interest is the unique human ability (Fitch, 2005; Hagmann & Cook, 2010; McDermott & Hauser, 2005, 2007) to quickly and spontaneously identify the beat in the context of musical rhythm. The beat is a perceived pulse that marks isochronous points in time, relative to which the timing of other events is measured (Large & Palmer, 2002; Parncutt, 1994). Although humans learn to identify the beat early in life (Cirelli et al., 2016; Honing et al., 2009; Ladinig et al., 2009; Phillips-Silver & Trainor, 2005; Winkler et al., 2009), exactly how beat perception arises remains unknown.

One hypothesis about how beat perception arises is through entrainment of neural oscillations (i.e., the cyclic changes in baseline excitability of populations of neurons; Lakatos et al., 2005) to the temporal structure of auditory rhythms (Large & Snyder, 2009; Nozaradan et al., 2011; van Noorden & Moelants, 1999). Entrainment explanations suggest that neural oscillations entrain to predictable, external stimuli such as repeated auditory tones or flashing lights (Henry et al., 2014; Henry & Obleser, 2012; B. Herrmann et al., 2016; Lakatos et al., 2007, 2008, 2005; Large & Snyder, 2009; Snyder & Large, 2005), such that the most excitable phase of the oscillation becomes aligned to the stimulus onset. Thus, during beat perception, it is hypothesized that the notes of a rhythm that are aligned with the excitatory neural phase elicit a greater neural response, resulting in them being perceived as accented, or more salient, than notes that occur in a less excitable phase. This results in subjective accenting of certain notes, giving rise to the percept of the beat.

The potential role of neural oscillations in beat perception is supported by recent work that focuses on power spectra (i.e., frequency-domain representations) of electroencephalography (EEG) data (Chemin, Mouraux, & Nozaradan, 2014; Cirelli et al., 2016; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011; Tierney & Kraus, 2014). In this work, the EEG power spectra of two different perceptual conditions are compared (Cirelli et al., 2014; Fujioka, Large, Trainor, & Ross, 2008a; Lakatos et al., 2008; Schroeder & Lakatos, 2009), or the EEG power spectrum is directly compared to that of the stimulus (Cirelli et al., 2016; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011, 2012a). Differences in spectral power (either between two perceptual conditions, or between the EEG and the stimulus) at note-related or beat-related frequencies are taken as evidence of neural entrainment. In particular, the power of the EEG signal at beat-related frequencies is assumed to scale with beat strength (i.e., the strength of the beat percept).

However, differences in spectral power at beat-related frequencies in the EEG signal may reflect more than just differences in neural entrainment. The power spectrum of the EEG signal is also sensitive to changes in evoked brain responses, independent of differences in entrainment. Evoked brain responses are influenced by the acoustic characteristics of a stimulus, such as pitch, note duration, onset/offset ramp duration, note rate, etc. (Alain et al., 1997; Hillyard & Picton, 1978; Kushnerenko et al., 2001; Muller, 1973; Onishi & Davis, 1968; Picton et al., 1978a, 1978b; Schweitzer, 1977). Altering a rhythm's acoustic characteristics necessarily affects the rhythm’s spectral power, including altering power at beat-related frequencies in the stimulus power spectrum, but does not alter beat strength (Henry et al., 2017). However, because acoustic effects have traditionally been studied using evoked responses (Alain et al., 1997; Hillyard & Picton, 1978; Kushnerenko et al., 2001; Muller, 1973; Onishi & Davis, 1968; Picton et al., 1978a, 1978b; Schweitzer, 1977), and neural entrainment has been studied by comparing power spectra (Cirelli et al., 2014, 2016; Fujioka et al., 2015a, 2009; Henry et al., 2014; Henry & Obleser, 2012; Lakatos et al., 2008; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011, 2012a; Schroeder & Lakatos, 2009; Tierney & Kraus, 2014) the effects of acoustic characteristics on the power spectra have not been well characterized.

Understanding the contributions of both the evoked response and the entrainment response is important because it is unclear if, or how, the evoked response induced by acoustic characteristics affects spectral power at frequencies traditionally used to make inferences about the strength of entrainment. Before we can assume that any differences in spectral power in the EEG signal at note or beat-related frequencies reflects differences in entrainment, and are an indication of differences in beat perception, we need to know how altering the acoustic characteristics of the rhythm affects power at those frequencies. The aim of the current study is to disentangle the contributions of the acoustic characteristics of the stimulus and perceived beat strength to the power spectrum of EEG data. To do this, we take advantage of the dissociation of beat percept from spectral stimulus characteristics (Henry et al., 2017) to characterize how acoustic characteristics and perceived beat strength each influence the spectral power of the neural response. Specifically, we conducted a series of three experiments in which we independently manipulated beat strength and acoustic characteristics (note duration and onset/offset ramp duration) in auditory rhythms. We hypothesize that, if the strength of entrainment scales with perceived beat strength, then manipulations that affect perceived beat strength should affect spectral power in the same direction. That is, temporal manipulations that increase beat strength should increase spectral power, and conversely, manipulations that decrease beat strength should decrease spectral power. Moreover, if spectral power at beat-related frequencies is a direct measure of beat perception (Nozaradan et al., 2011, 2012a), or beat perception ability (Cirelli et al., 2016; Nozaradan, Peretz, et al., 2016), then acoustic manipulations should not affect spectral power at beat-related frequencies. Finally, it is possible that both perceived beat strength and acoustic characteristics affect the spectral power in the neural response because differences in the evoked responses necessarily affect the power spectrum. In this study, we will characterize the changes in the neural power spectrum that result from beat strength versus acoustic characteristic manipulations.

2.2 Methods

2.2.1 Participants

51 participants (M_{age} = 20.47 years, *SD* = 2.72, 33 female) took part in all three experiments after providing written consent. Owing to either technical difficulties or attrition between testing sessions, 36 participants (M_{age} = 20.86 years, *SD* = 2.72, 21 female) completed the study. Participants completed a demographic questionnaire that asked about their history of music training. Thirty participants reported having at least some musical training (*M* = 7.15 years, *SD* = 5.05). Of those, 16 had more than five years' experience (*M* = 10.50 years, *SD* = 4.31), and of those, seven were currently

rehearsing at least one hour per week (*M* = 5.43 hours/week, *SD* = 6.63). Participants were remunerated either by receiving study credits for psychology courses or monetarily. This study was approved by the Research Ethics Board at the University of Western Ontario.

2.2.2 Auditory Stimuli

2.2.2.1 General auditory stimulus characteristics

Auditory rhythms for all experimental conditions were created by alternating narrow-band noise tones and silence. Narrow-band tones were used instead of pure tones to maximize the neural response to the stimuli (Rauschecker, Tian, & Hauser, 1995; Shahin, Roberts, Miller, McDonald, & Alain, 2007; Shahin, Roberts, Pantev, Trainor, & Ross, 2005). The narrow-band tones consisted of 30 sine-wave components sampled from a uniform distribution over a 500 Hz range, centred on 750 Hz. The phase of each sine-wave component, relative to the onset of the tone, was randomized, and the amplitude of each component decreased linearly with increasing distance to the centre frequency, such that components farthest from the centre frequency had the smallest amplitude. All tones were normalized with respect to peak amplitude and used linear onset/offset ramps. Manipulations of beat strength, tone duration, and onset/offset ramp duration were made by altering the timing, duration, or onset/offset ramp durations, respectively, of the tones in each rhythm as described in the following sections and are summarized in tables 1-3.

2.2.2.2 Experiment 1 – Beat Strength

Rhythms in Experiment 1 were created using narrow-band tones of 112.5 ms in duration with 10 ms linear onset/offset ramps. To examine the effect of beat strength on entrainment, three categories of rhythm were created: strong beat, weak beat, and non-beat. There were 5 unique rhythms in each beat strength condition for a total of 15 unique rhythms.

Rhythms in the strong beat condition were composed of four inter-onset intervals (IOIs): 250, 500, 750, and 1000 ms (Figure 1a). Thus, the duration of the silent period after each tone was the IOI minus the tone duration (112.5, 387.5, 637.5, or 887.5 ms, respectively). The IOIs of the strong beat rhythms were grouped into patterns designed to induce a beat percept (Grahn & Brett, 2007; Povel & Essens, 1985), in which a tone occurred in the "beat position" every 1000 ms. This gave the rhythms beat frequencies at 1 Hz (1000 ms), and at the harmonic of 2 Hz (500 ms), and potentially also at the minimum IOI frequency of 4 Hz (250 ms), although the latter is faster than the typical beat range (Demany & Semal, 2002; Drake & Botte, 1993; Martens, 2011; Repp, 2005).

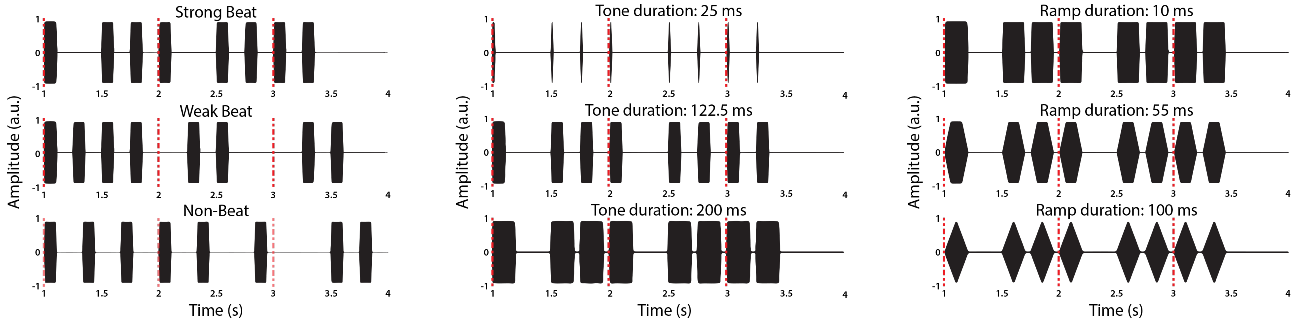

Figure 1: Waveforms of stimulus excerpts or Experiment 1(*left*), Experiment 2 (*middle*), and Experiment 3 (*right*). Black bars indicate the amplitude and duration of tones. Red, dashed lines indicate perceived beat location

For the weak beat condition, the order of the intervals in each of the 5 unique rhythms in the strong beat condition was pseudo-randomly permuted such that tones occurred on less than one-third of the "beat positions" defined in the strong beat condition (Figure 1). Fewer tones in beat positions reduces the amount of evidence for a steady beat, which weakened the strength of the beat percept in these rhythms (Shmulevich & Povel, 2000). Therefore, the rhythms were constrained such that no more than three consecutive beat positions could have tones. Lastly, to further prevent inducing a beat percept, consecutive repetition of any given measure (i.e., the sequence of IOIs between two consecutive beat positions) was not allowed.

For the non-beat condition, the order of intervals of each of the 5 strong beat rhythms was again permuted, but, unlike the weak beat condition, a tone still occurred every 1000ms. To prevent the perception of a beat, however, tone onsets were then jittered in duration so that the intervals of the non-beat rhythms were no longer integer multiples of the minimum IOI (Figure 1a). To jitter tone onsets in the non-beat rhythms, the silent period of all intervals was randomly adjusted such that 250 ms intervals either remained un-jittered (250 ms) or were made 33% longer (332.5 ms), 500 ms and 750 ms intervals remained un-jittered, were made 33% shorter (335.0 ms and 502.5 ms, respectively), or were made 33% longer (665.0 ms and 997.5 ms, respectively), and 1000 ms intervals either remained un-jittered or were made 33% shorter (670.0 ms). After jittering the intervals in the non-beat rhythms, the overall length of rhythms in each condition was checked to ensure that the length of rhythms in the non-beat condition did not differ significantly from the length of rhythms in the other two conditions.

Regardless of beat condition, rhythms all began with the same one-second sequence (an interval of 750 ms followed by an interval of 250 ms). The resulting transient stimulus onset response was later removed from the analysis (Nozaradan et al., 2012a). In each condition, this initial sequence was followed by 3 repetitions of one of the five unique 6-

second rhythms. Therefore, only data from the last 18 seconds of each trial were analyzed.

2.2.2.3 Experiment 2 – Tone Duration

Rhythms in Experiment 2 were composed of narrow-band tones with 10 ms linear onset/offset ramps and using the same patterns of IOIs as in the strong beat condition of Experiment 1. No weak or non-beat rhythms were used. To assess the effect of tone duration on behavioural rhythm percept, as well as on the resulting EEG response, rhythms with three tone durations were created: short tones (25 ms), medium tones (112.5 ms), or long tones (200 ms). Even though tone length differed, the IOIs remained the same as in the strong beat condition of Experiment 1, with all IOIs being integer multiples of 250 ms (Figure 1).

2.2.2.4 Experiment 3 – Ramp Duration

Rhythms in Experiment 3 were composed of narrow-band 200-ms tones (the same as the longest tone condition of Experiment 2) and using the same patterns of IOIs as in the strong beat condition of Experiment 1. No weak or non-beat rhythms were used. To assess the effect of tone duration on behavioural rhythm percept, as well as on the resulting EEG response, rhythms with three onset and offset ramp durations were created: fast (10 ms), medium (55 ms), or slow (100 ms) rise/fall times (Figure 1).

Table 1: Stimulus characteristics for Beat Strength manipulation (Exp. 1)

Condition	Beat Strength	Tone Duration (ms)	Onset/Offset Ramp (ms)
Beat 1^{t}	Strong	112.5	10
Beat 2	Weak	112.5	10
Beat 3	Non-beat	112.5	10

Note: Super-script label "t" indicates the condition was also used in Exp. 2.

Table 2: Stimulus characteristics for Tone Duration manipulation (Exp. 2)

Condition	Beat Strength	Tone Duration (ms)	Onset/Offset Ramp (ms)
Tone 1	Strong	25	10
Tone 2^{b}	Strong	112.5	10
Tone 3^{r}	Strong	200	10

Note: Super-script labels "b" and "r" indicates those conditions were also used in Exp. 1 and Exp. 3 respectively.

Table 3: Stimulus characteristics for Onset/Offset Ramp manipulation (Exp. 3)

Condition	Beat Strength	Tone Duration (ms)	Onset/Offset Ramp (ms)
Ramp1^{t}	Strong	200	10
Ramp 2	Strong	200	55
Ramp 3	Strong	200	100

Note: Super-script label "t" indicates the condition was also used in Exp. 2.

2.2.2.5 Target tones

To ensure attention to the stimuli, in one third of the trials, one of the stimulus tones was replaced by a target tone. Participants were instructed to make no response when they heard a target tone but were asked at the end of each trial whether a target was present or not. Target tones were identical to the standard tones in that trial apart from being wider in bandwidth (750 Hz). Although, the bandwidth expansion did not technically "whiten" the composition of the target tones, some participants described the targets tones as sounding more like white noise than the standard stimulus tones.

2.2.3 Procedure and Tasks

The testing session had three parts. Participants first gave informed consent and completed the demographic questionnaire, then they completed the EEG portion of the testing session in which data for all three experiments were collected, before completing the Beat Alignment Test (BAT) from the Goldsmiths Music Sophistication Index (Müllensiefen, Gingras, Musil, & Stewart, 2014) as an independent measure of beat perception skill. During EEG recording, participants were seated in a sound attenuated chamber, in front of a computer screen. The participants were instructed to avoid moving, and to focus on a fixation point on the screen during recording. A method of limits approach was used to determine individual hearing threshold (Leek, 2001) prior to the EEG experiment. During EEG, the auditory stimuli were presented 50 dB above the individual hearing threshold over headphones.

During EEG recording participants performed two tasks. The first was a beat strength ratings task, in which the participant rated how strong the beat was in each rhythm. Participants responded on a scale from 1 (*very weak beat*) to 9 (*very strong beat*) at the end of each trial. After making the rating, participants then indicated whether the rhythm had contained a target tone by pressing either the “y” or “n” key on a computer keyboard.

Participants completed a block of practice trials to ensure they were familiar with the behavioural tasks before beginning the experimental blocks. The training rhythms differed in beat strength, tone duration, and onset/offset ramp duration like in the experimental blocks, but the patterns of IOIs (i.e., unique rhythms) used in training were not used in the experiment.

To avoid fatigue and maintain focus during the EEG portion of the testing session, the EEG portion was divided into three sections (~ 45 min each). Each section was comprised of seven blocks (~ 6 min per block) with a break between each block. Each block consisted of 15 trials (three repetitions of each of the five unique rhythms) from a single experimental condition (e.g., 15 trials of non-beat rhythms or 15 trials of tones with 100 ms onset/offset ramp duration). Trials consisted of hearing a single 19.2 s auditory rhythm then making responses to the two behavioural tasks. The program waited for a response before advancing to the next trial. Blocks of trials for all three experiments were collected in each section, thus the designation into Experiment 1, 2, or 3 simply refers to which blocks of trials were selected for analysis. The order of the blocks of conditions was counterbalanced across participants.

After all EEG blocks were completed, participants completed the Beat Alignment Test (BAT) (Müllensiefen et al., 2014)to measure beat perception ability. The BAT takes ~10 minutes and has two components (each ~five minutes): beat production and beat perception. In the beat production task, participants listen to excerpts of music and tap along to the beat using a computer keyboard. In the beat perception task, participants judge whether a repeated tone, superimposed on the music excerpts, occurs on or off the beat of the music.

2.2.4 Behavioural Analyses

2.2.4.1 Ratings task.

Because participants rated each rhythm several times in the experiment, average beat strength ratings for each condition were calculated in two steps. First, the ratings for each individual rhythm were averaged. The averaged ratings from each rhythm were then averaged across beat strength condition (strong, weak, and non-beat). To determine how beat strength, tone duration, and ramp duration affected beat strength ratings, a series of 1x3 ANOVAs were conducted on beat strength ratings. For beat strength, the ratings across strong beat, weak beat, and non-beat conditions were compared. For tone duration, the ratings across 50 ms, 125 ms, and 200 ms tone lengths were compared. For ramp duration, the ratings across 10 ms, 55 ms, 110 ms ramp durations were compared.

2.2.4.2 Beat Alignment Test

2.2.4.2.1 Beat production task

Coefficient of Variation (CoV) and tapping asynchrony were calculated to determine how consistently and how accurately, respectively, participants tapped to the beat of the musical excerpts in the beat production task. Single trial CoV scores were calculated as the quotient of the standard deviation of the inter-tap intervals (ITIs) and the average ITI for each trial. The single trial CoV scores were then averaged across trials for each participant to give a single score of how consistently each participant tapped overall. Single trial asynchrony scores were calculated as the average of the absolute difference in time between each tap made by a participant and the closest beat in the musical excerpt. To compare asynchrony scores across excerpts with different tempi, this difference value was then divided by the average ITI for the trial (Repp, 2005; Repp & Su, 2013). These single trial values were then averaged across trials for each participant to give a measure of how accurately each participant tapped to the beat overall.

2.2.4.2.2 Beat perception task

Scores for the beat perception task were computed as a proportion of the total number of perception trials (n = 17) in which the participant correctly identified whether the superimposed tone was either on the beat or off the beat of the musical excerpt in that trial.

2.2.5 EEG Recording and Analyses

EEG was recorded from 64 Ag-AgCl electrodes mounted in a cap according to the 10-20 system. Signals were recorded continuously with a passband of DC to 400 Hz and digitized at a sampling rate of 1024 Hz. Data were also recorded from both mastoids for re-referencing during offline analyses. Electrode voltage offsets were kept below 25 kΩ to ensure low impedance.

The EEG data were analyzed offline using Fieldtrip software (Oostenveld, Fries, Maris, & Schoffelen, 2011) and custom Matlab (Mathworks, USA) scripts. Preprocessing included re-referencing to an averaged mastoid reference, high-pass filter (.65 Hz, 11792 points, Kaiser window), low-pass filtering (42 Hz, 90 points, Hann window), downsampling to 250Hz, segmenting the recordings into epochs (-1.5 to 19.5 s relative to stimulus onset), and submitting the data to ICA (runica; Delorme, Sejnowski, & Makeig, 2007). Components reflecting artifacts were identified (by visual inspection) and removed in order to avoid rejecting a large number of trials in the signal-range artifact rejection procedure which followed the ICA. Epochs were excluded if the signal range was larger than 120 mV in any of the electrode channels. Only data from this preprocessing pipeline were used in the subsequent analyses.

EEG time courses were averaged across trials to calculate the evoked (i.e., phase-locked) power spectrum (Ding & Simon, 2014). The average time-domain signals from each sensor were zero-padded and multiplied with a Hann window before transformation to the frequency domain using a Fast Fourier Transform (FFT). The resulting frequency resolution was 0.026 Hz. The resultant power spectra were normalized by subtracting, from each frequency bin, the median power of the 16 neighbouring frequency bins (8 on each side, i.e., the median over 0.042 Hz on either side of the centre frequency bin); this normalization was performed separately at each electrode to remove any unrelated, residual, broad-spectrum noise from the neural power to better estimate the entrained response (see Chemin et al., 2014; Nozaradan et al., 2012a).

Three separate 3 x 3 repeated measures ANOVAs were conducted on the spectral power values averaged over frontal central electrodes (AF3, AFz, AF4, F3, F1, Fz, F2, F4, FC1, FCz, FC2, C1, Cz, and C2; see Nozaradan et al, 2012, 2014), with frequency of interest (1, 2, and 4 Hz) and either beat strength (strong, weak, and non-beat), tone duration (50, 125, and 200 ms), or onset/offset ramp duration (10, 55, and 110 ms) as factors. Any significant results of the ANOVAs were followed up with post-hoc tests.

2.3 Results

2.3.1 Experiment 1: Beat Strength

2.3.1.1 Beat Strength Ratings.

To examine the effect of our beat strength manipulation on subjective ratings of beat strength, a 1 x 3 repeated measures ANOVA was conducted on the beat strength ratings with beat strength (strong, weak, and non-beat) as a factor. Ratings differed significantly between beat strength conditions, $F(1.78, 62.13) = 20.77$, $p < .001$, $\eta^2 = .37$ (Figure 2). Follow-up paired-samples t-tests revealed significantly higher beat strength ratings in the strong beat condition ($M = 6.52$, $SE = 0.21$) than in the weak beat ($M = 5.74$, $SE = 0.25$), $t(70) = 5.46$, $p <.001$, and non-beat conditions ($M = 5.95$, $SE = 0.24$), $t(70) = 4.53$, $p < .001$. Weak and non-beat conditions did not significantly differ, ($t(70) = 1.99$, $p = .055$).

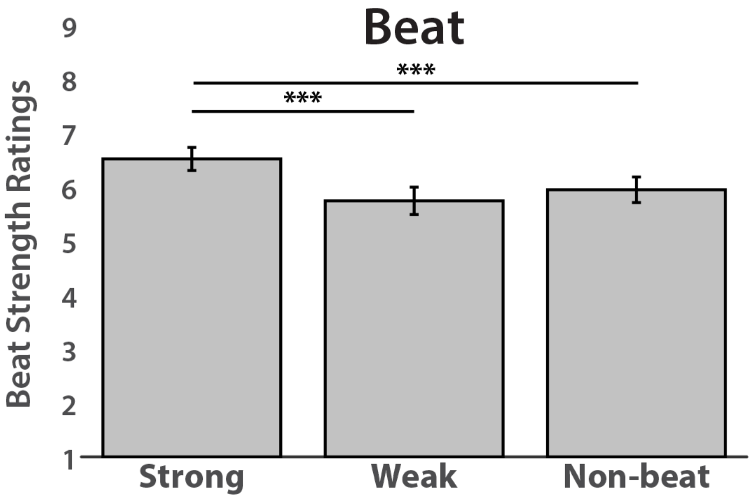

Figure 2: Beat strength ratings for beat condition; Error bars indicate +/- 1 within-subjects SEM; * indicates *p* < .001**

2.3.1.2 EEG Power.

A 3 x 3 repeated measures ANOVA on spectral power, with beat strength (strong, weak, and non-beat) and frequency (1 Hz, 2 Hz, and 4 Hz) as factors revealed significant main effects of beat strength, $F(2,68) = 3.94$, $p = .024$, $\eta^2 = .10$, and frequency, $F(2,68) = 44.77$, $p < .001$, $\eta^2 = .55$, on spectral power. The ANOVA also revealed a significant interaction, $F(4,136) = 3.31$, $p = .013$, $\eta^2 = .09$, indicating that the effect of beat strength differed for 1 Hz, 2 Hz, and 4 Hz power. To examine the simple main effects of beat strength at each frequency, one-way, repeated measures ANOVA were conducted, revealing a simple main effect of beat strength on spectral power at 2 Hz, $F(2, 70) = 5.01$, $p = .009$, $\eta^2 = .125$, but not at 1, $F(1.57, 55.07) = 0.72$, $p = .459$, or 4 Hz, $F(2, 70) = 0.30$, $p = .295$, as shown in Figure 3. In parallel with the ratings of beat strength, pair-wise comparisons of spectral power at 2 Hz revealed that strong beat rhythms had significantly greater spectral power than both the weak beat, $t(70) = 2.73$, $p = .010$, and non-beat rhythms, $t(70) = 2.42$, $p = .020$, which did not significantly differ from each other, $t(70) = 0.51$, $p = .614$.

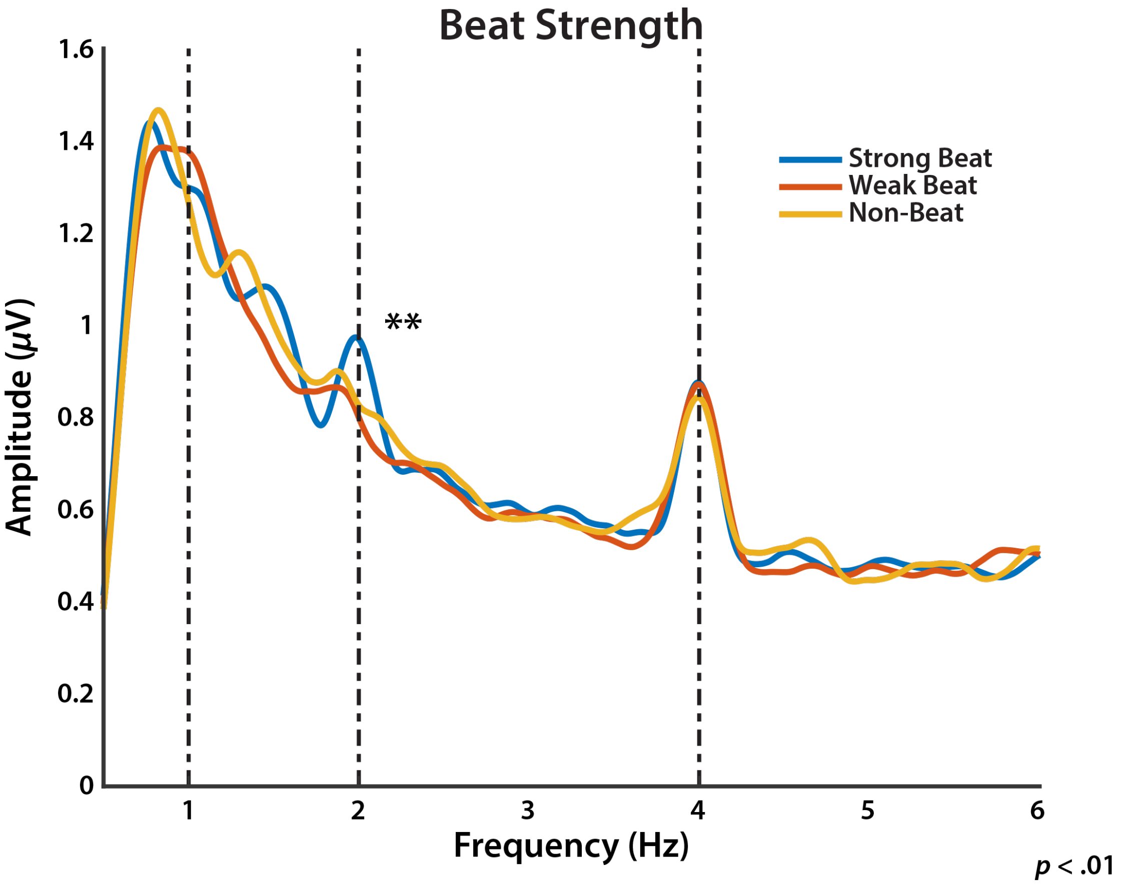

Figure 3: EEG amplitude for participants listening to strong (*blue*), weak (*red*), and non-beat (*yellow*) rhythms; Dashed lines indicate beat-related frequencies; ** indicates significant simple effect of beat strength at 2 Hz, $p < .01$

2.3.2 Experiment 2: Tone Duration

2.3.2.1 Beat Strength Ratings

To examine the effect of tone duration on ratings of beat strength, a 1 x 3 repeated measures ANOVA was conducted on the beat strength ratings with tone length (25, 112.5, and 200 ms) as a factor. Subjective beat strength ratings did not differ significantly between tone duration conditions, $F(1.27, 44.34) = 0.02$, $p = .992$, $\eta^2 < .01$ (Figure 4). Thus, the length of tone used in the rhythm did not affect perceived beat strength.

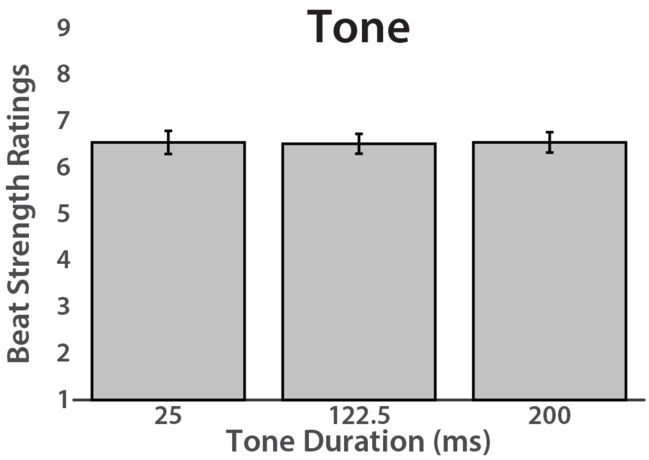

Figure 4: Beat strength ratings did not differ between tone duration conditions; Error bars indicate +/- 1 within-subjects SEM.

2.3.2.2 EEG Power

A 3 x 3 repeated measures ANOVA on spectral power, with tone duration (25, 112.5, and 200 ms) and frequency (1 Hz, 2 Hz, and 4 Hz) as factors revealed significant main effects of beat strength, $F(2,68) = 8.11$, $p = .001$, $\eta^2 = .19$, and frequency, $F(2,68) = 60.27$, $p < .001$, $\eta^2 = .64$, on spectral power. The effect of tone duration differed at 1 Hz, 2 Hz, and 4 Hz $F(4,136) = 2.85$, $p = .026$, $\eta^2 = .08$. To examine the simple main effects of tone duration at each frequency, 1 x 3 repeated measures ANOVAs were conducted on spectral power at 1 Hz, 2 Hz, and 4 Hz respectively, revealing a main effect of tone duration on neural spectral power at 1 Hz, $F(2, 70) = 5.86$, $p = .004$, $\eta^2 = .14$, and 2 Hz, $F(1.67, 58.58) = 5.36$, $p = .011$, $\eta^2 = .13$, but not 4 Hz, $F(2, 70) = 2.41$, $p = .097$. At 1 Hz, power was significantly greater for rhythms with 200 ms than 25 ms tones, $t(70) = 4.05$, $p < .001$. At 2 Hz, entrainment was significantly greater for rhythms with 112.5 ms than 25 ms, $t(70) = 2.79$, $p = .009$, and 200 ms tones, $t(70) = 2.29$, $p = .029$. No other pair-wise comparisons were significant.

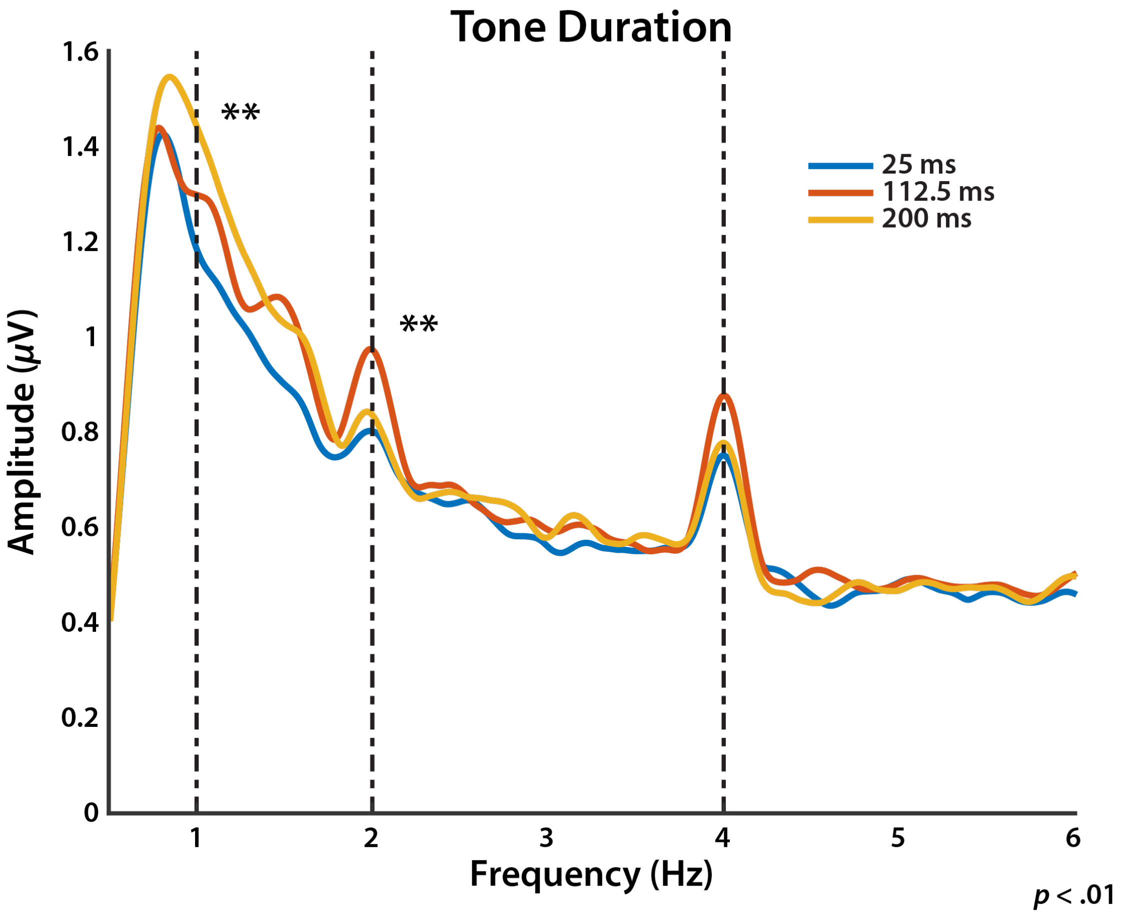

Figure 5: EEG amplitude for participants listening to strong beat rhythms with short (blue), medium (red), and long (yellow) tone durations; Dashed lines indicate beat-related frequencies; ** indicates significant differences in amplitude at 1 Hz and 2 Hz, $p < .01$

2.3.3 Experiment 3: Ramp Duration

2.3.3.1 Beat Strength Ratings

To examine the effect of onset/offset ramp duration on ratings of beat strength, a 1 x 3 repeated measures ANOVA was conducted on the beat strength ratings with onset/offset ramp duration (10, 55, and 100 ms) as a factor. Beat strength ratings did not differ significantly between onset/offset ramp duration conditions, $F(1.63, 57.10) = 2.26$, $p = .111$, $\eta^2 = .06$. Thus, onset/offset ramp did not affect perceived beat strength.

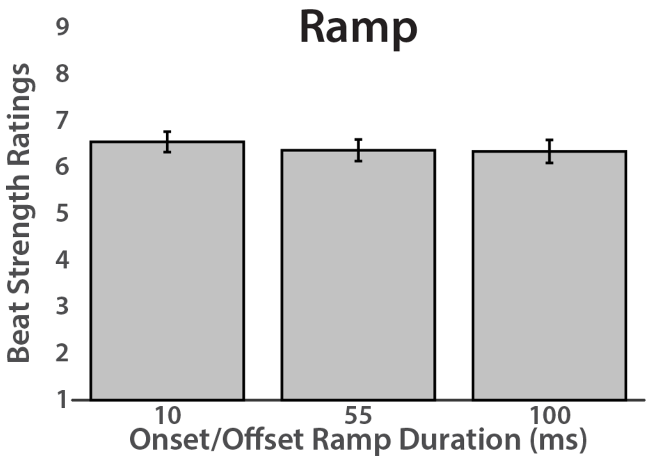

Figure 6: Beat strength ratings did not differ across ramp duration conditions; Error bars indicate +/- 1 within-subjects SEM.

2.3.3.2 EEG Power

A 3 x 3 repeated measures ANOVA on spectral power, with onset/offset ramp duration (10, 55, and 100 ms) and frequency (1 Hz, 2 Hz, and 4 Hz) as factors revealed only a significant main effect of frequency, $F(2,68) = 72.71$, $p < .001$, $\eta^2 = .68$, on spectral power. No other main effects or interactions were significant.

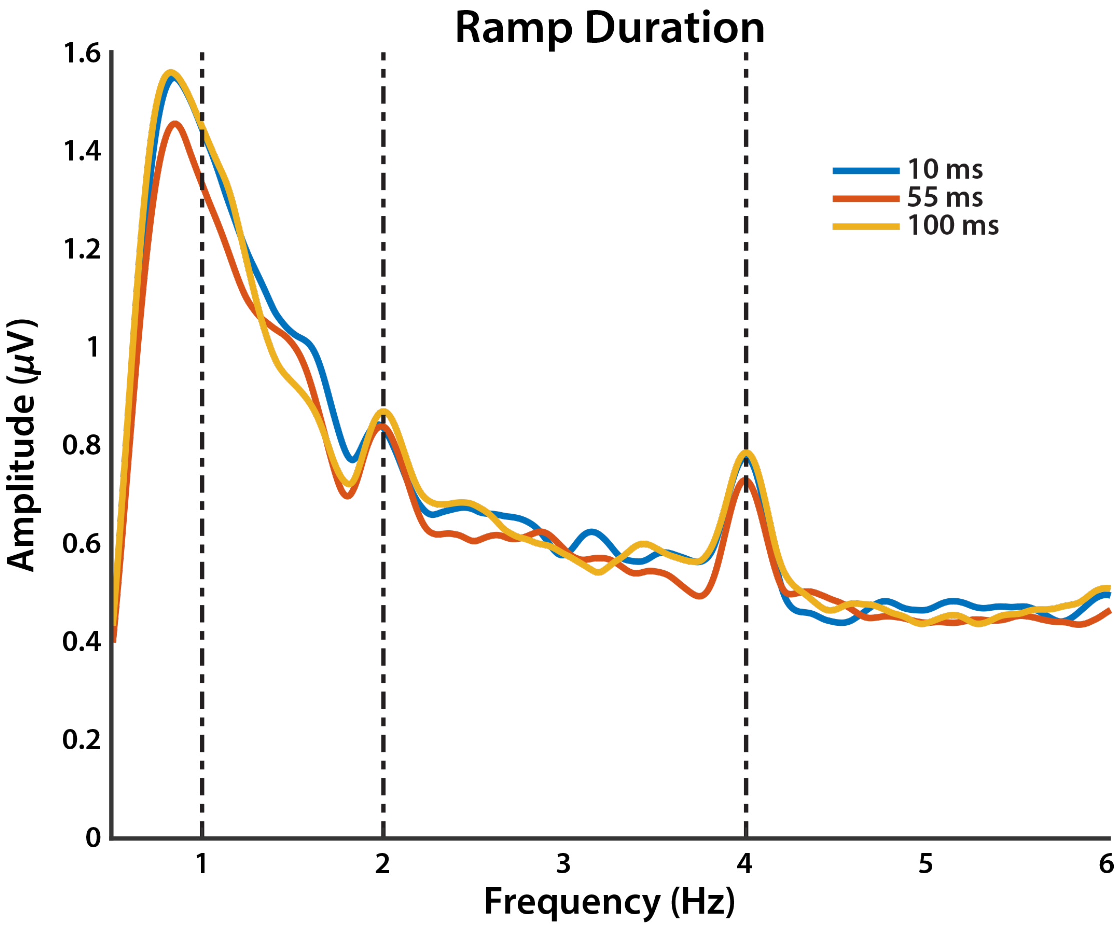

Figure 7: EEG amplitude for participants listening to strong beat rhythms with short (blue), medium (red), and long (yellow) onset/offset ramp durations; Dashed lines indicate beat-related frequencies.

2.3.4 Correlations and regressions of neural and behavioural measures of entrainment

2.3.4.1 Beat strength and Stimulus power

To examine how power at beat frequencies in the EEG data are related to both the stimulus-driven and entrained responses, we ran multiple linear regression analyses for each frequency of interest. For each participant we ran a multiple linear regression with EEG power at each beat frequency (separately for 1 Hz, 2 Hz, and 4 Hz) as the criterion variable, and beat strength ratings and stimulus power as predictors. EEG power at each frequency of interest and beat strength ratings were averaged across trials of each unique rhythm (45 presentations of each rhythm) to give a single value for each rhythm in each condition. Stimulus power was computed by transforming the stimulus amplitude envelope of each rhythm (obtained via Hilbert Transform implemented in MatLab) to the frequency domain using an FFT. The values EEG power, beat rating, and stimulus power were then transformed to z-scores to normalize the distribution of scores within each variable. A multiple linear regression using the z-scores of each variable was performed separately for each participant at each frequency of interest. The distributions of beta weights for each predictor and the interaction term across participants was tested against zero using a Wilcoxon signed rank test. The results of this analysis showed that power in the EEG at 1 Hz was predicted by stimulus power at 1 Hz (*Z*(35) = 2.53, *W*(35) = 494, *p* = .011) as shown in Figure 8. All other tests were non-significant.

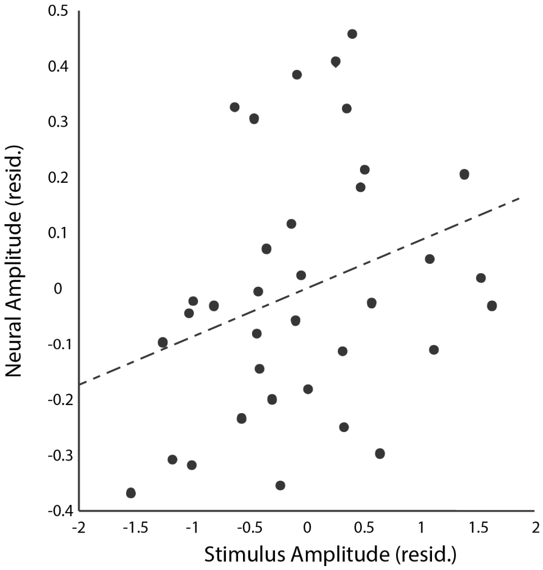

Figure 8: Residual variability of neural entrainment at 1 Hz and stimulus power at 1 Hz, after variability accounted for by beat strength ratings has been removed,

showing that more power in the stimulus envelope at 1 Hz predicts more power in the neural signal at 1 Hz also.

2.3.4.2 BAT performance

To investigate whether overall beat perception ability is predictive of power at beat frequencies in the EEG, we ran a multiple linear regression with EEG power as the criterion variable, and performance on the perception and production tasks (i.e., proportion of correct trials, and tapping asynchrony and CoV, respectively) of the BAT test as predictors. EEG power for 1 Hz, 2 Hz, and 4 Hz was calculated by averaging spectral power at each frequency across trials and then across strong beat conditions. As before, all values were z-scored to normalize the distribution of the variables before being submitted to the regression. None of the models obtained for EEG power at 1hz ($R^2 = .13$, $F(7, 28) = 0.58$, $p = .768$), 2Hz ($R^2 = .13$, $F(7, 28) = .58$, $p = .762$), or 4 Hz ($R^2 = .02$, $F(7, 28) = 0.09$, $p = .998$), were significant, nor were any of the partial correlations of the predictors or the interactions (*ps* > .132). These findings suggest that performance on the BAT test is not predictive of neural entrainment.

2.3.4.3 Musical experience

To further explore how prior musical experience relates to entrainment a multiple linear regression analysis was run with neural spectral power as the criterion variable and years of experience as the predictor variable. The steps for calculating spectral power in the EEG were the same as described in the BAT performance regression analysis. Again, none of the models for 1 Hz ($R^2 = .03$, $F(3, 32) = 0.36$, $p = .780$), 2 Hz ($R^2 = .05$, $F(3, 32) = 0.56$, $p = .643$), or 4 Hz ($R^2 = .14$, $F(3, 32) = 1.78$, $p = .171$) were significant. These findings suggest that musical experience was not related to neural entrainment to the rhythms in the current study.

2.4 Discussion

2.4.1 Comparisons of spectral power

2.4.1.1 Ratings of beat strength relate to spectral power at the beat frequency

Participants' behavioural beat strength ratings were higher for strong beat rhythms than weak or non-beat rhythms, meaning that the beat strength manipulation was successful. Moreover, spectral power at 2 Hz in the EEG signal was highest in the strong beat rhythms and lowest in the non-beat rhythms, indicating that stimuli that induced a beat also had greater neural power than stimuli that did not induce a beat. The finding of greater neural power for strong beat rhythms is consistent with previous work that suggests spectral power in the EEG signal reflects neural entrainment and may be a neural correlate of beat perception (Lenc et al., 2018a; Nozaradan et al., 2017, 2012a; Nozaradan, Schönwiesner, Caron-Desrochers, & Lehmann, 2016). However, these results should be interpreted with caution because stimulus power at 2 Hz was also higher in the strong beat condition than in the weak-beat and non-beat conditions (Figure 9). Thus, the differences in neural power at 2 Hz may have merely reflected stimulus differences, not entrained differences. A linear regression analysis (discussed below) was therefore conducted to determine the relationship between beat strength ratings and neural power when accounting for spectral differences between stimuli.

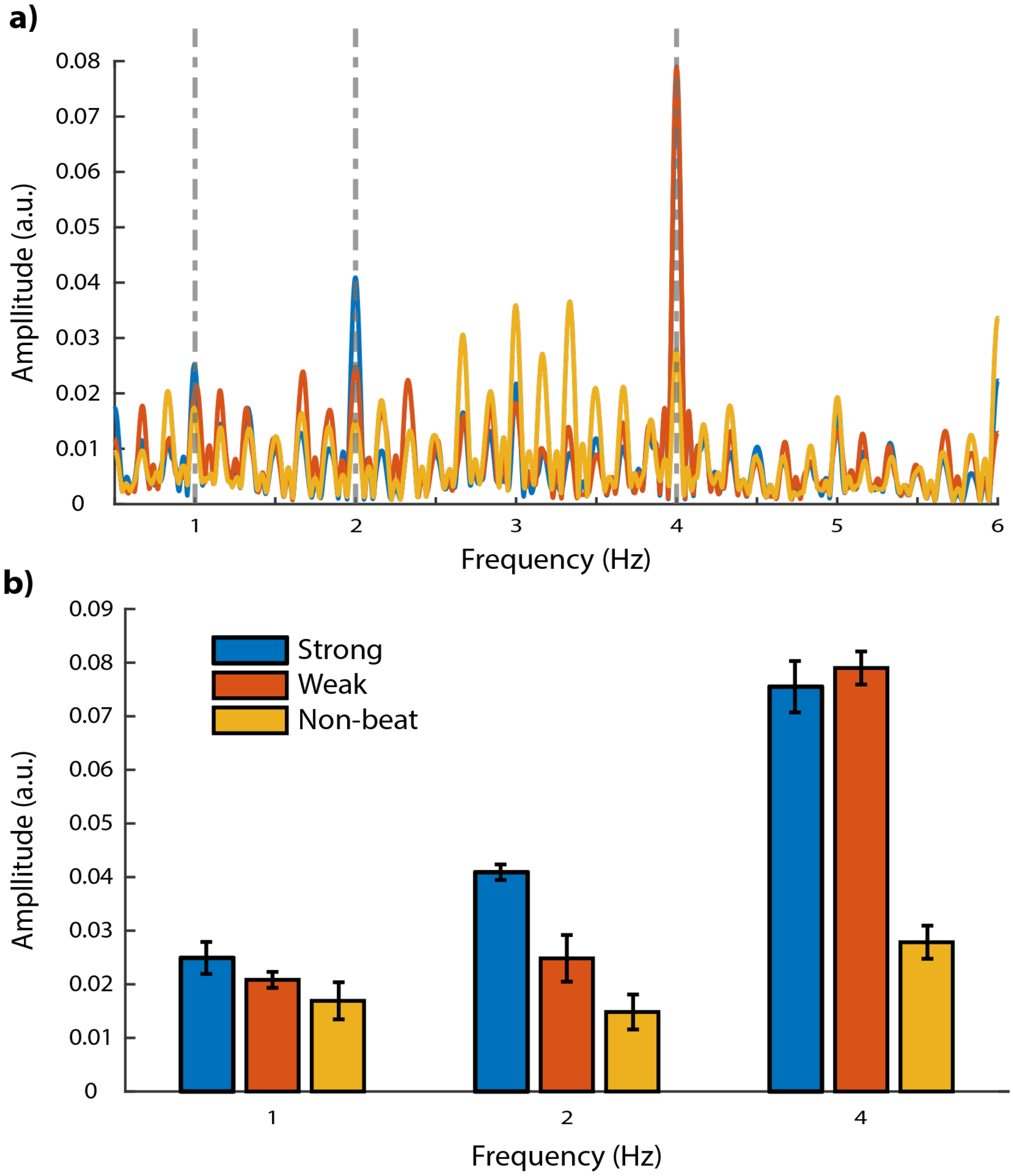

Figure 9: Amplitude spectrum of the stimulus envelope averaged across rhythms in the strong, weak, and non-beat condition (a). Amplitude of stimulus envelope at beat-related frequencies (b). Clusters of bars in (b) correspond to amplitudes at grey dashed lines in (a). Error bars indicate standard deviation of amplitude.

Although the observation of greater power at 2 Hz while listening to strong beat rhythms may support the current hypothesis about the relationship between neural entrainment and beat perception, one might also have predicted differences at the primary beat frequency of 1 Hz, which were absent (Figure 3). One explanation for this is that in the context of rhythm, regularities at multiple rates are perceived simultaneously – referred to as the metrical hierarchy (Essens & Povel, 1985; Parncutt, 1994; van Noorden & Moelants, 1999). One of the levels of the metrical hierarchy is perceived as the beat, but regularities are also perceived at other levels (e.g., twice as fast, or twice as slow). Therefore, while one person might feel the beat at a particular metrical level or rate, someone else might feel the beat of the same rhythm at twice the rate of the first person. Previous studies have shown that people are most sensitive to the beat at a rate of approximately 2 Hz (~ 500 ms) (van Noorden & Moelants, 1999). So, although our primary beat rate of 1 Hz (1000 ms) is within the normal range of 350 to 1500 ms in which people can perceive beat (Repp, 2005a; van Noorden & Moelants, 1999), participants may have entrained to a faster subdivision of the intended beat rate, hence the differences in spectral power occurring only at the faster, 2 Hz, beat rate.

2.4.1.2 Tone duration affects spectral power at the beat frequency.

Tone duration significantly affected spectral power across beat frequencies. Specifically, at 1 Hz, rhythms with long tones (200 ms) had significantly greater power than rhythms with short tones (25 ms). In contrast, at 2 Hz, rhythms with medium length tones (112.5 ms) had significantly greater spectral power than rhythms with either long or short tones. From the beat strength ratings, it is clear that beat strength did not significantly differ between the different tone length conditions (Figure 4), suggesting that spectral power differences between tone duration conditions are driven by the acoustic stimulus characteristics, independent of beat percept.

Although this is the first study to specifically investigate the effect that altering tone duration had on power at beat frequencies in the neural spectrum, the idea that the stimulus-driven response may be represented at beat frequencies in the neural spectrum is not new. Indeed, previous studies have attempted to account for the stimulus-driven response by subtracting power in the stimulus envelope from the neural power spectrum (Lenc et al., 2018a; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2012a, 2018). However, this subtraction relies on the assumption that that power differences in the neural response mirror power differences in the stimulus envelope unless beat perception, and thus the entrained response, is enhancing a beat-related frequency in the neural spectrum only. Here, beat perception was similar across the different tone duration conditions, so any beat perception-related enhancements should also be similar across all tone duration conditions, and thus enhancement at each beat-related frequency, relative to the stimulus spectrum, should be similar for each tone duration condition. Therefore, if beat strength, and thus beat-related enhancement, is the same across conditions, and power differences in the neural spectrum simply reflect power differences in the stimulus spectrum plus enhancement due to beat perception, which subtracting stimulus power from neural power implies, neural power at beat-related frequencies should be highest for conditions with the most stimulus power at beat-related frequencies. However, neural power at beat-related frequencies did not mirror stimulus power, nor did it appear to be simply an enhancement of the stimulus power at a particular frequency. For example, neural power was greater at 2 Hz for medium duration tone rhythms than for long tone rhythms (Figure 5), even though power in the stimulus envelope was greater at 2 Hz for long tones than medium tones (Figure 10), and beat percept was the same between the two conditions. These findings suggest that differences in neural power observed here are not just driven by differences in the stimulus power. Thus, simply subtracting the stimulus power at certain frequencies from neural power at those same frequencies, either by z score or other method (Nozaradan, Mouraux, et al., 2016; Nozaradan et al., 2012a) does not appropriately account for the stimulus-driven response. These findings further support recent literature that cautions against comparing the neural spectra to sound envelope spectra in general (Henry et al., 2017; Rajendran & Schnupp, 2019).

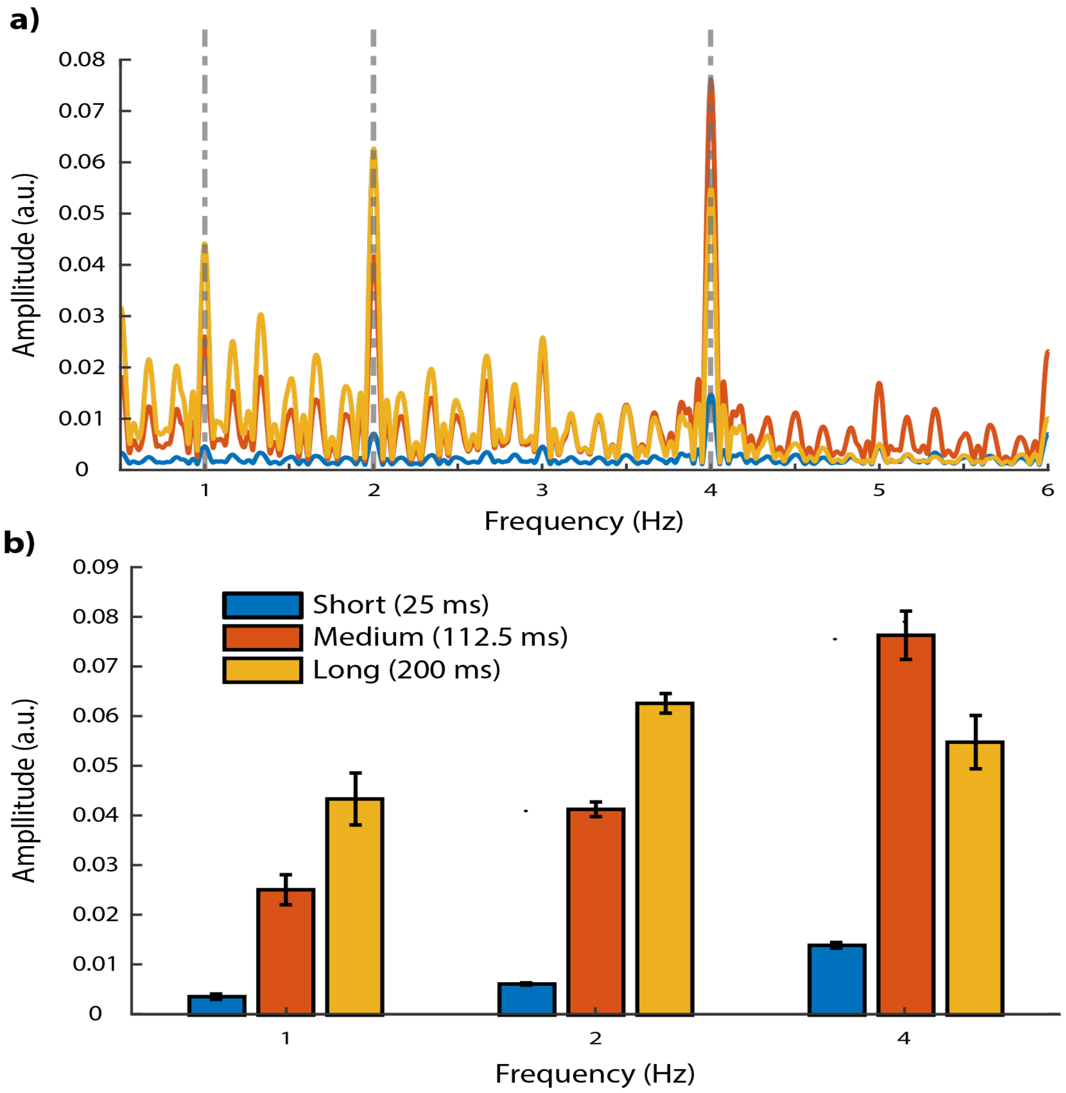

Figure 10: Amplitude spectrum of the stimulus envelope averaged across rhythms in the strong, weak, and non-beat condition (a). Amplitude of stimulus envelope at beat-related frequencies (b). Clusters of bars in (b) correspond to amplitudes at grey dashed lines in (a). Error bars indicate standard deviation of amplitude.

2.4.1.3 Onset/offset ramp duration does not affect spectral power.

Power at beat frequencies was not significantly affected by onset/offset ramp duration. It may be that ERPs to each tone differed based on ramp duration (Onishi & Davis, 1968), but that these ERP differences are not reflected in spectral power measures. Indeed, previous work has shown that onset ramp duration affects ERP latency, which does not affect spectral power, more than ERP amplitude or variability (Onishi & Davis, 1968), which do affect spectral power . Thus, spectral power at beat related frequencies in the neural spectrum would be unaffected by a latency shift in the evoked response provided that ramp duration was consistent within a rhythm.

However, changes in ERP latency and amplitude may have been reflected in spectral power at different frequencies than were tested in this study. Although ramp duration affects ERP latency more than ERP amplitude, longer onset ramps evoke a smaller amplitude difference between the N1 and P2 peaks of the ERP (Onishi & Davis, 1968). Thus, ramp-related amplitude differences in the ERP might be reflected in the neural spectra at frequencies related to the peak-to-peak timing (i.e., approx. 100 ms or 10 Hz), rather than slower, beat-related frequencies. If ramp duration does affect frequencies other than the ones tested here, it would explain why spectral power did not differ across ramp duration conditions in this study, despite evidence that ramp duration affects the evoked neural response. Finally, it is still unknown how ramp duration affects entrainment when multiple ramp durations occur within a rhythm, like rhythms we encounter in real music.

2.4.1.4 2.4.1.4 – Summary of Comparisons of Spectral Power

These analyses demonstrate that neural spectral power depends on both beat strength and acoustic stimulus characteristics. Critically, even though certain acoustic characteristics of the stimulus (e.g., tone duration, but not ramp duration) affect neural spectral power, they do *not* affect beat strength perception. Thus, observable changes in EEG power are not necessarily caused by changes in beat perception. These findings not only support previous studies calling for caution when interpreting differences in neural power for brain-to-stimulus comparisons (Henry et al., 2017; Novembre & Iannetti, 2018; Rajendran & Schnupp, 2019), but also provide evidence that the same caution is necessary when interpreting differences in neural power for brain-to-brain comparisons when stimulus power differs between rhythmic or beat strength conditions, as it did in the current study and many others (Chemin et al., 2014; Cirelli et al., 2016; Lenc et al., 2018a; Nozaradan et al., 2012a).

Furthermore, these findings demonstrate the need to consider the stimulus-driven response when trying to aggregate findings across studies. Beat perception has been studied using stimuli that range from sine-tones with filled and open intervals (Grahn & Brett, 2007, 2009; Grahn, Henry, & McAuley, 2011; Grahn & McAuley, 2009) to more naturalistic drum or woodblock sounds (Chen, Penhune, & Zatorre, 2008; Ladinig et al., 2009; Manning & Schutz, 2013; Winkler et al., 2009), and real musical stimuli (Iversen & Patel, 2008; Müllensiefen et al., 2014). Traditionally, comparing findings across studies did not pose a problem, because behavioural measures of beat perception are not significantly affected by most of these acoustic differences (Henry et al., 2017). However, when using neural measures, such as ERPs and spectral power, to investigate beat perception, it is important to account for stimulus differences, which affect the stimulus-driven response. Failure to do so results in inconsistency (e.g., studies using long duration tones may find effects of beat strength on entrainment at 1 Hz, whereas studies using medium duration tones may find the same effects at 2 Hz) when trying to aggregate findings across studies that use different stimuli.

2.4.2 Linear Regression Analyses

To better examine the relationship between neural spectral power and beat strength ratings, while accounting for differences in stimulus power, we conducted a series of linear regression analyses in which we generated the power spectrum for each of the 35 stimuli (five unique rhythms for each of the seven beat/tone/ramp combinations for a total of 35 individual stimulus spectra). This analysis accounts for the specific spectral power pattern on a stimulus by stimulus basis, rather than averaging power across stimuli within each condition as was done in the ANOVA (reported previously).

2.4.2.1 Stimulus power does not predict neural spectral power

Previous studies using isochronous stimuli to investigate entrainment, in general, find a strong relationship between the stimulus frequency and EEG power in the neural response (Henry et al., 2014; Nozaradan et al., 2011; Schroeder & Lakatos, 2009). However, in studies that use more complex, non-isochronous, rhythms, the relationship between stimulus power and neural power is less clear. The current results suggest that the degree of power in a complex stimulus may not reliably predict the degree of power in the neural spectrum. Previous studies which have used complex rhythmic stimuli have tended to focus their analysis on whether power at particular frequencies in the neural spectrum is enhanced (i.e., higher) relative to those frequencies in the stimulus spectrum (Lenc et al., 2018a; Nozaradan et al., 2012a, 2018; Nozaradan, Schönwiesner, et al., 2016), so the question of whether power in the stimulus spectrum predicts power in the neural spectrum has not been systematically explored. However, these results show that, when we do examine this question more systematically, there is not a clear, linear relationship between power in the stimulus and power in the neural spectrum. Even though the relationship exists at one beat-related frequency (1 Hz; see Figure 8), it does not at the other two frequencies (2 Hz and 4 Hz) where we would have also expected to find it. Thus, there is no clear "one-to-one" relationship between the stimulus envelope and neural power, and it remains to be seen how exactly the stimulus spectrum relates to power observed by EEG. Potentially, using cochlear models, or other models of transformation by the auditory system (Ghitza, 2011; Mesgarani, David, Fritz, & Shamma, 2009; Pasley et al., 2012), to predict stimulus-driven responses may improve this relationship, however, these techniques are currently more commonly applied to speech envelope tracking. Therefore, more research needs to be done to characterize the contribution of the stimulus-driven response to the neural power spectrum as rhythmic stimuli move beyond isochrony to more complex stimulus sequences.

2.4.2.2 Beat strength ratings do not predict neural spectral power

Curiously, when accounting for stimulus specific differences in power, the results of the regression analysis did not reveal a clear relationship between beat strength ratings and neural power at beat frequencies. Although both beat strength ratings and neural power were higher for strong beat rhythms than for weak or non-beat rhythms in the ANOVAs reported previously, this analysis finds no clear relationship between strength of beat perception and neural spectral power. One explanation is that although neural power differed across the tone duration conditions, beat strength ratings remained consistently high for strong beat rhythms across all tone duration conditions. Thus, even though the predicted relationship appears across different beat strength conditions (Henry et al., 2017), the relationship between beat strength ratings and neural power was altered by the tone duration conditions, in which neural power varied but beat strength ratings remained consistently high. This interaction between the acoustic features of the rhythm and the relationship between neural power and perceived beat strength suggests that interpreting neural power as a proxy measure of beat strength is problematic in some scenarios (Rajendran & Schnupp, 2019). These results again reinforce the importance of considering the stimulus-driven response when trying to interpret power differences in neural power spectra as the relationship between stimulus and beat perception is difficult to characterize.

2.4.2.3 BAT performance

The BAT was included in this study as an independent measure of beat perception ability, and I predicted that performance on the BAT would predict neural entrainment. However, BAT performance did not predict entrainment at any of the tested frequencies. The lack of relationship between BAT performance and entrainment could be because the stimuli used during EEG recording were different from the BAT stimuli. The EEG stimuli were composed of tones, and relied solely on the temporal structure of the rhythms to induce the beat (Grahn & Brett, 2007; Povel & Essens, 1985; Povel & Okkerman, 1981), whereas the BAT stimuli were real musical excerpts, containing many types of beat-inducing accents (e.g., note density, amplitude variations, etc.) in addition to beat-inducing temporal structures. Redundant cues in the music used in the BAT may have provided multiple ways for participants to feel the beat, whereas the rhythms in the EEG portion of the experiment potentially relies more heavily on entrainment to the temporal structure of the rhythm. Therefore, performance on the BAT, in which many cues are present, may be less reflective of entrainment to rhythms in which beat perception arises from the temporal structure of the rhythm alone.

2.4.2.4 Musical Experience

Musical experience was not related to spectral power in the EEG signal at any of the tested frequencies. Previous studies have found that experienced musicians are better at finding, maintaining, and synchronizing with the beat (Cameron, Potter, Wiggins, & Pearce, 2017; Repp, 2010; Repp & Doggett, 2007; Strait, Parbery-Clark, Hittner, & Kraus, 2012). Thus, one might predict that musical training might also be related to neural entrainment. However, we failed to find evidence of a relationship in the current data. Potentially, years of musical experience may not accurately reflect skill level, as there may be some variability in the skill of people who have played for the same length of time. However, years of musical experience highly correlated with self-reported skill level. Moreover, performance on the BAT test, which is related to musical skill (Iversen & Patel, 2008; Müllensiefen et al., 2014) was also unrelated to spectral power. Therefore, it seems unlikely that the lack of relationship between musical experience and spectral power is the result of variability in the skill level of the musical experience measure. Alternatively, perhaps musical experience was not related to neural entrainment because the rhythms were designed to induce beat perception in everyone, regardless of musical training. Previous research has shown that perceiving strong beat rhythms, such as those in the current experiment, induces beat perception in most people, even without special training or practice (Drake, 1998; Grahn & Brett, 2007). Thus, it is possible musical experience was not related to neural entrainment as those without musical training may have felt the beat as well those with musical training.

2.4.3 Conclusions

Taken together, these findings start to bridge the gap between traditional ERP analyses in the psychoacoustic literature, and the time-frequency analyses in the emerging entrainment literature. The current study found that neural responses are affected by both the beat percept and by the acoustic characteristics of the stimuli, which is consistent with both literatures (Large, 2008; Large & Palmer, 2002; Nozaradan, Peretz, Missal, & Mouraux, 2011; Alain, Woods, & Covarrubias, 1997; Hillyard & Picton, 1978; Kushnerenko, Ceponiene, Fellman, Huotilainen, & Winkler, 2001; Muller, 1973; Onishi & Davis, 1968; Picton, Woods, & Proulx, 1978a, 1978b; Schweitzer, 1977). These findings provide evidence that both the stimulus-driven response and the entrained response affect power in neural spectra. Moreover, these data support recent work suggesting that comparisons of neural spectra, to either stimulus spectra or other neural spectra, should be interpreted with caution (Henry et al., 2017; Novembre & Iannetti, 2018; Rajendran & Schnupp, 2019). In particular, tone duration affected neural power at beat-related frequencies, and that 1 Hz stimulus power predicts 1 Hz neural power, underscores the importance of disentangling the perceptual, entrained response from the acoustic, stimulus-driven response when trying to interpret the neural response. Previous studies have attempted to account for stimulus differences by subtracting power of the stimulus envelope from the neural power spectrum (Lenc et al., 2018a; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2012a, 2018). However, as this study has shown, accounting for the stimulus-driven response in complex, non-isochronous rhythms is more complicated than this subtraction accounts for. Failure to separate out the contributions of both the stimulus-driven and entrained responses increases the risk of stimulus differences being misinterpreted as perceptual differences. For example, these data show that significant differences in neural power at beat frequencies may reflect differences in tone duration rather than perceived beat strength. If we are going to understand how entrainment of neural oscillations relates to beat perception, it is important to control other factors that have the potential to affect the neural response.

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Chapter 3

3 Examining the influence of beat context on neural entrainment during a common rhythmic sequence

3.1 Introduction

Entrainment of neural oscillations is important for perception (Henry; Lakatos; Snyder; Schroeder) and has been shown to affect perception of rhythmic stimuli (Lakatos). Moreover, entrainment of neural oscillations has become increasingly popular as a proposed mechanism of beat perception (Cirelli et al., 2014; Fujioka et al., 2015a; Large, 2008; Nozaradan et al., 2011, 2012a). Several studies have demonstrated that strength and/or frequency of entrainment differs depending on the strength and/or frequency of the beat percept (Chemin et al., 2014; Cirelli et al., 2016; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2012a). This has been demonstrated by comparing frequency domain representations of neural or stimulus signals either to each other, or neural signals across different stimulus or listening conditions. More power at frequencies related to the beat, either in one condition compared to another, or in the neural signal compared to the stimulus signal, has been interpreted as greater entrainment.

However, entrainment is not the only factor that can affect power at a particular frequency. Changing either the acoustic or the temporal characteristics of the stimulus affects its spectral characteristics, which in turn affects the neural response. As seen in the previous chapter, changes to the acoustic characteristics of a stimulus (e.g., tone duration, onset/offset ramp duration, etc.) affect the neural signal independent of beat percept. To address this, previous studies have kept acoustic characteristics across stronger and weaker beat rhythm conditions, and shown that neural entrainment at beat frequencies is stronger to rhythms with a stronger beat than a weaker beat (Nozaradan et al., 2017, 2012a). However, the stronger and weaker beat rhythms differed in their temporal patterns, which is potentially problematic because it affects the spectral characteristics of the stimulus (Henry et al., 2017; Nozaradan et al., 2012a). However, it is unclear how these differences in the spectral characteristics are reflected in the neural response. To assess how beat perception relates to entrainment, ideally, we would compare entrainment when acoustic and temporal stimulus features are identical but beat percept differs.

Previous attempts to account for stimulus differences between conditions have involved comparing relative changes in the neural signal with relative changes in the stimulus spectra (Nozaradan, Mouraux, et al., 2016; Nozaradan et al., 2011). Frequency domain transformations are performed on both the stimulus and neural spectra, and power at beat-related frequencies is compared to power at unrelated frequencies in the <u>neural</u> signal, which are then compared to power differences at the same frequencies in the <u>acoustic</u> stimulus. Larger differences in the neural signal relative to the stimulus signal are attributed to entrainment. This calculation assumes, however, that the transformation between stimulus and neural signals is linear. However, the behaviour of resonating oscillators is inherently non-linear (Large, 2008). In other words, the baseline transformation (i.e., unrelated to beat perception) between stimulus and neural signals is not known, so it is difficult to tell how much of the difference between the neural responses in difference beat strength conditions is because of neural entrainment as opposed to stimulus processing. Although there is some work showing that behavioural ratings of beat strength can be altered without affecting the frequency domain representation of a rhythm (Henry et al., 2017), to date, few neuroimaging studies have attempted to disentangle the stimulus driven response from the entrained response (cf. chapter 2).

Additionally, theories of neural entrainment should make predictions about the phase of the entrained neural oscillations relative to the beat (Henry et al., 2014; Large, 2008; Obleser et al., 2017; Schroeder & Lakatos, 2009; ten Oever, Schroeder, Poeppel, van Atteveldt, & Zion-Golumbic, 2014). Specifically, the excitatory phase of the entrained neural oscillations should align with the beat in a musical rhythm. However, previous investigations of entrainment to musical rhythms have not typically reported findings about the phase of the neural oscillation when investigating entrainment. In particular, the power spectrum is calculated over the entire duration of the rhythmic stimulus, using a Fast Fourier Transform (FFT; Chemin, Mouraux, & Nozaradan, 2014; Cirelli, Spinelli, Nozaradan, & Trainor, 2016; Nozaradan, Peretz, & Keller, 2016; Nozaradan et al., 2012). However, information about the temporal dynamics of the neural signal is lost when examining power spectra taken over the entire length of a signal, as is the case with the majority of previous studies.

In this study we have two main goals. First, we aim to dissociate changes in entrainment caused by beat perception differences from changes caused by stimulus differences, and second, we aim to investigate the relationship between beat location and the phase of the entrained oscillations. To accomplish our first goal, we analyzed the neural responses to identical rhythmic sequences that were embedded in sequences with either a strong beat (i.e., the beat was easy to perceive) or a weak beat (i.e., the beat was either difficult or impossible to perceive). Thus, the surrounding rhythmic context induces beat perception differences, but the to-be-analyzed embedded sequence is identical across conditions, meaning that stimulus-driven effects are perfectly controlled between beat conditions. This way, we were able to manipulate the beat strength (and presumably, entrainment strength) while the stimulus driving response to the common sequence is kept constant.

One of the strengths of this manipulation is that it can also provide further evidence that entrainment is related to beat perception by examining how the phase of the underlying neural oscillation is related to the beat. To do this, we embedded the identical rhythm sequences into the strong beat rhythmic context such that the embedded sequence either started on a beat (in-phase), or between beats (anti-phase). We predict that the phase difference of the entrained, beat-frequency oscillation between the in-phase and anti-phase trials will differ by 180° within subjects. If phase differences in entrainment track beat percept, when overall beat strength and stimulus sequence is identical, it provides further evidence that entrainment of neural oscillations relates to beat perception.

3.2 Methods

3.2.1 Participants

Twenty-five participants (M_{age} = 20.33, *SD* = 2.88 years, 16 female) took part in the experiment after providing written consent. Twenty participants reported having previous musical experience (M_{years} = 10.99 years, *SD* = 7.53), of those, 11 reported having more than 10 years of training. This study was approved by the Western Research Ethics Board at the University of Western Ontario. Participants received monetary compensation for their participation in the study.

3.2.2 Stimuli

Rhythms in all conditions were approximately 14 s in length and were created by alternating narrow-band tones and silence. Narrow-band tones were used instead of pure tones to maximize the neural response to the stimuli (Rauschecker et al., 1995; Shahin et al., 2007, 2005). The narrow-band tones were composed of 30 sine-wave components sampled from a uniform distribution with a 500 Hz range centered on 750 Hz and were 100 ms in duration with a 10 ms linear onset/offset ramp. The phase of each sine-wave component, relative to the onset of the tone, was randomized, and the amplitude of the component was scaled linearly based on its inverse distance from the centre frequency; that is, components farthest from the centre frequency had the smallest amplitude.

To examine the effect of beat- and nonbeat-inducing rhythmic context on entrainment to an identical common sequence, three categories of rhythms were created: two categories of rhythm in which a strong beat percept was induced but the position of the common sequence differed relative to the beat percept (in-phase vs. anti-phase), and one category which did not induce a beat percept (non-beat). There were 45 unique rhythms in each rhythm category for a total of 135 unique rhythms in the experiment. For the “in-phase” condition, rhythms were composed of four inter-onset intervals (IOIs): 166.7, 333.3, 500.0, and 666.7 ms. Thus, the duration of the silent period after each tone was the IOI minus the tone duration (66.7, 233.3, 400.0, and 566.7 ms, respectively). These rhythms were designed to induce a strong beat percept (Grahn & Brett, 2007; Povel & Essens, 1985) in which a tone occurred every 666.7 ms (Figure 11a). This gave the rhythms a beat frequency at 1.5 Hz (666.7 ms), and at the harmonic of 3 Hz (333.3 ms), and potentially also at the minimum IOI frequency of 6 Hz (166.7 ms), although the latter is much faster than the typical beat perception range (Demany & Semal, 2002; Drake & Botte, 1993; Martens, 2011; Repp, 2005a).

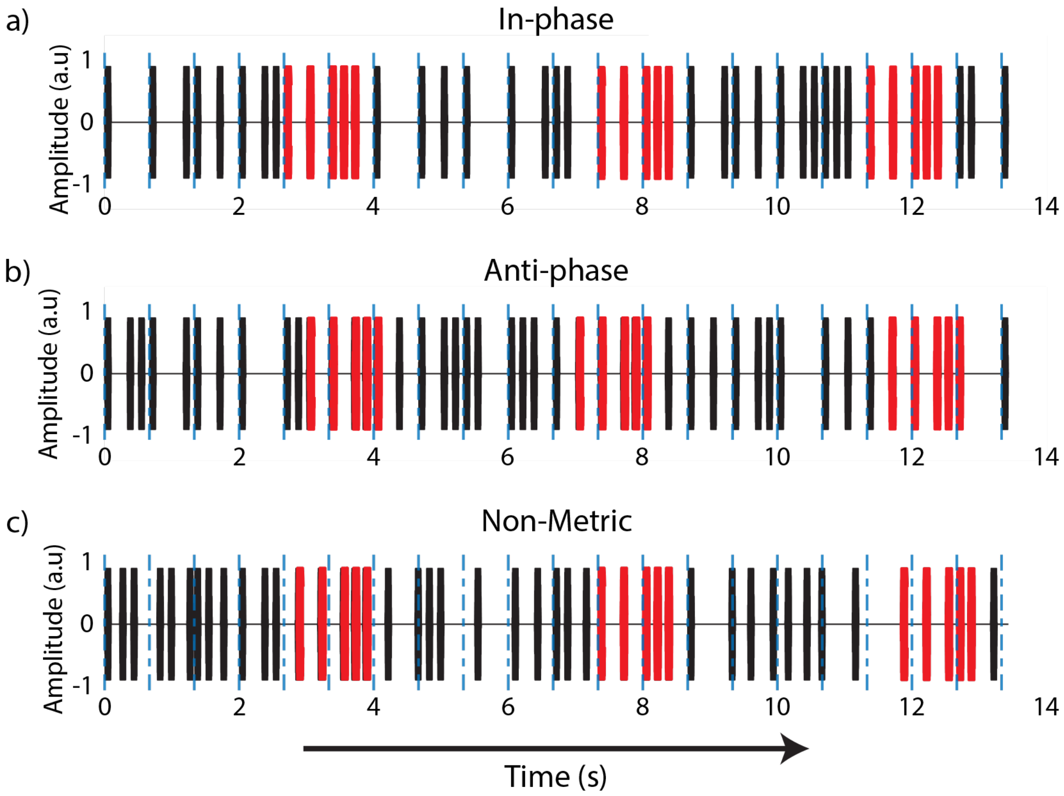

Figure 11: Waveforms of example stimuli in the in-phase (a), anti-phase (b), and non-metric (c) conditions. The blue dashed lines indicate where a beat occurs in the beat conditions (a & b), and where those same beat times would occur in the non-metric condition (c). The common rhythmic sequence is indicated in red and is identical in all conditions.

For the anti-phase condition, the order of intervals in each of the 45 in-phase rhythms was pseudo-randomly permuted but retained a tone onset every 666.7 ms. Thus, the anti-phase condition was similar to the in-phase condition in strength of beat percept as well as the beat frequencies (and harmonics) present in the rhythms. The characteristic that differed between in-phase and anti-phase conditions was the placement of the common sequence relative to the beat. In the in-phase condition, the common sequenced started on the beat (i.e., one of the tones that occurred every 666.7 ms), whereas in the anti-phase condition, the common sequence started anti-phase to the beat, i.e., half way between beats.

For the non-beat condition, the order of intervals in the in-phase condition was pseudo-randomly permuted such that tones occurred on less than one-third of the "beat positions" as defined in the in-phase condition. Fewer tones in beat positions reduces the amount of evidence for a steady beat, which weakens the strength of the beat percept (Shmulevich & Povel, 2000). Therefore, nor more than three consecutive beat positions could have tones. To further prevent inducing a beat percept, consecutive repetition of any given measure (i.e., the sequence of IOIs between two consecutive beat positions) was not allowed. Lastly, to further reduce the strength of the beat percept, tone onsets were jittered in duration so that the intervals of the non-beat rhythms were no longer integer multiples of the minimum IOI. The silent period of all intervals was randomly adjusted such that 166.7 ms intervals either remained un-jittered (166.7 ms) or were made 33% longer (221.7 ms), 333.3 ms and 500 ms intervals remained un-jittered, were made 33% shorter (223.3 ms and 335.0 ms, respectively), or were made 33% longer (443.3 ms and 665.0 ms, respectively), and 666.7 ms intervals either remained un-jittered or were made 33% shorter (446.7 ms). The overall lengths of each non-beat rhythm were checked to ensure they were the same length as the beat rhythms.

To control for the stimulus-driven response across rhythmic contexts, an identical common rhythm sequence was embedded in the rhythms of each condition (Figure 11), and comparisons across conditions were restricted to this common sequence. The common sequence was 1333.3 ms (i.e., two beats) long and was composed of the following intervals, which were present in all conditions: 333.3, 166.7, 166.7, 333.3, and 333.3 ms (Figure 11). The common sequence could occur once (11%), twice (56%), or three (33%) times in a rhythm. The positions of the common sequence within a rhythm were pseudo-randomized but began only after two beats (1333.3 ms) of the rhythm had elapsed, such that a beat percept could be established (Nozaradan et al., 2012a). In addition, in rhythms with two occurrences of the common sequence, one was in the first half and the other in the second half of the rhythm. In rhythms with three common sequences, common sequences were embedded in the first, middle, and final third of the rhythm.

The position of the common sequences within a rhythm was, on average, the same across conditions. The beginning of the common sequence was alternated between being half a beat position early and half a beat position late relative to in-phase trials (Figure 11a & 11b). Because beat-positions cannot exist in non-beat rhythms, common sequences in the non-beat condition started on the tone with the latency, relative to the start of rhythm, closest to that of the latency of common sequences in the in-phase trials.

3.2.3 Tasks & Procedure

After giving informed consent, participants completed a demographic questionnaire which contained questions pertaining to the participants' previous musical experience. The individual hearing threshold for each participant was then determined using a method of limits approach (Leek, 2001), followed by the EEG portion of the experiment. During EEG recording, participants were seated in a sound attenuated chamber, in front of a computer screen. The participants were instructed to avoid moving his or her body, and to focus on a fixation dot during recording. The auditory stimuli were presented 50 dB above individual hearing threshold (i.e. sensation level) over head phones. Participants completed a block of practice trials to ensure familiarity with the behavioural tasks before completing the experiment. The practice rhythms were not used in the rest of the experiment.

The experiment was divided into nine blocks (~8 min per block), with a break between each block. Blocks contained 15 trials from one stimulus condition and were counterbalanced across participants. Trials were 22 s long and consisted of three parts: a preparation period (2.00 s) in which the fixation dot was white, a listening period (13.33 s) during which the fixation dot was red, and a tapping period (6.67 s) in which the fixation dot was green. The preparation period was included so that participants weren't startled by the onset of the stimulus. During the listening period, participants listened to the rhythm without moving. When the fixation dot turned green, the participants then tapped along with the rhythm. The rhythm in the tapping period was a repetition of the first 6.67 s of the rhythm they heard in the listening period. Participants experienced the auditory stimuli in the listening and tapping periods as a single continuous rhythm.

3.2.4 Tapping Analysis

The coefficient of variation (tempo normalized measure of tapping stability; CoV) was computed as the quotient of the standard deviation of the inter-tap intervals (ITIs) for each trial and the mean ITI for that trial. The CoV was averaged across trials within each condition. A 1 x 3 repeated measures ANOVA, with stimulus condition (in-phase, anti-phase, non-beat rhythms) as the within-subjects factor, was conducted on the averaged CoV values for each condition.

To assess whether the common sequences were perceived as in-phase or anti-phase relative to the intended beat location in each trial, tapping phase, relative to the common sequences and not the trial onset, was computed for in-phase and anti-phase trials. Tapping phase was not computed for the non-beat condition because the non-beat rhythms do not contain a beat. Tapping phase was determined by comparing the timing of each tap during the listening phase of each trial to the timing of the closest intended beat. Trials were coded as 'in-phase' when the majority of extrapolated tap times fell within a time window of half the mean ITI, centered on each beat time (i.e., the beat time ± .25 * ITI). Conversely, trials were coded as 'anti-phase' when the majority of extrapolated tap times fell outside of this time window. Tapping phase of each trial was consistent with the intended rhythmic context condition in > 94% of trials.

3.2.5 EEG recording

EEG was recorded from 64 Ag-AgCl electrodes (BioSemi, Amsterdam, The Netherlands), mounted in a cap according to the 10-20 system and additional electrodes at both mastoids. Signals were recorded continuously with a passband of DC to 400 Hz and digitized at a sampling rate of 1024 Hz. Electrode voltage offsets were kept below 25 kΩ.

3.2.6 EEG analysis

EEG data were analyzed offline using Fieldtrip software (Oostenveld et al., 2011) and custom Matlab (Mathworks, USA) scripts. The EEG data were first re-referenced to the averaged mastoid reference. The then high-pass filtered (.65 Hz, 11792 points, Kaiser window) and low-pass filtered (42 Hz, 90 points, Hann window). Then the data were down sampled to 250Hz before being, dividing the recordings into epochs (-2 s to 2 s, relative to the onset of the embedded target sequence). After epoching, the data were submitted to ICA (runica; Delorme, Sejnowski, & Makeig, 2007). Components reflecting artifacts were identified (by visual inspection) and removed to avoid rejecting a large proportion of trials in the signal-range artifact rejection procedure following ICA. Epochs were excluded if the signal range was larger than 120 mV in any of the electrode channels. Only data from this preprocessing pipeline were used in the subsequent analyses.

3.2.6.1 Power

Time frequency decomposition was performed on the preprocessed data using a Morlet Wavelet convolution as implemented in fieldtrip (Oostenveld et al., 2011). Wavelets were 3 cycles and ranged from 0.5 Hz to 15 Hz in steps of 0.25 Hz, with a time range of 0 – 1.3 s in steps of 0.01 s. For statistical comparison, a 3 * 3 repeated measures ANOVA was performed on the power values, with Rhythmic Context (In-phase, Anti-phase, Non-beat) and Frequency (1.5, 3, and 6 Hz) as factors. Any violations of sphericity were corrected using the Greenhouse-Geiser method. Simple effects analysis of Rhythmic Context at each Frequency was performed by conducting separate 1 x 3 repeated measures ANOVA. Significant simple effects were followed up by conducting *post hoc* pairwise comparisons.

3.2.6.2 Phase

To calculate the phase difference between the beat frequency oscillation in the in-phase and anti-phase conditions for each participant, the resultant complex Fourier coefficients of the Wavelet convolution described previously were first averaged across trials within each phase condition, and then converted to phase-angle time series. Phase difference was then computed as the circular distance between instantaneous phase angles of the beat rate oscillation immediately prior to the tone onset in the middle of the common sequences (i.e., 666.67 ms after the start of the common sequence) using the “circ_dist” function in MatLab (Berens, 2009; Berens & Valesco, 2009). To assess whether the phase of beat rate oscillation differed significantly between the in-phase and anti-phase conditions, the circular distances were then compared to zero (no difference) and 180° (maximally different) using a Wilcoxon signed rank test. Although not reported, the pattern of phase differences was consistent across the duration of the common sequence. Thus, only the results from the middle of the common sequence (which minimizes potential influence from data points outside the common sequence) are reported.

3.3 Results

3.3.1 Behavioural tapping measures

3.3.1.1 CoV

To examine the effect of rhythmic context on beat tapping stability, a 1 x 3 repeated measures ANOVA was conducted on coefficient of variation with rhythmic context (in-phase, anti-phase, and non-beat) as a factor. Tapping stability differed significantly between rhythmic contexts, $F(2, 48) = 24.52$, $p < .001$, $\eta^2 = .51$ (Figure 12). Follow-up, paired-samples *t*-tests revealed that tapping was significantly less stable in the non-beat context ($M = 0.09$, $SE = 0.01$) than in either the in-phase condition ($M = 0.07$, $SE = 0.01$), $t(24) = -5.48$, $p < .001$, or the anti-phase condition ($M = 0.07$, $SE = 0.01$), $t(24) = -4.76$, $p < .001$. Tapping stability did not significantly differ between in-phase and antiphase beat conditions, $t(24) = -2.47$, $p = .061$.

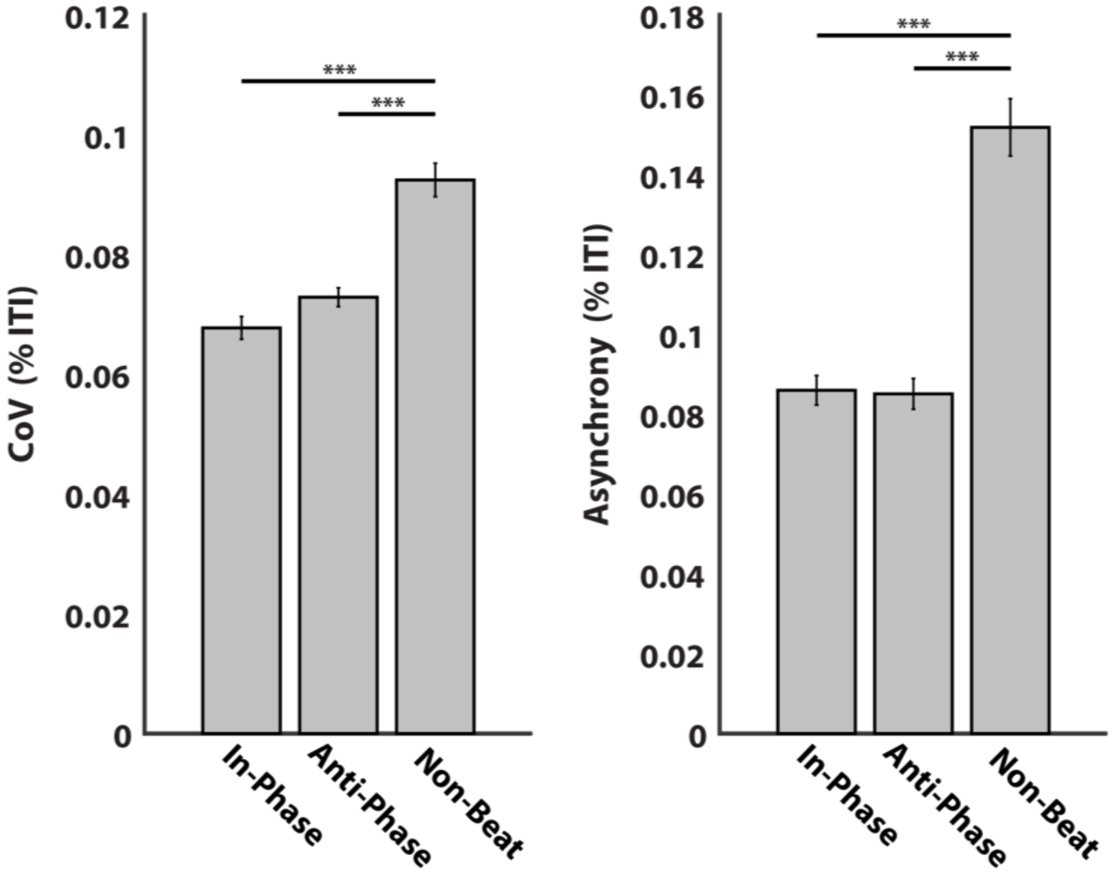

Figure 12: Values for CoV (*left*) and asynchrony (*right*) averaged across rhythm and participants within each rhythmic context; Participants tapped more consistently and more accurately to beat rhythms than non-beat rhythms; Error bars indicate +/- 1 within-subjects SEM. * indicates *p* < .001.**

3.3.1.2 Asynchrony

To examine the effect of the beat strength manipulation on tapping accuracy, a 1 x 3 repeated measures ANOVA was conducted on tapping asynchrony with rhythm condition (in-phase, anti-phase, and non-beat) as a factor. Tapping accuracy differed significantly between rhythm conditions $F(1.34, 32.10) = 24.52$, $p < .001$, $\eta^2 = .51$ (Figure 12). Follow-up paired-samples *t*-tests revealed that tapping accuracy was significantly lower in the non-beat condition ($M = 0.15$, $SE = 0.01$) compared to either the in-phase ($M =$

0.09, *SE* = 0.01), *t*(24) = -6.14, *p* < .001, or anti-phase condition (*M* = 0.09, *SE* = 0.01), *t*(24) = -6.13, *p* < .001. Tapping accuracy did not differ significantly between the in-phase and anti-phase conditions, *t*(24) = .39, *p* = .999.

3.3.2 EEG measures

3.3.2.1 Power

To examine the effect of beat percept on neural entrainment, a 3 x 3 repeated measures ANOVA was conducted on spectral power, with rhythmic context (in-phase, anti-phase, and non-beat) and frequency (1.5 Hz, 3 Hz, and 6 Hz) as factors. The ANOVA revealed there was no significant effect of frequency, *F*(2, 48) = 1.49, *p* = .236, η^2 = .06, but there was a significant effect of rhythmic context, *F*(2, 48) = 4.26, *p* = .020, η^2 = .15, and a significant interaction between rhythmic context and frequency, *F*(4, 96) = 3.43, *p* = .011, η^2 = .125, indicating that the effect of rhythmic context was not the same for each frequency (Figure 13). To better understand the interaction of rhythmic context and frequency, a series of 1 x 3 repeated measures ANOVAs were conducted on spectral power for each frequency separately, with rhythmic context as a factor. The results for these tests revealed a significant simple effect of rhythmic context at 1.5 Hz, *F*(2, 48) = 6.51, *p* = .003, η^2 = .21, and 6 Hz, *F*(2, 48) = 3.46, *p* = .040, η^2 = .13, but not at 3 Hz, *F*(2, 48) = 1.04, *p* = .361, η^2 = .04. At 1.5 Hz, paired-samples *t*-tests revealed that neural entrainment was significantly greater in the in-phase context than in either the anti-phase, *t*(24) = 3.27, *p* = .003 , or non-beat contexts, *t*(24) = 1.68, *p* = .050. Additionally, neural entrainment was significantly greater in the non-beat condition than in the anti-phase condition, *t*(24) = 2.18, *p* = .039. At 6 Hz, neural entrainment did not significantly differ between the in-phase and anti-phase contexts, *t*(24) = 0.26, *p* = .800, but was significantly lower in the non-beat context compared to both the in-phase, *t*(24) = 2.21, *p* = .037, and anti-phase contexts, *t*(24) = 2.00, *p* = .029.

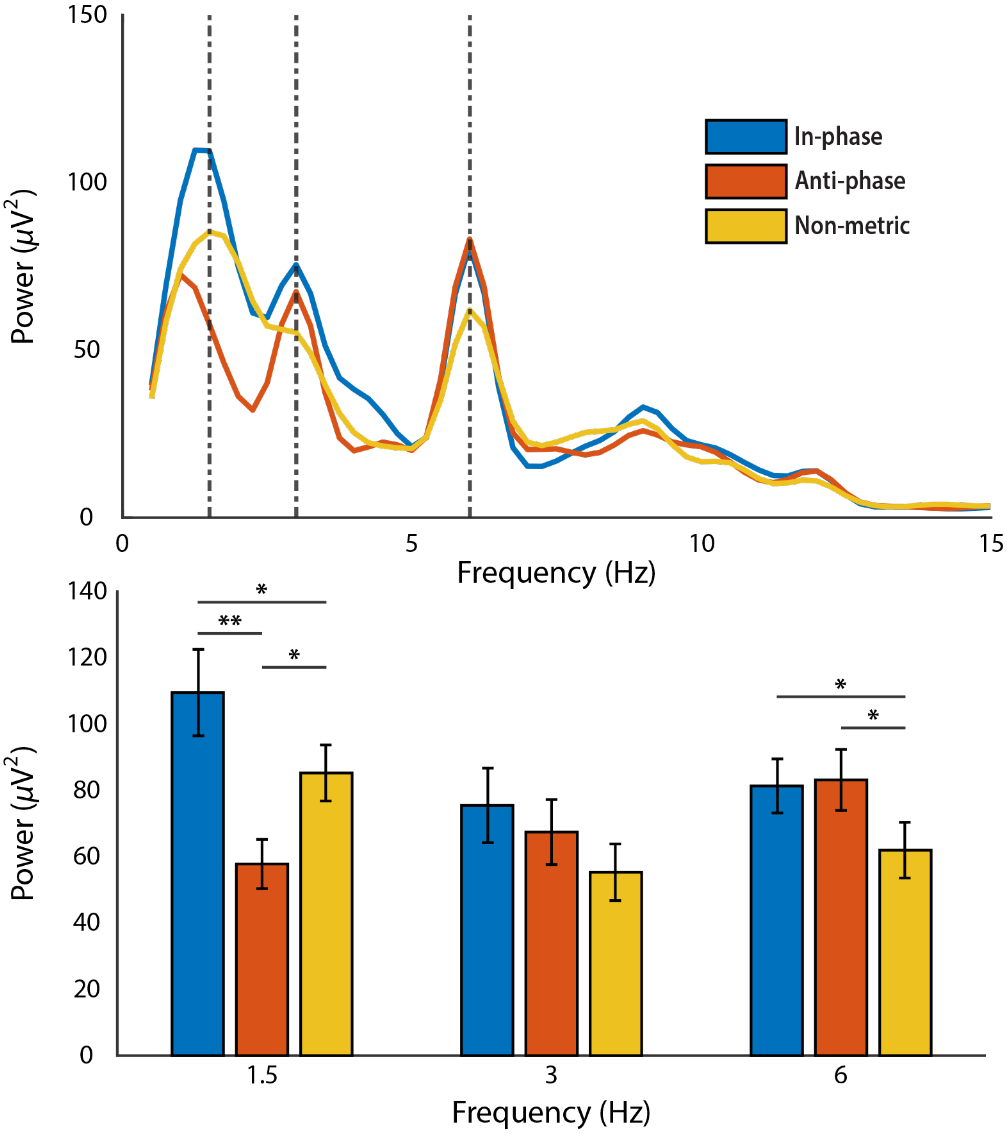

Figure 13: EEG power during the common sequence. (*top*) Power output of the wavelet analysis averaged across time points; grey dashed lines indicate beat-related frequencies; (*bottom*) Neural power at beat-reated frequences (at grey dashed lines). Error bars indicate +/- 1 within-subjects SEM, $p < .01$ and $p < .05$ are indicated by * and **, respectively.

3.3.2.2 Phase

To test for phase differences between the in-phase and anti-phase conditions, first the evoked phase of the 1.5 Hz oscillation was calculated by averaging the complex Fourier coefficients for each participant across trials within each condition (Figure 14a). The difference between the phase of the two conditions for each participant (Figure 14b) then was computed using the “circ_dist” function from the “CircStats” toolbox (Berens, 2009; Berens & Valesco, 2009) in Matlab (Mathworks). A Rayleigh’s test for nonuniformity of circular data was used to test if the phase difference between the in-phase and anti-phase conditions were uniformly distributed across participants (a non-significant result indicates uniform distribution). If the phase of the beat rate oscillation is not related to the location of the beat in the rhythm, phase differences between should be randomly distributed, and thus return a non-significant result. However, the phase difference between the rhythmic contexts were not uniformly distributed, $Z(24) = 3.69$, $p = .023$, indicating a relationship between oscillatory phase and the beat. However, it is possible that no difference exists between the two rhythmic conditions because the neural signal is comprised only of the stimulus driven response and does not differ because the common sequence is identical in both conditions. If this were the case, the phase differences between the two conditions would be non-uniformly distributed around zero. Thus, a one-sample Wilcoxon signed rank test was used to test if the median circular distance between the phases of the two rhythmic context conditions was different from zero (a non-significant test indicates no phase differences between in-phase and anti-phase contexts). The phase of the beat rate oscillation at 1.5 Hz, did differ significantly between the in-phase and anti-phase condition, $Z(24) = 4.37$, $W(24) = 325$, $p < .001$. However, the results of a second Wilcoxon signed rank test showed that the phase difference between the in-phase and anti-phase conditions was also significantly different than the 180° that was predicted, $Z(24) = -4.37$, $W(24) = 0$, $p < .001$. Taken together, these results suggest that although a relationship between beat location and oscillatory phase may exist, other factors may also affect the phase of the neural signal.

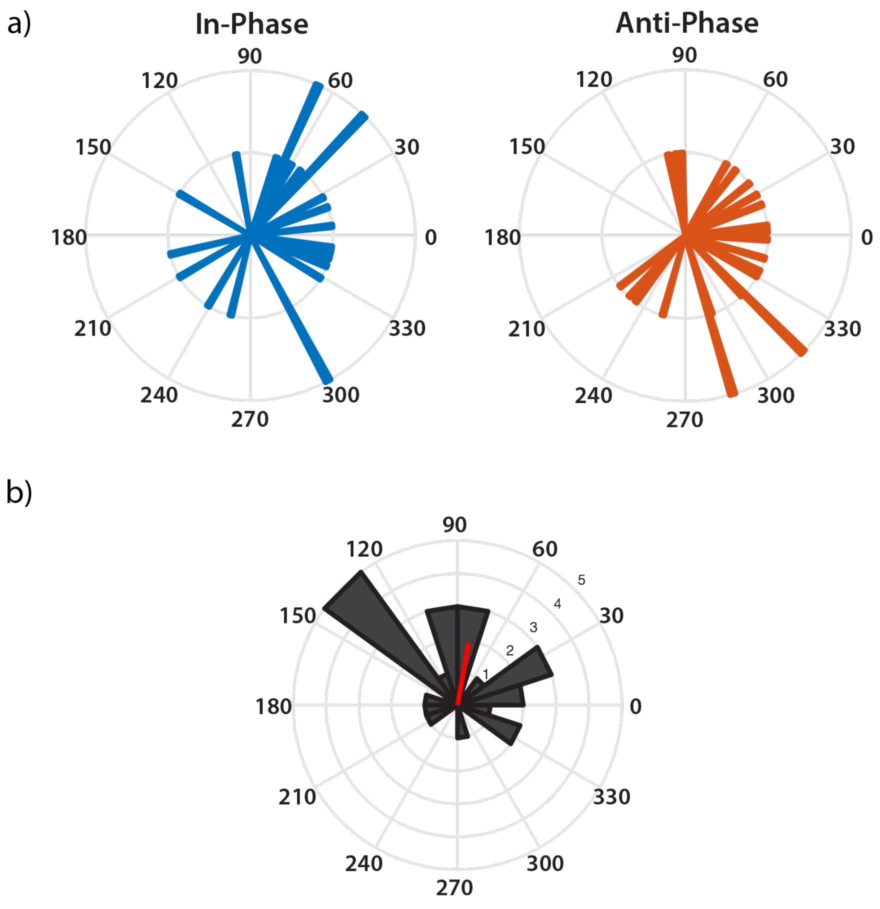

Figure 14: Circular histograms of 1.5 Hz (beat rate) oscillation during the common sequence, in all plots longer bars indicate more participants with that phase angle/difference; *a*) raw phase angle for each participant in the in-phase (*left*) and anti-phase (*right*) context; *b*) phase differences between rhythmic conditions in *a*) with the red line indicating mean phase difference.

3.3.3 Correlations between neural entrainment and behavioural measures.

To investigate how entrainment at beat frequencies was related to beat tapping, we ran multiple linear regression analyses with spectral power each frequency of interest (1.5 Hz, 3 Hz, and 6 Hz) as the criterion variable and CoV and asynchrony as the predictor variables. To test whether tapping measures predicted neural entrainment at a group level, a Wilcoxon signed rank test was used to test the median of the distributions of beta values for CoV, asynchrony, and the interaction against zero. The results of this analysis showed that power at 1.5 Hz (the primary beat rate) was predicted by both CoV, $Z(24) = 2.09$, $W(24) = 240$, $p = .037$, and asynchrony, $Z(24) = 2.14$, $W(24) = 242$, $p = .032$, but power at 3 Hz (*ps* > .510), and 6 Hz (*ps* > .581) was not (Figure 15). These results suggest that entrainment at the beat frequency is related to beat tapping performance. Specifically, participants with the most stable and accurate tapping show the greatest neural entrainment at the primary beat frequency.

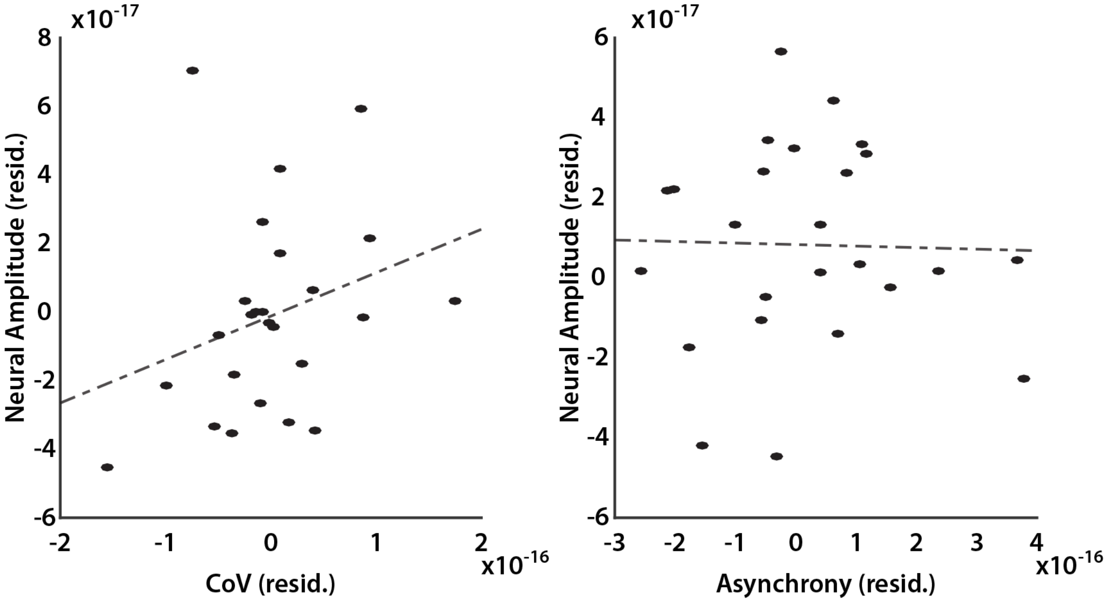

Figure 15: Partial correlations between neural entrainment at 1.5 Hz and CoV (*left*) and Asynchrony (*right*). Participants whose tapping was more stable and more accurate also showed greater entrainment at 1.5 Hz.

To investigate the relationship between neural entrainment and musical experience, separate linear regressions were conducted with spectral power for each combination of rhythmic context (in-phase, anti-phase, and non-beat) and spectral power at each frequency of interest (1.5 Hz, 3 Hz, and 6 Hz) as the criterion variable, and years of musical training as the predictor variable. Musical training did not predict spectral power at any of the frequencies of interest in any of the in-phase (all $R^2 < .01$, *Fs*(1, 23) < 0.31, *ps* > .582), anti-phase (all $R^2 < .09$, *Fs*(1, 23) < 2.19, *ps* > .152), or non-beat (all $R^2 < .04$, *Fs*(1, 23) < 0.98, *ps* > .332), rhythmic conditions.

3.4 Discussion

This study was designed to disentangle the stimulus-driven response from the entrained response to better understand how entrainment of neural oscillations relates to beat perception. To do this, we examined the neural response (i.e., the combination of the stimulus-driven and entrained responses reflected in the EEG signal) to a common rhythmic sequence that was embedded in either beat or non-beat contexts, thus equating the stimulus-driven response across contexts. Overall, the findings support our prediction of greater spectral power at beat frequencies when common rhythmic sequences were embedded in beat contexts than the non-beat context.

3.4.1 Spectral power at the beat frequency is related to tapping consistency accuracy

As stated above, we found greater neural power at beat frequencies when the common sequence was embedded in beat contexts than in the non-beat context. Specifically, we found more power for common sequences in the in-phase context than in the non-beat context at 1.5 Hz, and in both the in-phase and anti-phase contexts compared to the non-beat context at 6 Hz. Critically, the common sequence was identical in all rhythmic contexts, therefore the stimulus-driven response was also identical in all rhythmic contexts (Henry et al., 2017). Thus, the greater power at beat frequencies for beat than non-beat contexts (Figure 13) results from differences in neural entrainment between those contexts (Chemin et al., 2014; Cirelli et al., 2016; Nozaradan et al., 2011, 2012a; Schroeder & Lakatos, 2009). Moreover, participants tapped more consistently and more accurately to the beat contexts (i.e., in-phase and anti-phase) than the non-beat context (Figure 12), indicating that performance on the beat tapping task may be related to neural spectral power at the beat frequency. Indeed, previous works suggests that decreased accuracy in the non-beat context may reflect increased error correction in tap timing when the beat is less predictable, as in weak-beat or non-beat rhythms (Repp, 2005b; Repp & Su, 2013). Taken together, more power at beat frequencies, combined with more accurate tapping during beat than non-beat contexts, supports previous work that suggests neural spectral power reflects neural entrainment, and may be a neural correlate of beat perception (Large, 2008; Large & Snyder, 2009; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2012a).

Although these results support the hypothesis that entrainment of neural oscillations is related to beat perception, we would have also predicted that, because perceived beat strength did not differ between the two beat contexts (Figure 12), spectral power at the beat frequency would also be similar in the two beat contexts. Specifically, if beat perception is directly related to neural entrainment (Large, 2008; Lenc, Keller, Varlet, & Nozaradan, 2018b; Nozaradan et al., 2012a), power at the beat frequency should be similar for the two beat contexts, as they had similar beat strengths. However, there was significantly lower power at the beat frequency in anti-phase than in-phase beat contexts (Figure 13). One explanation for this may be that, although beat strength was the same in both contexts, temporal beat cues within the common sequence may align differently with the temporal beat cues in the in-phase and anti-phase contexts. Potential misalignment of temporal cues in common sequence with the cues in the rhythmic context could have unintentionally weakened or caused phase resetting of the beat rate oscillations in the anti-phase condition (Obleser et al., 2017; Povel & Essens, 1985; Povel & Okkerman, 1981). However, when we examine the intervals of the common sequence (i.e. 2-2-1-1-2), the only onset that might induce a slightly stronger perceptual accent than the others would be the final onset (i.e., the 2 of the 1-1-2), which is actually misaligned in the in-phase condition, not the anti-phase condition (Povel & Essens, 1985; Shmulevich & Povel, 2000). Thus, if misaligned temporal cues did cause differences in power between the phase conditions, the difference should be the opposite of what we observed. Therefore, we do not think that this is an explanation for why we see in-phase/anti-phase power differences.

Alternatively, features of the rhythmic context surrounding the common sequence may have differed in unexpected ways between the in-phase and anti-phase condition. However, great care was taken ensure that the intervals in each rhythmic context were controlled across conditions (see Methods for details of stimulus creation), and the intervals immediately preceding the common sequence did not significantly differ in length between conditions (analysis not reported). Therefore, it seems unlikely that differences in the rhythmic context, either overall or immediately preceding the common sequence, caused neural power differences between the in-phase and anti-phase conditions.

3.4.2 Phase

One of the key predictions of neural entrainment theories of beat perception is that the most excitable phase of the neural oscillation is synchronized to the onset of the beat (Henry et al., 2014; Large, 2008; Large & Jones, 1999; Zoefel et al., 2018). Therefore, the phase of the entrained oscillation should be maximally different (i.e., 180°) on the beat compared to halfway between beats. Here, the phase of the oscillation at the beat frequency (1.5 Hz) did significantly differ between in-phase and anti-phase rhythmic contexts. However, the phase difference between the two rhythmic contexts also differed from the 180° that “idealized” models of neural entrainment would predict (Henry & Herrmann, 2014; Large, 2008; Large & Jones, 1999). One possible explanation for the phase difference not being 180° is that the temporal characteristics of the common rhythmic sequence may be obscuring beat related changes in excitability.

For example, the intervals between tones in the rhythm are short enough that the neural signal is still being influenced by longer-latency ERP components from the previous tone when the next tone occurs (tone refs from ch 2). Thus, the phase of the neural signal may reflect a mix of the neural oscillation of the entrained response and the ERP of the stimulus driven response (Obleser et al., 2017). If so, even though using a common sequence allowed us to isolate power differences related to entrainment differences, the stimulus-driven response is still present, albeit consistent, in the neural signal. If the stimulus-driven response interacts unpredictably with the recording of the endogenous oscillation, then the evoked response to the tones in the common sequence could be shifting the subtle differences in the oscillations of neural excitability, preventing us from getting a pure estimation of the relationship between phase and beat location that we attempted to examine in this study.

However, even though our ability to observe the entrained, oscillatory response may have been altered by the stimulus-driven, evoked responses to the tones, we were able to observe how neural entrainment, locked to the beat location, influenced the neural signal. Specifically, if the phase of the neural signal was only comprised of the evoked response, the phase of the beat rate oscillation should be the same in both the in-phase and anti-phase contexts because the common sequence was the same in both contexts. However, the phase of the neural signal at the beat rate (1.5 Hz) is different between the in-phase and anti-phase contexts. This phase difference suggests that not only are we observing a mix of the evoked and entrained response, but also that the difference in the phase of the signal is related to the beat locations in the two rhythmic contexts. Taken together, these findings suggest that the specific phase of neural oscillations is also related to beat perception, consistent with previous work (Fujioka, Ross, & Trainor, 2015b; Henry & Herrmann, 2014; Henry et al., 2016; Lakatos et al., 2008; Large & Jones, 1999; Large & Snyder, 2009; Schroeder & Lakatos, 2009).

3.4.3 Regressions

We used a series of linear regressions to determine whether tapping performance related to neural entrainment. Power at 1.5 Hz, which was the primary beat frequency and also the rate that participants tapped at (Figure 12), was predicted by both CoV and asynchrony (Figure 15). Specifically, participants who tapped more consistently and accurately also showed greater neural power at 1.5 Hz than participants who tapped less consistently and accurately. This relationship between beat tapping performance and neural power at the beat frequency provides further evidence that neural entrainment is related to beat perception.

We were also interested in how musical experience affected entrainment. Previous behavioural studies have shown that musicians are better at beat perception tasks (Cameron et al., 2017; Repp, 2010; Repp & Doggett, 2007; Strait et al., 2012), thus, if neural entrainment is a neural correlate of beat perception one would predict that musicians would show greater entrainment than non-musicians. However, we did not find a link between musical experience, as measured by the number of years of musical training, and the strength of neural entrainment. Previous work has found a relationship between musical training and entrainment (Doelling & Poeppel, 2015; Nozaradan, Peretz, et al., 2016), however those studies specifically recruited expert musicians. Here, the participants were not recruited based on musical experience, therefore may not have been expert enough for a clear effect of musical training to be observed.

3.4.4 Conclusions

The findings are consistent with neural entrainment being associated with beat perception in rhythm (Large, 2008; Large & Jones, 1999; Large & Snyder, 2009; Nozaradan, 2014; Nozaradan et al., 2012a). Better performance on the beat tapping task in strong beat than non-beat contexts was accompanied by greater neural spectral power at beat frequencies during strong beat than non-beat contexts. This relationship was also reflected in the linear regression analysis that revealed that both tapping consistency and accuracy were predictive of neural spectral power.

Even though the results of both the power analysis and regression analysis support the relationship between neural entrainment and beat perception, not all analyses produced the predicted results. The evoked response, though identical across contexts, was still present in the neural signal, which potentially made it difficult to examine how the phase of neural oscillations was related to beat position. The presence of the stimulus-driven response in the neural signal may have influenced the overall neural response, making it challenging to directly observe how the specific phase of the entrained neural oscillation was related to the onset of each beat. These findings demonstrate that simply controlling the stimulus-driven response is not sufficient to completely disentangle it from the entrained response in the neural signal. Future attempts to examine the nature of the relationship between oscillatory phase and beat location may need to remove the stimulus-driven response from the neural signal altogether, rather than simply controlling the response across conditions.

To conclude, the goal of this study was to isolate the entrained response in the neural signal by controlling the stimulus-driven response. To do this we analyzed the neural response to identical sequences embedded in different rhythmic contexts. Because the stimulus was identical in all contexts, the stimulus-driven response was the same across all rhythmic contexts. Therefore, the observed differences in the power of the neural signal at the beat frequency were the result of differences in the listener's beat perception induced by rhythmic context. Taken together, these findings support the theory that entrainment of neural oscillations is related to beat perception (Large, 2008; Large & Jones, 1999; Large & Snyder, 2009; Lenc et al., 2018b; Nozaradan, 2014; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011, 2012a).

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Chapter 4

4 Investigating the influence of rhythmic entrainment on the persistence of neural oscillations through silence

4.1 Introduction

There is a growing body of evidence that neural oscillations are important to perception of predictable visual or auditory stimuli (Calderone et al., 2014; Henry & Obleser, 2012; C. S. Herrmann & Strüber, 2017; Lakatos et al., 2007, 2008; Large & Snyder, 2009; Schroeder & Lakatos, 2009; Snyder, 2015). Neural entrainment occurs when the cyclic changes in the excitability of populations of neurons entrain to (i.e., synchronize with) the onset of predictable, external stimuli, such as flashing lights or repeated auditory tones (Henry et al., 2014; B. Herrmann et al., 2016; Lakatos et al., 2007, 2008, 2013, 2005; Large & Snyder, 2009; Schroeder & Lakatos, 2009; Snyder & Large, 2005). In more complex, musical rhythmic stimuli, the entrainment (i.e., synchronization) of neural oscillations has been proposed to give rise to the phenomenon of beat perception (Cirelli et al., 2014; Fujioka et al., 2014, 2015a; Fujioka, Zendel, & Ross, 2010; Large & Jones, 1999; Large & Palmer, 2002; Nozaradan et al., 2011, 2012a; van Noorden & Moelants, 1999). Beat perception is the ability to perceive an isochronous pulse in musical rhythm (Large & Palmer, 2002; Parncutt, 1994).

Several studies have supported the role of entrained neural oscillations in beat perception by demonstrating that the strength and/or frequency of the entrained oscillations differs with the strength and/or frequency of the beat percept. These findings are based on studies in which researchers compared the power spectrum (i.e., the frequency domain representation) of EEG data to power spectrum of the stimulus envelope (Nozaradan et al., 2012a, 2018), or to the power spectra of EEG data acquired during different experimental listening conditions (e.g., strong vs. weak beat, low- vs. high-pitched tones, etc.) (Chemin et al., 2014; Cirelli et al., 2016; Lenc et al., 2018b; Trapp, Havlicek, Schirmer, & Keller, 2018). Differences in the power spectra, in either EEG-EEG or EEG-stimulus comparisons, at beat or beat-related frequencies are interpreted as evidence of differences in neural entrainment between conditions.

However, a difference in neural oscillatory entrainment is only one factor that can affect EEG power at beat frequencies. For example, changing the acoustic and temporal characteristics of the stimulus can affect power in both the stimulus and neural spectra (see Chapters 2 and 3; (Henry et al., 2017). Furthermore, even when the spectral characteristics of the stimulus are identical between listening conditions (see Chapter 3), there is a larger question about what power in the neural spectrum reflects. Currently, there is a debate about how to interpret neural power spectra (Henry et al., 2017; Novembre & Iannetti, 2018; Zoefel et al., 2018). The primary issue is that the spectral characteristics we see in the neural spectra may be influenced by internal representations of rhythm, such as whether or not a beat is perceived, as the entrainment literature suggests (Fujioka et al., 2009; Lakatos et al., 2008; Large, 2008; Large & Snyder, 2009; Nozaradan et al., 2011), or may simply arise from the evoked responses to tones in the stimulus (Novembre & Iannetti, 2018; van Ede et al., 2018). Disentangling whether internal representations play a role is important, because evoked responses to a rhythmic stimulus would also generate a rhythmic evoked response. Indeed, the power spectrum of a rhythmic evoked response could appear similar to the power spectrum of an entrained neural response (Novembre & Iannetti, 2018). Therefore, the neural power spectra could be generated solely by evoked responses to a rhythmic stimulus, rather than an internally-driven entrained response. If the former is true, then power in the neural spectrum reflects a purely stimulus-driven response.

Trying to determine the relative contributions of the stimulus-driven response and the entrained oscillatory response has proven difficult because most previous work has investigated the role of neural oscillations in perception during the presence of auditory or visual stimulation (Calderone et al., 2014; Henry et al., 2016; Henry & Obleser, 2012; Lakatos et al., 2007; Snyder et al., 2006; Wilsch et al., 2015). This means that the stimulus-driven response as well as the potential oscillatory response are both present in the neural signal in most previous investigations. For this reason, differences in the spectral characteristics of the neural response, compared to either the stimulus spectrum or the neural spectrum of a different listening condition, can be difficult to interpret with confidence.

However, one key feature of oscillators in general is that the oscillations generally continue for some period after stimulation ends. Once an oscillator has entrained to the stimulus onsets (as has been proposed in the theories of how neural oscillations give rise to beat perception), it continues to “resonate” at the entrained frequency after auditory stimulation has ceased (Baltus & Herrmann, 2015; Large & Snyder, 2009; van Noorden & Moelants, 1999; Velasco & Large, 2011). Recent findings indicate that electrical activity in the primary auditory cortex of monkeys continues phase-locked oscillations at the stimulation rate of a discontinued isochronous tone sequence (Lakatos et al., 2013). Relatedly, beat perception can also continue after a stimulus ends. Thus, if beat perception arises from entrained neural oscillators, not only should neural oscillations be entrained at the beat frequency in non-isochronous stimuli such as musical rhythms, but those oscillations should also continue for a short time after the auditory stimulus has ended. This is especially true if the stimulus ends at an unpredictable time—at least one cycle of beat perception is likely to continue before the listener can perceive that the stimulus has ended. By studying the neural response after stimulation has ended, we can investigate entrainment in the absence of the stimulus-driven response.

In addition, we can also investigate the *phase* of the entrained oscillations. Entrainment theories suggest that the cyclic changes in the excitability of neural populations entrain to (i.e., synchronizes with) the onset of predictable stimuli such that the stimuli occur during the most excitable phase of the neural oscillation (Henry et al., 2014; Lakatos et al., 2007, 2008, 2013, 2005; Large & Snyder, 2009; Schroeder & Lakatos, 2009; Snyder & Large, 2005). Although the phase of entrained neural oscillations is a key aspect in neural entrainment theories of beat perception, phase relationships remain relatively unexplored. The majority of studies examining how entrainment is related to perception have investigated only the power, not phase, of oscillations at the entrained frequency. However, increased power will unlikely aid perception unless the onset of the stimulus falls in the excitatory phase of the neural oscillation. Indeed, while the phase of entrained oscillations has been shown to be important in predicting perception in simple auditory and visual stimuli (Breska & Deouell, 2017; Henry & Herrmann, 2014; Henry et al., 2014; Henry & Obleser, 2012; Lakatos et al., 2013; Schroeder & Lakatos, 2009), there is little evidence about how the phase of neural oscillations relates to the beat in complex musical rhythms. If neural entrainment is truly related to beat perception, one would predict that the oscillations would be phase-locked to the beat.

Thus, our two main goals for this study are to investigate whether beat perception is the result of entrained neural oscillations, and to investigate the relationship between beat location and the phase of entrained neural oscillations in the absence of an evoked response. To accomplish our first goal, we analyzed the neural response in the silent period immediately following musical rhythms that either had a strong beat, or no beat (i.e., the beat was either difficult or impossible to perceive). Thus, the preceding rhythm induced a beat perception difference, but the to-be-analyzed silences after the rhythm were not only identical (thereby controlling the stimulus-driven response) but contained no evoked neural response because there was no stimulus. That way, we are able to manipulate differences in beat strength (and presumably entrainment strength) in the absence of any stimulus-driven response.

One of the strengths of this manipulation is that it can provide further evidence that entrainment is related to beat perception by examining the way that neural oscillations resonate (i.e. persist) after stimulation has stopped. This allows us to accomplish our second goal of examining how the *phase* of the underlying neural oscillation is related to the beat without being influenced by the stimulus-evoked response to the auditory rhythm. To investigate how phase of the entrained neural oscillation is related to the beat, we also created rhythms in which the final tone of the rhythm was either on-beat (in-phase), or between beats (anti-phase). Because each rhythm ended either on-beat or between beats, the time window in which data were analyzed began either in-phase (0°) or anti-phase (180°) relative to the beat in the rhythm. By comparing the phase of the neural response in these two phase conditions, we will be able to examine a key prediction of entrainment theories, which suggest that entrained neural oscillations are phase-locked to beat-locations in the rhythm (Arnal, Doelling, & Poeppel, 2014; Breska & Deouell, 2017; Fujioka et al., 2015a; Nozaradan et al., 2011, 2012a). That is, if neural oscillations are phased-locked to the beat, then the phase of the beat rate oscillation at a given point in the analysis window in the in-phase and anti-phase conditions should be maximally different because, relative to the beat, the beginning of analysis window is maximally different between the in-phase and anti-phase conditions.

If beat perception does arise from entrained neural oscillators, we predict that the entrained oscillations will continue into the silence after the stimulus has stopped playing, and that spectral power at beat and beat-related frequencies will be greater in the silences after strong beat rhythms than weak beat rhythms. Additionally, we predict that the entrained oscillations at the beat frequency will be phase-locked to the beat location in the stimulus and will therefore differ by 180°, within each subject, between the in-phase and anti-phase trials. If phase differences in entrainment track beat percept, it provides further evidence that beat perception arises as a result of entrained neural oscillators.

4.2 Methods

4.2.1 Participants

Twenty-eight participants (M_{age} = 23.18 (4.12) years, 20 female) took part in the experiment after providing written consent. Twenty-seven participants reported having previous musical experience (M_{years} = 6.71 years, SD = 5.21), of those, 10 reported having more than 10 years of training. This study was approved by the Western Research Ethics Board at the University of Western Ontario. Participants received monetary compensation for their participation in the study.

4.2.2 Stimuli

Rhythms in all conditions were approximately 10 s in length and were created by alternating narrow-band tones and silence. Narrow-band tones were used instead of pure tones to maximize the neural response to the stimuli (Rauschecker et al., 1995; Shahin et al., 2007, 2005). The narrow-band tones were composed of 30 sine-wave components sampled from a uniform distribution with a 500 Hz range centered on 750 Hz and were 100 ms in duration with a 10 ms linear onset/offset ramp. The phase of each sine-wave component, relative to the onset of the tone, was randomized, and the amplitude of the component was scaled linearly based on its inverse distance from the centre frequency; that is, components farthest from the centre frequency had the smallest amplitude.

To examine the effect of beat on persistence and phase of neural oscillations, three categories of rhythms were created: two categories of rhythm in which a strong beat percept was induced but the start of the analysis window differed relative to the beat percept (in-phase vs. anti-phase), and one category which did not induce a beat percept (non-beat). There were 60 unique rhythms in each rhythm category for a total of 180 unique rhythms in the experiment. For the “in-phase” condition, rhythms were composed of four inter-onset intervals (IOIs): 166.7, 333.3, 500.0, and 666.7 ms. Thus, the duration of the silent period after each tone was the IOI minus the tone duration (66.7, 233.3, 400.0, and 566.7 ms, respectively). These rhythms were designed to induce a strong beat percept (Grahn & Brett, 2007; Povel & Essens, 1985) in which a tone occurred every 666.7 ms (Figure 16). This gave the rhythms a beat frequency at 1.5 Hz (666.7 ms), and at the harmonic of 3 Hz (333.3 ms), and potentially also at the minimum IOI frequency of

6 Hz (166.7 ms), although the latter is much faster than the typical beat perception range (Demany & Semal, 2002; Drake & Botte, 1993; Martens, 2011; Repp, 2005a).

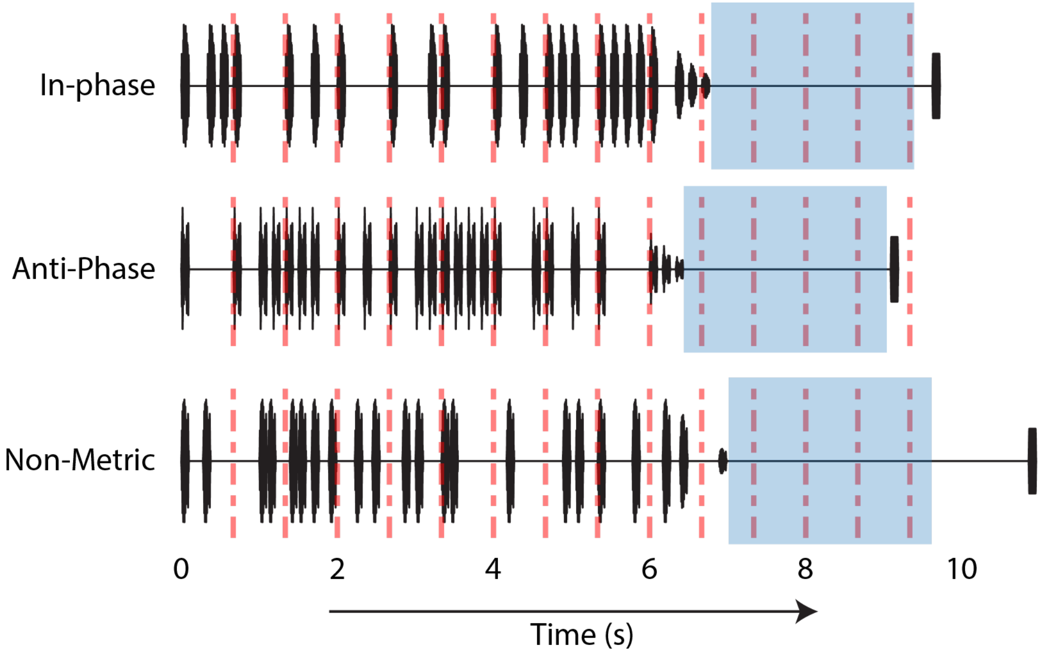

Figure 16: Waveform depiction of an example stimulus from the in-phase (*top*), anti-phase (*middle*), and non-metric (*bottom*) conditions. Light blue shaded regions indicate the time window in which EEG data was analyzed; the red vertical dashed lines indicate beat locations (or theoretical beat location in non-metric rhythms).

For the anti-phase condition, the order of intervals in each of the 60 in-phase rhythms was pseudo-randomly permuted but retained a tone onset every 666.7 ms. Thus, the anti-phase condition was similar to the in-phase condition in strength of beat percept as well as the beat frequencies (and harmonics) present in the rhythms. The characteristic that differed between in-phase and anti-phase conditions was start of the analysis window relative to the beat. In the in-phase condition, the analysis window started on the beat (i.e., one of the tones that occurred every 666.7 ms), whereas in the anti-phase condition, the analysis window started anti-phase to the beat, i.e., half way between beats.

For the non-beat condition, the order of intervals in the in-phase condition was pseudo-randomly permuted such that tones occurred on less than one-third of the “beat positions” as defined in the in-phase condition. Fewer tones in beat positions reduces the amount of evidence for a steady beat, which weakens the strength of the beat percept (Shmulevich & Povel, 2000). Therefore, nor more than three consecutive beat positions could have tones. To further prevent inducing a beat percept, consecutive repetition of any given measure (i.e., the sequence of IOIs between two consecutive beat positions) was not allowed. Lastly, to further reduce the strength of the beat percept, tone onsets were jittered in duration so that the intervals of the non-beat rhythms were no longer integer multiples of the minimum IOI. The silent period of all intervals was randomly adjusted such that 166.7 ms intervals either remained un-jittered (166.7 ms) or were made 33% longer (221.7 ms), 333.3 ms and 500 ms intervals remained un-jittered, were made 33% shorter (223.3 ms and 335.0 ms, respectively), or were made 33% longer (443.3 ms and 665.0 ms, respectively), and 666.7 ms intervals either remained un-jittered or were made 33% shorter (446.7 ms). The overall lengths of each non-beat rhythm were checked to ensure they were the same length as the beat rhythms.

In all conditions, a 666.7 ms linear offset ramp was applied to the end of the stimulus in each trial during which the amplitude of the tones was gradually reduced to 20% of the normalized amplitude of the rest of the tones (Figure 16). The amplitude reduction at the end of each trial was applied to attenuate any evoked response related to participants realizing rhythm abruptly stopped.

4.2.3 Tasks & Procedure

After giving informed consent, participants completed a demographic questionnaire which contained questions pertaining to the participants' previous musical experience. The individual hearing threshold for each participant was then determined using a method of limits approach (Leek, 2001), followed by the EEG portion of the experiment. During EEG recording, participants were seated in a sound attenuated chamber, in front of a computer screen. The participants were instructed to avoid moving his or her body, and to focus on a fixation dot during recording. The auditory stimuli were presented 50 dB above individual hearing threshold (i.e. sensation level) over head phones.

The experiment was divided into 12 blocks (~4.5 min per block), with a break between each block. Blocks contained 15 trials from one stimulus condition and were counterbalanced across participants. On average each trial was 18 s long and consisted of three parts: a listening period (~10 s) in which the rhythm played, a continuation period (~4 s) during which the volume of the rhythm faded out (.666 s), and participants continued the beat in their heads, and a response period (~ 4 s). The length of rhythms in the listening phase varied between 7 and 13 s. We randomized the length of the listening period so that participants would not be able to anticipate when the rhythm would fade out. The fade out was always one "beat" in length (666 ms) and was followed by a silent period of between 3 and 5 s which ended with the participants hearing a pure tone beep (Figure 16). We randomized the length of the silent period to accomplish two things: participants could not anticipate the timing of the tone, and tone was not be systematically on/off beat, which might advantage percept in one rhythmic condition more than another. Participants were told that the timing of the beep was unrelated to the beat in the rhythms, and not to use the timing of the beep as an indication of how well they were able to continue the beat during the continuation period. Participants were instructed to remain as still as possible during the listening and continuation period. After the ‘end-of-trial’ beep, in the response period, participants rated, on a scale of 1 – 9, how easy was it to continue the beat through the silent period (1 = very difficult, 9 = very easy).

4.2.4 Data Analysis

4.2.4.1 Ratings Analysis

Ease of continuation ratings were used as a manipulation check to ensure that participants felt the beat more strongly in the two beat conditions compared to the non-beat condition. To answer this question, we entered the ease of continuation ratings (which had been averaged across trials in each rhythm condition) into a 1 x 3 repeated measures ANOVA with rhythm condition (in-phase, anti-phase, and non-beat) as a factor.

4.2.4.2 EEG recording

EEG was recorded from 64 Ag-AgCl electrodes (BioSemi, Amsterdam, The Netherlands), mounted in a cap according to the 10-20 system and additional electrodes at both mastoids. Signals were recorded continuously with a passband of DC to 400 Hz and digitized at a sampling rate of 1024 Hz. Electrode voltage offsets were kept below 25 kΩ.

4.2.4.3 EEG analysis

EEG data were analyzed offline using Fieldtrip software (Oostenveld et al., 2011) and custom Matlab (Mathworks, USA) scripts. The EEG data were first re-referenced to the averaged mastoid reference. The then high-pass filtered (.65 Hz, 11792 points, Kaiser window) and low-pass filtered (42 Hz, 90 points, Hann window). The data were then divided into epochs (-1.5 to 3.5 s, relative to the onset of the analysis window), before being down sampled to 256. Next the epoched data were submitted to ICA (runica; Delorme, Sejnowski, & Makeig, 2007). Components reflecting artifacts were identified (by visual inspection) and removed to avoid rejecting a large proportion of trials in the signal-range artifact rejection procedure following ICA. Epochs were excluded if the signal range was larger than 120 mV in any of the electrode channels. Only data from this preprocessing pipeline were used in the subsequent analyses.

4.2.4.3.1 Power

Time frequency decomposition was performed on the preprocessed data using a Morlet Wavelet convolution as implemented in fieldtrip (Oostenveld et al., 2011). Wavelets were 3 cycles and ranged from 0.5 Hz to 10 Hz in steps of 0.25 Hz, with a time range of 0 – 1.3 s in steps of 0.01 s. For statistical comparison, a 3 * 3 repeated measures ANOVA was performed on the power values, with Rhythmic Context (In-phase, Anti-phase, Non-beat) and Frequency (1.5, 3, and 6 Hz) as factors. Any violations of sphericity were corrected using the Greenhouse-Geiser method. Simple effects analysis of Rhythmic Context at each Frequency was performed by conducting separate 1 x 3 repeated measures ANOVA. Significant simple effects were followed up by conducting *post hoc* pairwise comparisons. False discovery rate correction (Benjamini & Hochberg, 1995) was used to corrected for multiple comparisons.

4.2.4.3.2 Phase

Phase angle of the time-frequency data at each time point was computed using the complex Fourier coefficients which were output from the previous wavelet analysis. The Fourier coefficients for each participant were first averaged across trials within each condition before being converted to phase-angle time series. The phase difference between the beat-rate oscillation in the in-phase and anti-phase condition was then computed as the circular distance between the phase angles, using the “circ_dist” function in Matlab (Berens, 2009; Berens & Valesco, 2009). The circular distance scores for all participants were then submitted to a Wilcoxon-signed rank test which compared the mean difference between conditions to zero (indicating no phase difference between oscillations), and 180° (indicating maximally different oscillatory phase).

4.3 Results

4.3.1 Continuation Ratings

To investigate whether the different rhythm conditions did indeed induce the intended changes in perceived beat strength, participants rated how easily they were able to continue the beat in their heads through silence. The ratings from each participant were averaged across trials for each rhythmic condition before being submitted to a 1 x 3 repeated measures ANOVA with rhythm condition (in-phase, anti-phase, and non-beat) as a factor. Ease of continuation ratings differed significantly between rhythmic conditions, $F(1.01, 26.40) = 62.26$, $p < .001$, $\eta^2 = .71$, with a beat being more easily maintained throughout the silence in the in-phase ($M = 6.78$, $SE = 0.27$) and anti-phase ($M = 6.90$, $SE = 0.26$) conditions than non-beat condition ($M = 3.68$, $SE = .29$), $t(25) = 7.89$, $p < .001$, and $t(25) = 8.04$, $p < .001$, respectively. Ratings between the in-phase and anti-phase conditions did not differ significantly, $t(25) = 1.00$, $p = .335$ (Figure 17). These results confirm that the manipulation of beat strength had the intended effect on participants' beat perception. Specifically, the beat percept was much weaker for the non-beat rhythms, and there was no difference in beat strength between the in-phase and anti-phase conditions.

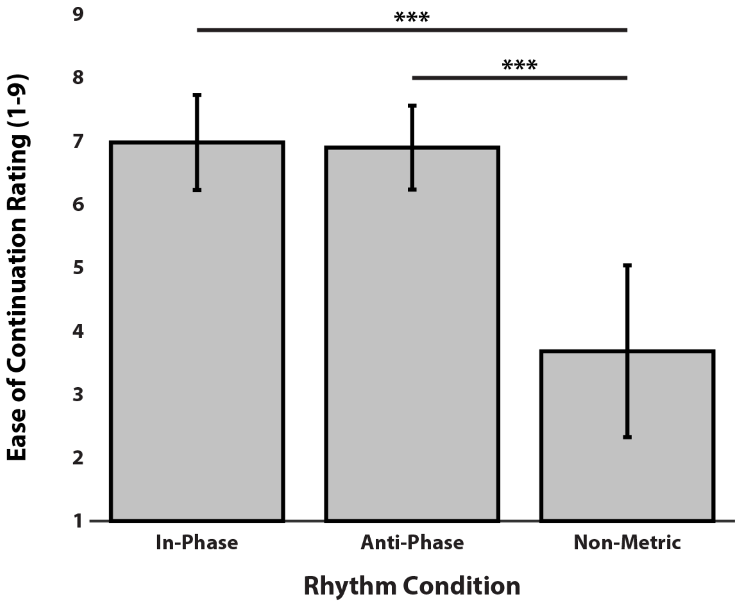

Figure 17: Ease of continuation ratings indicating how easily participants continued the beat through silence; Error bars indicate +/- 1 within-subjects SEM; * indicates *p* < .001.**

4.3.2 Neural measures

4.3.2.1 Power

To examine the effect of beat percept on neural entrainment, a 3 x 3 repeated measures ANOVA was conducted on spectral power, with rhythm condition (in-phase, anti-phase, and non-beat) and frequency (1.5 Hz, 3 Hz, and 6 Hz) as factors. The ANOVA revealed a significant main effect of frequency, $F(1.29, 32.15) = 76.34$, $p < .001$, $\eta^2 = .75$, with greater power at lower frequencies, as is typically observed in EEG spectra (Figure 18). Although numerically there was greater spectral power in the silence after beat rhythms (both in-phase [$M = 0.20$, $SE = .01$], and anti-phase [$M = .02$, $SE = .01$]) than in the silence after non-metric rhythms ($M = .18$, SE .01), neither the main effect of rhythm, $F(2, 50) = 0.94$, $p = .398$, $\eta^2 = .04$, nor the interaction between rhythm and frequency, $F(2.01, 50.14) = 1.04$, $p = .362$, $\eta^2 = .04$, were significantly different statistically. Despite failing to provide statistical support, the pattern of spectral power between rhythmic conditions suggests a promising relationship between neural entrainment and beat perception. Specifically, that rhythms with a strong beat may elicit a stronger entrained neural response, compared to non-beat rhythms, that continues to oscillate into the silence after rhythmic stimulation has stopped.

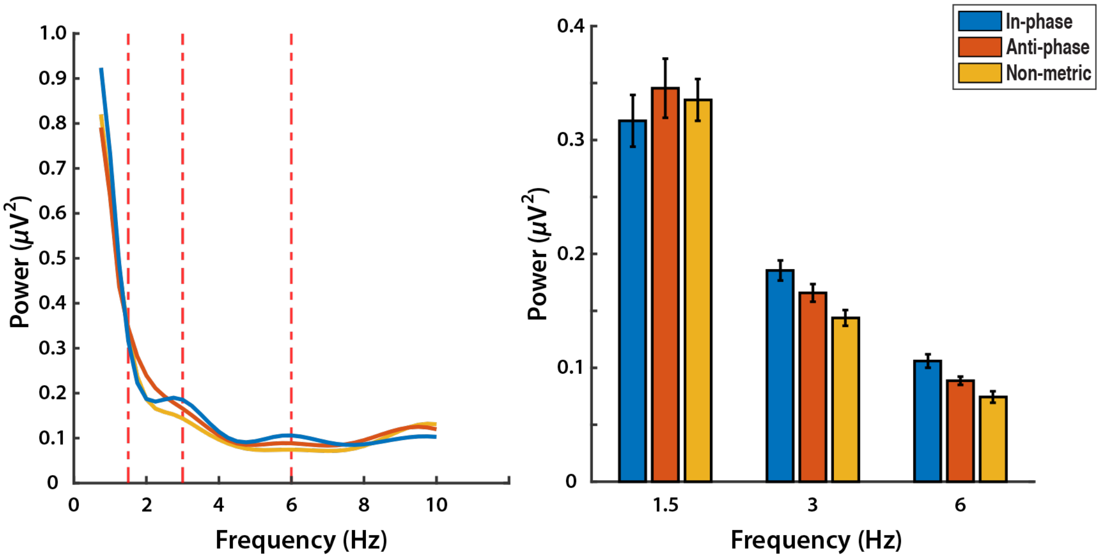

Figure 18: (*left*) Power spectrum of EEG during silent period immediately after rhythm perception; (*right*) Power at beat related frequencies, indicated by dashed red lines in *left*; Error bars indicate +/- 1 within-sujbects SEM.

4.3.2.2 Phase

To test for phase differences between the in-phase and anti-phase conditions at 1.5 Hz, first the evoked phase of the 1.5 Hz oscillation was calculated by averaging the complex Fourier coefficients across in-phase trials and anti-phase trials for each participant (Figure 19a). The circular distance between the phase of the two conditions for each participant (Figure 19b) then was computed using the "circ_dist" function from the "CircStats" toolbox (Berens, 2009; Berens & Valesco, 2009) in Matlab (Mathworks). A one-sample Wilcoxon signed rank test was used to test whether the median circular distance between the phases of the two rhythmic context conditions differed from zero (a significant test indicates phase differences between in-phase and anti-phase rhythmic conditions). The phase did differ significantly between the in-phase and anti-phase condition, $Z(25) = 4.46$, $W(25) = 351$, $p < .001$ (Figure 19). However, the results of a second Wilcoxon signed rank test revealed that the phase difference between the in-phase and anti-phase conditions was also significantly different from the predicted 180°, $Z(25) = -4.46$, $W(25) = 0$, $p < .001$. Taken together, the results of the two Wilcoxon tests suggest that although a relationship between beat location and specific phase of a neural oscillation may exist, other factors may also affect the persistence of the entrained oscillations through silence.

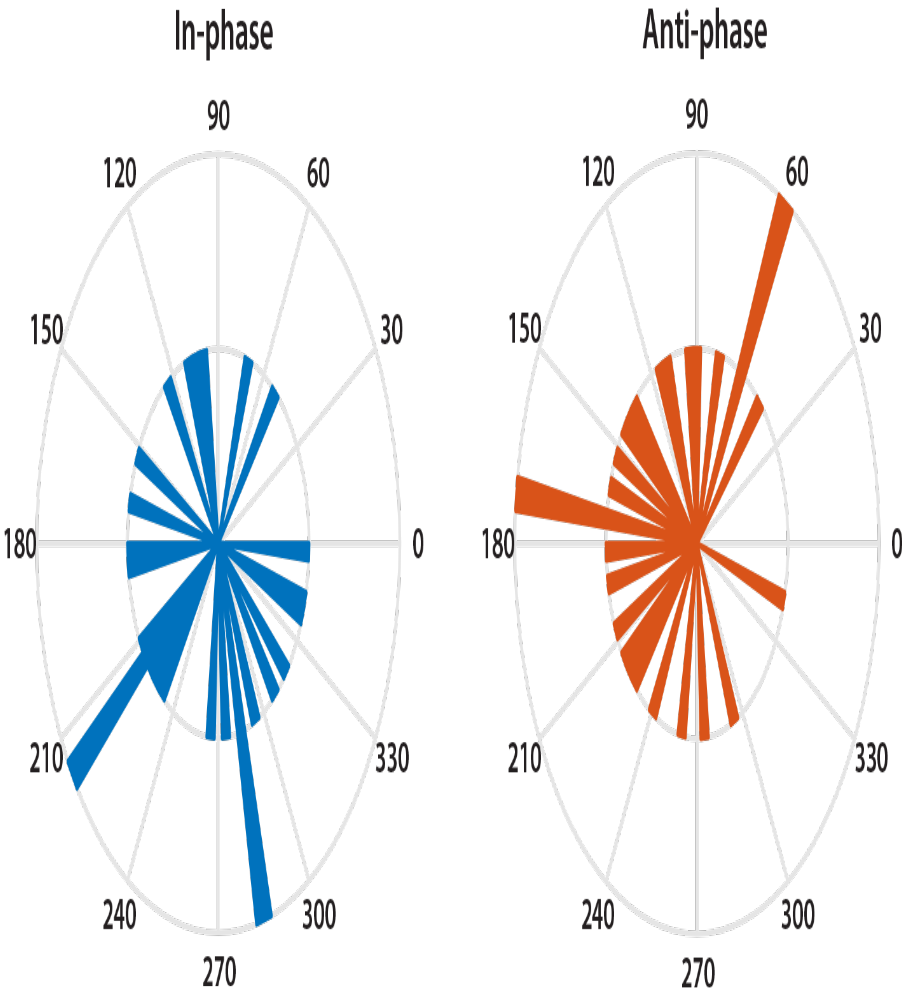

Figure 19: Circular histograms of 1.5 Hz (beat rate) oscillation during the common sequence, in all plots longer bars indicate more participants with that phase angle/difference; *a*) raw phase angle for each participant in the in-phase (*left*) and anti-phase (*right*) context; *b*) phase differences between rhythmic conditions in *a*) with the red line indicating mean phase difference.

4.3.3 Correlations between neural entrainment and behavioural measures

4.3.3.1 Neural entrainment and ease of continuation ratings

To explore the relationship between neural entrainment and ease of beat continuation a series of bivariate linear regression analyses were run, with spectral power at each beat frequency (1.5 Hz, 3 Hz, and 6 Hz) as the criterion variable and ease of continuation ratings as the predictor variable. For each participant, ratings from each trial were used to predict spectral power at each beat frequency. The resultant beta values at each frequency were then submitted to separate Wilcoxon signed rank tests. The results showed that spectral power was not predicted, at any beat frequency, by ease of continuation ratings, Zs < 0.51, Ws < 181, ps >. 603. Thus, the behavioural measure of beat strength did not predict the degree of neural entrainment during silence.

4.3.3.2 Neural entrainment and musical experience

To examine the relationship between musical training and entrainment, a series of bivariate regressions were conducted for each rhythmic condition (in-phase, anti-phase, and non-beat) at each beat frequency (1.5 Hz, 3 Hz, and 6 Hz) with spectral power as the criterion variable and years of musical training as the predictor variable. Musical training did not predict spectral power for any of the three rhythmic conditions at either 1.5 Hz (all $R^2 < .05$, $Fs(1, 24) < 1.35$, ps > .257), or 3 Hz (all $R^2 < .07$, $Fs(1, 24) < 1.68$, ps > .207). However, the number of years of musical training was predictive of spectral power in all three rhythmic conditions at 6 Hz (all $R^2 > .20$, $Fs(1, 24) > 6.08$, $p < .021$). Although not present at the anticipated beat frequencies of 1.5 and 3 Hz, these findings suggest a relationship between neural entrainment at 6 Hz and years of musical training (Figure 20). Specifically, participants with more musical training appear to entrain more to the note onset rate than participants with less musical training.

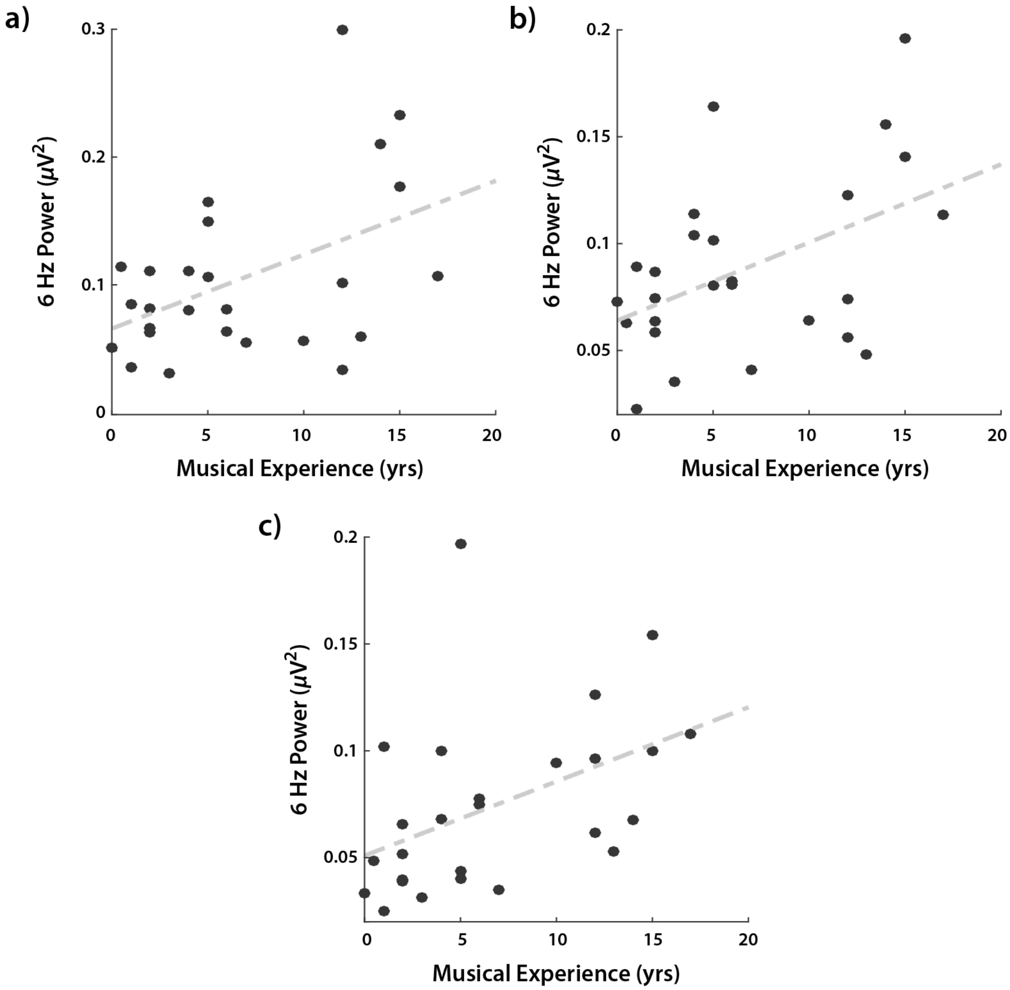

Figure 20: Correlations between neural entrainment at 6 Hz (tone onset frequency) and years of musical train in the in-phase (*a*), anti-phase (*b*), and non-metric (*c*) conditions.

4.4 Discussion

4.4.1 Continuation ratings

Participants' ratings of how easy it was to continue the beat were higher for strong beat rhythms (i.e., in-phase and anti-phase rhythms) than non-beat rhythms (Figure 17) indicating that the beat strength manipulation was successful. Unsurprisingly, ratings between in-phase and anti-phase conditions did not significantly differ, as both of these conditions were constructed to have a strong beat, and the difference between them only refers to whether the onset of the silent period coincides with the beat (in-phase) or half-way between beats (anti-phase). Although ease of beat continuation is not the most common measure of beat strength, it was appropriate here in order to index participants' experience during the period of interest—the silence after the rhythm. Furthermore, a behavioural pilot study (not reported here) found an almost perfect correlation between a more common measure—ratings of beat strength during the rhythm—and the ease of continuation ratings during silence, suggesting that ease of continuation is similar to more traditional measures.

4.4.2 Power

Power at the beat frequencies during the silent period was stronger during beat than non-beat conditions, however, these differences were not statistically significant. The power differences, although nonsignificant, were observed at 3 Hz and 6 Hz (Figure 18), suggesting that entrainment occurred at those frequencies, consistent with our original predictions, but not reliably enough to be significant. The pattern of beat and non-beat differences was as predicted, and the same sample size was sufficient to detect differences during a stimulus being played (Chapter 3), but perhaps was insufficient for differences that occurred during silence. It is also possible that participants' internal continuation of the beat was too weak during silence to be detected by our paradigm. Finally, we must consider the possibility that beat perception does not arise from neural entrainment.

An alternate theory about why greater power has been observed at beat-related frequencies in the power spectra is that attention enhances the evoked response to on-beat tones compared to off-beat tones (Barnes & Jones, 2000; Jones, 1976; Jones & Boltz, 1989; Large & Jones, 1999; Novembre & Iannetti, 2018), rather than beat perception entraining oscillations. If so, during silence, there are no evoked responses, and therefore nothing to be enhanced by attention, thus there would be no differences between silent periods following the beat and non-beat rhythms. The results of the current study are consistent with the possibility that increased neural power at beat frequencies reflects attentionally modulated evoked responses, and thus no beat versus non-beat differences are observed when the evoked response is removed.

Finally, it is also possible that the size of oscillatory differences during silence is much smaller than during auditory stimulation, for a variety of reasons. For example, the entrained oscillation may decay rapidly in the absence of a stimulus, with power at the entrained frequency disappearing rapidly in turn, making it difficult to detect differences in the signal. Alternatively, many people struggle to maintain a consistent imagined beat through silence, (Henry & Herrmann, 2014; C. S. Herrmann, Strüber, Helfrich, & Engel, 2016; Large & Jones, 1999; Manning & Schutz, 2013, 2015; McAuley, Jones, Holub, Johnston, & Miller, 2006), resulting in reduced temporal fidelity with the frequencies of interest and lower overall signal, weakening differences across trials.

4.4.3 Phase

At the beat rate (1.5 Hz), phase significantly differed between the in-phase and anti-phase conditions, as predicted (Figure 19). However, the difference was also significantly less than the 180° that would be expected by placing our target 180° apart in the anti-phase relative to the in-phase condition (Busch, Dubois, & VanRullen, 2009; Henry & Obleser, 2012; Large & Jones, 1999; Stefanics et al., 2010). One possibility for the smaller phase difference is that during the silence, the periodicity of the oscillation returns to the endogenous rate of the oscillator. Neural oscillators have their own endogenous (i.e., spontaneous) periodicity in the absence of external stimulus (Large, 2008; McAuley et al., 2006; Obleser et al., 2017). During entrainment, the periodicity adjusts to match that of the external stimulus (Baltus & Herrmann, 2015, 2016; Large, 2008). However, when the external stimulus ceases, the periodicity of the entrained oscillator gradually returns to the endogenous rate. The rate of return is called the decay rate. In the current study, the oscillations may have decayed very rapidly, or the decay rate may have differed across individuals, or even across trials, which may have affected calculations of phase when time-locking across trials. Thus, the findings suggest that there may be a relationship between oscillatory phase and beat location, but this relationship was not as expected. Previous research has shown that many factors, such as age (Drake, Penel, & Bigand, 2000; Henry et al., 2014; McAuley et al., 2006) or musical ability (Strait et al., 2012), are related to the ability to accurately continue a beat though silence, which may also affect the persistence of entrained oscillations through silence.

4.4.4 Regressions

A linear regression analysis failed to detect a relationship between beat continuation ratings and neural spectral power at any of the predicted frequencies. The most obvious reason for this is because the neural power at the beat frequencies wasn't significantly different between the three silence conditions. Thus, although the continuation ratings differed, the power at beat frequencies did not, and no relationship exists.

Thus, the regression failed to support neural entrainment as a neural mechanism of beat perception. There are a few possible explanations for why we did not observe a relationship even though one might exist. For example, continuation ratings only gauge how easily participants think they were able to continue the beat, not how accurately they did so. Once the rhythm faded out, participants' accuracy in maintaining the beat rate may have reduced without their awareness (Henry et al., 2014; Manning & Schutz, 2013, 2015). Altering the rate could affect the oscillation frequency of the entrained response (or vice versa) without affecting beat strength for the participant. This alteration could shift the frequency of the entrained response, causing wider, less pronounced peaks in the neural power spectrum (neural spectrum figure), compared to the narrow, sharp peaks that have been reported previously (Cirelli et al., 2016; Lenc et al., 2018b; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011, 2012a). This could be especially problematic in a regression analysis if the rate at which participants shifted beat rates during the silence varied from condition to condition, or from rhythm to rhythm while the ratings stayed constant. Future studies could include a measure of how accurately, in addition to how easily, participants were able to maintain the beat throughout silence.

Years of musical experience, although not predictive of spectral power at the beat frequencies (i.e., 1.5 or 3 Hz), did predict spectral power at the stimulus onset rate (i.e., 6 Hz). Specifically, participants with more musical experience appeared to entrain to the note onset rate more than participants with less experience (Figure 20). This relationship between musical experience and entrainment at the note rate is in line with previous findings that musicians are better able to discriminate the timing of single events within a rhythmic sequence (Jones & Yee, 1997; Rammsayer & Altenmüller, 2006; Yee, Holleran, & Jones, 1994). Indeed, maintaining a consistent tempo throughout silence is an important skill for musicians to have, particularly for musicians who play in large groups. This relationship between musical experience and entrainment at the note onset rate may reflect a potential neural mechanism for their superior performance. These findings are consistent with previous studies that have shown that musicians have less variable neural responses than non-musicians (Musacchia, Sams, Skoe, & Kraus, 2007; Strait & Kraus, 2011; Strait et al., 2012).

4.4.5 Conclusions

Overall, the results of the studies described in this thesis provide some evidence to support the idea that neural entrainment is reflected in the spectral power of the EEG signal and may be a neural correlate of beat perception (Lakatos et al., 2008, 2005; Large, 2008; Lenc et al., 2018a; Nozaradan et al., 2011, 2012a, 2018). These findings are relevant to the recent debate that has arisen over whether changes in neural power spectra reflect differences in entrainment, or differences in attention/prediction modulated evoked responses (Keitel, Quigley, & Ruhnau, 2014; Novembre & Iannetti, 2018; Zoefel et al., 2018). Overall, the pattern of spectral power may suggest a relationship between neural entrainment and beat perception, but without statistically robust evidence, further work remains to be done to determine whether entrainment of neural oscillators is a possible neural mechanism of beat perception (Large, 2008; Large & Jones, 1999; Large & Palmer, 2002; Nozaradan et al., 2011, 2012a; ten Oever et al., 2017).

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Chapter 5

5 General Discussion

5.1 Summary of Thesis

The ability to perceive a steady pulse in musical rhythm, called beat perception, is a uniquely human ability (Bispham, 2006; Hoeschele et al., 2015), which is present across all cultures from early in life (Phillips-Silver & Trainor, 2005; Trainor, 2009; Trehub et al., 2018; Zentner & Eerola, 2010). Not only does beat perception allow for activities such as dancing and making music with a group, the ability to perceive a beat also confers perceptual advantages, like being better able to discriminate between two rhythms (Grahn & Brett, 2007). Despite being a ubiquitous part of the "human experience", little is known about the underlying neural mechanisms that give rise to beat perception.

Recently, neural entrainment/resonance theories (Lakatos et al., 2007, 2013, 2005; Large & Jones, 1999; Large & Snyder, 2009; Lenc et al., 2018a; Nozaradan et al., 2011, 2012a; Obleser et al., 2017; Snyder & Large, 2005) have risen in popularity as a potential neural mechanism of beat perception. These theories suggest that cyclic changes in the excitability of populations of neurons entrain to (i.e., synchronize with) the events of a predictable external stimulus such that the events of the stimulus occur during times of maximal neural excitability (Calderone et al., 2014; Henry et al., 2014, 2016; Henry & Obleser, 2012; C. S. Herrmann et al., 2016; Lakatos et al., 2007; Schroeder & Lakatos, 2009; Wilsch et al., 2015). Applied to a musical rhythm, these theories suggest that beat perception is related to neural populations that not only entrain to, but resonate (i.e., non-linearly enhance power) at the frequency of the beat (Breska & Deouell, 2017; Large, 2008; Large & Jones, 1999; Large & Snyder, 2009; Nozaradan et al., 2011, 2012a).

The goal of this thesis was to better understand how neural entrainment is related to beat perception. The work here built on other studies using frequency-domain representations of EEG data to investigate changes in neural power spectra related to beat perception (Chemin et al., 2014; Cirelli et al., 2016; Nozaradan, Mouraux, et al., 2016; Nozaradan et al., 2011; Tal et al., 2017). Generally, previous studies found greater relative power at beat-related frequencies in neural spectra than stimulus spectra, suggesting a power enhancement may be related to beat perception. However, the neural signal recorded at the scalp is the sum of at least two components: one that reflects the brain's response to a sound irrespective of the context in which the sound was presented (i.e., the stimulus-driven response), and an additional component that reflects the capacity of that sound to entrain naturally occurring (i.e., endogenous) rhythmic oscillations in brain activity to the beat of the stimulus (i.e., the entrained response) (Henry et al., 2017). Although these two types of responses are conceptually separable, the degree to which basic acoustic characteristics, which may affect the stimulus-driven response (Alain et al., 1997; Hillyard & Picton, 1978; Kushnerenko et al., 2001; Muller, 1973; Onishi & Davis, 1968; Picton et al., 1978a, 1978b; Schweitzer, 1977; Schweitzer & Tepas, 1974), may influence the neural response remains unknown, despite implications for interpreting the role of entrainment in beat perception. Thus, to accurately assess the entrained component of the neural response, we designed a series of studies to characterize, isolate, and lastly remove the stimulus-driven response from the neural signal.

The goal of the first study was to characterize the effect of differing beat strength and acoustic characteristics of the stimulus on the neural power spectrum at beat frequencies. If rhythms that induced a stronger beat percept also better entrained oscillatory brain activity, then beat strength should be related to power at the beat frequency. However, because the neural response reflects the stimulus driven response as well as the entrained response, basic acoustic characteristics, such as tone duration and onset/offset ramp, may also influence the power spectrum of the neural signal. Thus, we designed a series of three experiments in which we manipulated the beat strength of musical rhythms, the duration of the tones that comprised the rhythms, and the onset/offset ramp duration of the tones in the rhythm. The results of this study showed power at beat frequencies in the neural signal was related to beat strength and tone duration but was not to ramp duration. Although, the finding that spectral power is related to beat strength supports previous literature (Chemin et al., 2014; Cirelli et al., 2014; Fujioka et al., 2008a, 2009; Large & Snyder, 2009; Nozaradan et al., 2017, 2012a), this study was the first to examine the effect of tone and ramp duration on spectra power at beat frequencies. That tone duration affects power at beat frequencies in the EEG signal but does not affect perceived beat strength has been demonstrated behaviourally (Henry et al., 2017) and indicates that one cannot equate differences in power and differences in beat perception.

The second study described here was designed with two main goals. The first goal was to build on the findings of the first study, by isolating the entrained response from the stimulus-driven response in the neural signal to better examine how differences in the entrained response related to beat perception. To accomplish this, we created a series of musical rhythms which had either a strong beat or no beat, and embedded a common rhythmic sequence, to which we confined our analyses, in all the rhythms. Overall, power at beat frequencies was higher when the common sequence was embedded in strong-beat rhythms than non-beat rhythms. Furthermore, because the stimulus was identical in all conditions, so too was stimulus-driven response, therefore the difference in spectral power is most likely the result of differences in the entrained response. Our finding of greater entrainment to strong-beat stimuli than non-beat stimuli is consistent with previous literature suggesting a relationship between beat perception and neural entrainment (Cirelli et al., 2014; Fujioka et al., 2009; Large & Snyder, 2009; Nozaradan et al., 2012a; Snyder & Large, 2005).

The second goal of the second study was to examine the relationship between the timing of the beat and the phase of the entrained neural oscillation. To accomplish this, the common sequence was embedded in the strong-beat rhythms such that the common sequence either started on a beat (i.e., in-phase), or halfway between beats (i.e., anti-phase), with the prediction that the phase of the entrained oscillation should be maximally different (i.e., 180°) on the beat, compared to halfway between beats (Calderone et al., 2014; Lakatos et al., 2007, 2005; Large & Palmer, 2002; Large & Snyder, 2009; Nozaradan et al., 2012a). The results showed that although the phase of the entrained oscillation in the in-phase placement significantly differed from the anti-phase placement, the phase difference between the two contexts was also significantly smaller than the 180° that "idealized" models of neural entrainment might predict. Potentially, the stimulus-driven response, which was identical in both conditions, made the phase of the neural response in both conditions more similar (i.e., less than 180° different) than entrainment theories predict. That is, longer latency components of the ERP response (approx. 450-550 ms) (Alain et al., 1997; Hillyard & Picton, 1978; Kushnerenko et al., 2001; Muller, 1973; Onishi & Davis, 1968; Picton et al., 1978a, 1978b; Schweitzer, 1977; Schweitzer & Tepas, 1974) may have influenced observed phase of the neural signal. Thus, although the finding that phase in the two contexts differs supports the idea that neural entrainment relates to beat perception, the finding that the phase difference is less than 180° suggests that the neural signal may reflect a mix of the neural oscillation in the entrained response and the ERP of the stimulus-driven response. These findings demonstrate that although the power analysis supports a relationship between neural entrainment and beat perception, the phase analysis may demonstrate the need to remove the stimulus-driven response altogether to better observe how the timing of the entrained response is related to beat perception.

The third study described here was designed to remove the stimulus-driven response neural signal, leaving only the entrained response, by analyzing EEG data collected during a silent period after a musical rhythm. The rhythms preceding the silence either induced a strong beat percept, or no beat percept, and silences in the strong beat conditions either started on a beat (in-phase), or between beats (anti-phase). This design allowed analysis of entrainment differences between strong-beat and non-beat rhythms, and analysis of specific phase of the entrained oscillation, in the absence of the stimulus driven response. We predicted that the silence after strong-beat rhythms should contain more power at the beat frequencies than the silence after non-beat rhythms (Cirelli et al., 2014, 2016; Fujioka et al., 2008a, 2009; Henry & Herrmann, 2014; Henry et al., 2014; Henry & Obleser, 2012; Lakatos et al., 2008, 2013; Large, 2008; Large & Jones, 1999; Large & Palmer, 2002; Lenc et al., 2018a; Nozaradan et al., 2011, 2012a, 2018; Obleser et al., 2017; Schroeder & Lakatos, 2009; ten Oever et al., 2017). Although there was numerically more power at beat frequencies during the silence after strong-beat than non-beat conditions, the difference was not significant. The lack of significant difference between the strong-beat and non-beat conditions in the absence of an evoked response may suggest that, in previous studies, the differences in neural spectral power at beat frequencies could reflect modulation of evoked responses to the stimuli in those studies (Barnes & Jones, 2000; Jones, 1976; Jones & Boltz, 1989; Large & Jones, 1999; Novembre & Iannetti, 2018), rather than entrained neural oscillations. However, it is also possible that entrained oscillations decay rapidly after the rhythms stops, or that participants were unable to continue the beat through silence with millisecond accuracy, to which EEG is sensitive (Henry & Herrmann, 2014; C. S. Herrmann et al., 2016; Large, 2008; Large & Jones, 1999; Manning & Schutz, 2013, 2015; McAuley et al., 2006). Either of these possibilities would make it difficult to observe differences in the neural signal. We also predicted that the phase of entrained, beat-frequency oscillations should be maximally different (i.e., 180°) between silences that started on the beat compared to silences that started between beats (Large & Jones, 1999; Large & Palmer, 2002; Lenc et al., 2018a; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011, 2012a). Phase differed significantly between the in-phase and anti-phase conditions, but again, this difference was significantly less than the predicted 180° of "idealized" models (Large & Palmer, 2002; Large & Snyder, 2009; Lenc et al., 2018a; Obleser et al., 2017). Potential explanations of these unpredicted phase differences are discussed below, in section 5.2.2.

5.2 Integration of findings

5.2.1 Spectral Power as an Index of Beat Perception

Overall these findings provide evidence that spectral power in the EEG signal may reflect beat perception, in line with a growing body of literature (Fujioka et al., 2008a, 2009; Large, 2008; Nozaradan, 2014; Nozaradan, Mouraux, et al., 2016; Nozaradan et al., 2011). Indeed, many studies including ones presented here (Studies 1 & 2) have shown evidence that more power at beat frequencies in neural spectra may be related to stronger beat percept (Chemin et al., 2014; Cirelli et al., 2016; Lenc et al., 2018a; Nozaradan et al., 2017, 2012a). However, previous studies have compared neural spectra elicited by different rhythm sequences, which introduces the issue of how compare neural spectra across conditions that have different stimulus spectra. Each rhythmic sequence has its own spectral power profile (Henry et al., 2017; Nozaradan et al., 2012a), and Study 1 shows that the spectral profile is affected by acoustic characteristics. Therefore, examining the spectral profile does not indicate clearly what frequencies will be perceived as the beat. Previous work has sought to account for stimulus differences by comparing the magnitude of peaks in the neural spectrum, normalized by either z-score (Nozaradan et al., 2012a) or percent difference (Nozaradan, Mouraux, et al., 2016), to the magnitude of similarly normalized peaks at the same frequencies in the stimulus spectrum. Increased magnitude of beat-related peaks in the neural spectrum relative to the corresponding peaks in the stimulus spectrum has been proposed to reflect “enhancement” due to neural entrainment (Large, 2008; Nozaradan et al., 2012a). The implicit assumption of this method is that deviations in the relative magnitudes of peaks in the brain signal compared to the stimulus envelope reflect neural entrainment. That is, in the absence of beat perception, spectral power in the brain signal and stimulus envelope would represent the rhythm in a similar way across beat and non-beat frequencies. However, in Study 1, when perceptual differences were accounted for, a reliable relationship between power in the stimulus and neural spectra was only found at the primary beat frequency (1 Hz), but not at other beat frequencies (2 Hz and 4 Hz), where it would be equally expected. These findings indicate that the relationship between the stimulus spectrum and neural spectrum is not consistent across beat frequencies, and suggests that using the stimulus spectrum may not be a reliable method of accounting for stimulus differences when comparing neural spectra elicited by different rhythms. This finding has implications for how we interpret the results of both past and future studies.

In fact, our finding that tone, but not ramp, duration affects power at beat frequencies potentially has implications for comparing across studies. For example, our finding that tone duration affects power at beat frequencies independent of beat percept suggests that directly equating enhancements in neural power to stronger beat perception is potentially problematic. Most studies keep stimulus characteristics consistent across conditions, which minimizes the impact of stimulus related differences within in a study, but stimulus variations still present challenges when trying to compare findings across studies that use different stimulus characteristics. For example, the results of our first study showed power at 1 Hz was greatest for long tones, whereas power at 2 Hz was greatest for medium length tones. Thus, if different studies use different length tones, it could appear that the beat entrains neural oscillations at different frequencies in different studies even though beat strength and beat rate are the same in both.

Ramp duration did not significantly affect neural power or beat strength (Study 1) but did affect the stimulus power at beat frequencies (Henry et al., 2017). This finding is important because previous investigations account for the stimulus-driven response by performing “normalization” or subtraction procedures to remove the stimulus-driven response from the entrained response (Chemin et al., 2014; Cirelli et al., 2016; Lenc et al., 2018a; Nozaradan et al., 2012a). The difference between the stimulus-envelope spectrum and the neural spectrum is then thought to reflect the entrained response, in turn reflecting beat perception. However, Study 1 finds that ramp duration is reflected in the power at beat frequencies in the stimulus spectrum, but not in the neural spectrum. Therefore, it is unclear that the stimulus spectrum is a reliable way to subtract out or account for stimulus differences, when comparing between neural spectral patterns elicited by different stimuli. Thus, our results support other work that questions whether comparing the neural response to the stimulus envelope is straightforward to interpret (Henry et al., 2017; Rajendran & Schnupp, 2019).

In light of finding that the stimulus characteristics like tone duration affect power at beat frequencies, we should also interpret the differences in power between beat strength conditions with caution. Even though tone duration was consistent across beat strength conditions, beat strength was manipulated by changing the temporal characteristics (i.e., grouping or during of the inter-onset intervals) of the rhythms, which, similar to altering tone duration, affects power at beat frequencies in the stimulus spectrum (Henry et al., 2017; Nozaradan et al., 2012a). Thus, part of the difference in neural power between beat conditions, which is thought to reflect a difference in beat perception in this study and others (Chemin et al., 2014; Cirelli et al., 2016; Lenc et al., 2018a; Nozaradan et al., 2017, 2012a), could also be the result of the differences in the stimulus-driven response. Therefore, interpretations of differences in neural spectral power must be made with caution, as accounting for the effects of stimulus differences on neural spectral differences is complex. Taken together, the results of the first study demonstrate that, although differences in beat strength may be reflected in the neural power spectra, so are differences in stimulus characteristics, and it is not clear how to account for the effect of stimulus characteristics. Therefore, to avoid the potential for confusing stimulus-related spectral differences and beat-related spectral differences, one approach is to isolate the entrained response from the stimulus-driven response.

To isolate the entrained response from the stimulus-driven response, our second study induced beat perception with a rhythmic context, but confined analysis of the neural signal to a common rhythmic sequence embedded in all conditions. As the stimulus was identical in all rhythmic contexts, the stimulus driven response was identical in conditions, and power differences should reflect differences in beat perception, not the stimulus. This is the first study to embed a common rhythm sequence across conditions, but not the first study to examine how changes in percept of the same rhythm affect the neural response (Chemin et al., 2014; Cirelli et al., 2016; Nozaradan et al., 2011). However, in the past, studies using a common stimulus have induced the beat, or changes in the beat, by asking participants to impose different groupings of isochronous tones together, or by moving along with the stimulus at different rates (Chemin et al., 2014; Cirelli et al., 2016). Although the study in which participants imposed a beat on the sequence provided a foundational demonstration that percept could be reflected in the EEG signal, imposing a beat is phenomenologically different than spontaneous beat perception naturally arising when listening to a rhythm (Demany & Semal, 2002; Povel & Essens, 1985). Furthermore, differences in beat percept induced by movement to a common stimulus are also phenomenologically different than natural beat perception, because motor synchronization with a stimulus affects the way that a stimulus is perceived, in both musical rhythm and speech (Falk & Dalla Bella, 2016; Manning & Schutz, 2013, 2015; Phillips-Silver & Trainor, 2007; Repp, 2005b; Repp & Su, 2013; Su & Pöppel, 2012). Therefore, the findings presented here are the first to examine the relationship between neural power and beat perception in a way that allows for the beat percept to arise naturally.

Although the first two studies found evidence that differences in beat perception relate to neural oscillatory differences, the third experiment, which examined the persistence of neural oscillations in silence, failed to detect significant differences in spectral power between the strong beat and non-beat contexts. Although the failure to find statistically robust differences does not support the relationship between neural entrainment and beat perception, the entrained response may be too subtle to be reliably detected in the absence of an ongoing rhythm. In line with this idea, although non-significant, numerically greater power was observed at 3 Hz and 6 Hz after strong-beat rhythms than non-beat rhythms (see figure 18), suggesting that entrainment may have occurred at those frequencies, but that the sample size was not sufficient to reliably detect the difference between the conditions.

5.2.2 Phase

Entrainment theories predict a specific relationship between a stimulus onset and the phase of an entrained neural oscillation when that onset occurs. Specifically, entrainment, by definition, is when the period and phase of an endogenous neural oscillation adjust to synchronize with a predictable stimulus, such that the stimulus occurs during the most excitable phase of the oscillation (B. Herrmann et al., 2016; Lakatos et al., 2007, 2008; Large, 2008; Large & Jones, 1999; Nozaradan et al., 2011; Schroeder & Lakatos, 2009) Therefore, we would expect the phase of the entrained oscillation to be maximally different (i.e., 180°) when comparing on the beat to halfway between beats (Busch et al., 2009; Henry & Obleser, 2012; Large & Jones, 1999; Stefanics et al., 2010; Zoefel & VanRullen, 2016). Two of the studies described here set out to test this prediction. In both studies, even though the phase of the beat frequency oscillation (i.e., 1.5 Hz) was significantly different between the in-phase and anti-phase conditions, the phase difference between the conditions was also not maximally different (i.e., 180°) as predicted.

Despite the phase not being as different as predicted, these data do show evidence that differences in oscillatory phase may have existed, particularly in Study 2. An alternate explanation for why greater power is observed at beat frequencies in the neural spectrum is that attention enhances the evoked responses of on-beat tones compared to off-beat tones (Barnes & Jones, 2000; Jones, 1976; Jones & Boltz, 1989; Large & Jones, 1999; Novembre & Iannetti, 2018). However, if this were true, and beat perception was not related entrainment of neural oscillations but rather was the result of enhancement of evoked responses, because the stimulus was identical in both conditions, the pattern of evoked responses would also identical, and thus the phase of the neural signal would be identical too. However, our results show a significant difference in the phase of the neural signal that attentional enhancement theories do not predict. Therefore, it is likely that beat rate oscillations are responsible for the observed difference in phase of the neural signal.

We also observed consistent phase differences in Study 3. Although, they are less than the 180° than predicted the fact that phase does differ between the two conditions is evidence against the idea of beat perception being the result of enhanced evoked responses. If beat perception were the result of attentionally modulated evoked responses (Barnes & Jones, 2000; Jones, 1976; Jones & Boltz, 1989; Large & Jones, 1999; Novembre & Iannetti, 2018), then beat-related neural activity would have ceased when stimulation ended, meaning that during silence, in the absence of evoked responses, neural activity would not reflect activity related to beat perception. Thus, any neural activity should be random with respect to the onset of the silence and cancel out eliminating any phase differences between conditions. However, the phase of the neural signal was systematically different during the silence, suggesting that beat-related neural oscillations may have continued after the stimulus ended.

It is probable that, in both studies, the phase differences between the two conditions are the result of entrained neural oscillations at the beat rate, and the discrepancy between predicted phase and observed phase differences are the result of the evoked response in the neural signal, or by variability in people's ability to accurately continue a beat through silences (Manning & Schutz, 2013, 2015, 2016). Thus, despite the discrepancy between theoretical predictions and the results of these studies, ultimately these data may be interpreted to support a relationship between entrainment of neural oscillations and beat perception.

5.2.3 Musician vs non-musicians

Musicians generally perform better on beat based tasks compared to non-musicians (Manning, Harris, & Schutz, 2016; Repp, 2010; Repp & Doggett, 2007). Thus, musicians may be expected to differ from non-musicians in their neural response as well. However, the data did not support this. It is possible that the lack of relationship here results from how beat perception has been measured previously. Much of the evidence of musicians showing superior performance to non-musicians has come from behavioural studies, but behavioural measures often rely on both perception and production. Musical experience may improve performance on rhythm production and even perceptually based rhythm discrimination tasks, as observed in previous studies (Grahn, 2012; Grahn & Rowe, 2009; Manning et al., 2016; Repp, 2010), but might not increase perceived beat strength in simple rhythms, such as the ones used in the current studies. This is particularly likely as the current rhythms were designed such that no expertise was required to perceive the beat. Therefore, it is possible that musical training had little effect on entrainment because the rhythms were simple enough that most participants perceived the beat, regardless of previous musical training. Potentially, the amount of music that we hear in our daily life enables non-experts to perceive beat in a simple musical rhythm.

Additionally, although there is evidence that musicians and non-musicians differ in their neural responses to rhythm (Geiser, Ziegler, Jancke, & Meyer, 2009; Musacchia et al., 2007; Strait & Kraus, 2011; Strait et al., 2012), there are key differences between the measures taken in previous studies and the measures described here. For example, previous work has found that musicians, compared to non-musicians, have higher fidelity of the frequency following response, which is recorded from the brainstem and reflects how accurately the brain follows the fine acoustic features of a stimulus (Musacchia et al., 2007; Strait & Kraus, 2011; Strait et al., 2012). However, the frequency following response is conceptually different than the cortical responses, which reflect encoding of broader structural features of a rhythm (e.g., beat), collected here. The distinction between acoustic features and structural features of the rhythm when examining the role of musical training has also been made in previous ERP research, which often finds that musicians have similar neural responses to the beat as non-musicians (Geiser et al., 2009). The differential role of musical training in the perception of acoustic versus structural features of rhythm is further supported by the current finding of a relationship between musical experience and neural entrainment was observed at the stimulus presentation rate (6 Hz), but not at beat frequencies (1.5 Hz and 3 Hz) during silence in Study 3. Specifically, people with more musical experience entrained more to the note onset rate than people with less musical experience. If musicians are better able to entrain the most excitable phase of stimulus rate oscillations to the onset of notes in a rhythm, the data presented here suggests that better entrainment may be a potential neural mechanism for the superior performance musicians have demonstrated on temporal discrimination tasks like detecting timing variations (Jones, Jagacinski, Yee, Floyd, & Klapp, 1995) and tempo changes (Drake & Botte, 1993; Schwartze & Kotz, 2013; Yee et al., 1994) in musical rhythms. However, this is purely speculative, and more testing is necessary to make that claim confidently.

5.3 Limitations and Future directions

Although we found evidence that neural entrainment is related to beat perception, we also failed to observe some of the predictions of resonance theories. For example, we observed a significant difference in the phase of beat rate oscillation when comparing in-phase and anti-phase trials. Even though this difference seems to support the relationship between neural entrainment and beat perception, we also observed that the phase difference was significantly less than the 180° that idealized entrainment theories have predicted. These findings are hard to interpret because do not fall in line with predictions of an existing theory. As previously discussed, the temporal characteristics of the common rhythmic sequence itself might have been a limiting factor in Study 2. Therefore, future studies should consider the full time-course of components in the evoked response when designing stimuli to examine oscillatory phase during stimulation. For example, measuring phase after longer inter-onset intervals in the rhythm (e.g., 750 – 1000 ms) would allow the influence of longer-latency components in the evoked response to wane before attempting to estimate phase of the neural signal.

In addition, we generally did not find relationships between musical training and neural entrainment. Although we included musical experience as a potential predictor of entrainment in each study, we did not specifically recruit for different levels of musical experience, thus limiting our ability to see training-related differences. Recruiting for extreme levels of training (no training to extensive training) could help understand how musical experience might affect neural responses.

5.4 Conclusions

Recently, studies have demonstrated that frequency-domain representation of EEG data may reflect the rate and strength of participants' perception of the beat (Chemin et al., 2014; Cirelli et al., 2016; Nozaradan, Peretz, et al., 2016; Nozaradan et al., 2011, 2012a). However, there is also discussion about the assumptions underlying the techniques used

(Henry et al., 2017; Rajendran & Schnupp, 2019), and whether beat perception arises from entrainment of neural oscillations at all (Novembre & Iannetti, 2018). The goal of this thesis was to clarify the relationship between neural entrainment and beat perception by first characterizing, then isolating, and finally removing the stimulus-driven response from the neural response to musical rhythms. Overall, the studies in this thesis demonstrate that differences in the neural power spectrum at beat frequencies can reflect differences in both perceived beat strength (Study 2) and acoustic characteristics (Study 1). The results of these studies support some of the previous conclusions about how neural entrainment is related to beat perception. However, we have also demonstrated that further research is necessary to characterize the relationship between the stimulus-driven response and neural spectral power before differences in neural spectral power can be interpreted with confidence. In conclusion, the results of the studies described here align with many theoretical predictions of entrainment theories, extends our understanding of the potential neural mechanisms of beat perception, and directly address the latest concerns/issues in the literature.

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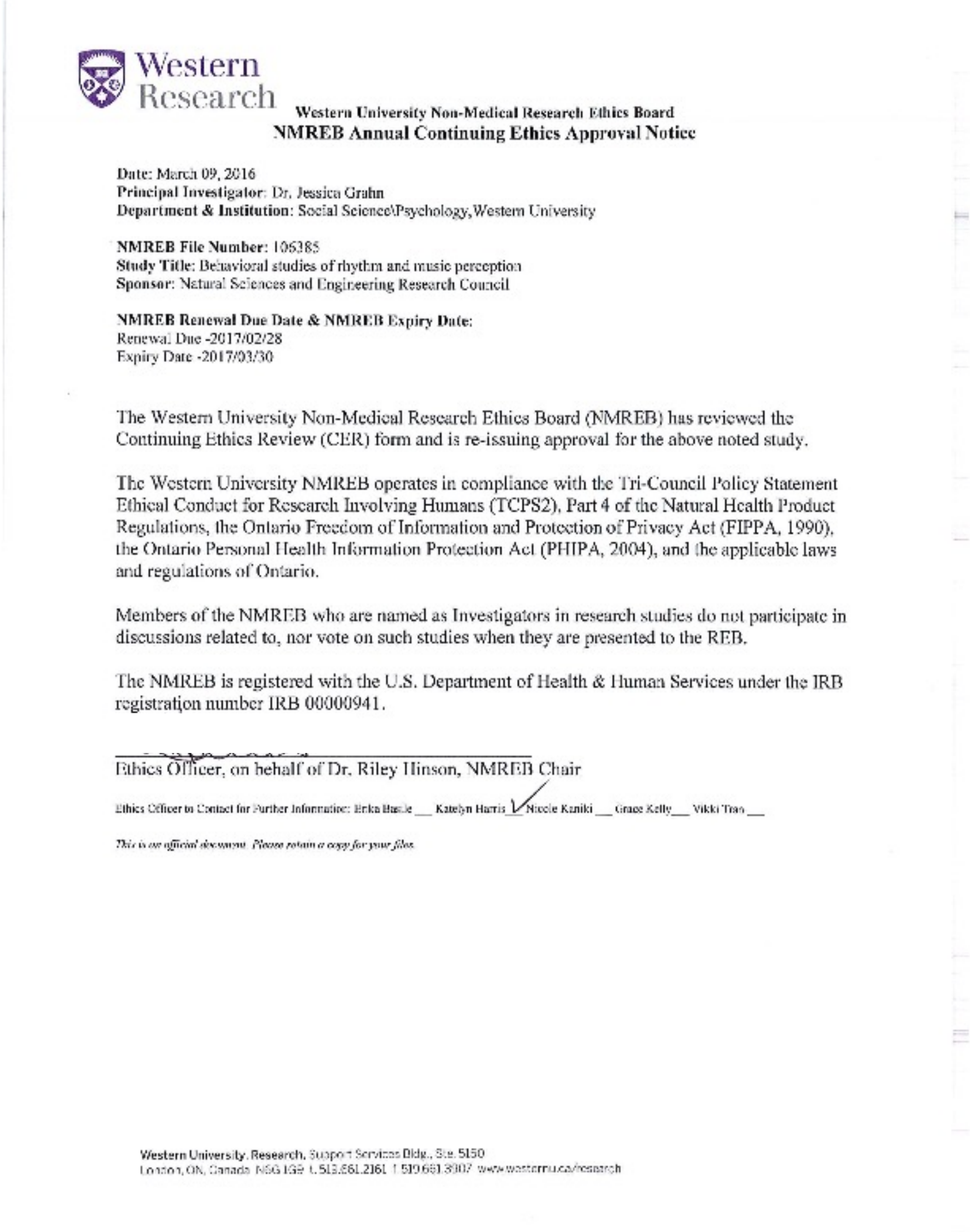
Appendices

Appendix A: Documentation of ethics approval



Western
Research

Western University Non-Medical Research Ethics Board

NMREB Annual Continuing Ethics Approval Notice

Date: March 09, 2016
Principal Investigator: Dr. Jessica Grahn
Department & Institution: Social Science\Psychology,Western University

NMREB File Number: 106385
Study Title: Behavioral studies of rhythm and music perception
Sponsor: Natural Sciences and Engineering Research Council

NMREB Renewal Due Date & NMREB Expiry Date:
Renewal Due -2017/02/28
Expiry Date -2017/03/30

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed the Continuing Ethics Review (CER) form and is re-issuing approval for the above noted study.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), Part 4 of the Natural Health Product Regulations, the Ontario Freedom of Information and Protection of Privacy Act (FIPPA, 1990), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

Ethics Officer, on behalf of Dr. Riley Hinson, NMREB Chair

Ethics Officer to Contact for Further Information: Erika Basile ___ Katelyn Harris ✓ Nicole Kaniki ___ Grace Kelly___ Vikki Tran ___

This is an official document. Please retain a copy for your files.

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London, ON, Canada N6G 1G9 t. 519.661.2161 f. 519.661.3907 www.westernu.ca/research

Curriculum Vitae

Aaron Gibbings
Department of Psychology
The Brain and Mind Institute
The University of Western Ontario

EDUCATION

Doctor of Philosophy, Psychology (expected July 2019)
Behavioural and Cognitive Neuroscience
Thesis Topic: Investigating how neural entrainment relates to beat perception by disentangling the stimulus-driven response.
Supervisor: Dr. Jessica Grahn
University of Western Ontario, London, ON

Master of Science, Psychology (August 2014)
Behavioural and Cognitive Neuroscience
Thesis Topic: How attention and beat perception modulate neural entrainment to rhythm.
Supervisor: Dr. Jessica Grahn
University of Western Ontario, London, ON

Honours Bachelors of Arts, Specialization in Psychology (May 2012)
Thesis Topic: The framing effects of language and social dominance orientation on the expression of prejudice towards non-human animals.
Supervisor: Dr. Lynne Jackson
King's University College at The University of Western Ontario, London, ON

AWARDS AND SCHOLARSHIPS

G. Keith Humphrey Memorial Award *(2017-2018)* - $650
Awarded to graduate student in Psychology or Neuroscience based on academic achievement

Rhythm Perception and Production Workshop Student Grant *(2017)* - £300
Awarded to student presenters based on strength of submitted abstract

Western Graduate Research Scholarship *(2014/2015, 2015/2016, 2016/2017, 2017/2018)* - $13,600
Awarded to eligible Doctoral students to fund research for their dissertation

NSERC Alexander Graham Bell Canada Graduate Scholarship – Master's *(2013/2014)* - $17,500
Awarded to students who demonstrate a high standard in undergraduate and graduate studies

Western Graduate Research Scholarship *(2012/2013, 2013/2014)* - $9,900

Awarded to eligible Masters students to fund research for their thesis

Ralph S. Devereux Award in Psychology *(2012)* - $1,000

Awarded to full time Masters student specializing in topics relating to Education or Children

Full-time Continuing Scholarship

2010; $2,000.00 – Average above 85% in previous academic year
2011; $1,500.00 – Average above 80% in previous academic year

Felix Giesen Award *(2011)* - $900.00

Granted to an upper year undergraduate student who balances work and school to afford his/her tuition

Dean's Honours List *(2009/2010, 2010/2011, 2011/2012)*

Cumulative academic average above 80% for the year

PUBLICATIONS

Peer reviewed

Jackson, L. & **Gibbings, A.**, (2016). Social dominance and legitimizing myths about animal use. *AnthroZoos, 29*(1), 151-160. DOI: 10.1080/08927936.2015.1082771

Gibbings, A., Grahn, J. A., (*in prep*). Neural oscillations entrained by rhythmic stimuli continue to resonate after stimulus stops.

Gibbings, A., Grahn, J. A., (*in prep*). Neural entrainment reflects beat strength when stimulus-driven response is equated.

Gibbings, A., Henry, M. J., Grahn, J. A., (*in prep*). Beat strength and sound envelope affect neural entrainment to rhythmic stimuli.

Gibbings, A., Henry, M. J., Cruse, D., Stojanoski, B. & Grahn, J. A., (*in prep*). Attention and beat perception modulate neural entrainment to rhythm.

Book Chapter(s)

Nguyen, T**., Gibbings, A.**, & Grahn, J. A., (2018). Rhythm and beat perception. In Springer Handbook of Systematic Musicology. Springer Publishing.

PRESENTATIONS

Talks

Gibbings, A., (2018). Using Musical Rhythm to separate stimulus-driven and entrained neural responses. Invited speaker at *Sleep Research* Laboratory, University of Ottawa, Ottawa, ON, Canada, November 2018.

Gibbings, A., & Grahn, J. A., (2018). The effect of beat percept on neural entrainment when the stimulus is the same. Research talk presented at *Symposium for Timing and Rhythm (STAR) Annual Conference,* London, ON, Canada, April 2018.

Gibbings, A., Henry, M. J., & Grahn, J. A., (2017). The effect of beat strength and sound envelope on neural entrainment. Research talk presented at *Neural Entrainment and Rhythm Dynamics (NERD) Workshop*. Boston, MA, USA, June 2017.

Gibbings, A., Henry, M. J., & Grahn, J. A., (2017). Investigating how changes in beat percept and sound envelope affect neural entrainment to auditory rhythms. Research talk presented at the *Symposium for Timing and Rhythm (STAR) Annual Conference*, Hamilton, ON, Canada, April 2017.

Gibbings, A., Cameron, D., Henry, M. J., & Grahn, J. A., (2016). Investigating the effect of attention on neural entrainment to simultaneous rhythms. Research talk presented at the *Symposium for Timing and Rhythm (STAR) Annual Conference* Lansing, MI, USA, April 2016.

Gibbings, A., Cruse, D., Stojanowski, B., & Grahn, J. A., (2015). Attention and presence of a beat modulate neural entrainment to rhythm. Research talk presented at the *Symposium for Rhythm and Timing (STAR),* London, ON, Canada, April 2015.

Posters

Gibbings, A., Henry, M. J., & Grahn, J. A., (2017). Investigating the effect of beat strength and sound envelope on neural entrainment to rhythmic stimuli. Poster presented at the *Rhythm Production and Perception Workshop (RPPW) 16,* Birmingham, UK, July 2017.

Gibbings, A., Henry, M. J., & Grahn, J. A., (2017). Investigating the effect of beat strength and sound envelope on neural entrainment to rhythmic stimuli. Poster presented at *The Neurosciences and Music – VI: Music, Sound, and Health,* Boston, MA, USA, June 2017.

Gibbings, A., Henry, M. J., & Grahn, J. A., (2017). Investigating how beat strength and physical envelope of an auditory rhythm affect neural entrainment. Poster presented at the *Lake Ontario Visionary Establishment (L.O.V.E.) Annual Conference,* Niagara Falls, ON, Canada, February 2017.

Gibbings, A., Cruse, D., Stojanowski, B., & Grahn, J. A., (2015). Attention and presence of a beat modulate neural entrainment to non-repeating rhythms. Poster presented at the *15th Rhythm Perception and Production Workshop (RPPW),* Amsterdam, Netherlands, July 6 – 9, 2015.

Gibbings, A., Cruse, D., Stojanoski, B., & Grahn, J. A., (2014). Attention and presence of a beat affect neuronal entrainment to rhythms. Poster presented at *The Neurosciences and Music - V: Cognitive Stimulation and Rehabilitation,* Dijon, France, May 29 - June 1 2014.

Gibbings, A., Cruse, D., Stojanoski, B., & Grahn, J. A., (2014). The effect of attention and beat salience on the steady state response to non-repeating rhythms. Poster presented at *Lake Ontario Visionary Establishment (L.O.V.E.) Annual Conference,* Niagara Falls, ON Canada, February 2014.

Gibbings, A., Stojanoski, B., Cruse, D., & Grahn, J. A., (2013). The effect of attention and beat salience on selective neuronal entrainment to non-repeating rhythms. Poster presented at the *Society for Music Perception and Cognition (SMPC) Biennial Meeting*, Toronto, ON, Canada, August 2013.

Guest Lecturer/Invited Speaker:

Psychology 3320F: Cognitive Neuroscience of Music (The University of Western Ontario)

Invited guest lecturer on electrophysiological techniques related to beat perception (2016)

Psychology 4891E*:* Honours Thesis (King's University College at Western University)

Invited panel member, discussing strategies, advice, and experience of graduate school applications, graduate degrees, and the culture of academia, for prospective graduates. (2012, 2013, 2014)

Psychology 3125G*:* The Creative Brain (King's University College at Western University)

Invited speaker on neuroimaging techniques related to beat perception. (2013)

TEACHING AND MENTORSHIP

Graduate Teaching Assistant (2012-Current) – Western University

Psychology 2032B: Psychology of Crime and Punishment

Tutoring on basic concepts and foundational theories of psychology (2019)

Psychology 2990B*:* Applications of Psychology (King's University College at Western University)

Guidance during development and feedback on proposals for applied psychology campaigns (2016/2017, 2018/2019)

Psychology 3800*:* Psychological Statistics using computers

Lab instruction, lecture supplemental course materials, teach skills for performing statistical analyses and interpreting results using computer software (e.g., SPSS, and DOS implementations) (2015/2016, 2016/2017, 2017)

Psychology 2840F/G: Behavioural Research Methods (King's University College at Western University)

Marking student research proposals, literature reviews, and proposed analyses. (2012/2013, 2014/2015, 2015/2016, 2016/2017, 2018/2019)

Psychology 1000*:* Introduction to Psychology

Marking assignments, supervisory hours, exam preparation lectures. (2015, 2018)

Psychology 3230F: Neuroscience of Music

Corresponding with students, marking assignments/exams, proctoring exams. (2014)

Psychology 2820: Research Methods and Statistical Analysis

Lecturing supplemental course material in lab sections, marking assignments, proctoring exams. (2012/2013)

Graduate Research Assistant (2013-2014) – Western University

Teaching Assistant Training Program (2012) – Western University

Completed training program offered by the Teaching Support Centre at Western to create more effective teachers.

Volunteer Teaching Assistant (2010)

Marked assignments for introductory psychology class at Fanshawe College

Marked assignments and presentations for Research Methods at King's University College

COMMITTEES & ORGANIZATIONAL CONTRIBUTIONS

Organizer

Society for Music Perception and Cognition Biannual Meeting (2014-2015)

Vanderbilt University, Nashville, TN, USA

3rd International Conference of the International Association of Music & Medicine (2014)

University of Toronto, Toronto, ON, CAN

Lake Ontario Visionary Establishment Annual Conference (2013-2014)

Niagara Falls, ON, CAN

Volunteer

Inaugural Brain and Mind Institute Symposium (2015)

The University of Western Ontario, London, ON, CAN

Lake Ontario Visionary Establishment Annual Conference (2013-2015)

Niagara Falls, ON, CAN

Member

Psychology Ethics and Subject Pool Committee (2015-*present*)

The University of Western Ontario, London, ON, CAN

Psychology Graduate Affairs Committee (2015-*present*)

The University of Western Ontario, London, ON, CAN

Brain and Mind Institute Graduate Student Committee (2014-*present*)

The University of Western Ontario, London, ON, CAN

Brain and Mind Institute Space Committee (2016-*present*)

The University of Western Ontario, London, ON, CAN

Brain and Mind Institute MOVE committee (2016-*present*)

The University of Western Ontario, London, ON, CAN

Brain and Mind Institute Furniture Committee (2016-*present*)

The University of Western Ontario, London, ON, CAN

COMMUNITY OUTREACH & PUBLIC ENGAGEMENTS

Demonstrator

EEG @ Western

(2016) *The University of Western Ontario, ON, CAN*

Conducted EEG demonstrations as part of an introductory EEG workshop

Mensa Tour

(2016) *The University of Western Ontario, ON CAN*

Conducted EEG demonstration, and answered methodological/research related questions for interested community members

Discovery Day

(2013, 2014, 2015, 2016, 2017) *The University of Western Ontario, ON, CAN*

Conducted EEG demonstration, and answered methodological/research related questions to encourage interest in the neurosciences amongst local secondary school students.

Take Your Kids to Work Day

(2013, 2014, 2015, 2016, 2016) *The University of Western Ontario, ON, CAN*

Conducted EEG demonstration, and answered methodological/research related questions to encourage interest in the neurosciences.

Volunteer

Brain Bee

(2015, 2016, 2017) *The University of Western Ontario, ON, CAN*

Group tour leader, and MC of trivia game based on knowledge of neuroscience related materials