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The Neural Mechanisms of Musical Rhythm Processing: Cross-Cultural Differences and the Stages of Beat Perception

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

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Abstract

Music is a universal human behaviour, is fundamentally temporal, and has unique temporal properties. This thesis presents research on the cognitive neuroscience of the temporal aspects of music: rhythm, beat, and metre. Specifically, this work investigates how culture is associated with behavioural and neural measures of rhythm processing, and the different neural mechanisms (with particular interest in the role of the striatum) that underlie different stages of beat perception, as musical rhythms unfold.

Chapter 1 presents an overview of the existing literature on the perceptual, cognitive, and neural processing of rhythm, including the entrainment of neural oscillations to rhythm and the neuroanatomical substrates of rhythm perception.

Chapter 2 presents research on cross-cultural differences in the perception and production of musical rhythm and beat. Here, East African and North American participants performed three tasks (beat tapping, rhythm discrimination, and rhythm reproduction) using rhythms from East African and Western music. The results indicate an association between culture and beat tapping and rhythm reproduction, but not rhythm discrimination.

Chapter 3 presents electroencephalographic (EEG) research on cross-cultural differences in neural entrainment to rhythm and beat. The degree to which neural oscillations entrained to the different regular ‘metrical levels’ of rhythms differed between groups, suggesting an influence of culture. Moreover, across all participants, the proportion of trials in which different rates were tapped was correlated with the degree of neural entrainment to those rates.

Chapter 4 presents functional magnetic resonance imaging (fMRI) research on the different neural mechanisms that underlie the different stages of beat perception (finding, continuation, and adjustment). Distinct regions of the striatum (dorsal vs. ventral putamen) were active to different extents in beat finding and adjustment, respectively. Activity in other regions (including the cerebellum, parietal cortex, supplementary motor area, and insula) also
differed between stages. Additionally, when rhythms were metrically incongruent (polyrhythmic), additional activity was found in superior temporal gyri and the insula.

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
Beat perception, Rhythm Perception, Music Cognition, Music Perception, Neuroscience of Music, Cross-Cultural, African Rhythm, Neural Entrainment, EEG, fMRI.
Chapter 1 contains a section from the following published paper:


Chapter 2 has been published in a different format:


Chapters 3 and 4 are in preparation to be submitted for publication.

All work presented in this thesis was designed and written in collaboration with Jessica Grahn. For Chapter 2, Jocelyn Bentley helped with data collection and analysis.

The format of Chapter 3 differs from that of Chapters 2 and 4 (Materials and Methods appears after Discussion) due to the requirements of the journal to which this chapter will be submitted.
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<tbody>
<tr>
<td>ANOVA</td>
<td>analysis of variance</td>
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<tr>
<td>ACC</td>
<td>anterior cingulate cortex</td>
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<td>BAT</td>
<td>beat alignment test</td>
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<td>CV</td>
<td>coefficient of variation</td>
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<td>EPI</td>
<td>echo-planar imaging</td>
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<td>EEG</td>
<td>electroencephalography</td>
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<td>FDR</td>
<td>false discovery rate</td>
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<td>FWE</td>
<td>family-wise error</td>
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<td>fMRI</td>
<td>functional magnetic resonance imaging</td>
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<td>GMSI</td>
<td>Goldsmiths Musical Sophistication Index</td>
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<tr>
<td>Hz</td>
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<td>IPL</td>
<td>inferior parietal lobule</td>
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<td>IBI</td>
<td>inter-beat interval</td>
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<td>IOI</td>
<td>inter-onset interval</td>
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<td>ITI</td>
<td>inter-tap interval</td>
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<tr>
<td>ICBM</td>
<td>International Consortium for Brain Mapping</td>
</tr>
<tr>
<td>IPS</td>
<td>intra-parietal sulcus</td>
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<tr>
<td>kΩ</td>
<td>kilohms</td>
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<td>MRI</td>
<td>magnetic resonance imaging</td>
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<tr>
<td>MP-RAGE</td>
<td>magnetization prepared rapid gradient echo</td>
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<td>µV</td>
<td>microvolts</td>
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<td>MidCC</td>
<td>middle cingulate cortex</td>
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<td>MTG</td>
<td>middle temporal gyrus</td>
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<td>ms</td>
<td>milliseconds</td>
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<td>PMC</td>
<td>premotor cortex</td>
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<td>ROI</td>
<td>region of interest</td>
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<tr>
<td>TR</td>
<td>repetition time</td>
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<td>s</td>
<td>seconds</td>
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<td>SVC</td>
<td>small-volume correction</td>
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<td>SEM</td>
<td>standard error of the mean</td>
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<td>SSEP</td>
<td>steady-state evoked potential</td>
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<td>ST</td>
<td>superior temporal</td>
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<td>STG</td>
<td>superior temporal gyrus</td>
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<td>SMA</td>
<td>supplementary motor area</td>
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<td>T</td>
<td>tesla</td>
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<td>TMS</td>
<td>transcranial magnetic stimulation</td>
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Chapter 1

1  General Introduction

1.1  The Perceptual Organization of Time in Music

Music is pervasive in human life, found in every known culture throughout the world. Music uses sound, organized with respect to various physical properties (e.g., pitch, harmony, timbre, intensity) to elicit aesthetic, emotional, and behavioural responses. Fundamentally, music is temporal: It unfolds over time and is strictly organized in time. Moreover, the temporal properties of music and musical behaviour are unique within human life, and indeed within biology. Given the pervasiveness and importance of music in human life, and its unique temporal organization, the neural mechanisms underlying the temporal aspects of music are worthy of cognitive neuroscientific investigation, and will lead to better understanding of the neural and cognitive bases of human music.

A critical aspect of music’s temporal organization is rhythm. Musical rhythms are sequences of sounds characterized by the time intervals between sound onsets (inter-onset intervals, or IOIs). When we listen to musical rhythms, we often perceive that certain sounds occurring at regular intervals are emphasized, relative to the others, and the perceived regular emphases—the beat—can persist even after the rhythm stops. The beat tends to be indicated by particular patterns of IOIs in a rhythm that cause certain sounds to be heard as stronger than others (Povel & Essens, 1985), according to certain perceptual rules (e.g., the second of two sounds tends to be perceived as stronger than the first). When these perceptual emphases occur in a regular (isochronous) fashion, perception of the resulting regular beat is induced. Once induced, the sense of beat tends to persist. Thus, although beat perception results, in part, from the temporal structure of rhythms, internal processes also support beat perception, enabling us to continue perceiving a steady beat across gaps in a rhythm, or to continue to clap along after the music stops. 
A variety of internally-driven factors influence rhythm perception. Some rhythms have temporal structures that make it possible for beat perception to occur at multiple rates and/or relative phase positions. However, even given an ambiguous context with multiple possible beat rates (metrical ambiguity, see London, 2012), only one beat rate is perceived as the beat (Poudrier & Repp, 2013). Thus, although flexible, beat perception is perceptually singular. Beat perception is also hierarchically structured, such that individual beat positions tend to be perceived as strong or weak relative to one another, in groups of two or more beats. For example, beats can be grouped into repeating patterns of two beats (e.g., Strong-Weak), three beats (e.g., Strong-Weak-Weak), or other numbers of beats. The phenomenon of cyclical patterns of strong and weak beats that musical rhythms usually induce and are subsequently perceived within, is called metre. Metrical structures support the hierarchical organization of rhythm. Different levels of the metrical hierarchy correspond to different regular temporal intervals (and thus to different rates). For example in a metrical structure of one strong beat followed by two weak beats, the beat rate itself is one level, as is the rate of strong beats, as shown in Figure 1. One can imagine a higher (slower) metrical level corresponding to every other strong beat, or a lower (faster) metrical corresponding to two evenly spaced positions per beat (Figure 8, in Chapter 3, depicts stimulus rhythms and different corresponding metrical levels in greater detail, as is relevant to the research presented in that chapter). Because of the hierarchical metrical structure of rhythm, individual listeners often select different metrical levels to tap along with. Thus, beat perception results from rhythm perception as well as internal factors that allow individual variability in perception and behaviour.

Overall, then, the perception of beat and metre arise from rhythms, but whereas rhythms are solely determined by their temporal structure, beat and metre are flexible, and depend on internal processes that lead to individual differences. Underlying contributors to individual differences in beat perception include musical training (Cameron & Grahn, 2014a; Grahn & Rowe, 2009; Palmer & Krumhansl, 1990), auditory working memory
span (Grahn & Schuit, 2012), age (McAuley, Jones, Holub, Johnston, & Miller, 2006), short-term experience with moving one’s body to rhythm (Phillips-Silver & Trainor, 2005), and long-term cultural experience (Hannon, Soley, & Ullal, 2012; Soley & Hannon, 2010). Although the causal mechanisms by which these factors influence perception are unclear, variability across individuals is a notable and essential aspect of the perception of rhythm, beat, and metre, underscoring the importance of internal factors in this domain of perception.

![Figure 1](Cameron & Grahn, 2014b)

Figure 1. A depiction of rhythm, beat, and metre. A rhythm is a sequence of auditory events, the onsets of which are separated by time intervals. The beat is the sequence of regular, salient time positions that are perceived in the rhythm. Metre is the hierarchical organization of beats into strong and weak (strong beats in the metrical structure are indicated in the top line). (This figure originally appeared in Cameron & Grahn, 2014b.)

In addition to perception, behaviour is highly relevant to understand music’s unique and fundamental temporal processing. Humans tend to entrain (or synchronize) their movements to auditory rhythms, and specifically to the perceived beat. How entrainment occurs, and varies across individuals, depends on various listener factors, but critically, entrainment of movement requires regularity in the stimulus. Relatedly, in addition to the human ubiquity of music, every known human culture has had a form of music that uses temporal regularity, suggesting a cultural and historical ubiquity of motoric entrainment to music (e.g., dance). The various stimulus and individual factors influencing motoric
Entrainment to rhythms have been widely investigated (Repp, 2005; Repp & Su, 2013), but one critical aspect of motoric entrainment is that it is anticipatory: When tapping along with the beat of an auditory rhythm, humans tend to tap slightly before the exact temporal position of the beat (Aschersleben, 2002; Franěk, Mates, Radil, Beck, & Pöppel, 1994). The anticipatory nature of entrained movement occurs without conscious intention to anticipate. The ongoing, implicit, anticipatory (or predictive) nature of beat perception is an important aspect of this universal human behaviour.

Overall, it is evident that human beat perception is a unique form of timing that involves dynamic, integrative, anticipatory processing and is subject to the influence of past experience. The research presented in this thesis will focus on the neural mechanisms underlying two aspects of rhythm and beat perception: 1) the association between culture and the perception and production of rhythm and beat, as well as its association with neural entrainment to rhythm, beat, and metre, and 2) the neural mechanisms that support the distinct stages beat perception as it unfolds over time.

1.2 Neuroscience of Rhythm and Beat Perception

Corresponding to the research presented in Chapters 3 and 4, it is relevant to here summarize the existing literature on neuroscience of rhythm and beat perception with respect to 1) entrained neural oscillations and 2) neuroanatomical correlates.

1.2.1 Neural Oscillations During Rhythm and Beat Perception

Neural populations are subject to fluctuations in excitability because of transient excitatory and inhibitory input. These fluctuations tend to oscillate between low and high excitability (making neural firing less or more likely, respectively) at various rates. These oscillations, and resulting neural activity, tend to entrain to incoming rhythmic stimuli (Buzsáki & Draguhn, 2004). Neural entrainment to rhythmic stimuli improves perception by aligning the excitatory phase of the neural oscillation to the expected onset of stimuli (Henry, Herrmann, & Obleser, 2014; Henry & Obleser, 2012; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). During perception of musical rhythms, neural oscillations
entrain to different metrical levels, and the degree of entrainment to different metrical levels differs between rhythms depending on their temporal structures (Nozaradan, Peretz, & Mouraux, 2012), although the strict relationship between rhythm structure and entrainment pattern to different metrical levels is not clear.

Much of the recent literature on neural entrainment to musical rhythms uses electroencephalography (EEG) to measure the magnitude of steady-state evoked potentials (SSEPs), essentially “tagging” the frequencies associated with a stimulus in EEG (Chemin, Mouraux, & Nozaradan, 2014; Cirelli, Spinelli, Nozaradan, & Trainor, 2016; Nozaradan, Peretz, & Keller, 2016; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan et al., 2012; Nozaradan, Zerouali, Peretz, & Mouraux, 2015). Although this method cannot determine with certainty what phase (i.e., relatively excitatory or inhibitory) of a neural oscillation is synchronized with the expected sounds in a rhythm, the measure does indicate the presence of entrainment between oscillations and stimuli.

The magnitude of SSEPs indicates that the magnitude of entrainment differs depending on stimulus factors, such as the temporal structure of the rhythm (Nozaradan et al., 2012). In addition, SSEPs are altered by internal factors. For example, when listening to an isochronous sequence (with sound onsets occurring at 2.4 Hz), neural oscillations entrain at the stimulus frequency (2.4 Hz). However, when listeners internally impose a metrical structure on the stimulus by imagining an emphasis on every second or every third onset, entrainment is then also observed at the metrical level being internally imposed (Nozaradan et al., 2011). The extent to which this increase in entrainment to 

\textit{intentionally-imposed} metrical levels resembles what would occur during \textit{naturalistic} beat and metre perception is not clear. Behaviour and experience can also influence the pattern of neural entrainment to metrical levels of auditory rhythms. Tapping the beat during listening to a rhythm increases entrainment to the metrical level that is being tapped (Nozaradan et al., 2015). Moreover, moving to particular metrical levels of a rhythm enhances subsequent entrainment to those metrical levels while hearing the same rhythm and not moving (Chemin et al., 2014). Previous experience listening to and
engaging with music can enhance entrainment to rhythms: for example, 7-month-old infants with experience in music classes have greater neural entrainment to rhythms than those without (Cirelli, et al., 2016). Thus, neural oscillations entrain to the frequencies of regularly occurring onsets in musical rhythms (metrical levels) during listening to rhythms, and besides stimulus-driven entrainment, internal factors enhance selective entrainment via both intentional and experience-dependent means. These interactions between neural oscillations and perception of musical rhythms shed some light on the neural dynamics of rhythm and beat perception, i.e., what the brain is doing during rhythm. However, these interactions, primarily understood via EEG data, have a limited potential to indicate which regions of the brain support rhythm and beat perception.

1.2.2 Neural Correlates of Rhythm and Beat Perception

In contrast to the temporally precise but spatially imprecise EEG methods that reveal neural dynamics (e.g., entrained oscillations) during rhythm perception, research using functional magnetic resonance imaging (fMRI), neurological patients, and transcranial magnetic stimulation (TMS) has revealed neural regions and networks involved in rhythm perception, albeit with lower temporal resolution than EEG. When humans listen to rhythms, widespread activity is observed in the cortical motor system, especially in the supplementary motor area (SMA) and premotor cortex (PMC), as well as subcortical regions such as the basal ganglia and cerebellum (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Lewis, Wing, Pope, Praamstra, & Miall, 2004; Mayville, Jantzen, Fuchs, Steinberg, & Kelso, 2002; Schubotz & von Cramon, 2001; Ullén, Forssberg, & Ehrsson, 2003). When listening to rhythms that elicit beat perception, activity is greater in the SMA and the basal ganglia compared to listening to rhythms that do not elicit beat perception (Grahn & Brett, 2007). The importance of the basal ganglia in beat perception is highlighted by the fact that patients with Parkinson’s disease have impaired perceptual discrimination of changes in beat-based rhythms compared to healthy controls, but not in non-beat rhythms (Grahn & Brett, 2009). This deficit in sensitivity to the beat structure in rhythms is presumably due to the degeneration of dopaminergic cells in a part of the basal ganglia called the substantia
nigra; the death of these cells deprives the basal ganglia of dopamine, causing
dysfunction. Overall, these findings suggest that the basal ganglia not only respond
during beat perception, but also are crucial for normal beat perception to occur.

In contrast to the basal ganglia, the cerebellum appears to play a different role in timing.
Whereas the basal ganglia are important for beat perception and beat-based timing (i.e.,
timing of events relative to a regular and predictable beat), the cerebellum has been
implicated in the perception of absolute time intervals (i.e., timing of events not relative
to a beat). Patients with cerebellar degeneration have showed a deficit in absolute timing
but not beat-based timing (Grube, Cooper, Chinnery, & Griffiths, 2010). Relatedly,
applying TMS over the cerebellum to transiently disrupt function in that structure
worsens performance in a single-interval timing task (i.e., a task that requires absolute
timing), but not in a regularity (beat) detection task (Grube, Lee, Griffiths, Barker, &
Woodruff, 2010). The dissociation in timing function between the basal ganglia and
cerebellum extends to wider networks in which they operate. Cerebellar regions and the
inferior olive are more active for absolute timing, and the basal ganglia, SMA, PMC, and
other frontal cortical regions are more active for beat-based timing (Teki, Grube, Kumar,
& Griffiths, 2011). Importantly, both of these dissociable networks are often active when
hearing musical rhythms, suggesting that absolute and beat-based timing mechanisms are
simultaneously engaged by rhythm processing.

Besides relative and absolute timing mechanisms, other network activity interactions
occur during the perception of musical rhythm. The effective connectivity (the direct
influence of one region’s activity on that of another region) between the basal ganglia and
several cortical areas, including the SMA, PMC and auditory cortex is greater during
listening to beat-based rhythms compared to non-beat rhythms (Grahn & Rowe, 2009).
The functional connectivity (the non-directional correlation in activation) between PMC
and auditory cortex increases as the intensity of tones in beat positions of an isochronous
sequence (or salience of the beat) increased (Chen, Zatorre, & Penhune, 2006). Findings
from these studies demonstrate that the connected activity, or coupling, between auditory and motor systems increases during rhythm and beat perception.

There is little known about how different networks (e.g., those supporting different timing mechanisms or auditory-motor interactions) operate over time during rhythm and beat perception. Beat perception is thought to have multiple stages: Initially, when a rhythm is first heard, the beat must be detected, or found. ‘Beat finding’ is followed by the creation of an internal representation of the beat, allowing the anticipation of future beats as the rhythm continues (‘beat continuation’). One fMRI study attempted to determine whether the role of the basal ganglia in beat perception was selective for finding or continuing the beat. Participants heard short, consecutive rhythms that either had a beat or not. Basal ganglia activity was low during the initial presentation of a beat-based rhythm, during which participants were engaged in beat finding. Activity was high when beat-based rhythms followed one after the other, during which participants had a strong and continuing sense of the beat, suggesting that the basal ganglia are more involved in beat-continuation than beat-finding (Grahn & Rowe, 2013). Somewhat conversely, another study found that basal ganglia activity (along with SMA, PMC, and other cerebellar, parietal, temporal, and frontal regions) was greater during beat finding (initial listening to a beat-based rhythm) compared to listening to an isochronous sequence (Kung, Chen, Zatorre, & Penhune, 2013). Thus, with conflicting evidence of increased activity during continuation and during finding (although different analytical methods were used) the role of the basal ganglia in beat finding versus beat continuation remains unclear.

Other regions contribute additional processing of rhythm and beat in more musically complex contexts: when tapping the beat to metrically ambiguous rhythms (for which multiple distinct metrical structures are theoretically perceptible) the anterior insula, inferior frontal gyrus, anterior cingulate, and right parietal regions are all active (Vuust, Roepstorff, Wallentin, Mouridsen, & Østergaard, 2006; Vuust, Wallentin, Mouridsen, Østergaard, & Roepstorff, 2011). How these and other regions and networks are involved
during perception of metrically ambiguous (i.e., without simultaneous tapping) remains unclear.

1.3 Introduction to the Research Chapters

The perception of musical time—rhythm, beat, and metre—is critical for music, and understanding the neural and cognitive underpinnings is critical for understanding both music and human behaviour. The following three chapters present research designed to contribute to our understanding human rhythm, beat, and metre perception. Specifically, Chapter 2 seeks to measure the association between long-term cultural experience and the perception and production of musical rhythms and beat using behavioural measures. Chapter 3 builds directly from the findings presented in Chapter 2, and measures the association between long-term cultural experience and neural entrainment to musical rhythms, with specific interest in differing entrainment patterns to different metrical levels, using EEG. Chapter 4 elucidates the distinct neural mechanisms that support the distinct stages of beat perception as it unfolds over time, as well as the mechanisms supporting beat perception during metrical ambiguity, using fMRI. Taken together, this research aims to provide novel understanding of the neural mechanisms of human rhythm and beat perception, and of cross-cultural differences.
Chapter 2

2 Cross-Cultural Influences on Rhythm Processing: Reproduction, Discrimination, and Beat Tapping

2.1 Introduction

Music exists in every known culture in history, suggesting that human perception of musical rhythm may be innate and universal (Nettl, 2000). In line with previous work, we define rhythm as a sequence of discrete temporal intervals, marked by (usually auditory) events (Fraisse, 1982; Clarke, 1999; Cooper and Meyer, 1960). In music, rhythms are usually structured such that the time intervals between events are related according to a temporal structure. The universal presence of rhythm may indicate that it has a central, common function. However, rhythmic structures in music vary across cultures, suggesting that culture also influences the perception and production of musical rhythm. Culture encompasses a tremendous range of complex societal constructs, including laws, beliefs, morals, and art. The relevant cultural influences on rhythm likely include, but are not limited to, the auditory experience of music, dance and other types of movement, and language. Despite much ethnomusicological research devoted to identifying and analyzing cultural differences in rhythmic structures, little empirical work has characterized how culture influences human perception and production of musical rhythms.

There may be aspects of rhythm perception that are universal due to common human cognitive processing, and/or physiological dynamics. For example, some work suggests that innate perceptual ‘rules’ govern the perception of accents in temporal groups (e.g., Povel & Essens, 1985), or that resonance in systems of neural oscillations underlie the perception of regularity in musical rhythms (Large & Snyder, 2009). However, experience is known to have an effect on some aspects of rhythm perception. Culture appears to influence rhythm perception as early as four months of age: American infants prefer rhythms with a regular metrical structure (found in both Turkish and Western
music) to rhythms with an irregular metrical structure (found in Turkish music, but not in Western music). Turkish infants do not have this bias, presumably due to their exposure to music with both regular and irregular metrical structures (Soley & Hannon, 2010). Moreover, both children and adults show superior memory for unfamiliar music from their own culture compared to unfamiliar music from an unfamiliar culture (Morrison, Demorest, & Stambaugh, 2008). Culture also influences the rhythm of language. Japanese and English speakers differ in their perception of rhythmic tone sequences in ways that are consistent with Japanese and English language rhythms (Iversen, Patel, & Ohgushi, 2008). In addition, music and language from a given culture share rhythmic properties. For example, English and French musical rhythmic structures are more similar to English and French speech rhythms (respectively) than to each other, in the sense that English music is more rhythmically variable than French music, and English speech is more rhythmically variable than French speech (Patel, Iversen, & Rosenberg, 2006).

Finally, broader cultural linguistic experience can improve rhythm perception. For example, learning a second language with different rhythmic characteristics than one’s first language improves perceptual discriminability of rhythmic tone sequences (Roncaglia-Denissen, Schmidt-Kassow, Heine, Vuust, & Kotz, 2013). Together, these studies show that enculturation to the rhythmic aspects of music and language occurs early in development and continues into adulthood.

Although it is clear that culture influences rhythm in music and language, the precise aspects of rhythm processing that are influenced by culture are unknown. Few studies have empirically investigated differences in musical rhythm perception between East African and Western music, and between participants from those cultures. As their musical rhythms have distinct characteristics (Temperley, 2000), these cultures are good candidates for comparing rhythm processing. The distinct characteristics of these rhythms lead to differences in perception of metre, the cyclical pattern of strong and weak beats that is perceived in rhythm. Ethnomusicological research on African rhythm has suggested that African music requires greater active engagement in order to maintain metre perception (Chernoff, 1979), puts greater importance on rhythm and metre than
Western music does (Chernoff, 1979), commonly has ongoing metrical tension (Agawu, 1995), and tends to be metrically ambiguous (see Temperley, 2000). Metrical ambiguity does not mean that listeners simultaneously perceive more than one metre when listening to a rhythm (e.g., Poudrier & Repp, 2013), but rather that different listeners may perceive different metres in the same musical rhythm. A recurring observation is that in specific cases of African music using cycles of 12 temporal units, African listeners tend to perceive 4 metrical beats of 3 temporal units each (e.g., a 12/8 metre), whereas Western listeners perceive 3 metrical beats of 4 units (e.g., a 3/4 metre) (Blacking, 1967; Locke, 1982). In addition to perceptual differences, cultural differences exist regarding aesthetics of rhythm, the evaluation of accuracy in rhythmic performance, and the relative importance of rhythm in music (see Kauffman, 1980; Agawu, 1995). For example, even within cultures, different styles of music might consider notated rhythms to be accurate when they are ‘swung’, or played ‘behind the beat’. Thus, we assume that different cultural groups have different notions about what rhythm is or should be, and we account for this in the design of our study.

As East African and Western music differ in their rhythmic structures (Kubik, 1962), we expected that using musical rhythms from these cultures to test participants from each culture (who differ in their exposure to the rhythms) would reveal influences of enculturation on rhythm perception. We assumed that culture, through exposure over time, would influence the processing of rhythm. Therefore, we hypothesized that the culture of the participant and the culture of the rhythmic stimulus would interact in their influence on performance, such that participants would have better performance with rhythms from their own culture. However, because exposure to Western music occurs nearly worldwide, including in the urban setting of our East African sample, our expectations were qualified to consider that both groups would have had exposure to Western musical rhythms, but only East African participants would have had exposure to traditional East African musical rhythms. This is consistent with a study that found that Africans’ and Americans’ ratings of melodic complexity differed for African folk songs,
but not for Western folk songs, presumably due to both groups’ familiarity with Western music, but not African music (Eerola, Himberg, Toivainen, & Louhivuori, 2006).

In addition to our predictions of superior performance (i.e., better ability to discriminate, reproduce, and tap to the beat of rhythms) for culturally familiar rhythms, we expected that culture would be associated with the range of beat rates that participants tapped. In metrical rhythms, multiple metrical levels (periodicities) are present, and each can legitimately be perceived as the beat. For example, in a 4/4 metrical structure, half notes, quarter notes and eighth notes could each be selected as the beat rate that a listener perceives and thus taps. As African music uses rhythms in which the metrical structure can be interpreted in multiple ways, (i.e., they are metrically ambiguous, see Temperley, 2000), we expected that participants would perceive, and therefore tap to, a greater number metrical levels for East African compared to Western rhythms. In addition, East African participants are assumed to have greater exposure to African music, as well as substantial exposure to Western music, therefore we expected they would tap to a greater number of metrical levels for all rhythms, compared to North American participants. We expected North American participants to tap to fewer metrical levels because their exposure to metrically ambiguous rhythms (such as those found in East African rhythms) is more limited.

Crucially, our a priori assumption was that group differences in performance accuracy would not be sufficient to demonstrate an influence of culture on rhythm processing. Rather, we would conclude that culture is associated with rhythm processing only if there was an interaction between the culture of the participant and the culture of the stimulus rhythm. That is, an association with culture would only be supported if the performance differences between the two types of rhythms also differed between the two groups. A simple group difference would be insufficient because other uncontrolled factors also differed between the groups and may have influenced performance on the tasks. These factors include familiarity with computer-based tasks, language barriers between experimenter and participant, conceptualization of regular beat tapping with auditory
rhythms, etc. Therefore, although we observed differences between groups, we cannot identify the specific cause of these differences, and it is the interaction between participant group and rhythm type that we interpreted.

2.2 Materials and Methods

2.2.1 Participants

Sixteen East African participants were recruited in Kigali, Rwanda (3 female, 23 mean years of age, 3.4 mean years of musical training, 2.5 mean years of dance training). Twenty-five North American participants were recruited in London and Toronto, Canada (13 female, 24.7 mean years of age, 4.7 mean years of musical training, 1.6 mean years of dance training). Musical training included any of the following: private lessons, instrumental or choral experience in school, church, or other organized setting (e.g., regularly performing traditional music ensemble). Dance training included any type of dance, but participants did not have to specify in which types they had training. All participants were over the age of 18, had normal hearing, and had spent the majority of their lives in the respective recruitment regions (East Africa or North America). Age, years of dance training, and years of musical training did not differ significantly between groups, as per independent samples t tests (p > .05). All participants gave informed consent prior to participating, and were compensated for their participation, as per approval by the ethics boards at the Centre Hospitalier Universitaire de Kigali and the University of Western Ontario.

2.2.2 Stimuli

East African rhythms were derived from two recordings of traditional East African music. These were an *embaire* performance called “Muliranwa” by the Ekidha Tobana Kabaliga Group in Bugwere village, Uganda, and an excerpt of a piece called *Chakacha*, performed by the Horizon Players Group and the choir from the Muslim Secondary School in Kisumu, Kenya (Barz, 2004). Three rhythms from each recording were used. The author (DC) transcribed the East African rhythms, and composed the Western rhythms. Western rhythms were composed to conform to norms of Western music in a
12/8 metrical structure, indicating a beat on every third position in the 12-position cycle. Rhythms were presented as sequences of sine tones or clicks, depending on the task in which they were presented (sine tones and clicks were used for the discrimination and reproduction tasks, and only sine tones were used for the beat tapping task, as described below). Sine tones were 100ms in duration, had intensity ramped up/down over the first/final 50ms, and were either 375 Hz or 500 Hz. Clicks were brief (6ms) excerpts of a generic snare drum sound from audio software (GarageBand). We used synthesized rhythmic tone sequences whose structures were derived from Western and East African music, rather than actual music or recordings of musical instruments, to avoid source-familiarity bias (Van de Vijver & Poortinga, 1997). All rhythms had a temporal structure of 12 units of equal duration; each unit either began with a sound or was silent. Importantly, rhythms were always presented in simultaneous pairs in each trial of each task. This was done to provide more rhythmic and metrical context than individual rhythms could alone, and to thus increase the perceptual differences between East African and Western rhythms. For each cultural rhythm condition, there were six individual rhythms, divided into two groups, each with three individual rhythms. Rhythms were simultaneously presented only with one of the others from the same group, as shown and described in Figure 2. The resulting ‘composite rhythms’ were used as stimuli for all three tasks. For example, the first East African group of rhythms was composed of rhythms 1-3, and the pairings were: rhythm 1 with rhythm 2, rhythm 1 with rhythm 3, and rhythm 2 with rhythm 3. Because an individual rhythm was created from one of two pitches/sounds, this made for a total of 12 rhythmic stimuli from each culture (e.g., rhythm 1 at 375 Hz with rhythm 2 at 500 Hz, or rhythm 1 at 500 Hz with rhythm 2 at 375 Hz). Each pair of rhythms was used in all tasks. Rhythms could be one of three tempi: each tempo had a unit duration of 180, 210, or 240ms, respectively. In all trials of all tasks, paired rhythms had the same tempo. Tempo was balanced across conditions in each task. See Figure 2 for a graphical depiction of rhythm stimuli.
Figure 2. Stimulus rhythms. Vertical lines denote onsets, dots denote rests. Each position (onset or rest) is of equal duration, one of 180, 210, or 240ms. A depicts individual rhythms. Rhythms were presented in pairs, as composite rhythms. Both rhythms in a given composite rhythm were selected from the same group of three rhythms (rhythms numbered 1-3, and 4-6). Therefore, within each type (Western and East African), rhythm pairings were 1-2, 1-3, 2-3, 4-5, 4-6, 5-6. For the discrimination and reproduction tasks, only the first cycle of each rhythm (the first 12 units, plus the subsequent downbeat) was used. B depicts examples of composite rhythms as used in the tasks. For the beat tapping task, entire rhythms as shown in section A were repeated cyclically (only two repetitions are shown in the example in section B).
For the beat tapping task, the two paired, simultaneously presented rhythms, which together constitute a composite rhythm, were composed of tones of different frequency (pitch), and rhythms were repeated for between 32-35s, to give participants enough time to perceive the beat, begin tapping, and stabilize the timing of their taps, as well as provide enough taps for robust measures of variability and accuracy. For the discrimination and reproduction tasks, one of the paired, simultaneously presented rhythms in each composite rhythm, was composed of a sine tone, and the other was composed of the click sound. This was to facilitate distinguishability of the rhythms since the tasks required reproduction or discrimination (from a potentially altered version) of only one of the two rhythms.

All tasks were presented using E-Prime software (Schneider, Eschman, & Zuccolotto, 2002a; 2002b) on a laptop and auditory stimuli were presented via headphones. Trial order was randomized for each task. All responses and tapping were executed on the laptop keyboard.

2.2.3 Procedure

2.2.3.1 Beat tapping task

Participants were instructed to tap the beat of the composite (paired) rhythms. The difference between isochronous beat tapping and non-isochronous rhythm tapping was explained. Participants were asked to listen to the stimulus and, as soon as they felt a sense of the beat, to begin tapping the beat on the ‘m’ key of the laptop keyboard along with the stimulus and to continue until the stimulus stopped. Participants were instructed that their perception of the beat might change over the course of the trial, and that their tapping might naturally adapt to their perception, but to avoid intentionally changing metrical interpretation or beat rate when not induced to by the stimulus (i.e., to not change when they tapped just to make the tapping more interesting). There were 12 trials of each condition for a total of 24 trials, plus two practice trials to begin.
2.2.3.2 Rhythm discrimination task

Participants were instructed to listen to three successive presentations of composite rhythms and decide if the third presentation was the same as or different from the first two presentations (which were always identical). During the task, the first composite rhythm was presented twice, accompanied by the text ‘Original rhythm: First Listen’ and ‘Original rhythm: Second Listen’, and the second composite rhythm was presented only once, accompanied by the text ‘SECOND rhythm’. Participants were then prompted to make their response by the text ‘Was the SECOND rhythm the same or different? If same, press (S) and if different, press (D)’. Participants responded by pressing keys on the laptop keyboard. Half of the trials in each cultural rhythm condition were ‘same’ and half were ‘different’. The composite rhythms were always made up of one sine tone sequence and one click sequence, and participants were told that only the tone sequence, not the click sequence, would sometimes contain a change, and only in the third presentation. For ‘same’ trials, all three presentations of the composite rhythms were identical. For ‘different’ trials, the rhythm in the third presentation was altered by switching (transposing) two intervals. This alteration occurred only in the individual rhythm that was composed of tones. The individual rhythm composed of clicks was always the same in the first and second composite rhythm (i.e., it was the same in all three rhythm presentations). There were 12 East African trials and 12 Western trials for a total of 24 trials, plus two practice trials to begin.

2.2.3.3 Rhythm reproduction task

Participants were instructed to reproduce a rhythm as accurately as possible after listening to it presented as part of a composite rhythm. They were explicitly instructed to reproduce the rhythms at the same tempo as the presented rhythms. In each trial, a composite rhythm was presented twice, accompanied by the text ‘rhythm’, followed by a screen signifying the start of the reproduction phase, accompanied by the text ‘tap back’. Participants tapped the individual rhythm that was presented as a tone sequence in the composite rhythm, on the ‘m’ key of the laptop keyboard. If the rhythm was reproduced
accurately, the participant would move on to the next trial. If inaccurate, the participant would attempt the same trial again, up to a maximum of five attempts per trial. Participants each completed 12 trials of each rhythm type for 24 total trials, plus three practice trials. Additionally, participants could repeat the three practice trials if they felt unsure of the task requirements.

Participants in Rwanda underwent EEG recording while listening to stimulus rhythms after completing all three behavioural tasks. These data are reported in Chapter 3.

2.2.4 Analyses

2.2.4.1 Beat tapping task

To measure tapping variability, inter-tap intervals (ITIs) were calculated. Individual ITIs were removed if they were less than 0.5 or greater than 1.5 of the mean ITI for each trial of each participant. This outlier removal procedure was performed once, then the mean ITI was recalculated and the procedure was performed again. 1.90% of ITIs were removed on this basis. The coefficient of variation (CV) of ITIs was calculated for each trial. The CV was equal to the standard deviation of ITIs divided by the mean ITI for that trial. Trials with a CV greater than 0.2 were removed, as they were considered too variable for the participant to have been intending to tap isochronously. 1.82% of trials were removed on this basis. Additionally, trials with fewer than 5 taps were removed, and 0.02% of trials were removed on this basis. Participants with 5 or more trials from each condition removed had their beat tapping data excluded from analyses entirely on the assumption that they did not understand the task requirements or were unable to execute the task consistently. The data from one North American participant was removed on these grounds. Four additional North American participants had no beat tapping data due to technical failure during testing.

To measure tapping accuracy, the absolute asynchrony between each tap and the nearest beat position was calculated. Beat positions occurred at each time point separated by the inter-beat interval (IBI), starting at zero. The IBI was determined by comparing the mean
ITI to potential IBIs that were multiples (1, 2, 3, 4, or 6 times) the tempo. This meant that accuracy could be meaningfully analyzed regardless of what metrical level of the rhythm the participant chose to tap to. The proportional average absolute asynchrony (mean absolute asynchrony divided by the mean ITI) was calculated for each trial to indicate beat tapping accuracy. The metrical level selected by each participant on each trial was determined by finding the multiple of the tempo (1, 2, 3, 4, or 6 times the tempo) closest to the mean ITI for that trial. The number of different metrical levels tapped for each rhythm type was calculated for each participant, giving a measure of the tendency of that participant to employ different metrical levels when tapping the beat.

In addition, to measure which of the five metrical levels were tapped to most frequently, for each rhythm type, we calculated the proportion of trials that each metrical level was selected as the beat rate tapped, for each participant.

2.2.4.2 Rhythm discrimination task

For the discrimination task, \( d' \) (sensitivity index) scores were calculated for each participant, for each rhythm type. This statistic measures a participant’s sensitivity to changes in the rhythms, taking into account the participant’s response bias (a bias to respond ‘same’ more often than ‘different’, or vice versa).

2.2.4.3 Rhythm reproduction task

For the rhythm reproduction task, the proportion of trials in which the rhythm was accurately reproduced was calculated for each participant, for each rhythm type. Rhythm reproduction was considered accurate when the correct number of intervals was tapped, and the duration of each tapped interval was within 20% of the presented duration.

For each task, dependent measures were analyzed separately in 2x2 mixed analyses of variance (ANOVA) with the between subjects factor of group (East African vs. North American) and the within subjects factor of rhythm type (East African vs. Western). The only exception was for the analysis of which metrical levels were tapped to most frequently in the beat tapping task. For this measure, a 2x2x5 mixed analysis of variance
was used, with the same two factors (group and rhythm type) and the repeated measures factor of metrical level (intervals of 1, 2, 3, 4, or 6 times the tempo). In cases where the assumption of sphericity was violated, Greenhouse-Geisser corrections were applied. Follow up $t$ tests were completed to investigate differences between individual conditions, in the case of significant interactions of group and rhythm type.

2.3 Results

2.3.1 Beat tapping task

Tapping variability (CV of ITI) did not significantly differ for rhythm type or group, and there was no significant interaction between those factors. However, North Americans tapped to the beat with greater accuracy (lower mean asynchrony) than East African participants (main effect of group: $F(1,34) = 11.29, p = .002$). There was also an interaction between group and rhythm type: each group tapped more accurately to the beat of rhythms derived from music of their respective culture ($F(1,34) = 3.48, p = .071$) as shown in Figure 3. Although the $p$ value of this $F$ test is not below .05, it is below 0.1, and we interpret this result because the direction of differences was predicted (thus, the equivalent of a one-tailed probability test is justified, and the $p$ value can be reported as .036).

Participants tapped to a greater number of metrical levels for East African rhythms than for Western rhythms (main effect of rhythm type: $F(1,34) = 7.13, p = .011$), and East African participants tapped to a greater number of metrical levels than North American participants (main effect of group: $F(1,34) = 3.11, p = .087$), as shown in Figure 4. We interpret the main effect of group, despite a $p$ value over .05, for the same reason described above: the $p$ value of this $F$ test is between 0.05 and .1, and the direction of differences was predicted (thus, the equivalent of a one-tailed probability test is justified, and the $p$ value can be reported as .044). The two factors did not interact.
Figure 3. Absolute asynchrony values of beat taps relative to beat positions in the rhythmic stimuli, averaged over each trial and proportionate (divided by) the tapping rate (mean ITI). Error bars indicate +/- 1 standard error of the mean (SEM). * indicates $p < .05$ (interaction between group and rhythm type).

Figure 4. Number of metrical levels tapped. Error bars indicate +/- 1 SEM. * indicates $p < .1$, and ** indicates $p < .05$. 
Participants across both groups selected certain metrical levels to tap to more often than others, irrespective of the type of rhythm, (main effect of metrical level: \( F(1,31) = 5.57, p = .004 \)). However, the proportion of trials tapped at each metrical level differed between East African and Western rhythms (interaction between metrical level and rhythm type: \( F(1,31) = 8.99, p < .001 \)), as shown in Figure 5. Participants selected the third metrical level more often for Western than East African rhythms (\( t(31) = 5.04, p < .001 \)), and the second and fourth metrical levels more often for East African than Western rhythms (second metrical level: \( t(31) = 3.79, p < .001 \); fourth metrical level: \( t(31) = 3.22, p = .003 \)). There was no indication that the two groups significantly differed in their use of metrical levels over others for the two types of rhythms (interaction between metrical level and group: \( F(1,31) = 2.05, p = .122 \)), or that the difference in proportion of metrical levels selected between the two types of rhythms differed between groups (interaction between metrical level, group, and rhythm type: \( F(1,31) = 1.82, p = .173 \)).

![Proportions of different metrical levels tapped as the beat for East African and Western rhythms by East African and North American participants.](image)

**Figure 5.** Proportions of different metrical levels tapped as the beat for East African and Western rhythms by East African and North American participants. Metrical levels are multiples of the tempo (the tempo in turn is the duration of the unit equal to an eighth note in a 12/8 metrical structure, thus, higher metrical levels are slower beat rates). Error bars indicate +/- 1 SEM.
2.3.2  Rhythm discrimination task
North American participants discriminated rhythms more accurately than East African participants (main effect of group: $F(1,37) = 4.53, p = .040$), but there were no main effects of rhythm type, nor interaction between group and rhythm type, as shown in Figure 6.

![Figure 6. $d'$ scores for the discrimination task, reflecting accuracy in discriminating rhythms. Error bars indicate +/- 1 SEM. * indicates $p < .05$.](image)

2.3.3  Rhythm reproduction task
East African rhythms were reproduced more accurately than Western rhythms (main effect of rhythm type: $F(1,38) = 18.00, p < .001$), and there was a marginally significant effect of group, suggesting that North American participants reproduced more rhythms accurately than East African participants did (main effect of group: $F(1,38) = 3.63, p = .064$). However, there was also a significant interaction between group and rhythm type ($F(1,38) = 5.5, p = .024$). Paired $t$ tests showed that both groups accurately reproduced a
greater proportion of East African rhythms than Western rhythms (East African participants: $t(15) = 4.02, p = .001$; North American participants: $t(23) = 2.45, p = .023$). Independent samples $t$ tests showed that North American participants were better than East African participants at reproducing Western rhythms ($t(38) = 2.59, p = .014$) but that the groups did not differ in proportion of accurately reproduced East African rhythms ($t(38) = 1.22, p = .273$), as shown in Figure 7.

Figure 7. Proportion of accurately reproduced rhythms. Error bars indicate +/- 1 SEM. * indicates $p < .05$, ** indicates $p < .01$.

2.4 Discussion

Overall, we find evidence of an association between culture and rhythm perception, rhythm production, and beat tapping. As predicted, culture was associated with performance on the beat tapping and rhythm reproduction tasks. Culture may influence rhythm perception by both active engagement with, and passive exposure to music, over time. The finding of an association with culture is consistent with past work suggesting rhythm perception is malleable by culture rather than innate and universal, and extends
beyond that work by using testing adults on multiple tasks using rhythms from two cultures with distinct musical rhythms.

Although North American participants generally performed better than East African participants, there were differences in the testing conditions between groups that prevent interpretation of group differences. Most notably, language and cultural barriers were present between participants and the experimenter for the East African group but not the North American group. Moreover, many North American participants were familiar with typical behavioural psychology experiments, instructions, testing environments, and equipment, which potentially biases the tests toward that group. Therefore, group differences in task performance may reflect differences in response to the testing conditions, rather than true cultural differences in rhythm and beat perception ability. As mentioned above, our *a priori* assumption was that a group difference in performance accuracy would not constitute evidence of an influence of culture. However, group differences in the *nature* of performance within a task (i.e., for the number of metrical levels tapped in the beat tapping task) are interpretable because that measure would not be sensitive to familiarity with the task instructions, environment, and equipment, and was predicted to differ between groups. Similarly, differences in task performance between the rhythm types, and interactions between group and rhythm type, are valid, as they are within-subject factors and thus resilient to testing biases between groups.

### 2.4.1 Beat tapping task

The results indicate that culture is associated with beat tapping accuracy. Participants from both groups tended to tap the beat with greater accuracy when tapping with rhythms derived from music of their own culture. Interestingly, tapping variability was not associated with culture. Cultural familiarity may therefore benefit the precision of identifying and anticipating beat positions in a rhythm, but not the ability to maintain a steady tapping rate. Another possibility is that the ability to tap steadily varies more across individuals than it does across cultures, in which case our measures may not have been sufficiently sensitive to demonstrate an effect.
Metrical interpretation varied across rhythm type as well as across group. As predicted, participants tapped to a greater number of metrical levels for East African rhythms than Western rhythms, presumably because East African rhythms allow more options for metrical interpretation than Western rhythms. Also as predicted, East African participants tapped to more metrical levels than North American participants, presumably due to their greater exposure to music containing rhythms that allow flexible metrical interpretations. East African participants would have had more opportunities to hear music with these rhythms, and moreover, to move to them (e.g., through dancing or clapping). This experience may have transferred to the simpler tapping movements required by the task.

In addition to analyzing the number of different metrical levels that were tapped across conditions, we also examined which of those metrical levels were tapped to most often across conditions. The specific metrical levels that participants chose to tap as the beat differed between East African vs. Western rhythms. Participants selected the third metrical level (a dotted quarter note in a 12/8 time signature) more often when tapping the beat with Western rhythms than East African rhythms. They selected the second and fourth (quarter note and half note) more often for East African than Western rhythms. These differences between tapping with East African and Western rhythms were significant, and presumably related to the different structural characteristics of the two types of rhythms. However, comparisons between the two groups (participants from East Africa and North America) did not reach significance, although, in terms of absolute proportions, East African participants tapped more often at the highest metrical level, a dotted half note in a 12/8 metre, than North American participants (see Figure 5). Overall, the data do not refute the null hypothesis that the groups do not differ in the metrical levels they select to tap to in the rhythms. Given the suggestions of ethnomusicological work, it may be that our study lacked sufficient power to demonstrate these differences (the $p$ value for the group by metrical level interaction was 0.12).
2.4.2 Rhythm discrimination task
No association with culture was found for accuracy for identifying whether a rhythm was the same as or different from another rhythm. Although the groups performed differently, this may be attributable to factors other than of rhythm perception differences, such as differences in familiarity with computer-based tasks and behavioural testing situations. There may be no true effect of culture on rhythm discrimination, or the task and stimuli may not have been optimal for detecting cultural influences on this perceptual task. The alteration of the rhythms for the ‘different’ trials in the discrimination task may have made the rhythms musically implausible, thus reducing the effect of cultural exposure to music. A lack of detection of a real effect is plausible, as previous studies have used purely perceptual measures of rhythm to demonstrate as association with culture (e.g., Soley & Hannon, 2010; Eerola, Himberg, Toivainen, & Louhivuori, 2006; Morrison, Demorest, & Stambaugh, 2008).

2.4.3 Rhythm reproduction task
An association with culture was also found for rhythm reproduction accuracy. Both groups reproduced East African rhythms more accurately than Western rhythms, but the difference between rhythm types was larger for the East African group than the North American group. This can be interpreted in two ways: East African rhythms were easier to reproduce overall, and the advantage of tapping those rhythms compared to Western rhythms was greater for East African participants than for North American participants. This suggests that East African participants benefitted from their cultural familiarity with East African rhythms. Another interpretation is that the Western rhythms were more difficult for East African participants than for North American participants, but that both groups found East African rhythms similarly easy. This suggests that tapping the culturally unfamiliar compared to familiar rhythms was more difficult for East African participants. In either case, the results are consistent with the prediction that cultural exposure to musical rhythms facilitates the reproduction of those rhythms.
2.4.4 General Discussion

Our findings demonstrate that culture is associated with the processing of musical rhythm and beat. If we assume that familiarity (e.g., as gained by cultural exposure) enhances performance generally, then the sensitivity of rhythm and beat production to culture are consistent with a function of musical rhythm being to facilitate synchronization. Musical rhythm may support cultural identity because it can facilitate interpersonal synchrony, consistent with theories that the function (i.e., adaptive value) of music and musical rhythm is to facilitate social cohesion (Huron, 2001). However, it is important to note that the function(s) of music may differ between cultures. Previous work (Jones, 1959; Blacking, 1967; Chernoff, 1979; Locke, 1982; Agawu, 1995), and the discipline of ethnomusicology, generally, provides greater detail and insight into the sociocultural contexts and functions of African and Western music.

Testing for associations with culture is challenged by the need for stimuli that avoid information that provide other musical context (i.e., stimuli that are well controlled, so that effects can be attributed to the differences in rhythm), but also accurately reflect the broader musical context from which rhythms were drawn and exert influence through exposure (i.e., stimuli that are ecologically valid, so that a real effect of culture can be detected). In this study, rhythmic stimuli consisted of synthesized tone sequences rather than real music or sounds from musical instruments in order to maintain control, and also consisted of paired, overlapping rhythms in order to create a musically realistic context. It is possible that our choices of rhythms were not ideal for demonstrating cultural associations with rhythm perception (e.g., due to a lack of sufficient cultural familiarity with the rhythms), or that other cultures have more distinct musical rhythms. Future studies may yield more sensitivity to the influence of culture on rhythm processing by comparing rhythmic stimuli and participants from cultures with more distinct musical rhythms.

Future studies could also combine cross-cultural approaches with neuroimaging methods to better understand the neural mechanisms of rhythm perception. In one neuroimaging
(fMRI) study, no differences were found in neural activations while listening to culturally familiar vs. culturally foreign music, despite the fact that music culture influenced performance on a recall task (Morrison, Demorest, Aylward, Cramer, & Maravilla, 2003). However, another approach could use cultural differences and fMRI to better understand rhythm perception: since most fMRI studies of rhythm have used Western rhythms and participants, having non-Western participants listen to rhythms perceived as irregular by Western participants but regular by non-Western participants, could reveal activations in either the same or different networks found for rhythm and beat perception in past studies. This approach could help elucidate the role of familiarity and regularity in the neural mechanisms of rhythm perception.

To conclude, this study provides empirical support for an association between culture and the perception and production of musical rhythm. Future studies could build on this work to investigate the cultural associations with neural mechanisms of rhythm and beat perception, and whether there are aspects of rhythm processing not associated with culture (i.e., are universal).
Chapter 3

3 Cross-Cultural Differences in Neural Entrainment to a Musical Beat

3.1 Introduction

The ability to synchronize, or entrain, movements to musical rhythm is universal among humans, across cultures and history (Nettl, 2000). Synchronization to rhythm relies on perception of a beat—a regular, perceived emphasis to which movements are entrained. In music, rhythms contain multiple hierarchical temporal (metrical) levels, with the perceived beat being one level of the metric hierarchy, and other levels being faster or slower than the beat rate (see Figure 8). Although the ability to entrain one’s movements to rhythm is universal, rhythm and beat perception are subject to individual differences and cultural familiarity (see Chapter 2; Morrison, et al., 2008; Hannon, et al., 2012; Iversen, Patel, & Ohgushi, 2008; Soley & Hannon, 2010). Specifically, different cultures tend to use metrical levels differently when entraining movements to the rhythm (see Chapter 2; Blacking, 1967; Locke, 1982). The cultural differences in the behaviours and perceptions associated with musical rhythm presumably arise via experience, including passive exposure to music as well as active engagement, such as making music and dancing.

The tendency to entrain movements to musical rhythms has been linked to neural excitability. Neural excitability fluctuates over time in regular oscillations, which tend to entrain to external rhythmic stimulation (Buzsáki & Draguhn, 2004). Neural entrainment to rhythmic stimuli optimizes perception of stimulus features (Henry, Herrmann, & Obleser, 2014; Henry & Obleser, 2012; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008) by aligning the peak of neural excitability with the anticipated occurrence of the stimulus. When hearing a musical rhythm, listeners’ neural oscillations have been shown to entrain to the different metrical levels (Nozaradan, Peretz, & Mouraux, 2012). Internal processes can alter the strength of neural entrainment to different metrical levels of a
rhythmic stimulus. For example, listening to a 2.4 Hz stimulus sequence causes neural entrainment at that same stimulus frequency—the stimulus will be ‘tagged’ in the frequency spectrum of brain activity, as a steady-state evoked potential (SSEP) in the electroencephalogram (EEG) of a listener. However, when listeners impose a metrical structure onto the stimulus by imagining an emphasis on every second or every third tone (at 1.2 Hz or 0.8 Hz, respectively), entrainment (SSEP amplitude) is enhanced at the imagined frequency (Nozaradan, Peretz, Missal, & Mouraux, 2011). Neural entrainment to rhythms is also associated with experience: Neural entrainment to rhythms is greater in infants with experience in music classes than those without (Cirelli, Spinelli, Nozaradan, & Trainor, 2016). Moreover, prior experience tapping the beat with rhythms at particular metrical levels enhances entrainment to those levels during later listening (Chemin, Mouraux, & Nozaradan, 2014). Thus, entrainment to the various metrical levels of musical rhythms is influenced by stimulus factors (e.g., rhythmic structure), internal phenomenology (e.g., imposition of emphases at specific beat rates), and experience (e.g., previous entrained movements to particular metrical levels). Each of these factors is subject to cultural influence: Musical rhythms differ cross-culturally (e.g., Kubik, 1962; Temperley, 2000), the metrical structures of rhythms differ cross-culturally (Blacking, 1967; Locke, 1982; Agawu, 1995; Temperley, 2000), and the practices of physically engaging with musical rhythm differ cross-culturally (i.e., the use of dance in a given society, as well as the specific metrical levels to which movement entrains; Blacking, 1967; Locke, 1982). Thus, although evidence exists for the influence of short-term experience moving to rhythms on neural entrainment, we do not know if long-term experience also changes how neural oscillations entrain to rhythms. Experience-dependent changes in brain responses are important for understanding neural underpinnings of human perception, but we do not know how long-term experience influences function at the level of neural oscillations.
Figure 8. Stimulus rhythms with depiction of the corresponding metrical levels. Vertical lines indicate sound onsets and dots indicate silence. Pairs of rhythms (within groups 1-3 and 4-6, for each of East African and Western rhythm types) were presented simultaneously for individual trials. Metrical levels (1, 2, 3, 4, and 6) correspond to the multiple of the minimum inter-onset interval (IOI) and to the duration indicated by musical notation, as shown.

Here, to test for an association between culture and neural entrainment to musical rhythms, participants from East Africa and from North America underwent EEG recording as they listened to rhythmic stimuli derived from the music of traditional East African music and from Western music. Three aspects of African and Western cultures differ in ways we hypothesize may influence neural entrainment: 1) rhythmic structures that are common to musical rhythms, 2) the perception of musical rhythms and their
metrical structures, and 3) behavioural experience with musical rhythms (e.g., dance). Although for pragmatic and theoretical reasons cross-cultural differences are notoriously difficult to assess empirically, we have previously demonstrated differences in rhythm perception and production between these cultural groups, including the same East African sample reported in Chapter 2. We predicted that the patterns of neural entrainment while listening to rhythms would differ between groups.

3.2 Results

For both groups, and for both types for rhythms, statistically reliable entrainment occurred at all metrical levels (single-sample t tests for each indicate significantly above-zero SSEP amplitudes at all metrical levels, at $p < .05$; see Fig. 9.).

East African and North American participants had different patterns of neural entrainment to metrical levels in the rhythms (group by metrical level interaction; $F(4,30)$ = 4.63, $p = .002$, $\eta^2_p = .134$), as shown in Fig. 10. Follow-up $t$ tests show that East Africans had greater relative entrainment to the fastest metrical level (1, equal to an eighth note in musical notation and IOIs of either 180 or 240ms for fast vs. slow tempi, respectively) than North Americans ($t(30) = 2.19$, $p = .036$), and North Americans had greater relative entrainment to the slowest metrical level (6, equal to a dotted half note in musical notation and IOIs of either 1080 or 1440ms for fast vs. slow tempi, respectively) than East Africans ($t(30) = 3.16$, $p = .004$). Additionally, East Africans had numerically (but marginally statistically) greater entrainment to the middle metrical level (3, equal to a dotted quarter note in musical notation and IOIs of either 540 or 720ms for fast vs. slow tempi, respectively) than North Americans ($t(30) = 1.76$, $p = .088$). The different patterns of entrainment for the two cultural groups occurred regardless of whether participants were listening to culturally familiar or unfamiliar rhythms (no significant interaction between group, metrical level, and rhythm type, $p > .1$). Participants listened to all rhythms presented at one of two possible tempi, but when included as a between-subjects factor, tempo did not influence SSEP amplitude as a main factor or in interaction with any other factors ($p > .1$).
Figure 9. Top: EEG amplitude for East African participants (left) and North American (right) participants during listening to East African rhythms (blue) and Western rhythms (red). Note that frequency here is relative, as data is collapsed over participants listening to rhythms with different tempi (and thus metrical levels have different absolute frequencies). Spectra were aligned at metrical levels and have equally spaced frequency bins between them. Metrical levels are indicated with black circles. Bottom: Mean normalized SSEP amplitudes at metrical beat frequencies for East African and Western rhythms. Error bars indicate +/- 1 SEM. Mean SSEP amplitudes significantly above zero are indicated by * for $p < .05$, ** for $p < .01$, and *** for $p < .001$. Because mean SSEP amplitudes in raw (smoothed) EEG data can be positive or negative, and therefore not significantly different from
zero under the null hypothesis, statistics are for raw SSEP amplitudes (in µV), not the normalized SSEPs shown in bar graphs (which, by contrast, are necessarily above zero).

Figure 10. Top: Mean SSEP amplitudes at all five metrical levels for each group, collapsed over rhythm types. East Africans had greater entrainment to the fastest metrical level (1, equal to an eighth note in musical notation) and marginally significantly greater entrainment to the middle metrical level (3, equal to a dotted quarter note in musical notation), compared to North Americans. North Americans had greater entrainment to the slowest metrical level (6, equal to a dotted half note in musical notation). Bottom: Mean SSEP amplitudes at all five metrical levels for each rhythm type, collapsed over groups. Entrainment to the slowest metrical level
and to the second fastest metrical level (2, equal to a quarter note in musical notation) was greater during listening to East African rhythms compared to Western rhythms. Entrainment to a different middle metrical level (3) was greater during listening Western rhythms compared to East African rhythms. Error bars indicate +/- 1 SEM.

In addition to differences between groups, we also found differences in neural entrainment between types of rhythm. Across participants in both groups, mean SSEP amplitude differed between metrical levels depending on the type of rhythm being listened to (interaction of metrical level and rhythm type; \( F(4,30) = 9.52, p < .001, \eta^2_p = .241 \)), as shown in Fig. 10. Follow-up paired \( t \) tests show that for the slowest metrical level (6) and the second fastest metrical level (2), SSEP amplitudes were greater for East African rhythms than Western rhythms (\( t(31) = 2.06, p = .048 \) and \( t(31) = 5.20, p < .001 \), respectively), and for the middle metrical level (3), SSEP amplitudes were greater for Western rhythms than East African rhythms (\( t(31) = 3.61, p = .001 \).

Importantly, the differences in neural entrainment reflected behavioural differences. Neural entrainment to metrical levels correlated with the likelihood of tapping those metrical levels (see Fig. 11). Mean SSEP amplitudes for individual metrical levels (for each rhythm type) significantly correlated with the overall proportion of beat tapping trials in which those individual metrical levels were tapped as the beat (Pearson’s \( r = .58, p = .040 \), 1-tailed).

The previously reported cross-cultural results of three behavioural rhythm perception and production tasks (Chapter 2) were not substantially changed by adding more North American participants to the original sample: Culture was associated with rhythm reproduction accuracy (\( F(1,61) = 5.77, p = .019, \eta^2_p = .086 \)), and beat tapping performance, in terms of both tapping accuracy (\( F(1,52) = 3.91, p = .027, \eta^2_p = .070 \)) and the number of metrical levels used as the beat (both groups used a greater variety of metrical levels for East African rhythms than Western rhythms; \( F(1,52) = 8.06, p = .006, \eta^2_p = .134 \), and East African participants used statistically marginally more metrical
levels overall than did North American participants, whereas in the original sample the difference was statistically significant; $F(1,52) = 2.43, p = .063, \eta^2_p = .045$). We did not observe an association between culture and rhythm discrimination accuracy ($p > .05$).

Figure 11. The relationship between neural entrainment (SSEP amplitude) to metrical beat frequencies of musical rhythms and the propensity to tap at those metrical levels in the beat tapping task. Blue circles indicate metrical levels tapped with East African rhythms and red circles indicate metrical levels tapped with Western rhythms. Number and musical notation labels of data points indicate metrical levels. Each data point indicates the mean SSEP value (in $\mu$V) and mean proportion of beat tapping trials in which that metrical level was tapped. The black line indicates the linear relationship between neural entrainment (mean SSEP amplitude) and the propensity to tap that metrical level as the beat (mean proportion of trials), over both types of rhythms and all participants.
3.3 Discussion

These data show that two cultural groups differ in their patterns of neural entrainment to the hierarchical metrical levels (different beat frequencies) of musical rhythms, suggesting that cultural experience alters neural entrainment to musical rhythms. East Africans had significantly greater entrainment to the fastest metrical level (1) and numerically (but not significantly) greater entrainment to the middle metrical level (3) than North Americans. North Americans had greater entrainment to the slowest metrical level (6) than East Africans.

Prior experience moving to particular metrical levels of rhythms enhances neural entrainment to those rhythms during subsequent listening (Chemin et al., 2014). In addition, previous work has reported that cultures differ in the metrical levels to which movement tends to be entrained to (i.e., in dance). For example, for certain rhythms, African listeners tend to entrain movements to the 3rd metrical level (or a dotted quarter note in musical notation) whereas Western listeners tend to entrain movements to the 4th metrical level (or half note) (see Blacking, 1967; Chernoff, 1979; Agawu, 1995; Locke, 1982). The statistically marginal group difference in neural entrainment at the third metrical level (East Africans had numerically greater entrainment than North Americans) corresponds to this previously reported difference in observed behaviour. Thus, it may be that extensive experience hearing certain rhythmic structures, and moving to particular metrical levels, influences the propensity of neural oscillations to entrain to those same metrical levels. This underlying connection between behavioural and neural entrainment is consistent with the positive correlation between the degree of entrainment to different metrical levels during passive listening to rhythms and the likelihood of tapping those metrical levels when listening to the same rhythms in a separate session.

The pattern of neural entrainment to rhythms across participants in both groups differed depending on whether the rhythms were derived from East African music or Western music. The different entrainment patterns for the two rhythm types correspond to music theoretical predictions of perception. The metrical level (3) is the level that would be
strongly predicted by Western music theory to be the primary beat (‘tactus’) and neural entrainment to that is greater than all other metrical levels, during listening to Western rhythms. By contrast, the degree of entrainment for East African rhythms is relatively even across metrical levels. This aligns with suggestions that African musical rhythm tends to give relatively equal importance to different metric levels, in contrast with the strongly hierarchical metrical structures of Western musical rhythm (Temperley, 2000; Kauffman, 1980; Arom, 1989; Magill, 1997; Agawu, 2006).

Other neural and cognitive processes associated with rhythm perception may be influenced by long-term cultural exposure to certain rhythms and by particular entrained movement to those rhythms, and may underlie the differences in neural entrainment to the metrical structure of rhythms. One possibility is that the dynamics of attention during rhythm perception change with experience, from both passive exposure to, and active engagement with musical rhythms. Directing attention to metrical structure (e.g., through explicit music education) may strengthen the enculturation of entrainment patterns (both neural and motoric). Implicit attention to the integration of rhythm and metre during other culturally-influenced activities (e.g., learning the words to communal songs in school, observing dance, hearing religious scripture with metrical phrasing, etc.), may support culture’s influence on entrainment to rhythms. Attention enhances the perception of metrical structure (Bouwer, Van Zuijen, & Honing, 2014; Chapin et al., 2010; Geiser, Ziegler, Jancke, & Meyer, 2009) and temporal allocation of attention is experience-dependent (e.g., Drake, Jones, & Baruch, 2000; Yashar & Lamy, 2013), suggesting that cultural differences in attention to stimuli could shape the pattern of neural entrainment to musical rhythms over time.

Finally, it is possible that genetic, rather than cultural, differences underlie the observed group differences. However, there is no evidence of neurophysiological differences between human groups that would explain differences in entrainment to auditory rhythms as observed here. Moreover, empirical evidence exists for the influence of experience: Even short-term experience of entraining movements to rhythms at different metrical
levels changes patterns of neural entrainment to those levels during subsequent listening (Chemin et al., 2014). For these reasons, we believe a genetic account for our findings is unlikely.

3.4 Materials and Methods

3.4.1 Participants

Sixteen East African adults were recruited from the Kigali, Rwanda region (3 female, 23 mean years of age, 3.4 mean years of musical training, 2.5 mean years of dance training), of which 13 underwent EEG recording. This East African sample is the same as reported in Chapter 2. Twenty-four North American adults were recruited from the London, Canada region (10 female, 22.2 mean years of age, 5.0 mean years of musical training, 1.4 mean years of dance training), of which three did not complete the EEG testing. Data from this North American sample was collected after data collection from the North American sample reported in Chapter 2, as those participants did not have EEG recorded. Behavioural data from the two North American samples were combined for analyses of those tasks in this chapter. All participants were over 18 years of age, had normal hearing, and had spent the majority of their lives in East Africa or North America, respectively. Groups did not significantly differ in age or years of music and dance training, as per independent samples t tests ($p > .05$). All participants were without hearing impairments, neurological or psychiatric disorders. All participants provided informed, written consent before participating. Translated letters of information and consent forms were available for participants in Kigali, as was a human translator when necessary.

3.4.2 Stimuli

Stimuli were the same as used in the beat tapping task, described in Chapter 2.
3.4.3 Procedure

For EEG recording, participants were instructed to sit comfortably, relaxed with eyes closed during presentation of rhythms. For East African participants, EEG was recorded via 18 Ag/AgCl electrodes with a portable GRASS amplifier, at a sampling rate of 400 Hz. Impedances were kept below 10 kΩ. For North American participants, EEG was recorded via 128 Ag/AgCl electrodes embedded in sponges, with an EGI amplifier, at a sampling rate of 250 Hz. Impedances were kept below 50 kΩ. Cz was used as an online reference for both groups, and data were filtered to remove fluctuations below 0.1 Hz at acquisition.

Participants heard 12 East African rhythm trials and 12 Western rhythm trials, all presented at one of two tempi. For the East African participants and seven of the North American participants, trials were presented as blocks (all East African trials then all Western trials, or vice versa, counterbalanced across participants). Fourteen North American subjects had rhythms presented in alternating order of rhythm type (East African and Western, counterbalanced) rather than blocked presentation. Analyses indicated that neural entrainment did not differ between the two subgroups of North American participants that heard trials in different orders, so analyses reported here are collapsed across all North American participants. After EEG recording, all subjects completed the three behavioural tasks: rhythm discrimination, rhythm reproduction, and beat tapping, in counterbalanced order.

3.4.4 EEG Preprocessing

Acquired EEG data were filtered to remove fluctuations below 0.1 Hz and above 50 Hz using a finite impulse response filter as implemented using EEGLab (Delorme & Makeig, 2004), and re-referenced to averaged mastoid electrodes. Six frontal electrodes (positions F7, F8, T3, T4, C3, and C4) were used, on the basis that the scalp locations of SSEPs at metrical frequencies in response to auditory rhythms are reliably located over bilateral frontal regions Nozaradan, Peretz, & Keller, 2016; Nozaradan, et al., 2011; Nozaradan, et al., 2012; Nozaradan, Zerouali, Peretz, & Mouraux, 2015; Chemin, et al., 2014; Cirelli, et
One East African subject had two additional channels (C3 and C4) removed because of artifacts. Additionally, because of the different numbers of original channels for the two groups (and low number of channels for the East African group), independent component analysis was not used for artifact rejection. Instead, individual trials with artifacts were removed by visual inspection (24.3% of trials were removed from East African participants’ data and 21.7% of trials were removed from North American participants’ data). One subject from each group was excluded on the basis of excessively noisy data.

### 3.4.5 EEG Analysis

EEG data recorded during each trial were trimmed to remove the first 1s, in order to remove the initial auditory evoked response to the onset of the rhythm. Trials were then subdivided into epochs equal to the duration of two repetitions of the rhythm (8.64s for rhythms with a 180ms tempo, 11.52s for rhythms with a 240ms tempo) for the 6 (for 180ms tempo) or 4 (for 240ms tempo) repetitions of each trial.

All epochs were averaged within condition (East African and Western rhythms) and the resulting average waveforms were transformed to the frequency domain using a Hanning-windowed fast Fourier transform. Amplitude values across frequencies were smoothed using the procedure standardly applied in previous research (Chemin, et al., 2014; Cirelli, et al., 2016; Nozaran, et al., 2011; Nozaradan, et al., 2012; Nozaradan, et al., 2015): For each frequency bin, the mean amplitude of four neighbouring frequency bins (+/- 3 and 4 frequency bins away from the centre bin) was subtracted from the amplitude. To obtain SSEP amplitudes for the metrical frequencies of interest—1, 2, 3, 4, and 6 times the minimum IOI (either 180ms or 240ms)—the maximum amplitude within frequency bins spanning +/- .05 Hz centred on the metrical frequencies. The above process was applied to each channel, and resulting SSEP amplitudes were averaged across channels, resulting in ten SSEP amplitudes: one for each of the 5 metrical levels in each rhythm type (East African and Western rhythms) for each participant.
SSEP amplitudes were normalized within-subject by dividing by the mean of absolute SSEP amplitudes for all metrical levels for both rhythm types. Normalizing amplitudes eliminated any systematic difference in overall EEG amplitude between groups due to the different EEG systems used to collect data. Normalized SSEP amplitudes were analyzed in a 2x5x2 mixed ANOVA for the repeated measures factors Rhythm Type (East African vs. Western) and Metrical Level (6, 4, 3, 2, and 1x the tempo), and the between-subjects factor of Group (East African vs. North American). Follow up independent- and paired-samples $t$-tests were applied for significant interactions between Group x Metrical Level and Rhythm Type x Metrical Level. To test for an association between neural entrainment and beat tapping behaviour, mean SSEP amplitudes (in $\mu$V—not normalized, because the two groups were not being compared separately) for each metrical level in each rhythm type (averaged across all participants) were tested for a correlation with the mean proportion of trials in the beat tapping task in which participants' tapped each metrical level for each rhythm type.

To rule out the possibility that results are confounded by differences between the two EEG systems used, we performed a control analysis on EEG recorded during silent periods between trials. The same analysis was performed for EEG data recorded during silence as was performed for the main analysis. EEG power at frequencies of interest during silence did not show the same differences between groups and metrical levels as found in EEG during rhythm presentation.
Chapter 4

Finding and Keeping the Beat: Neural Mechanisms Differ as Beat Perception Unfolds

4.1 Introduction

Detecting and anticipating regular events in the environment are critical functions of the human brain. Humans are particularly sensitive to certain auditory temporal regularities, which allow the detection and anticipation of beats (the regular emphases sensed in musical rhythms) in rhythmic sequences. Beat perception enables humans to synchronize movement to rhythm (e.g., tapping one’s toes on, not after, the beat; (Aschersleben, 2002), a behaviour that is not generally observed in non-human primates (e.g., Zarco, Merchant, Prado, & Mendez, 2009). The striatum is heavily implicated in beat perception (Grahn & Brett, 2007; 2009; Grahn & Rowe, 2009, 2013; Kung, Chen, Zatorre, & Penhune, 2013; Teki, Grube, Kumar, & Griffiths, 2011), perhaps because of its role in anticipation and prediction more generally.

Various striatal functions may be critical for beat perception. First, medium spiny neurons in the striatum are hypothesized to detect when the phases of different cortical oscillations coincide (Matell & Meck, 2004). The detection of coincidence between intrinsic neural oscillations and stimulus-driven neural oscillations can lead to phase-resetting of the intrinsic oscillations (Oprisan, Dix, & Buhusi, 2014), which enables entrainment of neural oscillations to regularities in sensory input, such as the beat in auditory rhythms. Detection of regularity is a prerequisite for beat perception, and striatal neurons may accomplish this by detecting coincidences and then resetting the phase of cortical oscillations. The possibility that the striatum detects regularity (the beat) via oscillatory coincidence detection is consistent with the prominent theory that beat perception arises from the interactions of neural oscillators entrained by rhythmic auditory stimuli (Large & Kolen, 1994; Large, 2008; Large & Snyder, 2009).
Second, the striatum supports the generation of temporal predictions based on the regularity that is detected (Kotz, Schwartze, & Schmidt-Kassow, 2009). Temporal prediction is a hallmark of beat perception (humans tend to tap slightly before the beat; (Aschersleben, 2002), and striatal activation during beat perception may result from prediction generation based on the beat.

Third, the striatum processes temporal prediction errors (McClure, Berns, & Montague, 2003), a critical function given that beat perception is not instantaneous, but unfolds over time, and thus requires ongoing integration of new temporal information to update the predictions of future beats. This integration is crucial to, for example, allowing beat perception to persist even as a rhythm’s beat rate gradually speeds or slows: any unexpected timing of incoming intervals is successfully integrated into ongoing temporal predictions. The striatum may be key to integrating temporal prediction errors, thereby supporting the persistence of beat perception through changes in incoming rhythms.

Detecting regularity, predicting regular events, and integrating temporal prediction errors are differentially important at different stages of beat perception. Upon initially hearing an auditory rhythm, regularity must be detected (beat finding). Then, temporal predictions based on that detected regularity persist to the extent that the auditory stimulus confirms those predictions (beat continuation). Finally, beat perception adjusts when rhythmic stimuli change, and the resulting temporal prediction errors are integrated into ongoing predictions (beat adjustment).

Because different processes are needed at different stages of beat perception, different regions of the striatum may be important at each stage. Some work suggests that the caudate nucleus is preferentially active during beat finding (Kung et al., 2013), and other work suggests the putamen is preferentially active during beat continuation (Grahn & Rowe, 2013). Other studies have not specifically distinguished stages of beat perception, but have found striatal activity during presentations of short beat-based rhythms, when beat finding was likely occurring (Grahn & Brett, 2007). Thus, the striatum has been implicated in both beat finding and continuation. However, no studies have examined
whether distinct subregions of the striatum respond during each of these stages, consistent with different processes occurring during finding versus continuation.

Here, we used fMRI to measure striatal activity during *beat finding*, *continuation*, and *adjustment*, which differentially require detection of regularity, generation of predictions, and integration of temporal prediction errors, respectively. To do this, we created novel, musically realistic rhythmic sequences, which allowed valid manipulation of the stages of beat perception that would rely differentially on the different functions of the striatum. We considered the possibility that the striatum performs multiple functions in beat perception, and that distinct regions of the striatum may support these distinct functions.

### 4.2 Materials and Methods

#### 4.2.1 Participants

18 participants (8 male, mean age 25.4 years) provided written, informed consent before completing two behavioural tasks and undergoing fMRI scanning. All participants completed the musical training subscale of the Goldsmiths Musical Sophistication Index (GMSI; Müllensiefen, Gingras, Musil, & Stewart, 2014), as well as the Beat Alignment Test (BAT) from the GMSI. Participants had an average overall GMSI training score of 29.5 out of a maximum possible score of 49.

#### 4.2.2 Stimuli

Stimuli were pairs of rhythms presented together, with one rhythm composed of 375 Hz sine tones and the other composed of 500 Hz sine tones. All tones were 100ms, with a linear rise and fall over the first and last 50ms, respectively. Within individual rhythms, inter-onset intervals (IOIs) were durations of 1, 2, 3, or 4 units, in which 1 was equal to one of five absolute durations (180, 195, 210, 225, or 240ms), and the other units scaled proportionately by 2, 3, or 4. The presented rhythm pairs were always based on the same absolute unit duration. Intervals within each rhythm were ordered to conform to either a duple or a triple metre (with a beat occurring on either every fourth unit or every third
unit, respectively). Individual rhythms were composed of repetitions of basic patterns of intervals summing to 16 units for duple rhythms or 12 units for triple rhythms.

The were four trial types, based on whether the rhythm pairs began *simultaneously* or in a *staggered* fashion, and whether the pairs were metrically *congruent* (both duple or both triple) or *incongruent* (one duple and one triple) as shown in Figure 12. In *simultaneous* trials, the two rhythms began and ended together, whereas in *staggered* trials, one rhythm started and the other rhythm began after a duration equal to the duration of one cycle of the second rhythm. The intensity of the first audible cycle of the second rhythm increased linearly from silence (i.e., faded in). After either four or five and one and one third total cycles of the first rhythm (for duple or triple rhythms, respectively), it stopped and the second rhythm continued for either one or one and one third cycles (for duple or triple rhythms, respectively).

As behavioural evidence indicates only a singular beat percept emerges, even when multiple different beat percepts are possible (Poudrier & Repp, 2013), we used metrically incongruent and congruent rhythm pairs to assess the neural mechanisms of beat perception in the context of one or multiple possible beat percepts being present. This allowed us to examine which brain regions’ activity during beat perception differs depending on whether multiple beat percepts are possible or not.
Figure 12. Examples of the four types of stimuli, each consisting of two rhythms. Waveforms of rhythms are presented in black. Blue and red arrows indicate beat positions. Rhythms were presented in simultaneous or staggered fashion. In staggered trials, the second rhythm faded in starting after a duration equal to that of one cycle of the second rhythm (the fade-in lasted for one cycle of the second rhythm), and, after four cycles of the first rhythm, the first rhythm ended, as the second rhythm continued for one cycle if it was a duple rhythm or one and a third cycles if it was a triple rhythm. In congruent trials, both rhythms had the same beat rate (duple or triple) and in incongruent trials, one rhythm had a duple beat rate and the other had a triple beat rate. In the incongruent trials shown, the bottom rhythm has a triple metre and the top rhythm has a duple metre.
4.2.3 Behavioural Tasks

Before scanning, participants completed a beat tapping task and a beat-strength rating task, using all trials used in the fMRI experiment. For each trial, participants tapped their perceived beat along with each rhythm. After each trial, they rated how difficult it was to maintain their beat percept, on a 5-point scale. Stimuli were presented by laptop via noise-cancelling headphones outside of the scanner, and tapping and ratings were collected by laptop.

In the scanner, the first seven participants performed the same beat-strength rating task that they had completed before scanning (with no simultaneous beat tapping task). The subsequent 11 participants performed the same beat-strength rating task for 2 sessions and performed a deviant detection task in the other 2 sessions. For the deviant detection task, 14 of the 104 trials contained a deviant (square) tone in place of one of the regular tones. The deviant never occurred during the finding stage of a trial. For the 11 participants who completed both tasks, the tasks alternated over the four sessions, in counterbalanced order over participants. For both beat rating and deviant detection tasks, responses were made on a 5-button response box. The addition of the deviant detection task was motivated by substantial activity in visual cortex in preliminary analyses (n=7), thought to be due to the visual instruction screen presented before and after each trial (always immediately following the final stimulus presentation stage; continuation in trials in which rhythms were presented simultaneously, and adjustment in trials in which rhythms were staggered). The deviant detection task had no visual instruction after trials (participants were instructed in advance to respond if and when they heard a deviant), but required attending to the auditory stimuli (91.8% of trials were detected). For both tasks, 0, 4, 6, or 12 seconds of silence separated trials (evenly distributed except for the 0s silence, which occurred once per session). Stimuli were presented in the scanner via pneumatic Sensimetrics insert earphones.
4.2.4 Image Acquisition and fMRI Design

FMRI data were collected on a 3-T Siemens Magnetom Prisma MRI scanner in 4 sessions of 240 echo-planar imaging (EPI) volumes. Each EPI volume had 43 slices of 3mm thickness and a resolution of 3x3mm. Repetition time (TR) was 2.5s. All analyses were completed with SPM8 (Wellcome Department of Imaging Neuroscience, London, UK). Anatomical images (magnetization prepared rapid gradient echo, or MP-RAGE) were collected for co-registration. For each participant, images were interpolated in time and spatially realigned to the mean image using 2\textsuperscript{nd} degree B-spline interpolation. The co-registered structural image was segmented using affine regularization and normalized at a resolution of 1x1x1 mm to a standard ICBM template in Montreal Neurological Institute space. EPI images were normalized to the template and spatially smoothed with a 8mm full-width half-maximum Gaussian kernel.

Within-subject first level modeling included 14 conditions: 1-2) the finding and continuation stages in simultaneous incongruent trials, 3-4) the finding and continuation stage in simultaneous congruent trials, 5) the finding stage in staggered trials, 6-8) the fade-in, continuation, and adjustment stages in staggered incongruent trials, 9-11) the fade-in, continuation, and adjustment stages in staggered congruent trials, and (12-14) instruction screen viewing, responses, and deviant tones. The durations of rhythm conditions are depicted in Figure 12. For all trials, each of the two rhythms had a total duration of either 4 or 5.33 cycles (for duple or triple rhythms, respectively). For trials with simultaneously presented rhythms, finding epochs had a duration equal to one cycle of triple metre ranging from 2.0 – 3.8 s. Continuation epochs in simultaneous trials began immediately following the finding epoch and continued for the remainder of the stimulus (4.33 cycles of a triple rhythm or 3.25 cycles of a duple rhythm). For trials with staggered rhythms, the duration of finding epochs was equal to 1 cycle of the second rhythm (the time from onset of the first rhythm to onset of the second rhythm). Fade-in epochs began at the onset of the second rhythm with the duration equal to 1 cycle of that rhythm (over which time the rhythm linearly increased from silent to full intensity). Continuation epochs began immediately after the fade-in epoch, and the duration was equal to the
remaining time of the first rhythm (which had a total duration of 4 or 5.33 cycles). Adjustment epochs began immediately after the continuation epoch, coinciding with cessation of the first rhythm, and had a duration equal to 1 cycle of duple metre or 1 1/3 cycles of triple metre.

Contrast images (conditions 1 to 11 > rest) from the first level analyses were included in a second-level, random-effects analysis for group effects. Two behavioural covariates were also included in the second-level model: beat tapping consistency and BAT score. Beat tapping accuracy and GMSI scores were omitted as covariates as they were significantly correlated with beat tapping consistency and BAT scores, respectively. The two covariates included were the two (of four) that were least correlated with each other.

Given our a priori interest in striatal function, and based on preliminary results (e.g., whole brain contrasts for all rhythm-listening conditions vs. rest), which showed striatal activation was focused in the putamen (rather than caudate), region of interest (ROI) contrasts were completed for a bilateral putamen ROI (defined by the Automated Anatomical Labeling Toolbox; Tzourio-Mazoyer et al., 2002) using a small-volume correction (SVC) with a voxel-level family-wise error (FWE) $p$ threshold of < .05.

For contrasts between stages (e.g., finding > continuation, or adjustment > rest), individual conditions from simultaneous, staggered, congruent, and incongruent trials were weighted equally. For contrasts with respect to metrical incongruence, different stages were weighted equally across congruent and incongruent conditions (fade-in and finding epochs from staggered trials were omitted). For all contrasts, results were considered at a cluster-level false discovery rate (FDR) $p$ threshold of < .05, based on a cluster-forming threshold of < .0001 uncorrected (for individual stages > rest) or < .001 (for all other contrasts).

4.2.5 Behavioural Analyses

For the beat-tapping task, we measured tapping consistency (coefficient of variation of inter-tap intervals) and tapping accuracy (mean absolute error between tap and beat
times) for congruent and incongruent trials, as per Chapter 2 and previous studies (Cameron & Grahn, 2014a). Mean ratings of beat strength for congruent and incongruent conditions were obtained for both pre-scan and during-scan rating sessions.

4.3 Results

4.3.1 Behavioural Results

Participants tapped the beat with greater accuracy (lower absolute tap-beat error) and greater consistency (lower CV of inter-tap intervals) for congruent compared to incongruent rhythms (accuracy: $t(17) = 4.33, p < .001$; consistency: $t(17) = 7.72, p < .001$). Tapping accuracy and consistency were correlated (Pearson’s $r = .495, p = .018$, 1-tailed). Congruent rhythms were rated as easier to maintain a sense of the beat, compared to incongruent rhythms, both before and during the scan (pre-scan: $t(17) = 12.24, p < .001$; in-scanner, $t(10) = 4.51, p = .001$, although in-scanner ratings from 7 participants were lost due to technical error). Neither measure of tapping performance correlated with either beat perception ability (BAT scores) or with musical training (GMSI scores). However, as expected, beat perception ability and musical training were correlated (Pearson’s $r = .457, p = .028$, 1-tailed). Figures for behavioural results can be found in Appendix A.

4.3.2 fMRI Results

Distinct regions of the striatum were differentially activated for the distinct stages of beat perception (see Table 1). During beat finding, when regularity is being detected, the dorsal putamen was more active than during continuation, when the beat has already been detected and is predictable. Although this activation was statistically significant for the right side, a subthreshold (SVC, FWE $p = .076$) peak was found for this contrast in the left dorsal putamen. In contrast, during continuation, the ventral putamen was more active (bilaterally) than during finding. In addition, this ventral region of the putamen was also more active for beat adjustment than both continuation (left) and finding (bilaterally). See Figure 13 (right panel) for images of activations from the putamen ROI.
contrasts (contrasts vs. rest are presented for clarity of visualization; peak voxels are similar for both the contrasts vs. rest and vs. other stages).

### Table 1. Putamen Peaks Across Different Stages of Beat Perception

<table>
<thead>
<tr>
<th>Finding &gt; Continuation</th>
<th>Region of Putamen</th>
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<th>z</th>
<th>t</th>
<th>p FWE</th>
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<tbody>
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<table>
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<th>z</th>
<th>t</th>
<th>p FWE</th>
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</thead>
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<th>z</th>
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<th>p FWE</th>
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</table>

Stereotactic coordinates (x, y, z) of peak voxels are in Montreal Neurological Institute space (mm).

In addition to differences in putamen activation, whole brain contrasts showed, unsurprisingly, significant activity in auditory cortices during each stage compared to rest. During continuation, activity expanded to regions including insula, operculum, cerebellum, superior parietal lobule, and precuneus. During adjustment, activity further expands to the insula and operculum, putamen, globus pallidus, cerebellum, and thalamus. Peaks of activity are listed in Appendix B and activity is shown in Figure 13.

At the whole-brain level, comparing stages directly reveals regions in which activity differs across stages (see Table 2 and Figure 14). For beat finding > continuation, the anterior and middle cingulate cortex had greater activity, as did left inferior parietal lobule (IPL), right supramarginal gyrus, cuneus and precuneus, and cerebellum (lobule
For beat *continuation* > *finding*, activity was greater in the insula, putamen, hippocampus, thalamus, inferior orbitofrontal cortex, and cerebellum (crus I). Regions with greater activity during beat *adjustment* > *finding* include insula, putamen, globus pallidus, hippocampus, and thalamus. For beat *adjustment* > *continuation*, activity was greater in supplementary motor area (SMA), putamen, and right frontal operculum.

Figure 13. Contrasts for each stage (beat finding, beat continuation, and beat adjustment) vs. rest, for whole brain (left panel) and putamen ROI small-volume correction (right panel) analyses. Highlighted voxels are statistically significant, at $p < .001$ uncorr.
<.001 uncorrected. STG = superior temporal gyrus, ST Pole = superior temporal pole.

Table 2. Peaks Across Different Stages of Beat Perception

<table>
<thead>
<tr>
<th>Finding &gt; Continuation</th>
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Cluster 1 = 3725 voxels; 2 = 321 voxels; 3 = 116 voxels; 4 = 131 voxels; 5 = 84 voxels.

<table>
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<th>Continuation &gt; Finding</th>
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<tr>
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Cluster 1 = 165 voxels; 2 = 189 voxels; 3 = 77 voxels; 4 = 2032 voxels; 5 = 127 voxels.

<table>
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<th>Adjustment &gt; Finding</th>
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Cluster 1 = 27 voxels; 2 = 415 voxels; 3 = 3342 voxels.

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Cluster 1 = 107 voxels; 2 = 61 voxels; 3 = 151; 4 = 48 voxels; 5 = 521 voxels; 6 = 129 voxels.

Stereotactic coordinates (x, y, z) of reported peak voxels (whole brain cluster-level FDR corrected < .05, clusters formed at < .0001 uncorrected) are in Montreal Neurological Institute space (mm).

---

**Figure 14.** fMRI results from direct contrasts of stages of beat perception.

Highlighted voxels are statistically significant, at $p < .001$ uncorrected.
Metrical incongruence was associated with activity in bilateral auditory and inferior frontal regions. During trials in which the two rhythms were metrically incongruent, compared to congruent trials, activity was greater in bilateral STG, left middle temporal gyrus (MTG), and right anterior insula as well as the frontal operculum (see Table 3 and Figure 15). The pattern of results (STG and insula/operculum) did not differ substantially for incongruent > congruent contrasts across the different stages (e.g., incongruent adjustment > congruent adjustment), although there was a subthreshold effect of incongruence during adjustment in insula, and a significant effect during finding and continuation in STG (see Figure 15).

Table 3. Peaks During Incongruent > Congruent Rhythms (All Stages)

<table>
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<tr>
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<th>y</th>
<th>z</th>
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</thead>
<tbody>
<tr>
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<td>7</td>
<td>4.37</td>
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Cluster 1 = 505 voxels; 2 = 120 voxels.
Stereotactic coordinates (x, y, z) of reported peak voxels (whole brain cluster-level FDR corrected < .05, clusters formed at < .001 uncorrected) are in Montreal Neurological Institute space (mm).

Beat tapping consistency and beat perception ability were associated with greater activity in temporal and parietal regions (see Table 4 and Figure 16). Activations in bilateral STG, right superior temporal pole, and left supramarginal gyrus were greater for participants with better beat tapping consistency (lower coefficient of variation of inter-tap intervals). Activations in right posterior STG and MTG were greater for participants with better beat perception (higher BAT scores).

As expected, comparison between tasks revealed greater activity in occipital cortex for the rating task compared to deviant-detection task (cluster-level FDR < .05).
Figure 15. fMRI results contrasting listening during metrically incongruent > congruent trials. Highlighted voxels are statistically significant, at $p < .001$ uncorrected. Bar graphs indicate means and SEM for incongruent > congruent contrasts for each individual stage (beat finding, continuation, adjustment), for peak voxels in the three regions.

Table 4. Correlations Between Behaviour and fMRI Activity

<table>
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<th>Tapping Consistency (CV)</th>
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<th>Cluster</th>
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<td>63</td>
<td>2</td>
<td>-5</td>
<td>4.36</td>
</tr>
<tr>
<td></td>
<td>R Superior Temporal Pole</td>
<td>2</td>
<td>60</td>
<td>8</td>
<td>-8</td>
<td>4.14</td>
</tr>
</tbody>
</table>

Cluster 1 = 97 voxels; 2 = 89 voxels.

Stereotactic coordinates ($x, y, z$) of reported peak voxels (whole brain cluster-level FDR corrected < .05, clusters formed at <.001 uncorrected) are in Montreal Neurological Institute space (mm).

BAT % correct

<table>
<thead>
<tr>
<th>Brain Area</th>
<th>Cluster</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
</tr>
</thead>
</table>
Figure 16. fMRI correlates of beat perception (% correct on BAT) and negative correlates beat tapping variability (CV of inter-tap intervals from beat tapping task). Highlighted voxels are statistically significant at $p < .001$ uncorrected.

4.4 Discussion

4.4.1 Differing Neural Mechanisms Across Stages of Beat Perception

The results suggest that distinct regions of the striatum respond during the different stages of beat perception, indicating that distinct functions may be occurring at each stage. The dorsal putamen was most active during beat finding, which requires the detection of regularity. We propose that detection of regularity may be supported by
medium spiny neurons in the dorsal putamen that detect the coincidence of cortical oscillations (Matell & Meck, 2004), and in turn reset the phase of cortical oscillators (Oprisan et al., 2014).Resetting the phase of neural oscillations to entrain them to the onsets of regular stimulus events, such as the beat positions in a musical rhythm, is a likely necessary step in initiating beat perception.

The ventral putamen was more active during continuation and even more so during adjustment, compared to finding, suggesting that that region supports ongoing temporal prediction during beat perception (as per Kotz et al., 2009), and the integration of the temporal prediction errors (as per McClure et al., 2003) that occur during adjustment, into the ongoing, perceived beat structure.

“Actor” and “critic” functions have been associated with dorsal and ventral regions of the striatum, respectively, and these may correspond to their differential activation over the stages of beat perception roles. The actor-critic model suggests that in learning, the actor (dorsal) region of the striatum uses temporal prediction errors to modify stimulus-response associations in order to select actions, whereas the critic (ventral) region uses temporal prediction errors to update successive predictions based on the state of external-internal environment dynamics (O'Doherty et al., 2004; O'Doherty, Hampton, & Kim, 2007). This view suggests that temporal predictions are constant, and the striatum processes temporal prediction errors in all stages of beat perception, but with different functions. With respect to our results, the “critic” (ventral putamen) is most active during beat adjustment, the stage requiring the integration of temporal prediction error processing into ongoing predictions in order to maintain persistent beat perception (the internal state) in the face of changing auditory rhythm (the external state). The “actor” (dorsal putamen) is more active during beat finding, the stage requiring the initial assessment of the stimulus in order to select the appropriate response (e.g., a beat rate to be perceived or motorically entrained to). Beat and metre perception can be thought of as an attentional behaviour (London, 2004) that is inherently motoric, and as such, the notion of beat finding as modifying stimulus-response associations seems apt. Thus, beat
finding and adjustment may resemble previously proposed “actor—critic” functions of dorsal and ventral striatal regions, respectively, which are preferentially active for those stages.

Beyond functions supported by the striatum, the results point to mechanisms involving other regions across the distinct stages of beat perception. During beat finding, before the beat is detected, temporal intervals may be processed as absolute durations, rather than as durations relative to the beat, as no beat has yet been detected. Consistent with absolute timing occurring during finding, we found that activity in cerebellar lobule 8 was greater during finding than during continuation, as previous evidence shows that the cerebellum supports absolute timing (Teki et al., 2011). Additionally, during finding, attention orients in time to prospective beat positions. We found that activity in left inferior parietal cortex was greater during finding than continuation, consistent with previous evidence of its role in orienting attention to time (Bolger, Coull, & Schön, 2014; Coull & Nobre, 1998; Davranche, Nazarian, Vidal, & Coull, 2011; Cotti, Rohenkohl, Stokes, Nobre, & Coull, 2011). Moreover, during beat finding, the rhythmic stimulus is novel, and draws the listener’s attention. This general shift in attention to the rhythm may correspond to the greater anterior cingulate cortex activity in finding than continuation, given its role in attention to relevant external stimuli (Botvinick, Cohen, & Carter, 2004; Totah, Kim, Homayoun, & Moghaddam, 2009). Thus, in addition to striatal functions, the cerebellum, left inferior parietal cortex, and anterior cingulate may support the absolute timing, and orienting of attention in time, that occurs during beat finding.

After finding, during which the beat is detected and encoded, beat continuation enables the ongoing beat to be maintained and retrieved, in order to generate temporal predictions. The duration of the inter-beat interval is used in real time to predict the onsets that will occur in the ongoing stimulus. The observed activation in the posterior hippocampus for continuation (to a greater extent than for finding) may be in support of the maintenance and retrieval of the beat interval, consistent with recent evidence of a posterior hippocampal role in auditory working memory, specifically in the “analysis of
auditory stimuli in real time” (Kumar et al., 2016). Additionally, previous research found hippocampal activation, though more anteriorly, during beat continuation (Grahn & Rowe, 2013).

The anterior insula is more active during both continuation and adjustment compared to finding, suggesting it supports ongoing beat perception. Insula activity has been widely observed in temporal auditory processing (e.g., Pastor, Macaluso, Day, & Frackowiak, 2006; Steinbrink, et al., 2009; Bamiou, et al., 2003), and during beat perception it may support the integration of auditory and motor processing (Kurth, Zilles, Fox, Laird, & Eickhoff, 2010; Mutschler et al., 2007; Mutschler et al., 2009; Zarate & Zatorre, 2005). The integration of auditory processing (i.e., rhythm perception) and motor processing (i.e., motoric entrainment, motor system activation) is the phenomenological hallmark of beat perception. However, auditory-motor integration is less involved in beat finding, during which auditory rhythm perception has not yet induced motoric entrainment, compared to continuation and adjustment. Thus, the observed anterior insula activation during continuation and adjustment (compared to finding) may be due to its role in auditory-motor integration.

### 4.4.2 Metrical Incongruence

Human beat perception tends to persist during listening to metrically incongruent (e.g., polyrhythmic) stimuli. Even when listening to rhythms specifically designed to have an ambiguous metrical structure, allowing for multiple regularities to be perceived as the ‘beat’, listeners only track one rate as the ‘beat’ (Poudrier & Repp, 2013). This persistence of stable beat perception occurs in musical contexts in which different instruments produce distinct rhythms conforming to different metrical structures (metrical ambiguity, see London, 2012). When tapping the beat in metrically ambiguous compared to unambiguous rhythmic contexts, greater activity is found in inferior frontal regions, right anterior insula, and right inferior parietal cortex (Vuust, Roepstorff, Wallentin, Mouridsen, & Østergaard, 2006; Vuust, Wallentin, Mouridsen, Ostergaard, & Roepstorff, 2011), suggesting that these regions are part of a network relevant in
integrating and cohering temporal information. We thus used metrically congruent and incongruent trials to compare the neural mechanisms of the maintenance of beat perception in the face of metrical incongruence in the rhythmic stimulus.

The right anterior insula was more active during metrically incongruent rhythms than congruent rhythms, when beat perception was persisting despite conflicting cues about beat structure. This is highly consistent with the aforementioned work on beat perception in metrically incongruent and congruent contexts, which found greater right anterior insula activity for incongruent compared to congruent contexts (Vuust et al., 2006). The function of the anterior insula in metrical incongruence may be similar to its function integrating auditory and motor processing in continuation and adjustment (compared to finding), as discussed above. That is, metrical incongruence may require the anterior insula’s integration of auditory and motor processing to a greater extent (than for metrical congruence) in order to maintain beat perception, because of the difficulty in maintaining beat perception when there are multiple, conflicting metrical cues (participants had less consistent and less accurate beat tapping for incongruent rhythm, and rated them as being more difficult to maintain a sense of the beat for, compared to congruent rhythms).

4.4.3 Behavioural Correlations
Correlations between behavioural performance and fMRI data showed that bilateral STG was more active for participants with superior beat tapping consistency (lower variability of inter-tap intervals) and right STG was more active for participants with superior beat perception (greater proportion of correct trials in the BAT). Greater STG activity may be associated with more attention to the rhythms, which would lead to more accurate behavioural performance.

4.5 Conclusion
The striatum plays an important role in the processing of temporal regularity and the prediction of regular events. The results here indicate that dorsal and ventral regions of the putamen have distinct functions in the different stages of beat perception during
listening to musical rhythms. Dorsal regions were more active for *beat finding* (possibly because of detection of coincidence and phase resetting of neural oscillations) and ventral regions were more active during *beat adjustment* (possibly because of the processing of temporal prediction errors). Overall, we can place these striatal functions within the broader neural mechanisms that support the distinct processes of beat perception: mechanisms that vary in time (e.g., initial *beat finding* followed by *beat continuation*), mechanisms that depend on the unfolding and dynamic nature of the auditory rhythm (e.g., *beat adjustment*), and mechanisms that are arise by stimulus characteristics (e.g., metrical incongruence).
Chapter 5

5 General Discussion

The research presented in the previous three chapters was conducted to better understand the neural processes that underlie the perception, cognitive processing, and behavioural consequences of musical rhythm. Broadly, the data demonstrate that 1) culture is associated with how we perceive, produce, and thus how our brains process, auditory rhythms, 2) neural entrainment to rhythms depends on more than stimulus characteristics and differences in entrainment are associated with culture, and 3) distinct neural mechanisms support distinct stages of beat perception as it unfolds.

5.1 Discussion of Chapters 2-4 in a Wider Context

In Chapter 2, participants from two cultures (East African or North American) completed three tasks, which, critically, used rhythms that were designed to be culturally familiar to either East Africans or to North Americans. We observed an association between culture and rhythm reproduction, beat tapping accuracy, and the nature of beat tapping (the tendency to use a greater number of metrical levels across trials). Because the cultures were likely to differ in ways that were unrelated to the hypotheses of interest (e.g., familiarity with testing conditions and equipment, whether or not participants had a common first language with the experimenter, etc.), two distinct cultural groups and stimulus sets were used so that interactions, rather than main effects, could be assessed. This design takes into account that cultural groups may differ in ways that are unrelated to the hypotheses, but that nevertheless influence the results. Several existing cross-cultural studies have used the same 2x2 design (Demorest et al., 2010; Hannon, Soley, & Ullal, 2012; Iversen, Patel, & Ohgushi, 2008; Soley & Hannon, 2010). Critical to this 2x2 cross-cultural design is that an influence of culture is only interpreted for statistically reliable interactions of Group and Rhythm Type (and not for simple group differences) for accuracy of task performance (e.g., beat tapping variability, or rhythm discrimination scores), as it is plausible that these differences may have arisen from differences in
familiarity with equipment or language, as mentioned above. However, group differences in the nature of task performance—the way in which the task is performed, rather than strictly how well it is performed (e.g., the number of metrical levels chosen over all beat tapping trials, rather than how accurate the tapping is)—may indicate an association with culture, as group differences in these cases are not easily attributed to plausible confounds. Specifically, it is unclear how unfamiliarity with testing or barriers between participant and experimenter would result in a participant using a greater number of metrical levels over all beat tapping trials than it is that actual cultural differences between East African and North Americans would lead to this difference in the nature of task performance.

The observed association between culture and rhythm reproduction and beat tapping contributes to the rather sparse literature on experimental, cross-cultural research in music perception and cognition. Experimental, cross-cultural research in cognitive neuroscience is practically challenging (e.g., equating testing conditions in different regions), but also theoretically challenging. For example, it is difficult to predict the effect size of cross-cultural differences, as not all cultures are equally distinct from one another, in terms of musical rhythms. For the present study, our research benefitted from the fact that the distinctions between musical rhythm and rhythm-related behaviour of the broader cultures tested here (African and Western) are well-established (see Temperley, 2000). Thus, the cross-cultural 2x2 (Group x Stimulus Type) design and the use of two cultures with highly distinct musical rhythms maximized our ability to observe real effects of culture.

The two behavioural tasks for which we observe an association with culture involve motor production: rhythm reproduction and beat tapping. By contrast, in the non-motor task (rhythm discrimination) we do not observe a significant association with culture. As suggested in Chapter 2, it may be that the ways in which culture influences the processing of rhythm do not influence how rhythms are perceived during this particular task, or, it may be that we were unable observe a real effect of culture on rhythm discrimination.
because of stimuli that did not maximally exploit cultural differences and/or insufficient data (number of trials per participant and/or number of participants). One possibility is that effects were observed in the motor tasks specifically because motor tasks are more sensitive to differences in the processing of rhythm and beat, possibly for reasons related to the close connection between musical rhythm, the brain’s motor system, and movement.

The effect of culture on the number of the different metrical levels tapped across different rhythm types stands out as an example of how the nature of beat production, and possibly beat perception, can be associated with culture. East African participants used more metrical levels as the beat during the beat tapping task than did North American participants. Both groups tapped more metrical levels for the East African rhythms than for the Western rhythms. These two effects may be related: East African participants’ tendency to tap more metrical levels may be due to their relatively greater exposure to and experience with the type of rhythms (East African) to which listeners in general tap more metrical levels. Though this proposed causal relationship cannot be demonstrated with the present data, it is plausible.

The difference in how participants tapped the beat in East African and Western rhythms corresponds with the difference in how neural activity entrained to different metrical levels in the two types of rhythms. In Chapter 3, we observed different patterns of neural entrainment to metrical levels of rhythms in East African and North American participants. These results extend the observed effects of culture on rhythm production (Chapter 2) and contribute to the extremely limited body of cross-cultural, neuroscientific research on music and musical rhythm (although see Demorest et al., 2010; Morrison, Demorest, Aylward, Cramer, & Maravilla, 2003) for two cross-cultural fMRI studies of music perception). The differences in neural activity between the two cultural groups are made more interpretable by the fact that behaviour differs (critically using identical stimuli for behavioural and neural measures), and vice versa. Across all participants, the tendency to tap particular metrical levels was reliably correlated with neural entrainment
to them (during passive listening). Any causal relationship between these correlated measures, however, is unknown and unmeasurable from the present data. The correlation may be driven by correlations at the single-trial level: entrainment strength for particular metrical levels may correspond to tapping those metrical levels in individual rhythms. If so, it is plausible that during initial listening, before beat tapping begins, the metrical levels with stronger entrained neural oscillations cause motor programs to more readily select those metrical levels as the frequency to tap. It is also plausible that both neural entrainment and beat tapping tendency are related to past experience moving with rhythms (i.e., that the metrical levels that have been motorically entrained to in past experience are more likely to be chosen for as the beat to tap, and also strengthens neural entrainment those levels). This is consistent with previous evidence that prior (short-term) experience entraining movements to particular metrical levels of rhythms enhances neural entrainment to those same levels during later listening (Chemin, Mouraux, & Nozaradan, 2014), and to a lesser extent with evidence that infants with music class experience have enhanced neural entrainment to particular metrical levels during rhythm listening. The broader interpretation of the correlation between beat tapping tendency and neural entrainment in terms of an underlying link between neural entrainment, behaviour, and perception could be aided by further work connecting neural entrainment to perception and behaviour, especially for musically realistic rhythms.

Neural entrainment is likely influenced by many factors besides the listener’s experience entraining their movements at particular metrical levels. Primarily, a rhythm’s temporal structure will influence the degree of entrainment to the different frequencies that correspond to metrical levels because neural activity entrains to stimuli that occur regularly. Thus, we expect entrainment to occur at all metrical levels during listening to rhythms (as all metrical levels correspond to rates of real event onsets in stimuli). However, only one metrical level can be selected as the beat to entrain single-effector movements to (such as tapping the beat with a finger) (Poudrier & Repp, 2013). Together, it is not surprising then, to see a less than perfect association between neural and behavioural measures. As an example, although we expect neural entrainment to
occur at the fastest and slowest metrical levels (1 and 6, respectively) as they correspond to event rates in the stimuli, we also expect that they are less likely to be tapped because they are furthest from the preferred rate that humans tend to entrain movements to (roughly 500-600ms; see London, 2004), and also, in the case of the fastest metrical level, challenge motor constraints. We cannot fully assess the extent to which behaviour or perception correspond to enhancement of neural entrainment to certain metrical levels—but we find evidence that they are related.

As noted above, East African participants tapped more metrical levels during the beat tapping task, compared to North American participants, and both groups tapped more metrical levels along with East African rhythms compared to Western rhythms. The latter difference may also be related to observed patterns of neural entrainment: Over all participants, entrainment did not differ between metrical levels during listening to the East African rhythms. By contrast, during listening to Western rhythms, entrainment to metrical level 3 was greater compared to all others, and entrainment to a different metrical level (2) was lesser than all others. The absence of a clear metrical hierarchy in neural entrainment to East African rhythms compared with the presence of one for Western rhythms, corresponds to previous descriptions of metre in these types of music. African music has a flatter metrical hierarchy, in terms of the salience of different metrical levels, compared to Western music (Temperley, 2000; Kauffman, 1980; Arom, 1989; Magill, 1997; Agawu, 2006).

In Chapter 4, we used fMRI to investigate the distinct neural mechanisms that underlie different processing and perceptual stages of beat perception. This experiment expanded on previous fMRI studies of beat perception (Grahn & Brett, 2007; Grahn & Rowe, 2009; 2012). This literature has focused on how regions of the motor system, and the striatum in particular, support rhythm and beat perception. However, the methods and stimuli applied here differ from previous studies in multiple relevant ways.

First, whereas previous studies contrasted activation during listening to beat-based and non-beat-based rhythms to identify regions selectively activated during beat perception
(as opposed to perception of simply rhythm), all stimuli used here were beat-based rhythms. While contrasting beat and non-beat rhythms successfully isolates beat perception from rhythm perception, it eliminates the possibility of uncovering regions whose activation is required for beat perception but occurs in response to both beat-based and non-beat-based rhythms. Specifically, during beat finding, the processing required to detect regularity \textit{when it is present} may occur during perception of all rhythms, but is successful in detecting the predictable regularity that subsequently induces beat perception only when the perceived rhythm is beat-based. Contrasting perception of beat-based and non-beat-based rhythms may eliminate the possibility of revealing this mechanism. In this way, our experimental design may capture real neural mechanisms involved in beat finding that were missed in beat vs. non-beat contrast designs.

Second, and also related to stimulus characteristics, the stimuli used here are more ecologically valid than the stimuli used in the two fMRI studies investigating different stages of beat perception (Grahn & Rowe, 2012 and Kung, et al., 2013). Grahn and Rowe (2012) presented consecutive, short, beat-based and non-beat-based rhythms, of varying tempi. Beat-based rhythms following silence or following non-beat rhythms were considered beat finding, beat-based rhythms following a beat-based rhythm with the same rate were considered beat continuation, and beat-based rhythms that had a slower or faster rate than the preceding (beat-based) rhythm were considered as distinct forms of beat adjustment. The finding condition in the present study always followed silence, more closely resembling the experience of hearing real music, starting from silence, in which the initial sounds provide cues about what the metrical and other structures of the music are. By contrast, a beat-based rhythm immediately following a non-beat-based rhythm (as used in Grahn & Rowe, 2012) could be understood as akin to beat adjustment, in the sense that auditory inter-onset intervals were being perceived and processed before a beat structure could be (gradually) detected and used for prediction. In addition, the beat adjustment stage in our design always presented temporal intervals that fit with the metrical structure of the stimulus heard up to that point (IOIs corresponded to metrical levels, even in the incongruent trials). Thus, our adjustment stage allowed ongoing
perception of a pulse (at a faster metrical level than was typically tapped as the beat) and the higher-level beat structure could either be the same or different. Again, this is more akin to real music (e.g., metrical ambiguity, see London, 2012), compared to the shifting temporal structures used previously (Grahn & Rowe, 2012). Thus, the stimulus sequences in that study were less similar to real music than those used here, in that beat rates changed more rapidly than occurs in music, whereas the rhythms used here had a continuous beat structure, as occurs in real music. In another previous study, Kung and colleagues (2013) presented beat-based rhythms but required tapping along with the rhythms after an initial ‘finding’ stage (that had no tapping). In contrast, our finding stage was purely perceptual, with no inclusion of tapping preparation occurring in the beat finding condition.

Third, two rhythms were presented simultaneously, and were either metrically congruent or incongruent (but inducing beat perception in both cases), compared to the vast majority of previous rhythm and beat perception studies in which only one rhythm is presented at a time. This stimulus construction was critical to create our beat adjustment stage, but it is also ecologically valid, as real music is most often polyphonic, with different voices or instruments producing distinct rhythms that together induce a single beat percept.

5.2 Limitations

The 2x2 cross-cultural design of Chapters 2 and 3 has the limitation of being quasi-experimental: participants had pre-existing cultural backgrounds and thus were not subject to random assignment. For this reason, we are unable to say with the certainty that culture causes the observed group differences. As mentioned above, it is possible that genetic (or other) differences account for the results, although this seems unlikely. There were specific group differences that may have contributed to performance on the behavioural tasks: specifically, participants in the East African sample were, anecdotally, far less familiar with psychology/neuroscience testing and using a laptop compared to the North American participants. They were also less fluent with English (although this
varied widely across the sample) and translation was used for some participants. For this reason, successfully communicating task requirements was more challenging when testing East African participants than North American participants. Together, these factors may have contributed to the overall main effects of group: East Africans performed worse overall on the rhythm discrimination and reproduction tasks, and had worse beat tapping accuracy. However, as discussed above, the interaction of the group difference with the influence of the type of rhythm being heard (in the reproduction and beat tapping tasks) allows us to interpret these otherwise confounding group differences, as confounding factors are equally likely to affect performance for both types of rhythms. Thus, the Group x Rhythm Type interactions likely indicate that the groups responded differently to the two types of rhythms—an association with culture.

Data collection in East Africa was, to a certain extent, opportunistic, thus, because of external circumstances (e.g., equipment availability) and time constraints, only 16 East African participants were able to participate (and only 13 of those involved EEG recording). In addition, different EEG systems were used for East African and North American participants, but differences between the two systems are unlikely to have confounded our results as reported, as discussed in Chapter 3, because EEG power at frequencies of interest during silence did not show the same differences between groups and metrical levels that were found in EEG during rhythm presentation.

The association between brain and behaviour reported in Chapter 3 is a key finding—neural oscillations not only entrain to rhythm and beat, and are associated with cultural experience, but relate to beat tapping behaviour. The methods used here preclude observing a 1:1 association between neural entrainment and behaviour for individual rhythms, because both neural and behavioural data were averaged over trials. Other designs could enable direct comparisons, for example by obtaining EEG recordings from multiple trials of the exact same rhythm, and separately, beat tapping with the same rhythm, which would give a strong prediction for each individual rhythm as to the metrical levels to which neural and behavioural entrainment should occur, rather than
averaging over all rhythms of the same type, in which rhythm-specific signals are lost to averaging.

A general limitation of EEG methods is the challenge of localizing the source(s) of observed neural activity. For this reason, we cannot interpret where in the brain the observed neural entrainment occurs. However, the observed correlation between behavioural tapping and frequencies of neural entrainment lends support to entrainment as a potential neural mechanism of beat perception, although, as noted above, better understanding of how neural entrainment relates to perception and behaviour would further this interpretation. Ideally, future research will enable interpretation of the present results within a broader mechanistic view, with better understanding of which neural regions entrain to rhythms and how different regions entrain to one another.

One limitation of the fMRI data is that seven of the 18 participants performed one task (rating the strength of the perceived beat after each trial), while the other 11 performed that same task for half of the trials and another task (responding when they heard a deviant tone) for the other half. As discussed in Chapter 4, the change from one to two tasks was made to clarify whether activations in visual cortex that were observed in a preliminary analysis (of the first seven participants’ data) were caused by the visual aspect of the beat rating task. Indeed, visual activations were reduced during the deviant detection task, which, unlike the rating task, did not have a standard display screen asking for the participant’s response at the end of each trial. Given the logic of fMRI in cognitive neuroscience—that the cognitive processes associated with the task performed in the scanner are related to the acquired signal from the brain—the task difference between these groups of 7 and 11 participants is worth noting. However, this difference does not invalidate the interpretations of our results. Our a priori interest was the phenomenon of beat perception—which arises due to perception of a beat-based auditory rhythm—rather than the explicit task or cognitive intention performed in the scanner, and both tasks were designed to ensure attention to the auditory stimulus was maintained. Moreover, previous studies using different in-scanner tasks have found highly similar
results for the same beat rhythms > non-beat rhythms contrast (e.g., Grahn and Rowe (2012) used a beat rating task, Grahn and Rowe (2009) used a deviant detection task, and Grahn and Brett (2007) used a rhythm discrimination task, and all three studies show robust striatal and SMA activations for beat > non-beat listening contrasts).

The stimulus design used in the fMRI study allows for a novel investigation of a particular phenomenon: ‘switching’ from one beat rate and metrical structure to another, within a continuous rhythmic stimulus. This is a real musical phenomenon. However, we did not find significant results for the contrast that isolates this phenomenon (Incongruent Adjustment > Congruent Adjustment), and using a relaxed statistical threshold, results strongly resembled those reported in the overall Incongruent > Congruent contrast. The lack of results for this particular phenomenon may be due to a number of factors. The contrast may have been underpowered (too short a duration for the adjustment stage, too few trials per participant, and/or too few participants). The phenomenon may also have been too variable: We did not expect that all participants’ sense of the beat would switch at the exact same time relative to the stimulus, and indeed some participants may not have switched; either due to hysteresis of beat perception induced by the first part of the rhythmic stimulus (they kept the same beat rate going), or due to insufficient exposure to the new metrical structure (they lost sense of the initial beat rate, but did not regain a new sense of beat). A different task may be able to better isolate this phenomenon for improved temporal alignment of fMRI data by requiring participants to indicate when their perception of the beat switches, or training participants to internally switch their perception when cued to do so, although both of these possibilities would require further changes to the experimental, stimulus, and task designs. Despite not isolating the particular phenomenon of beat ‘switching’, we remain confident in the interpretation of results with respect to beat adjustment and metrical incongruence, both of which may reveal mechanisms that contribute to beat ‘switching’ (e.g., the right anterior insula).

In order to investigate the neural mechanisms of beat perception, we used univariate, general linear model analyses to assess whether acquired fMRI data revealed differences
in neural activation between the different stages of beat perception and between metrical congruent vs. incongruent rhythms. With this approach, observed differences in the data we believe to be reasonably and validly interpreted as reflecting differing neural mechanisms. However, applying other analytic methods (e.g., connectivity) could further reveal aspects of the mechanisms underlying the stages of beat perception. Such analyses could elucidate different networks by revealing which regions have correlated activity, and differences in those correlations across the different stages. As a specific example, in addition to the observation that dorsal and ventral regions of the putamen respond differently during beat finding and beat adjustment, respectively, the broader neural mechanisms related to these perceptual stages could be informed by observing in which neural regions activity correlates with that of dorsal vs. ventral putamen during respective beat perception stages. Such observed regions may or may not be similar to those observed in the univariate contrasts (e.g., parietal and cerebellar regions during beat finding, and hippocampal and insular regions during beat adjustment).

As in the cross-cultural EEG study, fMRI data correlated with behavioural measures. Participants with better beat tapping performance had greater activity in bilateral STG and left supramarginal gyrus during rhythm perception, and those with better beat perception ability (BAT scores) had greater activity in right STG during rhythm perception. However, while interpretable (see Chapter 4), these behavioural measures have a limited ability to reflect our primary interest, the unfolding dynamics of beat perception as a stimulus unfolds over time. We lack a valid and reliable behavioural measure of beat perception that would be sensitive to changes over time (i.e., in response to the stimulus manipulations used here). Beat tapping is a valid index of beat perception, but varies across individuals in ways that challenge its use in different perceptual stages. For example, when instructed to tap the beat with a rhythm, individuals vary in how quickly they begin tapping: some begin quickly after the rhythm starts and their tapping variability and accuracy tends to gradually improve as beat perception stabilizes, whereas others will begin tapping later, after they are confident about the beat timing, in which case tapping is more stable and accurate from the start. Another major challenge to using
beat tapping as an index of perception is that beat tapping affects beat perception (Manning & Schutz, 2013). For our stimulus design, this is primarily a concern for the incongruent adjustment stage, in which we expect that the act of tapping would support hysteresis of the original beat as perceived up to that stage. The study of beat perception’s unfolding dynamics over time would benefit from behavioural measures that reliably assess perception in this regard, without confounds related to tapping.

5.3 Broader Interpretations and Future Directions

The research presented in Chapters 2-4 links behaviour, perception, and neural activity as measured with EEG and fMRI, contributing to greater understanding of the neural mechanisms that support rhythm and beat perception. EEG and fMRI provide distinct perspectives on neural mechanisms, and were used here to show an association between culture and entrainment of neural oscillations to auditory rhythms, and to examine the neural activity underlying different stages of beat perception, respectively. These two perspectives provide useful insight about neural mechanisms, but are not easily linked together: We can neither say from these data where the entrained neural oscillations arise (or how entrained oscillations in different regions interact), nor what oscillatory dynamics of neural activity occur in the regions identified as differentially active for different stages of beat perception. Future research could integrate these aspects of neural mechanisms. Specifically, one can ask which neural populations give rise to different entrained oscillations (in terms of oscillatory frequency). The literature shows that neural oscillations in different frequencies bands entrain differently to different auditory rhythms. In addition to entrainment to the relatively slow frequencies of metrical levels (as in Chapter 3; Chemin et al., 2014; Cirelli, Spinelli, Nozaradan, & Trainor, 2016; Nozaradan, Peretz, & Keller, 2016; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Peretz, & Mouraux, 2012; Nozaradan, Zerouali, Peretz, & Mouraux, 2015), entrainment also occurs in the power fluctuations of relatively faster activity (in the beta band, 15-25 Hz). Importantly, beta power fluctuates in an anticipatory fashion (Fujioka, Trainor, Large, & Ross, 2012). However, these two frequency bands of entrainment (beat rate and beta band) have not been thoroughly connected or dissociated in the context of
musical rhythm, so their functional relevance to one another in rhythm and beat perception remains unknown. One possibility is that entrainment to the relatively slower beat rate in a rhythm occurs in the auditory system, due to auditory cortex responses to individual sound onsets, whereas entrainment of beta fluctuations occurs in the motor system (given beta activity’s importance in motor function and frequent localization to the motor system; see Baker, 2007; Salmelin, Hämäläinen, Kajola, & Hari, 1995; Salmelin & Hari, 1994). Thus, stimulus driven entrainment in the auditory system may drive entrainment of beta activity in the motor system.

Although this possible entrainment-based interaction between auditory and motor systems assumes that stimulus properties drive entrainment in the auditory system, other ‘top-down’ factors are clearly important, including experience and culture (Chemin et al., 2014; Cirelli et al., 2016; Chapter 3). Thus, besides stimulus properties, ‘top-down’ input (e.g., temporal attention, expectations, memory, movement, etc.) influence slower entrainment to frequencies embedded in rhythms. Biases in processing that underlie individual differences in neural entrainment could occur in the auditory system, for example, due to experience-driven synaptic strengthening between primary auditory cortex and specific neural populations in secondary auditory cortex whose oscillatory properties match the entrained frequency. Alternatively, top-down influences on auditory system entrainment to slow frequencies could result from input from elsewhere. For example, specific entrained oscillations could be enhanced by inferior parietal regions known to direct attention to specific points in time (Cotti, Rohenkohl, Stokes, Nobre, & Coull, 2011; Coull, Vidal, Nazarian, & Macar, 2004; Davranche, Nazarian, Vidal, & Coull, 2011) as beat perception unfolds, or by inferior frontal regions known to be active when familiar music is recognized (Demorest et al., 2010; Leaver, Van Lare, Zielinski, Halpern, & Rauschecker, 2009; Watanabe, Yagishita, & Kikyo, 2008) and thus allowing accurate predictions about the upcoming rhythms and beat structure. Linking to the fMRI results in Chapter 4, another possibility is that auditory responses in primary auditory cortex inform the striatal activity that supports the predictive aspects of beat perception,
which in turn contributes to entrainment in cortical oscillations elsewhere (possibly via beta band activity; see Bartolo, Prado, & Merchant, 2014).

This speculative proposal is intended as an example of plausible oscillatory-network mechanisms of rhythm and beat perception through which the results, particularly in Chapters 3-4, could be integrated. There is currently insufficient evidence to support a full theory of the brain-wide mechanistic interactions involved in rhythm and beat perception. To understand the neural mechanisms at the levels of brain function suggested here, future research will require further combinations of methods, including intracranial electrophysiological recordings from nonhuman primates and human patient populations.

5.4 Conclusion

The research described in this thesis contributes to our understanding of the human brain processes that underlie perception, cognition, and behaviour as it relates to musical rhythm, notwithstanding the limitations described above. The experimental designs, stimuli, analyses, and interpretations involved in this research have been primarily motivated within the perspective of cognitive neuroscience (i.e., uncovering how the brain supports perceptual, cognitive, and behavioural phenomena such as rhythm and beat perception), however, this work also adds to understanding of music. It informs ethnomusicological perspectives and provides a basis for future research designs related to cross-cultural perspectives as well as real time phenomenology of rhythm, beat, and metre. More generally, it can inform expansion of cognitive neuroscientific methods to research in the humanities. Overall, this work contributes to our understanding of how brain functions change over time during beat perception and how long-term experience influences rhythm perception and neural entrainment to rhythms. Together, these provide new knowledge about how brain functions underlie the pervasive and uniquely human phenomena of music.
References


Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J Neurosci, 18*(18), 7426-7435.


Appendix A. Figure of behavioural results for Chapter 4. Clockwise from top left: 1) Both tapping consistency (coefficient of variation, or CV, of inter-tap intervals) and tapping accuracy (absolute difference between tap and beat times as a proportion of the beat interval) were better for congruent compared to incongruent trials. 2) Congruent trials were also rated as have greater beat strength than incongruent trials (note that lower ratings reflect greater beat strength), for ratings made both before and during the fMRI scan (ratings did not differ between those two instances). Error bars indicate standard error of the mean, and * indicates \( p < .05 \).

3) Tapping accuracy and consistency were positively correlated. 4) Beat perception (proportion of correct trials on the BAT) and musical training (training subscale of the GMSI) were positively correlated.
## Appendix B. Table of Peaks Across Stages of Beat Perception

### Finding > Rest

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### Continuation > Rest

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### Adjustment > Rest

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</table>

Cluster 1 = 1915 voxels; 2 = 1640 voxels; 3 = 1087 voxels; 4 = 203 voxels; 5 = 51 voxels

Stereotactic coordinates (x, y, z) of reported peak voxels (whole brain cluster-level FDR corrected < .05, clusters formed at < .001 uncorrected) are in Montreal Neurological Institute space (mm).
Appendix C. Ethics approval, letters of information and consent forms for participants in North America and East Africa (English and Kinyarwanda).

![Western logo]

**Project Title:** Investigating Cultural Influences on Rhythm Perception in East Africa and Canada

**Principal Investigator:**
Rhodri Cusack, PhD; Departments of Psychology and Medical Biophysics; Brain and Mind Institute, University of Western Ontario

**Letter of Information**

1. **Invitation to Participate**
   You are being asked to participate in this research study investigating the neural mechanisms of rhythm perception because you have indicated that you are interested in participating and that you have lived in North America for most of your life. We are interested in the differences in patterns of brain activity during perception of rhythms common in East African and North American. This research will be conducted in Canada as well as in Kenya and Rwanda.

2. **Purpose of the Letter**
   The purpose of this letter is to provide you with the information required to understand the methods and goals of our research so that you can make an informed decision regarding participating in this research. We encourage you to ask the research investigators any questions you may have related to the study.

3. **Purpose of this Study**
   The purpose of this study is to better understand the influence of culture on brain processes during rhythm perception. Since the music in East Africa and North America are strikingly different, we can investigate the different ways in which people from these regions perceive the rhythmic aspects of music.
4. **Inclusion Criteria**

   Adults over the age of 18 with normal or corrected-to-normal hearing who have lived in North America for the majority of their lives are eligible to participate in this research.

5. **Exclusion Criteria**

   Participants with impaired hearing or any neurological condition (including epilepsy) are not eligible to participate in this study.

6. **Study Procedures**

   If you participate in this study, you will be asked to fill out a questionnaire regarding your experience with music and musical training. You will take part in a rhythm perception task requiring you to listen to and compare auditory rhythms. You will perform a rhythm reproduction task requiring you to listen to an auditory rhythm and then tap it back on a computer keyboard. You will also complete a task requiring you to tap to the ‘beat’ as you listen to rhythms.

   Some participants will have the option to undergo a second part of the study using electroencephalography (EEG) to measure brain responses to rhythms.

   The EEG component of the study will require application of an alcohol swab to your scalp to prepare the skin, application of conductive gel to help record EEG signals, and the application of (14-128) electrodes to your scalp. Once this preparation is complete, you will be asked to sit still and listen to various auditory rhythms. The EEG system provides a non-invasive and safe method of recording brain activity.

   We expect that testing will last approximately 60 minutes for each participant completing only the behavioural tasks (reproducing and discriminating rhythms, and tapping the beat with rhythms). We expect behavioural and EEG testing to last approximately 90-120 minutes. Testing will occur at Western University’s Brain and Mind Institute, and at the University of Toronto. There will be 30 participants completing only the behavioural portion of the study. An additional 20 participants will complete both the behavioural and EEG portions.

7. **Possible Risks and Harms**
There are no health risks involved in this experiment for those participants not undergoing EEG recording.

The application of EEG electrodes on the scalp requires the use of an alcohol scrub and conductive gel. Some participants may experience a mild skin irritation as a result, however this does not represent a significant health risk. EEG requires participants to remain still and minimize eye blinks, which can become strenuous. If you become uncomfortable and do not wish to continue, the experiment will be terminated immediately.

8. Possible Benefits

You will not directly benefit from participating in this study but information gathered may provide benefits to society as a whole. These include a better understanding of the brain mechanisms underlying auditory and motor function. Better understanding of these mechanisms can lead to novel applications in neurological health and development.

9. Compensation

You will be compensated $5 per hour for your participation in the behavioural tasks and $10 per hour if completing both EEG and behavioural tasks.

10. Voluntary Participation

Participation in this study is voluntary. You may refuse to participate, refuse to answer any questions or withdraw from the study at any time with no effect on your compensation or future (academic status, etc.).

11. Confidentiality

Your identity will not be published or made public in anyway due to participation in this study. All data collected will remain confidential and accessible only to the investigators of this study.

12. Contacts for Further Information
If you have any questions or would like more information about this research project, or your participation, you may contact Rhodri Cusack, Daniel Cameron, or Jocelyn Bentley. If you have any questions about your rights as a research participant or the conduct of this study, you may contact The Office of Research Ethics, email:

13. Publication

Results from this study may be published in peer-reviewed academic journals in the fields of psychology, neuroscience, and music cognition.

This letter is yours to keep for future reference.
Project Title: Behavioural and EEG Study of Adult Rhythm Perception in East Africa and North America

Principal Investigator:
Rhodri Cusack, PhD; Departments of Psychology and Medical Biophysics; Brain and Mind Institute, University of Western Ontario

Letter of Information

1. Invitation to Participate
   You are being asked to participate in this research study investigating the neural mechanisms of rhythm perception because you have indicated that you are interested in participating and that you have lived in East Africa for most of your life. We are interested in the differences in patterns of brain activity during perception of rhythms common in East African and North American. This research will be conducted in in Canada as well as in Kenya and Rwanda.

2. Purpose of the Letter
   The purpose of this letter is to provide you with the information required to understand the methods and goals of our research so that you can make an informed decision regarding participating in this research. We encourage you to ask the research investigators any questions you may have related to the study.

3. Purpose of this Study
   The purpose of this study is to better understand the influence of culture on brain processes during rhythm perception. Since the music in East Africa and North America are strikingly different, we can investigate the different ways in which people from these regions perceive the rhythmic aspects of music.
4. Inclusion Criteria

Adults over the age of 18 with normal or corrected-to-normal hearing who have lived in East Africa for the majority of their lives are eligible to participate in this research.

5. Exclusion Criteria

Participants with impaired hearing, neurological injury or neurological diseases (including epilepsy) are not eligible to participate in this study.

6. Study Procedures

If you participate in this study, you will be asked to fill out a questionnaire regarding your experience with music and musical training. You will take part in a rhythm perception task requiring you to listen to and compare auditory rhythms. You will perform a rhythm reproduction task requiring you to listen to an auditory rhythm and then tap it back on a computer keyboard. You will also complete a task requiring you to tap to the ‘beat’ as you listen to rhythms. The Electroencephalography (EEG) component of the study will require application of an alcohol swab to your scalp to prepare the skin, application of conductive gel to help record EEG signals, and the application of (14-128) electrodes to your scalp. Once this preparation is complete, you will be asked to sit still and listen to various auditory rhythms. The EEG system provides a non-invasive and safe method of recording brain activity.

We expect that testing will last approximately 90 minutes for each participant. Testing will occur at University of Nairobi Hospital in Nairobi, Kenya, and at University Hospital in Kigali, Rwanda. There will be 60 participants split between Nairobi and Kigali.

7. Possible Risks and Harms

The application of EEG electrodes on the scalp requires the use of an alcohol scrub and conductive gel. Some participants may experience a mild skin irritation as a result, however this does not represent a significant health risk. EEG requires participants to remain still and minimize eye blinks, which can become strenuous. If you become uncomfortable and do not wish to continue, the experiment will be terminated immediately.
8. Possible Benefits

You will not directly benefit from participating in this study but information gathered may provide benefits to society as a whole. These include a better understanding of the brain mechanisms underlying auditory and motor function. Better understanding of these mechanisms can lead to novel applications in neurological health and development.

9. Compensation

You will be compensated 420 KES / 3,000 RWF per hour for your participation.

10. Voluntary Participation

Participation in this study is voluntary. You may refuse to participate, refuse to answer any questions or withdraw from the study at any time with no effect on your compensation or future (employment, academic status, etc.).

11. Confidentiality

Your identity will not be published or made public in anyway due to participation in this study. All data collected will remain confidential and accessible only to the investigators of this study.

12. Contacts for Further Information

If you have any questions or would like more information about this research project, or your participation, you may contact Rhodri@cusacklab.org or Daniel Cameron (dcamer25@uwo.ca; 0787885788). If you have any questions about your rights as a research participant or the conduct of this study, you may contact The Office of Research Ethics (519) 661-3036, email: ethics@uwo.ca.

13. Publication

Results from this study may be published in peer-reviewed academic journals in the fields of psychology, neuroscience, and music cognition.

This letter is yours to keep for future reference.
CONSENT FOR RESEARCH STUDY

Investigating Cultural Influences on Rhythm Perception in East Africa and Canada

I have read the letter of information, have had the nature of the study explained to me and I agree to participate. All questions have been answered to my satisfaction.

Dated in _____________________, this__________ day of______________, 20______.

Name of Participant: _______________________________________________________

(Please Print)

Signature of Participant: ____________________________________________________

Name of Person Responsible for Obtaining Consent: ______________________________

(Please print)

Signature of Person Responsible for Obtaining Consent: _________________________

Version Date: 02/18/2013

Participant Initials____
Umutwe w'umushinga: gukoresha ubuhanga buhendutse mu gusuzuma ubwonko bw’ impinja muri Afurika y’iburasirazuba.

Abashakashatsi b’ibanze: Dr Raissa Teteli; ibitaro bya kaminuza bya Kigali
Rhodri Cusack,PhD; Department of Psychology and
Medical Biophysics; Brain and Mind Institute, Western
University.

Ibaruwa yo kumenyesha

1. Ubutumire bwo kugira uruhare mubushakashatsi

Mwebwe n’umwana manyu mutumiwe kugira uruhare mubushakashatsi bugamije kureba uburyo buhendutse bwo gusuzuma ubwonko bw’ impinja. Utumiwe muri ubu bushakashatsi kuberako dushaka gusuzuma ubuziranenge n’imihindagurikire by’uburyo bukoreshwa gusuzuma ibibazo bitandukanze ubwonko bw’ abana bushora kuba bwahura nabyo duhereye kubana bazima. Kurundi ruhande hasuzumwa abana bivekeko ko bavukanye ikibazo bitandukanze mu bwonko. Ibi bikazaba bigamije gushaka ubuhanga bw’ inyongera abaganga bakwifashisha mugihe kiza kugufashiza abana bavukanye ibibazo mu bwonko.

2. Impamvu y’iyinyandiko

Iyinyandiko igamije kugufasha kwitabira ubu bushakashatsi wumwa neza impamvu yabwo. Ntampungege mukubaza abashakashatsi ikibazo icyaricyo cyose kirebana no kwitabira ubu bushakashatsi mbere yo kubwinjiramo.

3. Impamvu y’ubushakashatsi

Ubu bushakashatsi buzashyiraho uburyo buhendutse kandi bworoshye gukoresha mugusuzuma imikorere n’imiterere y’ubwonko. Hazifashihwa uburyo bubiri butandukanze mugukora ubu bushakashatsi:

Uburyo bwa mberere tuzifashisha akuma gasuzuma imikorere y’ubwonko( EEG), ni uburyo butagira icyo buhungabanyo kumubiri bukorwa hashyirwa utwuma K’umutwe w’umwana tugakukirana imikorere y’ubwonko. Ubu byo buzifashishwa mugusuzuma uburyo ubwonko bw’ uruhinja bwakira amajwi naho bihuriye n’imikurire y’umwana.
Hazifashishwa kandi icyuma kikareba imirere y’ubwonko murwego rwo kureba niba ntakibazo bufite.

Ubu buryo bwombi buzadufasha kubaka bushobozii mugusuzuma uburwayi bujyanye n’imikorere cyangwa imerere y’ubwonko umwana ashobora guhura nabyo igihe avuka.

4. Abemerewe kuja mu bushakashatsi

Impinja zose byemejwe na muganga wa CHUK k’o ntakibazo zifite zemerewe kuja muri ubu bushakashatsi.

5. Abatemerewe kuja mu bushakashatsi

Impinja zose zagize ikibazo mugihe ziri kuvuka cyangwa nyuma yo kuvuka ntizizajya muri ubushakashatsi. Abana bose bakekwa kuba bafite ibizo byo kutumva ntibazajya mubushakashatsi kubera ko mumvura neza aribyo bizatuma ubushakashatsi bushoboka.

6. Uburo ubushakashatsi buzakorwa.

Niwemera kuza muri ubu bushakashatsi, umwana wawe azakorerwa ibizamini bibiri bitandukanye byo gusuzuma ubwone, aribyo EEG na US.

Umwana ukorerwa irisuzumwa agumya gukurikiranwa buri munsi cyangwa buri minsi ibiri kugeza asezerewe mugitaro. Niwemera kuguma muri ubu bushakashatsi umwana azagumya gukurikiranwa n’abaganga mu mikurire ye hifashijwe kubonana na muganga mu isuzumiro cyangwa kubazwa ibibizo byerekeranye n’imikurire y’umwana kuri telephone. Kugirango bigende neza kandi, ibi bikorwa uzaja ubifashwamo kubijyanye n’ubushobozii.

Kubijyanye no gusuzumwa hakoreshhejwe icyuma gisuzuma imikorere y’ubwonko (electroencephalograph), umwana abanza guhanagurwa k’umutwe hakoreshhejwe agatambaro koroshye kugiranga havanehe imyanda ishobora kubangamira imigendekere myiza y’isuzuma. Hanyuma utwuma dusuzuma imikorere y’ubwonko dushyirwa k’umutwe w’umwana. Mugihe k’isuzumwa umwana abayumvishwa amajwaji atandukanye hakorejwe utwuma dushyirwa k’umutwi ye kugirango dusuzume uburo ubwo busesegura amajwaji bwakira.

Kubijyanye no gusuzumwa hakoreshhejwe icyuma kireba imiterere y’ubwoneko (ultrasound machine), ikizamini gikorwa hifashijwe amavuta asigwa kugitwariro cy’umutwe w’umwana agashasa icyuma kureba ibice bigomba gusuzumwa. Mbere y’uko isuzuma ritangira no mugihe riri kuba hakoreshwa akuma gakurikirana imihumekere y’umwana, ako kuma gashyirwa kugatoki. Mugihe isuzumwa rikorwa akuma gafotora ibice by’ubwoneko gashyirwa k’umutwe w’umwana ahasizwe amavuta hanyuma ukagenda ukarebesha mubice bitandukanye kugirango usuzume ubwone ko bwose.
Ubu bushakashatsi buzifashishwa nanone nk’uburyo bworoshye kandi buhendutse bwo gutahura uburwayi ubwonko bw’abana bushobora kugira mugihe cyo kuvuka no gukurikirana ingaruka bishobra kugira ku mikurire yabo. Ibyo bibazo rimwe narimwe ntibikunze guhita byigaragaza. Bizoroshyya kandi gutanga ubuvuzi bukenewe mugihe.

9. Ibihembo

Uztabira ubu bushakashatsi azajya ahabwa ingurane y’amafaranga agera kubihumbi bitatu na maganatanu (3500frws) ku isaha mugihe azaba ari muri ububushakashatsi.

10. Kwitabira k’ubushake.

Kwitabira ubu bushakashatsi ni ubushake. Ushobora kwanga kubwitabira, kwanga gusubiza ibibazo runaka cyangwa kuva muri ubu bushakashatsi igihe cyo aricyo cyose kandi ntibigire ingaruka k’ubufashwa ubahwa kwa muganga mugihe kizaza.

11. Ibanga.

Umwirondoro w’umwana wawe ntuzigera ushyirwa ahagaragara mu buryo ubwo aribwo bwose kubera kwitabira ubu bushakashatsi. Amakuru azava muri ubu bushakashatsi azagirwa ibanga gusa akazifashishwa nabakora ubu bushakashatsi.


Ushatse kugira ikibazo ubaza cyangwa andi makuru wifuza kumenya kubijyanye n’ubuntu bushakashatsi wakwifashisha iyi imeyili Rhodri@cusacklab.org.

13. Kumurika ibyavuye mu bushakashatsi

Nihabaho kumurika ibyavuye mu bushakashatsi, izina ry’umwana ntirizigera ritangazwa. Ushatse guhabwa inyandiko y’ibyavuye muri ubu bushakashatsi wabaza Dr Rhodri Cusack.
**KWEMERA KUJYA MU BUSHAKASHTSI.**

**Inyito y’umushinga:** gukoresha ubuhanga buhendutse mu gusuzuma ubwonko

bw’impinja muri Afurika y’iburasirazuba

**Amazina y’umushakashatsi:** [Redacted]

Maze gusoma no gusobanukirwa neza imiterere y’ubushakashatsi nemeye kubwitabira.
Ibabazo byose nabajije byasubije muburo bunyuze.

Amazina y’umwana

Amazina y’umubyeyi/ umuhagarariye wemewe n’amategeko

Umukono w’umubyeyi/umuhagarariye  Itariki

Amazina y’umushakashatsi wakiriye ukwemera k’umurwayi

Umukono w’umushakashatsi  Itariki

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Paji |  Itariki: Wer/11/2013  Impine z’amazina z’umurwayi - - - -
Appendix D. Ethics approval, letter of information, and consent form for Chapter 4.

Use of Human Participants - Ethics Approval Notice

Principal Investigator: Dr. Jessica Grahn
File Number: 105605
Review Level: Delegated
Approved Local Adult Participants: 810
Approved Local Minor Participants: 0
Protocol Title: Neural mechanisms of rhythm and music perception - 18087E
Department & Institution: Social Sciences/Psychology
Sponsor: Natural Sciences and Engineering Research Council

Ethics Approval Date: February 27, 2013 Expiry Date: May 31, 2016
Documents Reviewed & Approved & Documents Received for Information:

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<th>Comments</th>
<th>Version Date</th>
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<td>Revised Western University Protocol</td>
<td>Revised protocol (adds 3T MRI to the 3T MRI already specified, very minor revisions)</td>
<td>2013/02/13</td>
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This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/CIHC Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the University of Western Ontario Updated Approval Request Form.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

The Chair of the HSREB is Dr. Joseph Gilbert. The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000946.

Ethics Officer to Contact for Further Information

This is an official document. Please retain the original in your files.
LETTER OF INFORMATION FOR NEUROIMAGING PARTICIPANTS

The neural mechanisms of rhythm and music perception

Principal Investigator:
Jessica A. Grahn, Ph.D.,
Department of Psychology, The University of Western Ontario, London, ON

Introduction
You are being invited to participate in a research study investigating the regions of the brain that are active when people perceive sequences of events that form a rhythm. The purpose of this research is to map and characterize areas of the human brain which are involved in our natural sense of musical rhythm and "feeling the beat". This letter contains information to help you decide whether or not to participate in this research study. It is important for you to understand why the study is being conducted and what it will involve. Please take the time to read this carefully and feel free to ask questions if anything is unclear or there are words or phrases you do not understand.

Research Procedures
If you agree to participate in this study, you will undergo functional magnetic resonance imaging (fMRI) at the Robarts Research Institute. Functional MRI is a noninvasive brain imaging technique that uses the same machine that is used in MRI for patients. MRI uses a strong magnet and radio waves to make images of the brain. It does not involve x-rays or radiation. When a specific region of the brain is involved in processing information, there is an associated change in brain metabolism and blood flow to that region. These changes can be detected by the MRI scanner as changes in the image signal intensity. These changes are particularly prominent with stronger magnetic fields, which is why we use a 3 Tesla scanner.

Eligible participants will also be asked to remove any metallic personal effects (jewellery, watch, hair clips, wallet) to be stored in a safe place while being scanned. At the beginning of the session, you will lie down on a table that slowly slides inside the long hollow tube at the centre of the MRI machine. The space within the large magnet is somewhat confined, although we have taken many steps to reduce any "claustrophobic" feelings. The session will last up to two hours, during which you must keep as still as possible, especially during periods lasting approximately five minutes during which the magnet is beeping continuously. You will be made comfortable with pillows, blankets, and foam to help keep your head still. You will hear a muffled banging and beeping noises throughout the scanner operation, but the hearing protection will reduce the sound level to an acceptable level. You will be in voice contact with the operator while you are in the scanner. Between scans we will remind you of specific instructions of the next task. If you want to alert the operator during a scan (i.e., if you find the sound uncomfortably loud), you can use the squeeze ball to end the scan session. Of course, you may ask the operator to end the experiment at any time.
During the functional scans, you will look at images or real objects. You may be asked to look at the displays passively, to make perceptual judgments about the displays, and/or to interact with them by moving your eyes or reaching out to touch or grasp them.

Voluntary Participation

Participation in this study is voluntary. You may refuse to participate, refuse to answer questions or withdraw from the study at any time with no effect on your academic or employment status. You should ask to stop the experiment if you feel uncomfortable, claustrophobic or tired.

Compensation

You will be compensated $25/hr to cover your time, parking and the inconveniences associated with participating in the study.

Benefits

While this study will not result in any direct benefit to you, it may help clinicians understand how the brain responds to rhythmic information and therefore be of some benefit to patients in the future.

Risks

The Food & Drug Administration (USA) has indicated that for clinical diagnosis an 'insignificant' risk is associated with human MRI exposure at the intensities used in this project. Current Canadian guidelines follow the USA guidelines. Although very rare, injury and deaths have occurred in MRI units from unsecured metal objects being drawn at high speeds into the magnet or from internal body metal fragments of which the subject was unaware or had not informed MRI staff. To minimize this latter possibility it is essential that you complete a screening questionnaire. Other remote but potential risks involve tissue burns and temporary hearing loss from the loud noise inside the magnet. The latter can be avoided with ear protection that also allows continuous communication between you and the staff during the study.

Participant Exclusion Criteria

The most important safety concern with MRI is to avoid having any metal in your body that is deemed unsafe in a strong magnetic field. Prior to participating, you will be asked to fill out a screening checklist to evaluate whether you meet the eligibility criteria for participation in this fMRI study. These include precautions to ensure you have no unsafe metal in your body and, if you are female, that you are not pregnant or at risk of conceiving a child. If you have any history of head or eye injury involving metal fragments, if you have ever worked in a metal shop or been a soldier, if you have some type of implanted electrical device (such as a cardiac pacemaker), if you have severe heart disease (including susceptibility to arrhythmias), you should not have an MRI scan. Some surgical implants (e.g., hip or joint replacements) are made of alloys (e.g., titanium) that are non-magnetic and are therefore safe in the MRI scanner. To certify that your surgical implant is safe for the MRI, we must have documentation from your physician before you will be able to participate in the experiment.

Confidentiality

Any information obtained from this study will be kept confidential. In the event of publication, any data resulting from your participation will be identified only by case number, without any reference to your name or personal information. The data will be
stored on a secure computer in a locked room. Both the computer and the room will be accessible only to the experimenters. After completion of the experiment, data will be archived on storage disks and stored in a locked room for five years, after which they will be destroyed.

Representatives of the University of Western Ontario Health Sciences Research Ethics Board may require access to your study-related records or may follow up with you to monitor the conduct of the study.

**Estimate of participant’s time and number of participants**

Each experiment will last approximately two hours. The entire research project will involve approximately 800 subjects.

**Consent Form**

You do not waive any legal rights by signing the consent form. You will be provided with a copy of this letter of information and the consent form.

**Contact Information**

If you would like to receive a copy of the overall results of the study, or if you have any questions about the study please feel free to contact the Principal Investigator at the contact information provided above.

If you have any questions about your rights as a research participant or the conduct of the study you may contact:

The Office of Research Ethics
The University of Western Ontario

[Version Number], Last Modified April 28, 2011

Participant’s Initials _______
CONSENT FOR RESEARCH STUDY

The neural mechanisms of rhythm and beat perception

I have read the letter of information, have had the nature of the study explained to me and I agree to participate. All questions have been answered to my satisfaction.

Dated in _____________________, this ____________ day of __________________, 20______.

Name of Participant (Please print) ___________________________ Name of Principal Investigator: ___________________________

Signature of Participant: ___________________________ Signature of Principal Investigator: ___________________________

Name of Person Responsible for Obtaining Consent: ___________________________

(Please print)

Signature of Person Responsible for Obtaining Consent: ___________________________

Dated in _____________________, this ____________ day of __________________, 20______

[Version Number], Last Modified April 28, 2011  Participant’s Initials _______
Curriculum Vitae

DANIEL J CAMERON

Education

2012-16  PhD (candidate): Neuroscience, University of Western Ontario
            Supervisor: Dr. Jessica A. Grahn
2010-11   MSc (Distinction): Music, Mind and Brain, Goldsmiths, University of London, UK
            Thesis: Perception of Similarity in Musical Rhythm: Factors and Models
            Supervisor: Dr. Marcus T. Pearce
2009-10   Undergraduate courses, Dept. of Psychology, University of Winnipeg
2003-07   BMus (honours): Music Performance, min. Religion Studies, University of Toronto

Employment and Research Positions

2015   Teaching Assistant/Tutor (Psychology), Indigenous Services, University of Western Ontario
2015   Research Intern, Instituto de Neurobiologia, Universidad Nacional Autónoma de México,
                Querétaro, Mexico
2013   Research Intern, Kenyatta Hospital, University of Nairobi, Kenya
2013   Teaching Assistant, Dept. of Psychology, University of Western Ontario
2012-present  Research Assistant, Brain and Mind Institute, University of Western Ontario
2010-11   Research Assistant, Institute of Cognitive Neuroscience, University College London
2010-11   Research Assistant, Dept. of Psychology, Goldsmiths, University of London
2010   Research Assistant, Behavioural Neuroscience Laboratory, University of Winnipeg

Awards and Scholarships

2015-16   IODE War Memorial Doctoral Scholarship ($15,000)
2015-16   LIVElab seed grant: “The role of social context in intersubject synchronization between
            audience members during musical performance”, Daniel Cameron (PI), Molly Henry (co-PI),
            Jessica Grahn (Co-I) ($11,400)
2015   Mitacs Globalink Research Award ($5,000)
2014   Attendance Scholarship, Neurosciences of Music – V, Mariani Foundation (€350)
2013   Invited participant, Visceral Mind Summer School, Bangor University, UK ($1,500)
2013-16  Postgraduate Scholarship (PGS-D), National Sciences and Engineering Research Council of
            Canada ($63,000)
2013   Students for Development Internship for research in Rwanda and Kenya: “Using affordable
            technology to measure the newborn brain in East Africa” ($6,500)
2013   Student Award, Society for Music Perception and Cognition International Conference ($250)
2012   Attendance Bursary (International Conference for Music Perception and Cognition) (€100)
2012   Alexander Graham Bell Canada Graduate Scholarship (CGS-M), National Sciences and
            Engineering Research Council of Canada ($21,000)
2012-16  Western Graduate Research Scholarship, University of Western Ontario ($8,000/year)
2010-11  Goldsmiths International Postgraduate Scholarship Goldsmiths (University of London) (£5,000)
2008-09  Arts Fellowship for music research/training, Shastri Indo-Canadian Institute ($7,000)

Publications Submitted and in Preparation
Cameron, D.J., Potter, K., Wiggins, G., Pearce, M.T. (Submitted). Perception of rhythmic similarity is asymmetrical, and is influenced by musical training, expressive timing, and musical context.


Peer-Reviewed Publications


Conference Proceedings


Stober, S., Cameron, D.J., & Grahn, J.A. (2014). Does the beat go on? Identifying rhythms from brain waves recorded after their auditory presentation. *Proceedings of the 9th Audio Mostly Conference (AM’14)*.


Selected Conference Presentations


Volunteer and Service positions

2016 Program Organizer, Rhythm and Timing Symposium, Michigan State University
2015-present Advisor (cycling policy) to City Councilor Jesse Helmer, London, ON, Canada
2015 Graduate Program Reviewer, Masters of Public Administration, University of Western Ontario
2015 Lead Organizer, Rhythm and Timing Symposium, Western University
2014-16 Organizer, Coffee Talk Series, Brain and Mind Institute, University of Western Ontario
2014-15 Graduate Student Rep., Steering Committee, Brain and Mind Institute, University of Western Ontario
2014-15 Member, Psychology Colloquium Series Committee, University of Western Ontario
2014-15 Councilor, Society of Graduate Students, University of Western Ontario
2013-present Graduate student Rep., University Disciplinary Appeals Committee, University of Western Ontario
2013-present Volunteer speaker and organizer, various public outreach events (Brain and Mind Institute, University of Western Ontario, Retiring With Strong Minds, British Science Festival)
2001-present Drumming workshop leader, various organizations, Canada, UK

Invited Talks

2016 Neuroscientific Investigations of Beat Perception: Mechanisms, Dynamics, and Human-Specificity
Institute for Cognitive and Computational Sciences, Georgetown University, Washington DC
2015 FMRI Investigations of Beat Perception and Temporal Predictability in Auditory Rhythms
Instituto de Neurobiología, Universidad Nacional Autónoma de México, Querétaro, Mexico
2014 Investigating Rhythm and Beat Perception: Complexity, Probability, and Experience
Center for Functionally Integrative Neuroscience, University of Aarhus, Denmark
2014 Investigating Rhythm and Beat Perception: Complexity, Probability, and Experience
Brain and Cognition Center, University of Amsterdam, Netherlands
2013 Stages of Beat Perception and the Influence of Metrical Incongruity
Institute of Neuroscience, Newcastle University, UK

Public Outreach Media

2015 Interview for GradCast radio program, Western University campus radio/podcast
2015 Interview for Campus Confidential radio/podcast, Fanshawe College

Ad-Hoc Reviewing


Conference Submissions: International Conference of Students of Systematic Musicology (SysMus)
## Teaching and Supervision

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