Finding Groove in Behaviour and the Brain

Tomas Matthews

A Thesis
In the Department
of
Psychology

Presented in Partial Fulfillment of the Requirements
For the Degree of
Doctor of Philosophy (Psychology) at
Concordia University
Montréal, Québec, Canada

April 2021

CONCORDIA UNIVERSITY
SCHOOL OF GRADUATE STUDIES

This is to certify that the thesis prepared

By: Tomas Matthews
Entitled: Finding Groove in Behaviour and the Brain

and submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY (Psychology)

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

Signed by the final examining committee:

______________________________ Chair
Dr. Michael Sacher

______________________________ External Examiner
Dr. Petr Janata

______________________________ External to Program
Dr. Richard Courtemanche

______________________________ Examiner
Dr. Mickael Deroche

______________________________ Examiner
Dr. Emily Coffey

______________________________ Thesis Supervisor
Dr. Virginia Penhune

Approved by: ______________________________
Dr. Andrew Chapman, Graduate Program Director

05/31/2021 ______________________________
Dr. Pascale Sicotte
Faculty of Arts and Sciences

Abstract

Finding Groove in Behaviour and the Brain

Tomas Matthews, Ph.D.
Concordia University, 2021

Movement, perception, and reward are fundamental processes underlying much of our behaviour which, although separable, are strongly linked. For example, moving to music requires the extraction of timing information from auditory input to synchronize movements to musical rhythms, a process that often leads to pleasure. But why does it feel good to move to music, and what aspects of the music make us want to move? Further, what are the brain networks underlying this urge to move? One approach to answering these questions is to study the sensation of groove, which is defined as the pleasurable urge to move to music. The work presented in this thesis investigated groove using behavioural and neuroimaging methods to shed new light on music's ability to move us and the fundamental processes that support this phenomenon.

Groove has been shown to be strongly influenced by rhythm, however, other aspects of music are likely to contribute. Article 1 investigated the role of harmonic complexity, showing that it interacts with rhythmic complexity in determining groove. A mediation analysis showed that harmonic complexity affects groove primarily via its impact on pleasure.

There is some evidence that moving to music increases groove. However, it is unclear if this depends on whether listeners feel as though they are synchronizing accurately. Article 2 compared the relative impact of perceived and measured synchrony on groove. Perceived synchrony showed a stronger relation with groove indicating that 'feeling in sync' is a crucial driver of groove.

Separate lines of research have investigated the brain networks involved in rhythm perception and music-induced pleasure. Groove provides the opportunity to investigate these processes together. Article 3 investigated the brain regions underlying groove using functional magnetic resonance imaging. Groove elicited activation in motor timing and reward networks with the basal ganglia implicated in both.

Together, these studies provide novel insight into groove and its underlying processes. These results are discussed in the context of the integration of predictive coding and dynamic attending treatments of rhythm perception and groove. I suggest that predictive timing processes form the foundation on which groove is built.

Acknowledgements

Firstly, I thank my Master's and PhD supervisor Dr. Virginia Penhune. Virginia provided me with so much support over the (many) years, both academically and in life. I really felt I could go to her with anything. Thank you for reining in my various dives down analysis rabbit holes, helping to structure my flailing ideas, and providing an amazingly supportive space for me to learn and grow. I have always looked forward to our discussions.

This work was supported by Erasmus Mundus Student Exchange Network in Auditory Cognitive Neuroscience, the Fonds de Recherche du Quebec – Nature et Technologies, and the Natural Sciences and Engineering Research Council of Canada. I am also grateful to Concordia's faculty of Arts and Sciences and School of Graduate Studies for financial support.

I am very grateful to have collaborated closely with Dr. Maria Witek and Dr. Peter Vuust. Maria has been and continues to be a great mentor and friend throughout all these years and many projects together. Working with Maria has been nothing but fun and I have learned so much from her. I feel lucky to have worked with Peter. His boundless excitement for research and approachability is an inspiration for me to continue pursuing an academic career.

I also feel very lucky to have met and worked with so many great people within the Penhune lab. Thanks to Dr. Kierla Ireland for your energy and enthusiasm and for always being there when I needed to talk. Thanks to Joe for all the patient guidance and wisdom. Thanks to Dr. Chris Steele for being a mentor in the early days of my graduate career. Thanks to Dr. Chiara Giascoco, Dr. Dilini Sumanapala, Dr. Lucia Vaquero, Dr. Fiona Manning, Brian Gunther, Jake Shenkar, and Alex Albury for all your help and wisdom over the years.

I also want to thank members of the Montreal music neuroscience community who have given me friendship and guidance over the years, including Dr. Dominique Vuvan, Dr. Pauline Trenchant, Dr. Megha Sharda, and Dr. Benjamin Gold.

Thanks also to Dr. Ole Heggli, Dr. Torben Lund, Dr. Rick Gurnsey, and Dr. Alexandre Morin for their help and guidance, and generosity with their time. Thanks to Sallamaari Vainio, Alessandra Brusa, and Dr. David Quiroga-Martinez for help collecting data, and to Dr. Michael Conway for use of his space. Thanks to Dr. Elvira Brattico for helping to get me to Aarhus and helpful comments on Article 1. Thanks also to Dr. Gabe Nespoli for analysis suggestions in Article 1. I am grateful to Dr. Robert Zatorre for helpful comments on Article 3 and to his lab members for helpful feedback.

I am thankful to my parents for their unwavering support and kindness over all these years. Finally, thank you to Dr. Jessica Thompson. Without her patience, wisdom, and caring support, I would not have finished this thesis.

Contribution of Authors

Article 1: The sensation of groove is affected by the interaction of rhythmic and harmonic complexity

Tomas E. Matthews	Conceptualized the research question and paradigm, generated stimuli, ran the statistical analyses, generated visualizations, and wrote and edited the manuscript
Maria A. G. Witek	Contributed to the conceptualization, stimuli generation, statistical analyses, visualization, and editing of manuscript
Ole A. Heggli	Generated and hosted web interface for online testing
Virginia B. Penhune	Contributed to the conceptualization, and editing of manuscript
Peter Vuust	Contributed to the conceptualization, stimuli generation, and editing of manuscript

Matthews, T. E., Witek, M. A., Heggli, O. A., Penhune, V. B., & Vuust, P. (2019). The sensation of groove is affected by the interaction of rhythmic and harmonic complexity. *PloS one*, *14*(1), 1-17. https://doi.org/10.1371/journal.pone.0204539

Article 2: Perceived motor synchrony with the beat is a stronger predictor of groove than measured synchrony

Tomas E. Matthews	Conceptualized the research question and paradigm, modified existing stimuli, ran the statistical analyses, generated visualizations, and wrote and edited the manuscript
Maria A. G. Witek	Generated original stimuli. Contributed to the conceptualization, statistical analyses, visualization, and editing of manuscript

Joseph N. L. Thibodeau	Created data collection (tapping) apparatus, pre-processed tapping data
Sallamaari Vainio	Contributed to data collection
Peter Vuust	Contributed to the conceptualization, and editing of manuscript
Virginia B. Penhune	Contributed to the conceptualization, and editing of manuscript

Matthews, T. E., Witek, M. A., Thibodeau, J. N. L., Vuust, P., & Penhune, V. B. (2021). Perceived motor synchrony with the beat is a stronger predictor of groove than measured synchrony**.** Under review at *Music Perception* (Article ID: MP-2021-0023).

Article 3: The sensation of groove engages motor and reward networks

Tomas E. Matthews	Conceptualized the research question and paradigm, generated stimuli, collected data, ran the statistical analyses, generated visualizations, and wrote and edited the manuscript
Maria A. G. Witek	Contributed to the conceptualization, stimuli generation, data collection, statistical analyses, visualization, and editing of manuscript
Torben Lund	Contributed to data collection, preprocessed the fMRI data, and contributed to statistical analysis
Peter Vuust	Contributed to the conceptualization, stimuli generation, and editing of manuscript
Virginia B. Penhune	Contributed to the conceptualization, and editing of manuscript

Matthews, T. E., Witek, M. A., Lund, T., Vuust, P., & Penhune, V. B. (2020). The sensation of groove engages motor and reward networks. *NeuroImage*, 214 (116768), 1-12. https://doi.org/10.1016/j.neuroimage.2020.116768

Table of Contents

List of Figures

List of Tables

CHAPTER ONE:

GENERAL INTRODUCTION

1.1 General Introduction

Whether unconsciously tapping your foot, or dancing to your favourite song, moving to music is a ubiquitous behaviour. These examples illustrate two fundamental yet still mysterious aspects of music's power over us: It makes us want to move and doing so gives us pleasure. But why are we compelled to move to music? And why does it feel good? One way to address these questions is by studying the sensation of groove, which is defined as the pleasurable urge to move to music. Over the last two decades, studies on groove have provided novel insights into which rhythmic musical features engender a pleasurable desire to move. Meanwhile, neuroimaging studies on rhythm perception and the pleasure associated with music-listening have provided some clues as to the brain regions involved. However, although theoretical accounts have provided some suggestions, the underlying mechanisms are still unclear.

As the definition implies, groove is likely to involve the integration of auditory, motor, and reward processes. One commonality between these processes, and something that is likely crucial to groove, is the role of prediction. Many psychological theories, going back to Helmholtz in the mid-19th century, suggest that prediction is fundamental to perception and behaviour, and the perception of music is likely no exception. In fact, the highly structured nature of music, both in time and in content, makes it particularly amenable to predictive processes. Indeed, the pleasure derived from listening to music is theorized to be largely driven by the confirmation and violation of predictions regarding what will happen and when it will happen. These predictions are based on the combination of explicit and implicit knowledge of musical structure and the preceding musical context (Cheung et al., 2019; Huron, 2006; Juslin & Västfjäll, 2008; Meyer, 1956; Salimpoor, Zald, Zatorre, Dagher, & McIntosh, 2015).

Groove is strongly linked to musical rhythm, therefore, the temporal predictions that support rhythm perception are particularly relevant. Rhythm perception, and temporal prediction in general has been linked to the motor system, with motor cortical and subcortical brain areas involved in the processing of a regular beat and metre (Araneda, Renier, Ebner-Karestinos, Dricot, & De Volder, 2016; Bengtsson et al., 2009; Burunat, Tsatsishvili, Brattico, & Toiviainen, 2017; Chapin et al., 2010; Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009, 2013; Kung, Chen, Zatorre, & Penhune, 2013; Schubotz, Friederici, & von Cramon, 2000; Thaut, Trimarchi, & Parsons, 2014). In addition, moving to music is a predictive rather than reactive process as it requires anticipatory initiation of movements for them to be temporally aligned to the musical beat. Therefore, the sensation of groove can be thought of as the interaction of auditory, motor, and reward processes, with temporal prediction as a common mechanism. This makes groove a powerful phenomenon through which we can investigate how prediction drives the interaction of these fundamental processes. Further, the ubiquitous, highly structured, and modifiable nature of rhythmic music makes it a near-ideal tool with which to elucidate many of the processes of interest to psychologists and cognitive neuroscientists.

However, many aspects of groove have yet to be investigated, including the influence of non-rhythmic musical features as well as the underlying brain networks. In addition, it is still unclear whether rhythmic movements enhance groove and why this might be the case. Therefore, the work presented in this thesis focuses on investigating these questions using behavioural and neuroimaging methods in order to better our understanding of the perceptual, cognitive, and neural processes underlying this powerful response to music. Article 1 describes a study investigating the impact of harmonic complexity, and its interaction with rhythmic complexity, on groove. Article 2 describes a study investigating the relative influence of perceived and measured tapping synchrony on groove. In Article 3, functional magnetic resonance imaging was used to elucidate the brain regions involved in groove. In addition to contributing to our understanding of groove, this work can also help us understand fundamental processes such as temporal prediction, audition, action, and reward, and how they interact.

1.2 Rhythm and Groove

Rhythm, the temporal organization of sequences of sounds and silences, is crucial to groove as it creates the structure with which we align our movements. Musical rhythms are organized around a beat, which is the repeating, regular (i.e., isochronous) temporal pulse. This regular beat is what we tap our foot or bob our head to, and which determines the tempo of a musical passage. The beat provides a rhythmic anchor such that the timing of all other events is perceived in relation to it. The beat may be marked by sounded events on each iteration but will also be perceived, and will persist, when sounds fall on only some of the beats. Therefore, beat perception arises from the combination of external stimuli and endogenous processes (Large & Palmer, 2002). The pattern of strongly and weakly accented beats is called the metre (London, 2012). For example, in some marches, the first strong beat is emphasized followed by three weaker beats, while in a waltz, the strong beat is followed by two weak beats. Together, beat and metre lead to temporal predictions about where onsets will fall, with stronger predictions that onsets will fall on the beat versus off the beat and on stronger beats versus weaker beats. Syncopations, which are key to the sensation of groove, occur when an onset falls on a weak beat followed by a silence on a strong beat (Fitch & Rosenfeld, 2007; Longuet-Higgins & Lee, 1984). Syncopations contradict temporal predictions and can therefore be conceptualized as providing counterevidence to the beat or metre.

Syncopation is strongly linked with the sensation of groove. Musicians use syncopation to increase groove (Madison & Sioros, 2014) and rhythms with medium degrees of syncopation are rated higher in groove than those without syncopation or with high degrees of syncopation (Sioros, Miron, Davies, Gouyon, & Madison, 2014; Witek, Clarke, Wallentin, Kringelbach, & Vuust, 2014). Too little syncopation and a rhythm can seem boring, whereas too much syncopation makes a rhythm hard to follow. This suggests an inverted U-shaped relationship between degree of syncopation and groove. This inverted U-shaped function, known as the Wundt curve, has been proposed as a general relationship between complexity and aesthetic pleasure in art (Berlyne, 1971). For example, this relationship has been shown between preference and the verbal complexity of poems (Kammann, 1966) and the number of elements in abstract paintings (Rump, 1968). In the context of music, this relationship has been shown between objective and subjective measures of musical complexity, and ratings of liking or pleasantness with a variety of musical stimuli, from classical piano compositions to popular music (Heyduk, 1975; North & Hargreaves, 1997). These authors have suggested that this relationship reflects the degree to which stimuli increase arousal, with low arousal leading to disengagement and high levels of arousal having a deterring affect – and a sweet spot of moderate arousal that produces maximum engagement. This aligns with a recent study showing that high groove music and syncopated drum patterns elicited greater arousal as measured by ratings and pupil dilation, compared to low groove music and un-syncopated patterns (Bowling, Ancochea, Hove, Fitch, & Madison, 2019). The inverted U is likely to depend on musical expertise and personality factors (e.g., sensation seeking). For example, one study showed a 'flattening' of the inverted U as musical training increases, suggesting other factors beyond complexity may become stronger determinants of liking as one gains musical expertise (Orr & Ohlsson, 2005). In order to explore the effect of musical expertise, the articles presented here involved either recruitment of participants with a wide range of musical training (Article 1) or separate musician and non-musician groups (Articles 2 and 3). This allowed us to test the effects of training using both regression and group-comparison approaches.

Based on early descriptions of groove, which focused on the expressive timing deviations that give music a certain rhythmic 'feel' (Danielsen, 2006), early experimental work on groove focused on the degree to which these microtiming deviations elicit groove. However, experiments testing the effect of microtiming have shown mixed results, with only one study showing a positive relation between the degree of microtiming deviations and ratings of groove (Kilchenmann & Senn, 2015), and others showing a negative relation (Butterfield, 2010; Davies, Madison, Silva, & Gouyon, 2013; Frühauf, Kopiez, & Platz, 2013; Madison & Sioros, 2014). However, these mixed results likely reflect the difficulty in studying such a phenomenon in the laboratory. Several other rhythmic features have been shown to be consistently associated with groove. For example, pulse clarity (the degree to which a rhythm induces perception of a beat), beat salience (how periodic the beat is), and event density (the number of between-beat onsets), have shown positive relations with ratings of groove (Madison, Gouyon, Ullén, & Hörnström, 2011; Stupacher, Hove, & Janata, 2016). Other musical features, such as timbre, melody, and harmony can affect beat and metre perception. For example, chord changes or melodic contour can cue a strong beat point or the start of a phrase even while onset timing is kept constant (Dawe, Platf, & Racine, 1993; Hannon, Snyder, Eerola, & Krumhansl, 2004). In this way, these musical features may interact with rhythmic timing to influence groove. Harmony is likely to impact the affective component of groove as it can elicit emotional reactions even with a single chord (Lahdelma & Eerola, 2014). Article 1 focuses on the impact of harmonic complexity, and its interaction with rhythmic complexity, on groove.

1.3 Tapping Studies

Article 2 describes a study in which participants tapped to the beat of rhythms of various degrees of complexity. Participants' perception of how well they tapped were compared to how well they actually tapped in terms of their relative influence on their sensation of groove. Therefore, the next section briefly summarizes relevant literature on sensorimotor synchronization, focusing on the degree to which conscious awareness and automaticity influence this process.

1.3.1 Finger Tapping as a way to Investigate Sensorimotor Synchronization

Sensorimotor synchronization (SMS) is the coordination of movements in time with a predictable stimulus (Repp, 2005). SMS relies on sensorimotor integration and temporal prediction processes as it requires participants to transform perceived timing information into motor timing information such that movements can be predictively aligned to the timing of stimulus onsets. In the context of metrical rhythms, participants can be asked to move to the beat or to other metrical levels. Therefore, SMS can provide overt indices of these psychological constructs and measure how they are affected by rhythmic context. Finger tapping tasks are the most common way of assessing SMS in the lab. Due to inherent variability in perceptual and motor processes, timing errors are intrinsic to SMS. Therefore, much work has focused on error correction processes in order to gain insight into the underlying perceptual, motor, and temporal prediction processes (Repp, 2005). In SMS, error comes in two forms: accuracy (often referred to as asynchrony), which is the difference between the onset of the tap and the onset of the stimulus; precision (often referred to as variability), which is the consistency of the tap-timing within or across trials.

When tapping in synchrony to regular sequences, responses tend to be early by 10 to 80 ms relative to the stimulus onset, a phenomenon known as negative mean asynchrony (Aschersleben, 2002; Repp, 2005). Although a full explanation of this phenomenon remains elusive, it has been shown to be reduced by training. That is, the negative mean asynchrony tends to be smaller in musicians (Repp, 2010) and is reduced in non-musicians following prolonged practice (i.e., 10 sessions of the same task) when accompanied by performance feedback (Aschersleben, 2002). Tapping precision is also enhanced in musicians and often covaries with regularity or predictability of the sequence (Matthews, Thibodeau, Gunther, & Penhune, 2016).

Error correction is also thought to come in two forms: phase correction and period correction. Phase correction, where the timing of individual taps is altered to better align with target onsets following a perturbation, is thought to be automatic and independent of conscious awareness. For example, phase correction occurs even when participants are asked to ignore the perturbation and despite the fact that phase correction is counterproductive in this case (Repp, 2002). In addition, participants will employ phase correction in response to local phase shifts, wherein the phase of an onset and all following onsets is shifted, even when this shift is so small as to be subconscious (Repp, 2000, 2001). Conversely, period correction, which is when one maintains synchrony with a sequence that is changing in tempo, is thought to be under intentional, conscious control (Repp, 2005; Repp & Keller, 2004). For example, period correction depends on whether participants are aware of the tempo change, whether they are instructed to actively maintain synchrony with the tempo-changing sequence, and whether they are engaged in a distractor task (Repp & Keller, 2004). This relates to an influential model of SMS which suggests that natural variability in SMS comes from two sources; an internal timekeeper and peripheral motor processes (Wing & Kristofferson, 1973). It has been suggested that the internal timekeeper may be responsible for intentional period correction, while phase correction is an automatic motor process (Repp & Keller, 2004), thus explaining the lack of reliance on conscious awareness. However, recent work has suggested that motor kinematics and feedback from sensory consequences of motor actions influences timekeeping (Ross & Balasubramaniam, 2014), thus suggesting that peripheral and internal timekeepers are not as independent as previously assumed.

1.3.2 Tapping to Musical Rhythms

Tapping to the beat of a musical rhythm is thought be a special case of SMS, since the beat results from the combination of stimuli timing and endogenous process rather than an acoustic referent. Therefore, tapping to the beat, as well as the associated error correction, requires a combination of internally and externally driven timing processes (Repp & Su, 2013) and is susceptible to rhythmic context. For example, increased syncopation leads to a decrease in both tapping precision (Toiviainen & Snyder, 2003) and accuracy (Fitch & Rosenfeld, 2007). Metre also affects tapping, likely by affecting the temporal predictions. For example, as the perception of a clear metre increases by increasing the difference in volume between accented and non-accented tones, the duration of taps (i.e., the time that the finger is in contact with the surface) aligned with those accents also increases (Chen, Zatorre, & Penhune, 2006). In another study, participants tapped to metrical rhythms and a metronome (Patel, Iversen, Chen, & Repp, 2005). Although performance was not better for the metrical rhythms overall, tap asynchrony was lower for the strong first beat of a phrase compared to the weaker following beats. This suggests that tap timing, and thus the temporal prediction that drives this tap timing, is more accurate for strong compared to weak beats. Finally, musical training also affects tapping to the beat, likely via the strength of beat-based temporal predictions. For example, the use of tapping to find the underlying beat of a rhythm is more beneficial to non-musicians then musicians (Su & Pöppel, 2012). This suggests that musicians have a stronger endogenous representation of the beat and therefore can rely less on overt movements.

1.3.3 Tapping and Groove

There are very few studies looking at the effects of SMS on groove. One study showed that tapping precision was not significantly associated with ratings of groove (Stupacher et al., 2016). Another study showed that, although the degree of synchronization of head movements was related to ratings of groove, tap synchronization was not (Hurley, Martens, & Janata, 2014). These studies suggest that moving to music, but not tapping, can increase groove. However, as part of their seminal study on groove, Janata et al. (2012) showed that tapping increased the ratings of experienced groove, which the authors distinguish from perceived groove, compared to not moving, particularly for high-groove music. In addition, the degree to which taps synchronized with the music positively correlated with experienced groove. Finally, the perceived difficulty of synchronizing taps to the music was a strong predictor of groove. Together these results show that moving to music, and doing so accurately, increases the sensation of groove, and further that the feeling that one is successful in synchronizing is an important predictor of groove. This relates to the idea of fluency, which is the degree to which one is able to quickly and efficiently process task-relevant information. Fluency within a sensorimotor task has been linked to positive affect (Cannon, Hayes, & Tipper, 2010) and has been associated with lower tapping variability in a finger tapping task (Stupacher, 2019). Therefore, although it is still unclear whether the degree of tap synchronization is positively related to groove, it is likely that the feeling that one is able to synchronize their movements with music is associated with the pleasurable component of groove. This hypothesis is tested in the experiment reported in Article 2.

1.4 Theoretical Treatments of Rhythm Perception and Groove

Rhythm perception and groove have been generally discussed in the context of two theoretical frameworks; predictive coding and dynamic attending. These frameworks, along with their relatives, have been applied to a broad set of functions, and across sensory modalities. Both frameworks emphasize the proactive and predictive nature of perception and its integration with motor control (cf., active inference, active sensing). That is, these frameworks assume that perception is a combination of top-down and bottom-up processes. In particular, these frameworks rely on the concept of temporal predictions to explain rhythm (and groove), and therefore, despite their distinct ways of formalizing these predictions and how they come about, they are generally compatible.

1.4.1 Predictive Coding

Predictive coding (PC) is based on Bayesian inference and proposes that a core principle of information processing in the brain is the minimization of prediction error (Friston, 2005; Rao & Ballard, 1999). Because the brain only has indirect access to the environment via noisy sensory information, it generates internal models, or predictions regarding what will happen next and when it will happen. Inevitably there is a mismatch between the prediction and the incoming sensory information, resulting in a prediction error. It is this prediction error, rather than direct sensory information, that is passed to other brain regions for higher level processing. Prediction errors force the brain to adjust the existing internal model, thus refining these predictions to better align with sensory input. The precision, or certainty (here I will use certainty so as to avoid confusion with tapping precision), of the prediction determines the weight that is given to the prediction error, that is, the degree to which it will lead to an update in the internal model (Koelsch, Vuust, & Friston, 2019). Another way to minimize prediction error is by moving one's body to alter the sensory input to better match the model. Further, efference copies of motor commands can function to suppress processing of the sensory consequences of self-generated actions (e.g., the sounds of one's own steps), which may serve to down-weight prediction errors (Brown, Adams, Parees, Edwards, & Friston, 2013).

As prediction errors lead to model refinement and thus learning, they are considered to be inherently rewarding (Vuust & Witek, 2014; Vuust, Witek, Dietz, & Kringelbach, 2018). That is, prediction errors can signal new information that can improve the model, thus acting as a form of intrinsic motivation serving the innate need for competence (Ryan & Deci, 2000; White, 1959). However, this depends on the context. For example, many strong prediction errors, particularly in a relatively uncertain context, can be aversive. In the context of music listening, relatively sparse prediction errors regarding a specific aspect of a musical passage (e.g., the rhythm) are likely rewarding, creating a pleasant sense of surprise (Gebauer, Kringelbach, & Vuust, 2012). This is partially because the listener is expecting some degree of prediction error, otherwise the music would be boring. Therefore, musical prediction errors are rewarding particularly when they are themselves predictable (Koelsch et al., 2019).

In the context of rhythm perception and groove, the internal model consists of the beat and/or metre (Vuust & Witek, 2014), thus aligning with the view that these are psychological constructs. These models engender predictions regarding when future onsets will occur with stronger or weaker predictions reflecting the metrical structure. These temporal predictions are conceptualized as probability distributions (or probability density functions) around a given timepoint, with the center of the distribution determining the point estimate, and the width of the distribution (in time) reflecting the certainty of the prediction (Koelsch et al., 2019). Prediction errors, for example in the form of syncopations, may lead to an updating in the model depending on the certainty of the antecedent prediction. This certainty will depend on the rhythmic context. For example, a metronome is perfectly regular and consistent, therefore certainty is high, as reflected by a narrow probability distribution. However, when a performer is playing a complex rhythm including both syncopations and microtiming deviations, certainty will be lower. Attention can also influence the degree to which a prediction error leads to an update in the model. For example, if the rhythm is complex and the listener is having trouble determining whether it is a duple or triple metre, the certainty of the predictions will be low. However, these predictions may nonetheless be strongly weighted by attention as the prediction error has the potential to resolve the uncertainty as to which metre is intended by the performer or composer. In this case, the listener will focus attention to each event and thus highly weight each prediction error until they can determine which metre is intended, and uncertainty is resolved.

According to this framework, the inverted U-shaped relationship between the degree of syncopation and groove results from the fact that rhythms with medium levels of syncopation result in moderately certain predictions and produce a moderate degree of prediction error (Koelsch et al., 2019; Vuust & Witek, 2014). These rhythms are regular enough to allow the generation of temporal predictions, but the certainty of these predictions is only moderate due to the uncertainty created by syncopations, creating a pleasurable balance or tension. Further, the prediction errors, in this case, are themselves relatively predictable as the syncopations are expected, either due to familiarity with the particular piece or musical genre, or due to repetitions of the same rhythmic pattern. Conversely, low degrees of syncopation elicit little-to-no prediction errors therefore these rhythms are less engaging, while highly syncopated rhythms subvert the ability to perceive a beat or metre and thus the ability to generate predictions in the first place. According to PC, rhythms with a medium degree of syncopation also increase the urge to move in order to test predictions and refine the internal model (beat or metre) or to down-weight prediction errors that may signal an incorrect model (e.g., to maintain a given metre while some onsets suggest another metre). Therefore, by balancing predictability and prediction error, rhythms with medium syncopation elicit greater reward and a greater urge to move associated with groove (Vuust & Witek, 2014).

PC is, generally speaking, a brain-based theory, therefore evidence for this framework tends to come from neural recordings. For example, many studies have focused on the mismatch negativity (MMN) which is an event-related neural response, measured by electroencephalography (EEG) or magnetoencephalography (MEG), that follows a perceptual deviant within a stream of 'standards'. Based on this work, the MMN is thought to be a neural index of prediction error. In the context of music, MMNs occur in response to both rhythmic (Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009) and melodic (Quiroga-Martinez et al., 2019) deviants. MMNs associated with violations of rhythm-based temporal predictions have been localized to the parietal and auditory cortices (Lappe, Steinsträter, & Pantev, 2013). The parietal cortex is part of the dorsal auditory stream (Rauschecker, 2011; see section 1.5.4) and has been implicated in both rhythmic (Ross, Iversen, & Balasubramaniam, 2018b) and non-rhythmic timing (Davranche, Nazarian, Vidal, & Coull, 2011). Interestingly, Vuust et al. (2009) showed higher amplitude MMNs for syncopations on strong beats compared to weak beats, and for expert musicians compared to non-musicians, supporting the suggestion that musical training strengthens metrical models. Similarly, the amplitude of MMNs in response to small temporal perturbations decreased as rhythmic complexity increased (Lumaca, Haumann, Brattico, Grube, & Vuust, 2019). This suggests that prediction errors, as reflected by MMNs are weaker for weaker metrical models and therefore also reflect the certainty or weight of the prediction error.

1.4.2 Dynamic Attending and Neural Resonance

The dynamic attending theory (DA) builds on dynamical systems theory to describe how temporal predictions come about and in turn lead to rhythm perception (Large & Jones, 1999). According to this framework, attention is a rhythmic process, formalized as an endogenous oscillator, or set of oscillators, continuously fluctuating between low and high states. These oscillators are entrained by rhythms in the environment, such as music or speech, thus aligning periods of relatively high attention with relevant timepoints in the auditory stream. The coupling strength, describes the force with which a rhythm in the environment draws attention, thus determining how fast the attentional oscillator aligns with the environmental rhythm. Synchronization describes the consistency of the temporal relation between attentional oscillator and external rhythm and thus the degree of entrainment. In the context of rhythm perception, high phases of the attentional oscillator reflect temporal predictions. That is, once entrainment is established, rhythmic onsets are expected to occur at high rather than low phases of the attentional oscillator. As in PC, temporal predictions have varying degrees of precision depending on the rhythmic context and this precision is formalized as the width of a probability distribution. In DA, this distribution is referred to as the focus of attention, defined as rhythmic pulses of attention or 'concentrations of attentional energy' over time (Large & Jones, 1999, pg. 129). Therefore, as in PC, the width of attentional focus will be broader when the rhythmic context engenders uncertainty, for example, when no note falls within the focus of attention and the temporal prediction is violated.

The neural resonance theory, which is based on DA, proposes that attentional oscillations are instantiated in neural oscillations, which reflect the periodic increases and decreases of excitability in neuronal ensembles (Large & Snyder, 2009). These oscillations can be entrained by regularly timed stimuli such that phases of high neural excitability align with relevant time points in the stimuli, thus facilitating perception. Evidence for this comes from EEG and MEG studies involving perceptual target detection or discrimination within rhythmic or pseudo-rhythmic streams. Within these tasks, task performance is predicted by the phase alignment between perceptual targets and neural signals (Auksztulewicz, Myers, Schnupp, & Nobre, 2019; Henry, Herrmann, & Obleser, 2014; Henry & Obleser, 2012; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). Therefore, these studies provide a neural basis of the faciliatory effects of temporal prediction on perception.

Neural oscillations are also thought to coordinate communication between brain regions, with higher frequency oscillations supporting local (e.g., within a brain region) communication and lower frequency communication supporting longer distance (e.g., between brain regions) communication (Buzsáki, 2006). Further, high frequency oscillations can be nested within low frequency oscillations, thus providing a mechanism by which local and long-distance processes can be synchronized in time, for example, to facilitate multisensory integration (Bauer, Debener, & Nobre, 2020). This nesting is often measured via phase-amplitude coupling in which the high-excitability phase of the low frequency oscillation correlates with high power or amplitude in the high frequency oscillation (Samiee & Baillet, 2017). Therefore, according to the neural resonance view, rhythmic neural activity is a fundamental component of neural computation, accounting for attentional sensory selection, temporal prediction mechanisms, and multi-sensory integration. Although, not measured in the projects discussed in this thesis, low-frequency neural oscillations may provide a neural substrate for beat-based predictions while coupling between low and high frequency oscillations may determine the precision of these predictions. In addition, this coupling may govern the timing of motor outputs, for example in an SMS task.

Based on the above discussion, it is clear that there is strong overlap between the PC and DA frameworks in how they conceptualize and formalize temporal predictions, and their certainty, in the context of rhythm perception. However, the ways in which these frameworks account for the neural mechanisms of rhythm perception, and the degree to which they have been applied to groove, diverge. For example, the link between DA and neural resonance theories to rhythm and beat perception has been widely tested and discussed (see section 1.3.3), however, the link to groove has yet to be firmly established. Exceptions include a study linking subjective feelings of entrainment, including the urge to move and a subjective feeling of changes in bodily rhythms, to positive affect in the context of music listening (Labbé & Grandjean, 2014) and another showing a positive relation between neural entrainment and ratings of groove (Cameron et al., 2019). Conversely, PC has been repeatedly applied in the investigation of groove and its underlying mechanisms (Koelsch et al., 2019; Vuust & Witek, 2014; Vuust et al., 2018; Witek et al., 2014). The methodological approaches associated with these two frameworks also diverge. For example, due to the reliance on oscillatory processes, the neural correlates of DA have largely been tested using methods that can capture the temporal (e.g., phase) relationships between neural activity, as measured by EEG or MEG, and auditory rhythms. Conversely, the emphasis on prediction errors in PC has led to the focus on the event-related brain responses such as event-related potentials (with EEG) and event-related fields (with MEG), as well as event-related functional magnetic resonance imaging (fMRI).

In the current context, these theoretical frameworks are most relevant for Article 2 in which they are used to generate hypotheses and interpret the relative contribution of perceived and measured tapping synchrony to groove. Within the context of that study these frameworks make generally the same predictions. However, the final chapter will provide a more in-depth discussion of how these frameworks may explain the sensation of groove in general.

1.5 The Neuroscience of Rhythm, Beat Perception, and Music-Derived Reward

There is now an abundance of work on the neural correlates of rhythm and beat perception and production, however, very little work has focused on the sensation of groove. One consistent result from neuroimaging studies on beat and rhythm perception is the involvement of motor regions of the brain, even during passive listening and with no intent to move (Araneda et al., 2016; Bengtsson et al., 2009; Burunat et al., 2017; Chapin et al., 2010; Chen et al., 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009, 2013; Kung et al., 2013; Schubotz et al., 2000; Thaut et al., 2014). Given that the urge to move is fundamental to the sensation of groove as well as the importance of rhythm perception in groove, it is sensible to expect that even passive listening to groove-based music would engage the motor regions of the brain. There has also been a number of neuroimaging studies showing that music listening engages reward networks in the brain (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011; Salimpoor et al., 2013) corresponding to those involved in the processing of primary and secondary rewards such as food and money (Sescousse, Caldú, Segura, & Dreher, 2013). However, neuroimaging work investigating the reward associated with groove is lacking. Article 3 investigates whether the motor networks and reward networks involved in rhythm perception and music-derived pleasure are involved in the sensation of groove. Therefore, these two sets of literature are briefly summarized in the next two sections.

1.5.1 The Brain Regions Involved in Rhythm and Beat Perception

Exploiting its high spatial resolution, researchers have used fMRI to investigate the brain regions involved in beat perception. The most common approach to the design and analysis of fMRI studies involves contrasting the blood oxygen-level dependent (BOLD) response between two or more conditions. Studies contrasting rhythms with a strong beat to those with no discernible beat (e.g., random onsets) show activity in brain regions associated with motor processes including the primary motor (M1), the dorsal and ventral premotor cortices (dPMC; vPMC), the supplementary motor area (SMA), the basal ganglia (BG) and the cerebellum (Araneda et al., 2016; Bengtsson et al., 2009; Burunat et al., 2017; Chapin et al., 2010; Chen et al., 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009, 2013; Kung et al., 2013; Schubotz et al., 2000; Thaut et al., 2014). Many of these regions have been specifically implicated in both motor and perceptual timing tasks. The BG is thought to be involved in beat-based timing of regular repeating intervals in the hundreds of milliseconds range. In contrast, the cerebellum is implicated in timing of single intervals and in the fine-grained, automatic correction of movements (Breska & Ivry, 2018; Teki, Grube, & Griffiths, 2012; Teki, Grube, Kumar, & Griffiths, 2011).

Based on the above work, it has been proposed that a network formed by the BG, PMC, and SMA (BG-SMA-PC; and likely other regions, such as the thalamus) is responsible for endogenous beat generation (Merchant et al., 2015). This is supported by behavioural work with Parkinson's Disease patients. Parkinson's Disease affects dopamine release by the substantia nigra to other regions of the BG. Patients with Parkinson's Disease show a reduced ability to use the beat in a rhythm discrimination task compared to healthy controls (Grahn & Brett, 2009). Conversely, patients with cerebellar degeneration show decrements in duration-based (e.g., a single interval) but not beat-based timing tasks (Grube, Cooper, Chinnery, & Griffiths, 2010). A similar result was shown when cerebellar activity was disrupted using transcranial magnetic stimulation (TMS; Grube, Lee, Griffiths, Barker, & Woodruff, 2010). In addition, activity in the BG-SMA-PMC respond to the beat across auditory, and vibrotactile modalities (Araneda et al., 2016; Grahn, Henry, & McAuley, 2011). In addition, oscillatory activity in these regions has been shown to track the beat and metre (Li et al., 2019; discussed further below).

The BG-SMA-PMC hypothesis is also congruent with more general models of timing, such as the pacemaker-accumulator model and striatal beat frequency model, which are based on interval timing studies in animals. Both models implicate the BG and motor cortical regions, including the SMA, as crucial nodes in a core timing network (Coull, Cheng, & Meck, 2011; Matell & Meck, 2004; Merchant, Pérez, Zarco, & Gámez, 2013). Although based on interval timing tasks, these models are also compatible with beat perception and beat-based timing (Hartcher-O'Brien, Brighouse, & Levitan, 2016). These models provide promising accounts of how basic timing mechanisms within cortico-striatal networks may explain beat perception and generation, however, empirical evidence is still lacking. Further, these regions provide likely candidates for connecting rhythm perception and the urge to move in the context of groove, a hypothesis that is tested in Article 3.

1.5.2 Using Brain Stimulation to Investigate Rhythm and Beat Perception

TMS allows for the investigation of the causal involvement of cortical regions in beat or rhythm perception. TMS involves the application of electric current to a specific brain region via electromagnetic induction which leads to either excitation or inhibition of activity in this region. The effects of this stimulation on motor and perceptual processes is then measured. One approach is to deliver a single pulse of TMS over M1 and then use electromyography, for example with a surface electrode placed on the muscle controlling finger movements, to measure the resulting motor evoked potential (MEP). The amplitude of the MEP is related to corticospinal excitability which is considered an index of motor preparation. Using this method, studies have shown larger MEPs for rhythms with a strong beat compared to a weak beat (Cameron, Stewart, Pearce, Grube, & Muggleton, 2012) and enhancement of MEP amplitudes in response to stimuli with rates around participants' spontaneous tapping tempo (Michaelis, Wiener, & Thompson, 2014). Finally, one study showed larger MEPs for high-groove compared to low-groove music and that this effect was greater on the beat compared to off the beat (Stupacher, Hove, Novembre, Schütz-Bosbach, & Keller, 2013). Together these results show that beat perception and groove causally affect motor preparation.

Another approach is to use TMS to excite or inhibit activity in cortical regions and then measure changes in behaviour via beat perception or tapping tasks. As this approach does not rely on measuring changes in muscle activity, it can be used to investigate the involvement of regions other than M1 in beat or rhythm perception. Using this approach, one study showed that inhibitory TMS over the right dPMC during a rhythm reproduction task affected tap asynchrony but not the accuracy of produced intervals (Giovannelli et al., 2014). Inhibitory TMS over left dPMC and the SMA did not affect tapping performance. Two recent studies with perceptual rhythm and timing tasks showed that inhibitory TMS over the right dPMC affected performance on an interval timing and an inter-beat interval task, but not a phase-shift detection task (Ross, Iversen, & Balasubramaniam, 2018a). In a separate study, inhibitory TMS over the left parietal cortex reduced phase shift detection but stimulation over the SMA did not affect performance on either beat-based or interval timing-based tasks (Ross, Iversen, & Balasubramaniam, 2018b). Although supporting the role of the PMC in beat-based timing, these results contradict the previously discussed results suggesting involvement of the SMA in beat perception (see also the next section). Therefore, the specific contributions of these two regions have yet to be clarified.

1.5.3 The Role of Neural Oscillations in Beat and Rhythm Perception

Unlike fMRI, EEG provides high temporal resolution and therefore the ability to measure brain activity at and above frequencies corresponding to rhythmic stimuli. This makes EEG an excellent method for investigating neural resonance theory in the context of rhythm perception. One popular method is to ‘tag’ frequencies in the EEG frequency spectrum that correspond to those found in the spectrum of rhythmic stimulus and compare the amplitudes of these EEG signals across conditions (Nozaradan, 2014). For example, one study using this approach showed that when participants impose a metre on an isochronous rhythm, by imagining an accent on every second onset, EEG signals with frequencies corresponding to both the rhythm and metre were observed (Nozaradan, Peretz, Missal, & Mouraux, 2011). In addition, tapping to either the event or beat frequency enhances the amplitude of the corresponding EEG signal (Chemin, Mouraux, & Nozaradan, 2014). This approach was also applied to patients with BG or cerebellum lesions. Results indicated that BG patients had reduced signal amplitudes at slower tempos especially for more complex rhythms while cerebellum patients showed reduced signal amplitude for faster tempos (Nozaradan, Schwartze, Obermeier, & Kotz, 2017). A recent study combined this frequency-tagging approach with fMRI, showing that the putamen, caudate, SMA and thalamus tracked both metre and beat frequencies (Li et al., 2019). In addition, by contrasting beat and metre tracking conditions, the authors showed that the SMA showed greater tracking of the beat versus metre while putamen showed greater tracking of the metre compared to the beat. A recent study used a similar approach, but with MEG recordings and with syncopated rhythms with few or no onsets falling on the beat (Tal et al., 2017). Analysis of the MEG signal showed a significant peak corresponding to the beat frequencies in the right auditory cortex, thus providing a neural correlate of an endogenous beat.

Other studies of beat entrainment using MEG have focused on activity in the beta band (12.5 -30 Hz), a frequency range associated with motor preparation (Engel & Fries, 2010). Studies using a similar paradigm, where participants imagine or impose metrical accents on un-accented stimuli, have shown beta power modulations following imagined accents (Fujioka, Ross, & Trainor, 2015; Iversen, Repp, & Patel, 2009). Further, they have shown that beta power tracks rhythmic onsets (Fujioka, Trainor, Large, & Ross, 2009) and that this tracking is consistent across tempos, suggesting that this oscillatory response is predictive rather than simply reflecting a stereotypic evoked response (Fujioka, Trainor, Large, & Ross, 2012). Beta activity has been generally associated with motor functions (Engel & Fries, 2010) and may be generated in motor cortex (Baker, 2007). This has led to the suggestion that beta activity encodes predictive timing signals that facilitate auditory processing in a rhythmic context (Arnal, 2012; Patel & Iversen, 2014; Teki & Kononowicz, 2016). This conception has been recently given experimental support by a study showing directed signaling in the beta range from motor to auditory cortex during both covert and overt tracking of the beat (Morillon & Baillet, 2017). In addition, source localization of the beta activity associated with rhythmic onsets and imagined accents shows a large network of cortical and subcortical motor, auditory, parietal and frontal regions (Fujioka et al., 2015; Fujioka, Fidali, & Ross, 2014; Fujioka et al., 2012). Therefore, studies using EEG and MEG corroborate the involvement of a motor, frontoparietal, and auditory network supporting beat and rhythm perception as shown by the fMRI studies discussed above. Further, these studies provide evidence for entrainment-driven temporal predictions as the underlying mechanism.

1.5.4 Dorsal Pathways and Rhythm and Beat Perception

Evidence demonstrating the involvement of auditory, parietal, premotor and prefrontal regions in both fMRI and MEG studies of rhythm and beat perception, is in line with the importance of the dorsal auditory stream in predictive motor control (Rauschecker, 2011) including speech (Hickok & Poeppel, 2004, 2007, 2016) and rhythm (Karabanov, Blom, Forsman, & Ullén, 2009; Kornysheva & Schubotz, 2011). This network is thought to be crucial for translating acoustic representations, such as speech, into motor commands in a feedforward manner, that is, generating a motor command based on the desired or predicted auditory output (Hickok & Poeppel, 2016). These networks are also thought to generate efference copies of a motor signal and send this signal to sensory regions, allowing for the facilitation or suppression of the resulting sensory input. A similar network, consisting of the dorsal premotor and posterior parietal cortices, is thought to be responsible for the coding of domain-general simulation of actions allowing for the manipulation of abstract representations such as that involved in mental rotation or melody transpositions (Foster, Halpern, & Zatorre, 2013; Ptak, Schnider, & Fellrath, 2017). The feedforward generation of motor commands, and their efference copies, is thought to occur for covert or simulated actions as well as those actually carried out. In the context of rhythm perception, the action simulation for auditory prediction (ASAP; Patel & Iversen, 2014) hypothesis suggests that the endogenous beat consists of covert actions generated in dorsal networks, along with the BG. The efference copies of these covert motor commands provide the pacing signal that focuses attentional and sensory processes to the predicted beat points (Kotz, Brown, & Schwartze, 2016). Specifically, covert motor signals, likely in the beta range, are thought to result in a phase reset of the slow neural oscillations in auditory cortex, thus enhancing or maintaining neural entrainment to rhythmic or pseudo-rhythmic input (Rimmele, Morillon, Poeppel, & Arnal, 2018). Activity in the parietal cortex has been implicated in focusing attention in time (Coull et al., 2011), for example when expecting a perceptual target to fall on a certain metrical beat, in both perceptual and motor tasks (Bolger, Coull, & Schon, 2014; Davranche et al., 2011). This likely relates to the purported role of the parietal cortex as the interface between efference motor signals and incoming sensory signals thought to support the comparison between temporal prediction and input (Rauschecker, 2011).

1.5.5 The Brain Regions Involved in Music-Derived Reward

Given that the sensation of groove involves a positive affective response, it is likely to engage regions involved in processing reward, including the caudate and nucleus accumbens (NAcc) in the basal ganglia as well as the medial orbitofrontal cortex (mOFC). Current research suggests that these regions are involved in processing music-derived pleasure (Salimpoor et al., 2015) in addition to processing primary (e.g., food and sex) and secondary (money) rewards (Sescousse et al., 2013). The NAcc has been shown to be active during peak moments of music-derived pleasure while the caudate is active in anticipation of these moments (Salimpoor et al., 2011), suggesting differential roles in the anticipation and experience of reward. In addition, activity in the NAcc predicted the reward value of music as measured by the amount of money participants were willing to pay for each song (Salimpoor et al., 2013). Further, functional connectivity between the NAcc and auditory cortex, as well as structural connectivity between NAcc and mOFC, and between NAcc and the mOFC is associated with the degree to which listening to music induces reward (Martinez-Molina, Mas-Herrero, Rodríguez-Fornells, Zatorre, & Marco-Pallarés, 2019; Martínez-Molina, Mas-Herrero, Rodríguez-Fornells, Zatorre, & Marco-

Pallarés, 2016). Together these results show that music-derived pleasure is supported by a network formed by the NAcc, mOFC, and auditory cortex.

Activity in NAcc and other BG regions during positive emotional experiences, including those related to music listening, rely on dopaminergic signaling that is thought to reflect prediction processes (Gebauer et al., 2012; Juslin & Västfjäll, 2008; Koelsch & Skouras, 2014; Salimpoor et al., 2011). Dopamine release within subcortical regions including the substantia nigra and ventral tegmental area (VTA) are thought to code for reward prediction errors, for example when a stimulus is better than predicted (Schultz, 2016). Therefore, the pleasure experienced during music listening and the associated BG activation are thought to reflect the interaction between predictions about what and when musical elements will occur, and the value assigned to these elements (Hollerman & Schultz, 1998). This is supported by recent work showing that reward prediction errors related to melodic passages are coded in the NAcc (Gold, Mas-herrero, Zeighami, Benovoy, & Dagher, 2019). In addition, activity in the VTA and NAcc during music listening is highly correlated suggesting dopamine release from the VTA may be associated with NAcc activation (Menon & Levitin, 2005). The use of positron emission tomography allows for the tracking of dopamine release within the brain. Studies using this technique have shown greater dopamine release in the NAcc during moments of peak music-induced pleasure (Salimpoor et al., 2011). Further, ingestion of a dopamine precursor led to increased pleasure ratings and electrodermal activity, during music listening, as well as increased money spent per song, compared to placebo (Ferreri et al., 2018). Ingestion of a dopamine agonist led to the opposite effect. This suggests a causal role of dopamine in music-derived pleasure.

Together these studies show the importance of BG regions, along with the mOFC, in the experience of musical pleasure, with dopaminergic signaling as the likely neurobiological mechanism. The motor system as well as frontoparietal activity are also sensitive to reward incentive (Bundt, Abrahamse, Braem, Brass, & Notebaert, 2016; Etzel, Cole, Zacks, Kay, & Braver, 2016; Galaro et al., 2018) suggesting that cognitive, motor, and reward processes interact during incentivized task performance. This also relates to reward-based motor learning in which the BG has been shown to integrate reward value for action selection and optimization, a process that is also likely to rely on dopaminergic signaling (Graybiel, 2008; Graybiel & Grafton, 2015). As discussed above, the BG are also thought to be crucial for rhythm and beat perception and production with dopamine likely playing a crucial role (Grahn & Brett, 2009; Koshimori et al., 2019). Therefore, the BG seems a likely candidate for the integration of the motor-driven rhythm-based temporal prediction and reward processes associated with groove. For this reason, Article 3 focuses on BG, as well as whole-brain, activity associated with the sensation of groove.

1.6 Introduction to the Research Chapters

Studying the sensation of groove helps us to better understand music's power to move us both emotionally and physically, while also providing a powerful tool to further our understanding of how motor-driven timing and reward processes interact. In the following chapters, three research articles will be presented investigating perceptual, behavioural and neuroscientific aspects of groove. In Article 1, I investigate the degree to which harmonic complexity, and its interaction with rhythmic complexity, affects groove. This takes the investigation of groove beyond rhythm while elucidating how different aspects of music affect the pleasure and urge to move components of groove differentially. Article 2 focuses on whether 'feeling in sync' with a rhythm predicts groove to a greater degree than measured synchrony by comparing the effects of tapping accuracy and precision, and tap ratings, on groove. In Article 3, I use fMRI to elucidate the brain regions involved in groove by investigating the neural correlates of both musical properties and subjective ratings. Together, this research aims to further our understanding of groove while investigating the fundamental processes that underlie this powerful aspect of music.

CHAPTER TWO:
ARTICLE 1

The sensation of groove is affected by the interaction of rhythmic and harmonic complexity

Matthews, T. E., Witek, M. A., Heggli, O. A., Penhune, V. B., & Vuust, P. (2019). The sensation of groove is affected by the interaction of rhythmic and harmonic complexity. *PloS one*, *14*(1), 1-17. https://doi.org/10.1371/journal.pone.0204539

Abstract

The pleasurable desire to move to music, also known as groove, is modulated by rhythmic complexity. How the sensation of groove is influenced by other musical features, such as the harmonic complexity of individual chords, is less clear. To address this, we asked people with a range of musical experience to rate stimuli that varied in both rhythmic and harmonic complexity. Rhythm showed an inverted U-shaped relationship with ratings of pleasure and wanting to move, whereas medium and low complexity chords were rated similarly. Pleasure mediated the effect of harmony on wanting to move and high complexity chords attenuated the effect of rhythm on pleasure. We suggest that while rhythmic complexity is the primary driver, harmony, by altering emotional valence, modulates the attentional and temporal prediction processes that underlie rhythm perception. Investigation of the effects of musical training with both regression and group comparison showed that training increased the inverted U effect for harmony and rhythm, respectively. Taken together, this work provides important new information about how the prediction and entrainment processes involved in rhythm perception interact with musical pleasure.

Introduction

When listening to music we often find ourselves spontaneously tapping or moving to the beat. This has led to the study of groove, which is the pleasurable desire to move to music (Janata, Tomic, & Haberman, 2012; Witek, 2009; Witek et al., 2014). Certain types of music are more likely to induce the sensation of groove than others. However, which specific aspects of music contribute to this sensation is less clear. Research on groove has focused on rhythmic complexity, but other musical properties may contribute as well. The harmonic complexity of simultaneous notes forming a chord is a likely contributor because it modulates affective responses (Pallesen et al., 2005), however, this may be influenced by musical expertise (Lahdelma & Eerola, 2014). Therefore, in the current study we investigated whether rhythmic and harmonic complexity work together to affect the sensation of groove and whether this depends on musical training.

Early definitions of groove focused on the degree to which a piece of music will induce the desire to move to the beat (Madison, 2006; Pressing, 2002). Moving along with music, especially through dance, is often accompanied by feelings of pleasure. In a seminal study on groove, responses to a survey emphasized both the desire to move and the associated positive affect (Janata et al., 2012b). Since then, several rhythmic aspects have been studied in terms of their effectiveness in inducing groove. Music with a strong beat leads to higher groove ratings (Madison, Gouyon, & Ullen, 2009; Madison et al., 2011) and is more likely to induce whole body movements, compared to music with a weak beat (Burger, Thompson, Luck, Saarikallio, & Toiviainen, 2013).

A strong beat may be necessary for groove but is likely not sufficient. A ticking clock could be considered to have a strong beat but is unlikely to be something people want to dance to. Syncopation, when a note falls on a weak beat, and is then followed by a silence on a strong beat (Fitch & Rosenfeld, 2007; Longuet-Higgins & Lee, 1984), is a critical component of groove. It is often found in musical genres associated with groove, such as jazz, soul, funk, Afro-Cuban, and Hip Hop (Danielsen, 2006; Greenwald, 2002), and is used by musicians intentionally to create groove (Madison & Sioros, 2014). Meter is the pattern of differentially accented groupings and subdivisions of strong and weak beats which may or may not be acoustically present in the rhythm. Syncopation works against the meter by emphasizing a weak beat and de-emphasizing a strong beat. This creates tension with the established meter, violating expectations

(Huron, 2006; London, 2012; Meyer, 1956). Listeners rate syncopated sequences as more enjoyable and sounding happier than non-syncopated sequences (Keller & Schubert, 2011), but this depends on the degree of syncopation. An inverted U-shaped relationship has been shown between degree of syncopation, and ratings of pleasure and the desire to move, where moderately syncopated rhythms are rated higher than rhythms with low or high degrees of syncopation (Witek et al., 2014).

Non-rhythmic musical features have also been shown to contribute to groove, such as bass frequency content and variability in dynamics (Stupacher et al., 2016). While no current studies directly address whether harmony affects groove, there is evidence that consonance (i.e., a pleasant relation between notes in a chord) affects motor synchronization (Komeilipoor, Rodger, Craig, & Cesari, 2015) and feelings of entrainment (Trost et al., 2014). In the present study we tested the effect of harmony in single chords rather than chord sequences, therefore harmonic complexity was operationalized as the degree of consonance. Although chords most often occur in music as part of a sequence, some groove-based genres, such as salsa, funk, and house music, frequently feature only one or two chords (James Brown's 'The Payback' is a well-known example). Recent studies have shown that the harmonic complexity of single chords affects ratings of emotion and arousal (Lahdelma & Eerola, 2014) and that chords of intermediate complexity are preferred over highly consonant or dissonant chords (Lahdelma & Eerola, 2016). This result supports the inverted U hypothesis which, as discussed above, has been shown for rhythmic complexity, and is theorized to be a domain-general phenomenon (Berlyne, 1971). The use of single chords here allows for the modulation of affective responses by consonance alone, thus avoiding a confound with responses to violations of harmonic expectations from chord sequences.

As affective, aesthetic and embodied effects of music are highly subjective and dependent on experience, musical training likely influences how individuals experience groove. However, the results of studies comparing musicians and non-musicians are somewhat contradictory. Musicians have shown a greater effect of syncopation on groove ratings (Senn, Kilchenmann, Bechtold, & Hoesl, 2018), stronger motor response to high groove music (Stupacher et al., 2013), and larger error-related neural response to rhythmic violations, compared to non-musicians (Vuust et al., 2009). Conversely, several studies have suggested that musical training has little or no effect on groove ratings (Stupacher et al., 2013; Witek et al.,

2014) or leads to lower groove ratings (Hurley et al., 2014). Furthermore, it has been suggested that the inverted U-shaped relationship between overall complexity and liking disappears as musical training increases and other 'learned aesthetic criteria' become stronger predictors for music preference (Orr & Ohlsson, 2005), pg. 608). These contradictory results may be due to the fact that these studies differ in how musicianship is defined and tested (i.e., as a continuous regressor or via group comparison). For harmonic complexity in the context of chords the picture is somewhat clearer, as musicians show higher liking ratings (Lahdelma & Eerola, 2014), greater differences in ratings of consonance (Arthurs, Beeston, & Timmers, 2017; Pallesen et al., 2005), and larger mismatch negativity brain responses (Brattico et al., 2008). These results suggest that musical training leads to a greater sensitivity to consonance-dissonance manipulations, which may translate to greater affective response in the context of groove.

Taken together, current evidence shows that the sensation of groove involves both a motor and affective response, and is predicted by syncopation, while the contribution of harmonic complexity and the impact of musical training are less clear. Therefore, in the present study we created stimuli that varied in both rhythmic and harmonic complexity. These stimuli were then rated for pleasure and wanting to move by a large sample of people with a broad range of musical training using an online paradigm. Based on previous research (Witek et al., 2014), rhythmic complexity was expected to show an inverted U-shaped relationship with ratings of both pleasure and wanting to move. Harmonic complexity was also expected to show an inverted U-shaped pattern with pleasure ratings and affect wanting to move only indirectly, if at all. Harmonic complexity was also expected to enhance the effect of rhythm via its effect on emotional valence. In order to reduce methodological bias, the contribution of musical training was investigated both as a continuous regressor and by comparing sub-groups of highly trained, practicing musicians to non-musicians. Musical training was expected to increase sensitivity to both harmonic and rhythmic complexity.

Methods

Ethics statement

This study investigates subjective experiences of music via a web-based survey. The study was conducted through the Centre for Music in the Brain at Aarhus University, therefore, ethics were governed by the Central Denmark Region Committees on Health Research Ethics. According to their Act on Research Ethics Review of Health Research Projects (Act 593 of 14

July 2011, section 14.1), only health research studies shall be notified to the Committees. Our study is not considered a health research study (section 14.2) and therefore did not require ethical approval nor written/verbal consent, regardless of participants' age. When recruited, participants were informed that their responses would be used for research purposes. Participants were anonymized, and no IP addresses were collected or stored. They were free to exit the survey at any time and were provided with an email address at the end of the survey to which they could address any questions or concerns.

Participants

Two hundred and one participants between the ages of 17 and 79 (*M* = 34.74 *S*D = 13.24) completed the survey (96 reported as female). Participants reported their nationality as being from countries in six different continents, with a majority in Europe (n = 130) and North America (n = 47). As can be seen in Table S2.1, there was a large range of musical training backgrounds. A majority (n = 189) of participants reported no university-level music degree. Of those currently playing music, a majority played piano (n = 50), guitar (n = 44) or sang (n = 25) and had 14.5 (*SD* = 5.31) years for formal music training. Musician responders played largely classical (n = 69) or pop/rock (n = 62) genres.

For the group analysis, two subsets of the total sample were categorized as musicians (n = 58, 15 F) and non-musicians (n = 51, 18 F). Musicians were defined as those who reported at least eight years of formal music training (*M* = 14.5, *SD* = 5.31) and were currently practicing on a weekly or more frequent basis (hours per week: *M* = 6.52, *SD* = 8.51). Non-musicians were defined as those who reported less than three years of formal training (*M* = 0.21, *SD* = 0.49) and were not practicing on a weekly or more frequent basis. Participants falling between these categories were excluded from the group analysis only.

Stimuli

The stimuli consisted of short musical sequences with three levels (Low, Medium, High) of both rhythmic and harmonic complexity. There were three different rhythm patterns for each level of rhythmic complexity and three different chords for each level of harmonic complexity. These were combined into nine versions of each rhythmic and harmonic complexity combination, of which six were selected for inclusion in this study, resulting in a total of 54 stimuli. All stimuli were created using Cubase Pro version 8.0.30 (Steinberg Media Technologies).

Each sequence consisted of a rhythmic chord pattern with one repeated chord in a piano timbre presented at 96 beats per minute in common time (see example stimuli in Figure 2.1). Each sequence also included an isochronous hi-hat pattern with an inter-onset interval (IOI) of .3125 seconds, corresponding to an eighth note. The hi-hat provided a metrical context for the rhythms and prevented participants from perceptually shifting the beat of the high-complexity rhythms to reduce perceived complexity. Each piano chord lasted approximately .373 seconds including the full decay and were considered as eighth notes except in two of the high complexity rhythms which included IOI's of .234 seconds corresponding to a dotted sixteenth note. Each sequence lasted one bar which was repeated four times for a total length of ten seconds.

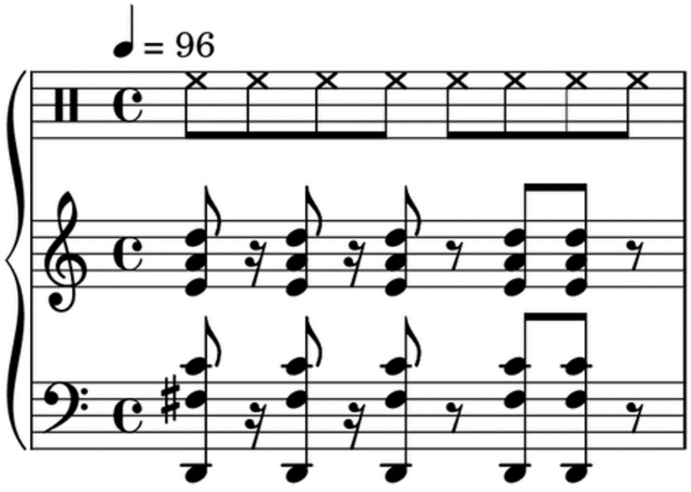

Figure 2.1. Stimuli example. Transcription of an example stimuli with a medium complexity rhythm (son clave) and a medium complexity chord (four note chord with extensions). The upper bar denotes the hi-hat.

Rhythmic complexity

Rhythms at all three levels of complexity consisted of five onsets in a 3+2 rhythmic pattern, that is, the first half of the bar consisted of 3 onsets, and the latter of 2 onsets. Medium complexity rhythms consisted of the son clave and the rumba clave, which are popular Afro-Cuban five-stroke rhythm patterns, as well as an experimenter-created rhythm (see Figure S2.1 for a schematic depiction of all rhythms). The claves were chosen as they induce a strong sense of beat despite including syncopations. The son clave and rumba clave are widely used in South American and particularly Afro-Cuban music but are also found in many forms of western music including pop, jazz and electronic dance music. Low complexity rhythms followed the same 3+2 rhythmic pattern as the medium complexity rhythms with all syncopation removed so that all onsets fall on strong beats. High complexity rhythms also followed the 3+2 rhythmic pattern, however only the first of the five onsets fell on strong beat points.

The degree of syncopation was quantified using the syncopation index created by Fitch and Rosenfeld (Fitch & Rosenfeld, 2007) based on the formalization of syncopation by Longuet-Higgins and Lee (Longuet-Higgins & Lee, 1984). Each syncopation in a sequence was given a weight based on the position of the rests and preceding notes involved, then these values are summed for an overall index for that sequence. The syncopation indices are summarized in Figure 2.2A. C-scores were also calculated for each rhythmic sequence (see Figure 2.2B). The C-score, created by Povel and Essens (Povel & Essens, 1985), measures the amount of counterevidence a rhythm provides against a given metrical interpretation based on the number of weak accents and silences falling on predicted beat points. C-scores and syncopation indices were highly correlated ($r(7) = 0.99, p < .05$) and both were highly consistent within each level of rhythmic complexity.

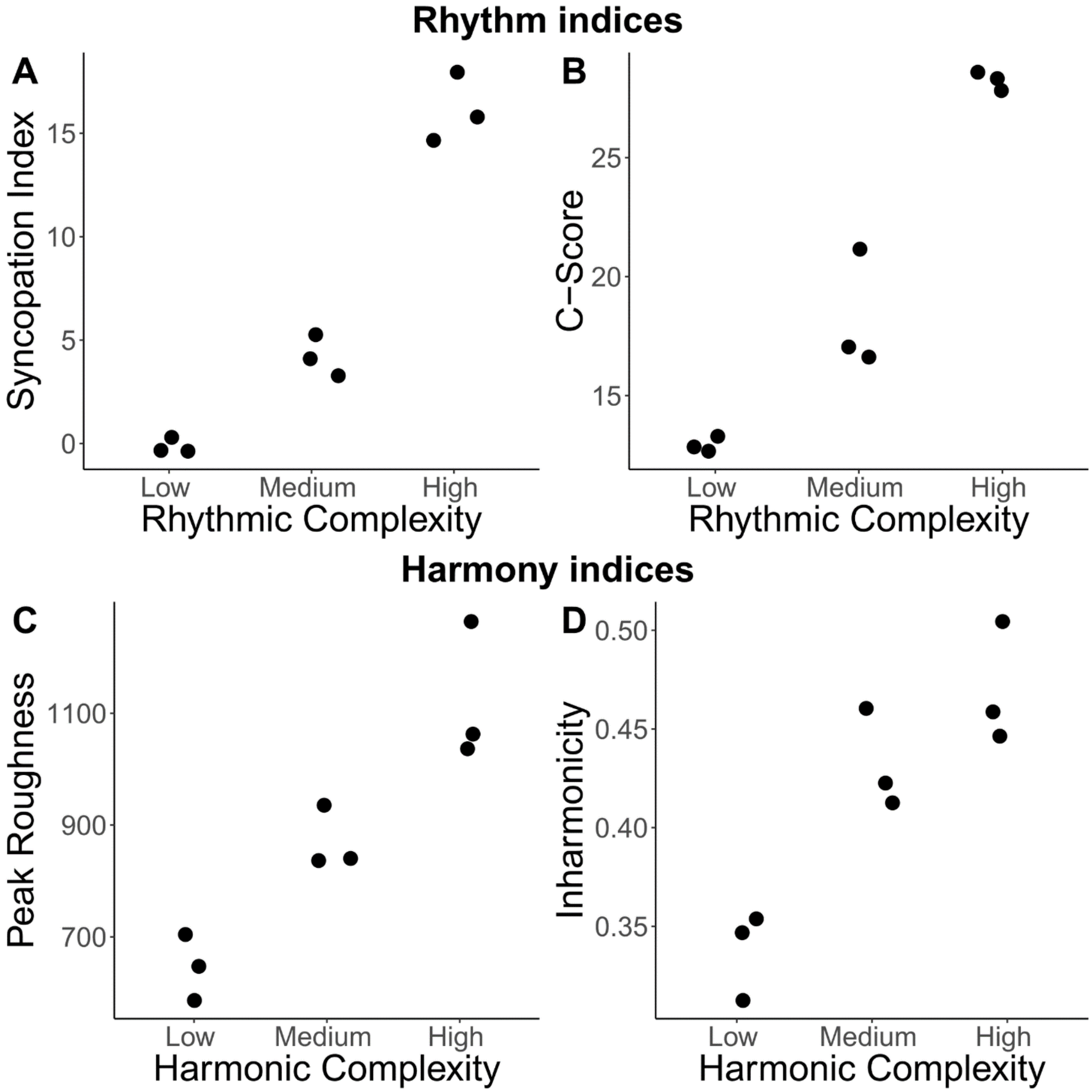

Figure 2.2. Indices of rhythmic and harmonic complexity. Scatterplots of measures of rhythmic complexity: (A) syncopation indices and (B) C-scores; and of harmonic complexity: (C) peak roughness and (D) inharmonicity.

Harmonic complexity

There were three chords for each of the three levels of harmonic complexity (Low, Medium, and High). All chords were in the key of D major and included six notes spanning four octaves (D2 to #D5; see Figure S2.2). Low complexity chords consisted of the D major triad and two inversions. Medium complexity chords consisted of four note chords with extensions. High complexity chords included a flat ninth interval between chord note and extension which is considered highly dissonant, when not specifically occurring as flat 9th on major 7th chord, according to contemporary harmonic theory (Freeman & Pease, 1989; Levine, 2011; Nettles & Ulanowsky, 1987).

Measures based on both acoustic and harmonic theory were used to quantify chord consonance. The acoustic measures of roughness and inharmonicity were calculated with the MIRtoolbox (Lartillot, Toiviainen, & Eerola, 2007). Roughness is due to combining sounds with similar frequencies, which causes beating and sensory dissonance (Plomp & Levelt, 1965; Sethares, 2004). Inharmonicity is the degree to which the partials in a chord are integer multiples of the fundamental frequency (Lartillot et al., 2007). A measure of consonance based on harmonic theory, called the aggregate dyadic consonance (ADC) (Huron, 1994) uses relations between pitch class sets rather than acoustic properties. Each interval class is given a consonance value which is multiplied by the number of occurrences of this interval class then summed for each chord.

As can be seen in Figure 2.2C, peak roughness increased with level of harmonic complexity. Mean roughness shows a similar pattern (see Figure S2.3). Inharmonicity increased with level of harmonic complexity, however the medium and high complexity levels showed similar values (see Figure 2.2D). The ADC shows an inverted U-shaped pattern where the medium complexity chords have the highest value (see Figure S2.3). This is because ADC is dependent on the number of distinct notes in a harmonic set, leading to increased potential for consonant intervals as the number of notes increases (Huron, 1994; Lahdelma & Eerola, 2016).

Procedure

Participants were recruited to visit a website hosting the survey via social media, email lists and word of mouth. Participants were offered the chance to win one of two Amazon gift cards worth 50 euros. First, participants completed a questionnaire regarding demographics, musical training, and musical preference. Participants reported years of formal training in music, the age at which they began formal training, and how often they currently practiced. Information regarding participants' interest in groove music, how often they listen to groove music, their enjoyment of dancing and how often they dance, were collected on five-point rating scales (see Figure S2.4). All questions required an answer before proceeding.

Participants then heard two sequences similar to the stimuli used in the survey and were asked to adjust the volume on their computer to a comfortable level. They were told to maintain the chosen volume throughout the survey. The two sequences, which were not used in the actual experiment, illustrated the range of possible levels of rhythmic and harmonic complexity. The survey then began during which each stimulus was presented once in a randomized order. After each stimulus was presented, two rating scales appeared for the two questions: ‘How much does this musical pattern make you want to move?’ and ‘How much pleasure do you experience listening to this musical pattern?’. Participants used their mouse to select their rating on the two five-point scales where one indicated ‘not at all/none’ and five indicated ‘very much/a lot’. Participants were not able to proceed to the next stimulus until each stimulus had been presented in its entirety and a rating had been selected on both scales.

Analysis

Only data from participants who completed all 54 trials were saved. Therefore, the analysis was implemented with no missing values. In order to reduce the number of predictors in the main analysis, ratings regarding interest and frequency of listening to groove music were combined using a principle component analysis (PCA) and are henceforth referred to as groove engagement PCA. The identical approach was taken with the two questions regarding whether participants enjoy dancing and how often they dance (referred to as dance PCA) as well as hours of practice per week and years of formal training (referred to as musicianship PCA).

Analysis of the main effects and interactions of rhythmic and harmonic complexity, as well as the effects of musical training, and enjoyment of dancing and groove music, were carried out using linear mixed effects regression in *R* (version 3.4.1) and *RStudio* (version 1.0.143), using the lme4 package (Bates, 2010). Random intercepts for participants were included as well as by-participant random slopes for the effects of rhythm and harmony, which accounted for inter-individual differences in average rating and effects of complexity, respectively (Barr, Levy, Scheepers, & Tily, 2013). By-item random intercepts were also included, which accounted for differences in ratings among the versions of stimuli within each level of rhythmic and harmonic complexity. This also allowed for analysis of the raw rather than by-level aggregated ratings. Note that boxplots show ratings aggregated within complexity level for visualization purposes.

A hierarchical approach was used, starting with an intercept-only model including all random effects. Predictors were then added incrementally and increases in model fit were assessed using the likelihood ratio test (Baayen, Davidson, & Bates, 2008). A final model including all significant predictors and random effects was then used to test follow-up contrasts. Along with visual inspection, inverted U-shaped relationships between harmonic and rhythmic complexity and ratings were tested using quadratic contrasts, which apply the contrast weights of 1, -2, and 1, corresponding to the three levels of rhythmic and harmonic complexity. Therefore, inverted U-shaped relationships result in negative contrast estimates (*b*). Following a significant interaction, pairwise contrasts were used to test whether the result of the quadratic contrast for rhythmic complexity differed across levels of the other predictors (i.e., harmonic complexity and group). Linear contrasts were not included as they compare low and high levels of complexity which was not of interest here. Contrasts were carried out using the *emmeans* package in *R* (Lenth, Singmann, Love, Buerkner, & Herve, 2018). Confidence intervals were calculated using degrees of freedom approximated with the Satterthwaite method and were adjusted for multiple comparisons using the multivariate *t* method. As all contrasts involved comparing the estimates (*b*) to zero, confidence intervals not only reflect the precision of the estimate but also were used as two-tailed significance tests where an interval excluding zero indicates a statistically significant result. Diagnostic plots of the residuals from all models were inspected for violations of the assumptions of normality and homoscedasticity. No violations were detected.

Linear regression models have been shown empirically to be robust to the potential violations of assumptions associated with Likert data (Norman, 2010). However, many believe that parametric statistics such as linear mixed effects models are not appropriate for Likert data (Jamieson, 2004). However, cumulative link mixed models (CLMM; from the *ordinal* package in *R*; Christensen, 2015), which are a standard method for analyzing ordinal data in a mixed effects context, do not allow for by-participant random slopes and are therefore less generalizable than linear mixed effect models (Barr et al., 2013). Furthermore, simulations suggest that CLMMs are more prone to Type I errors than linear mixed effects models for Likert data (Kizach, 2014). In the current study, secondary analyses were carried out using CLMMs to compare with the linear mixed effects approach. Overall, the pattern of results was very similar for both types of models with slightly more statistically significant beta estimates in the CLMM models. Given their increased generalizability and potentially lower Type I error rates compared to CLMMs, only the results of the linear mixed effects models are reported here.

Mediation Analysis

Harmonic complexity was expected to affect pleasure directly and wanting to move only indirectly, while rhythmic complexity was expected to affect both variables directly. Therefore, following the main analysis, a mediation analysis was carried out to further examine the effect of harmonic and rhythmic complexity on *wanting to move* ratings, specifically to test whether their effects were mediated by *pleasure*. This analysis involved comparing two models predicting *wanting to move* ratings; one identical to that in the main analysis, and another including the addition of pleasure ratings as a predictor. If pleasure is a significant mediator, then the contributions of rhythmic and/or harmonic complexity will be reduced in the second model.

The mediation effect was assessed using the *mediation* package (Tingley, Yamamoto, Hirose, Keele, & Kosuke, 2014) which provided point estimates and 95% confidence intervals for the mediation (indirect) and direct effects after taking the mediators' effects into account. The mediation and direct effect estimates were considered significant if the confidence interval did not contain zero. Confidence intervals were calculated using a quasi-Bayesian Monte Carlo simulation with the number of simulations set to 1000. Given the limitations of the mediation package, the models included a by-subject random intercept only and only the medium versus high and medium versus low pairwise contrasts were tested.

Group Analysis

In addition to the main analysis which regressed a continuous musicianship variable on ratings, an additional group analysis was carried out to compare the ratings of two subsets of the whole sample; those who were trained musicians (n = 58) and those with little-to-no training (n = 51; see Table S2.1 for musical background information). First, groove engagement and dance PCA scores were compared between the musicians and non-musicians to test whether musical training affected interest in groove and dance. A linear mixed effects analysis compared ratings between groups and tested for interactions between group and rhythmic and harmonic complexity.

Results

Wanting to move

For the *wanting to move* ratings, likelihood ratio tests showed that model fit was significantly improved by adding rhythmic complexity ($\chi^2(2) = 280.46$, $p < .001$) and harmonic complexity ($\chi^2(2) = 134.71$, $p < .001$). Follow-up contrasts showed that both rhythmic ($b(198) =$ 2.269, 95% CI [-2.530, -2.008]) and harmonic complexity ($b(199) = -0.327$, 95% CI [-0.431, -0.223]) showed significant quadratic trends, with rhythmic complexity showing a more pronounced trend. As can be seen in Figure 2.3A, rhythmic complexity showed a clear inverted U with highest ratings for medium complexity rhythms compared to both low and high. For harmony, despite a significant quadratic trend, an inverted U-shaped relationship was not shown as low and medium complexity chords were rated similarly, with a drop in ratings for high complexity chords.

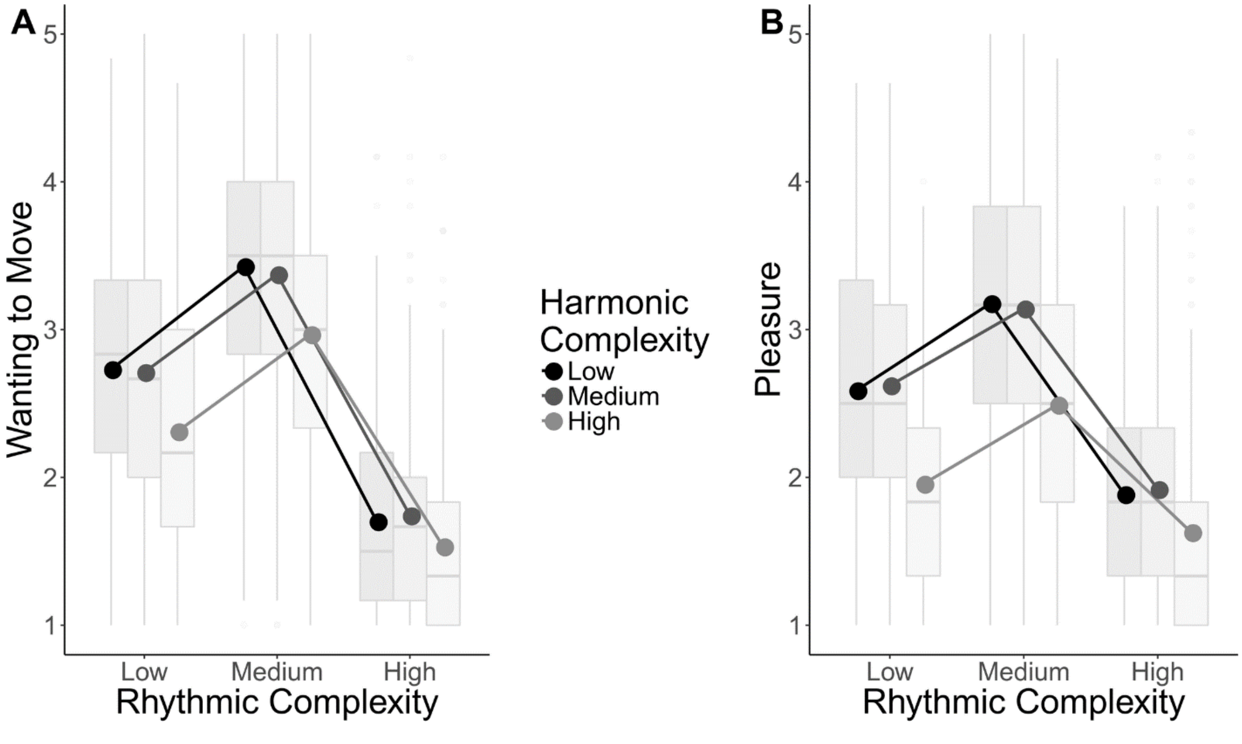

Figure 2.3. Ratings as a function of complexity. Boxplots showing the interaction between rhythmic and harmonic complexity for wanting to move ratings (A) and pleasure ratings (B). Boxplots represent ratings aggregated over items within each level of complexity for

visualization purposes. Center line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; points, outliers. Dots represent means calculated from the raw ratings.

Likelihood ratio tests also showed a significant interaction between rhythmic and harmonic complexity ($\chi^2(4) = 55.27$, $p < .001$). Follow-up contrasts showed a greater quadratic trend for rhythmic complexity when combined with medium harmonic complexity than high harmonic complexity ($b(9840.02) = 0.201$, 95% CI [-0.005, 0.406]) suggesting a more prominent inverted U-shaped relationship. However, this difference did not reach statistical significance after correction for multiple comparisons. There was a smaller difference in the quadratic trend between medium and low complexity chords which was also not significant ($b(9840.02) = 0.129$, 95% CI [-0.076, 0.335]). Musicianship PCA scores showed a significant interaction with harmonic complexity ($\chi^2(2) = 12.26$, $p < .01$) with the follow-up contrast showing a more prominent quadratic trend as musicianship increased ($b(199) = -0.108$, 95% CI [-0.212, -0.004]). This was driven by lower ratings for low complexity chords as musicianship increased.

Dance PCA scores showed a significant main effect ($\chi^2(1) = 8.20$, $p < .01$). Those with greater interest in dancing showed higher *wanting to move* ratings overall ($b(195.77) = 0.154$, 95% CI [0.033, 0.275]). There were also significant interactions between rhythmic complexity and both dance PCA ($\chi^2(2) = 7.14$, $p < .05$) and groove PCA ($\chi^2(2) = 6.79$, $p < .05$) scores however, the follow-up contrasts were not significant .

Pleasure

For *pleasure* ratings, a likelihood ratio test revealed that there was a main effect of rhythmic complexity ($\chi^2(2) = 227.49$, $p < .001$). When harmonic complexity was added, the model failed to converge (Barr et al., 2013). Therefore, the main effect of harmonic complexity was added at the same step as the harmony by rhythm interaction, which together significantly improved model fit ($\chi^2(6) = 295.69$, $p < .001$). Follow-up contrasts showed that both rhythmic ($b(198) = -1.673$, 95% CI [-1.900, -1.446]) and harmonic complexity ($b(199) = -0.546$, 95% CI [-0.681, -0.411]) showed significant quadratic trends. As in the *wanting to move* results, rhythm showed a pronounced inverted U shape, whereas harmonic complexity did not, as low and medium complexity chords were rated similarly, with a drop in ratings for high complexity chords (see Figure 2.3B).

Follow-up contrasts for the rhythm by harmony interaction showed that the quadratic trend for rhythmic complexity was significantly more pronounced for medium than high complexity chords (*b*(9840.02) = 0.345, 95% CI [0.137, 0.553]). There was a smaller, non-significant difference in the trend between medium and low complexity chords (*b*(9840.02) = 0.138, 95% CI [-0.069, 0.347]). Therefore, the inverted U relationship between rhythm complexity and *pleasure* was more pronounced for medium complexity chords compared to high complexity chords. As in the *wanting to move* results, there was a significant interaction between musicianship PCA scores and harmonic complexity ($\chi^2(2) = 19.39$, $p < .001$) showing that as musicianship increased, so did the quadradic trend (*b*(199) = -0.014, 95% CI [-0.023, 0.039]).

Likelihood ratio tests showed significant interactions between rhythmic complexity and both musicianship PCA ($\chi^2(2) = 6.04$, $p < .05$) and Dance PCA scores ($\chi^2(2) = 7.25$, $p < .05$). Due to convergence issues, both Dance and Groove PCA scores were added together which significantly improved model fit ($\chi^2(2) = 7.06$, $p < .05$). However, follow-up contrasts based on these effects were not significant suggesting that these were weak effects or, in the case of the interactions, were not related specifically to the quadratic trend of rhythmic complexity.

Mediation Analysis

Based on our finding that harmonic complexity affected wanting to move ratings and given that harmonic complexity was only expected to affect wanting to move ratings indirectly, we used a mediation analysis to test the extent to which the effects of rhythmic and harmonic complexity on *wanting to move* were mediated by their effects on *pleasure* ratings.

For rhythmic complexity, adding *pleasure* ratings led to a significant drop in the effect of rhythmic complexity for the medium versus low contrast (*b* = 0.378, 95% CI [0.329, 0.430]). However, the direct effect of rhythm complexity for this contrast remained significant in the mediation model (*b*(1634.9) = 0.294, 95% CI [0.227, 0.361]). The identical pattern was seen in the difference in ratings between the medium and high complexity rhythms. Adding *pleasure* ratings significantly reduced the effect of this contrast (*b* = 0.777, 95% CI [0.718, 0.840]), while the direct effect remained significant (*b*(1729.54) = 0.821, 95% CI [0.741, 0.900]). Therefore, for both the medium versus low and medium versus high rhythm complexity contrasts, *pleasure* showed a significant mediation effect, while the direct effect remained significant.

For harmonic complexity, the difference in ratings between medium and low complexity chords was not significant in the initial model (*b*(1592) = 0.012, 95% CI [-0.075, 0.099]) or the mediation model (*b*(1591.03) = 0.019, 95% CI [-0.044, 0.081]). For the medium minus high harmonic complexity contrast, adding *pleasure* ratings led to a significant drop in the estimate (*b* = 0.371, 95% CI [0.323, 0.420]) with the direct effect going from significant in the first model (*b*(1592) = 0.339, 95% CI [0.252, 0.426]) to non-significant in the mediation model (*b*(1633.31) = -0.031, 95% CI [-0.098, 0.036]).

These results, summarized in Figure 2.4, show that *pleasure* ratings fully mediated the effect of harmonic complexity on *wanting to move* ratings. However, *pleasure* only partially mediated the effect of rhythmic complexity on *wanting to move* ratings such that a direct effect of rhythmic complexity remained.

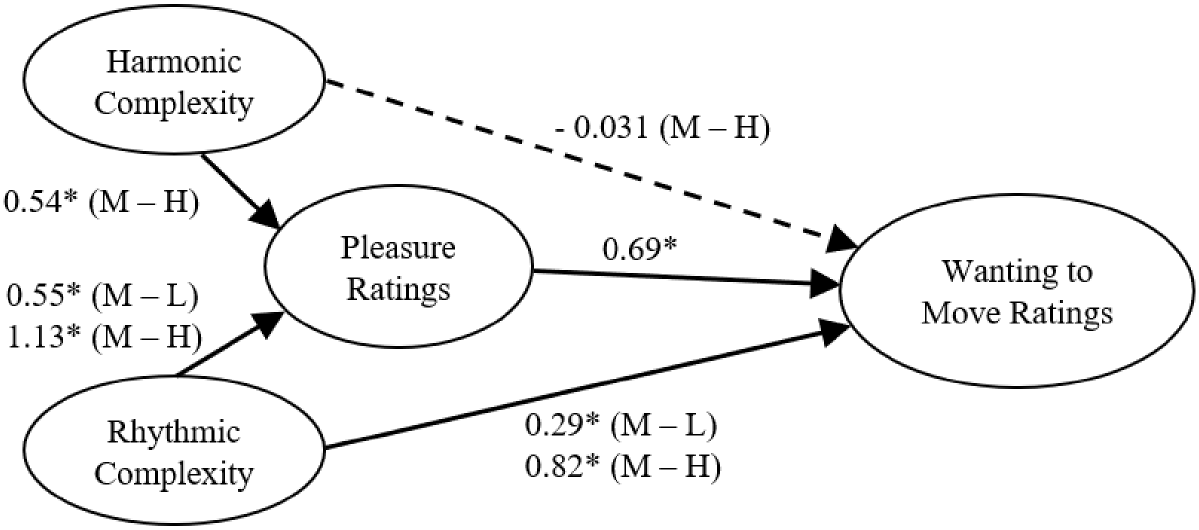

Figure 2.4. Path model. Path model based on the mediation analysis showing the relations between the predictors – rhythmic and harmonic complexity; the mediator – pleasure ratings; and the outcome variable – wanting to move ratings. Regression estimates for the effects of rhythmic and harmonic complexity on wanting to move ratings are from the mediation model that takes into account the effect of pleasure ratings on wanting to move ratings. The dashed line indicates that the direct effect of the medium – high harmonic complexity contrast was no longer significant once pleasure ratings were included in the model. L = Low, M = Medium, H = High; * *p* < .05.

Musician vs non-musicians

Dance and groove engagement PCA scores were not significantly different between musicians and non-musicians (*b*(106.31) = 0.324, 95% CI [-0.257, 0.906]: *b*(105.61) = - 0.099, 95% CI [-0.675, 0.477]) and were thus excluded from the analysis.

Wanting to move

There was no significant main effect of group ($\chi^2(1) = 0.0014$, $p > .05$), but there was a significant interaction between group and rhythmic complexity ($\chi^2(2) = 7.47$, $p < .05$) on *wanting to move* ratings. A follow-up contrast showed that the quadratic trend for rhythmic complexity was greater for musicians than non-musicians (*b*(109) = 0.770, 95% CI [0.213, 1.331]; see Figure 2.5A). Therefore, musicians showed a more prominent inverted U-shaped relationship between rhythmic complexity and *wanting to move* than non-musicians.

Pleasure

There was a significant effect of group ($\chi^2(1) = 4.52$, $p < .05$) showing that musicians had higher *pleasure* ratings overall compared to non-musicians (*b*(107) = 0.227, 95% CI [0.023, 0.431]; see Figure 2.5B).

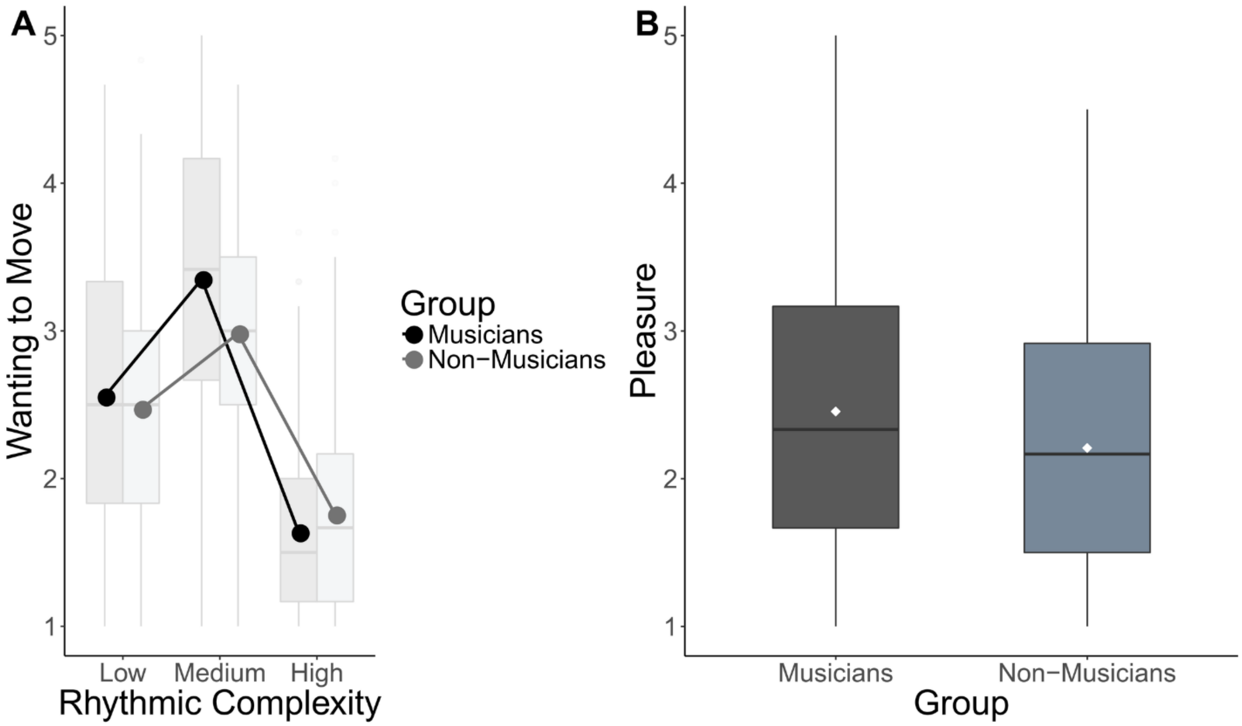

Figure 2.5. Ratings as a function of musical training. A) Box plot showing the interaction between group and rhythmic complexity. Lines represent means calculated from raw ratings. B) Box plot of the effect of musical training on pleasure ratings. Boxplots represent ratings aggregated over items within each level of complexity for visualization purposes. Center line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; points, outliers. Dots represent means calculated from the raw ratings.

Discussion

This study used ratings of *pleasure* and *wanting to move* to assess whether harmony and rhythm work together to affect the sensation of groove. Rhythm showed a strong inverted U-shaped relationship with both *pleasure* and *wanting to move* ratings while harmony did not. Consistent with our hypotheses, rhythm and harmony interacted such that medium complexity chords enhanced the inverted-U effect of rhythm complexity, particularly for *pleasure* ratings. Mediation analysis showed that rhythm directly affected both *wanting to move* and *pleasure* while the effect of harmony on *wanting to move* was driven by *pleasure*. Together these results suggest that rhythm plays a primary role in generating the sensation of groove, with harmony providing a modulatory role through its effect on *pleasure*.

In the group analysis musicians showed a stronger effect of rhythmic complexity on *wanting to move* ratings and higher *pleasure* ratings overall. Further, musicianship was associated with greater sensitivity to harmonic complexity. Together these results show that musical training strengthens the connection between syncopation and the desire to move and leads to greater reported pleasure. Finally, for all participants, interest in dance was associated with higher *wanting to move* ratings.

The inverted U effect of rhythm complexity on ratings may be interpreted in the context of predictive processes whereby listeners develop internal models, or musical expectancies, based on prior experience (Huron, 2006; London, 2012; Meyer, 1956). The strongest responses arise when listeners can make predictions, but expectancies are subtly violated, creating a balance between predictability and uncertainty (Salimpoor et al., 2015). In the current context, medium levels of syncopation achieve this balance by creating an optimal level of tension between a predictive model – the meter – and the current sensory input – the rhythm (Vuust et al., 2009, 2018; Vuust & Witek, 2014). According to this view, *pleasure* ratings show an inverted U-shaped relationship with rhythmic complexity because this tension between model and input engenders prediction errors, or violations of expectations, which are rewarding as they lead to further predictions and thus learning (Vuust & Witek, 2014). Similarly, the desire to move is highest for medium syncopation because this tension encourages the listener to reinforce and/or test their model by synchronizing their movements and fill in the gaps in the rhythmic surface created by syncopations (Patel & Iversen, 2014; Witek, 2017). It is also possible that familiarity may have contributed to the U-shaped relationship observed here because the medium complexity rhythms consist of son and rumba claves that are common to many types of popular music. However, the stimuli used here were entirely novel, and therefore would not be individually recognizable.

Harmonic complexity modulated the inverted U-shaped relationship between rhythmic complexity and pleasure and to a lesser degree, the desire to move. Combined with the results of the mediation analysis, this suggests that harmony primarily influences groove by modulating the affective component of music. Positive mood has been shown to broaden auditory attention in a musical context (Putkinen, Makkonen, & Eerola, 2017). By contributing to positive affect, pleasant chords may broaden attention to rhythmic aspects of the stimuli thus enhancing the effect of rhythmic complexity, while unpleasant chords may focus attention on harmony. The interaction between rhythm and harmony may also be accounted for by rhythmic entrainment. Theories of entrainment suggest that attentional focus predictively aligns with the onsets of a periodic stimulus thereby enhancing perceptual processing (Large & Jones, 1999), which is crucial for meter and beat perception (Large & Kolen, 1994; Large & Snyder, 2009). Subjective feelings of entrainment predict positive affective responses to music (Labbé & Grandjean, 2014) which is in line with the idea that entrainment at neural, cognitive, physiological, and social levels results in a positive affective response (Trost, Labbé, & Grandjean, 2017). Harmony, by modulating affect, may therefore alter the degree of entrainment to rhythmic stimuli thus affecting the precision of the temporal prediction processes that rely on this entrainment. Although this hypothesis has yet to be tested, promising evidence comes from a study showing that auditory-motor synchronization, which relies on precise temporal predictions, was reduced for dissonant compared to consonant tones (Komeilipoor et al., 2015). Intriguingly, motor regions in the brain are thought to be the origin of the neural processes underlying temporal predictions (Morillon & Baillet, 2017). Therefore, one possibility is that enhancement of entrainment by pleasant stimuli may also enhance motor activity leading to a greater desire to move, thus providing a possible mechanism for the interaction seen here.

Overall, harmonic complexity did not show an inverted U-shaped pattern because low and medium complexity chords were rated similarly, and only high complexity chords were rated lower. This may be because low and medium complexity chords are both relatively common in groove music while high complexity chords are uncommon, and thus were not only perceived as unpleasant but also violated expectations. In addition, rhythmic features appear to dominate for these stimuli, which may have reduced the attention paid to harmonic complexity. Another possibility is that the range of harmonic complexity was too limited to capture an inverted U-shaped relationship. The addition of lower complexity chords such as the octave, might lead to lower ratings than the low complexity chords used here. However, as musicianship increased, ratings for the low complexity chords decreased, making the relationship more U-shaped. This adds to evidence suggesting that musical training leads to greater sensitivity to harmonic complexity in the context of single chords (Arthurs et al., 2017; Pallesen et al., 2005). Although, this interaction effect occurred for both pleasure and wanting to move ratings, given the results of the mediation analysis, it is likely that this effect was driven by pleasure ratings. Therefore, those with higher levels of musical training and who practice more frequently may be more susceptible to the effects of harmony on groove.

In the group analysis, musicians showed a more prominent inverted U-shaped relationship between rhythm and wanting to move. Musical training may lead to an increased awareness and appreciation of syncopation and its effect on the desire to move. For example, musicians have been shown to use syncopation intentionally to convey groove (Madison & Sioros, 2014) and musical expertise has been positively linked with the effect of syncopation on groove ratings (Senn et al., 2018). Musical training may lead to more developed internal models that lead to stronger rhythmic expectations. This is supported by studies showing that musicians have greater error-related neural responses to rhythmic violations (Vuust et al., 2009) and enhanced neural entrainment to natural music (Doelling & Poeppel, 2015). Finally, a stronger connection between sound and movement may also account for the greater effect of rhythm on wanting to move in musicians (Alluri et al., 2017; Stupacher et al., 2013). Consistent with previous work (Witek et al., 2014), enjoyment and interest in dancing was also associated with higher wanting to move ratings overall. This further supports the link between motor processes and groove-based music in those with strong associations between music and movement.

The musician group also showed greater overall pleasure ratings compared to non-musicians. This is consistent with evidence that musicians demonstrate greater enjoyment of and increased neural reward activity for a range of musical stimuli (Alluri et al., 2015; Chapin, Jantzen, Kelso, Steinberg, & Large, 2010; Lahdelma & Eerola, 2014). Some studies have shown no effect of musicianship (Witek et al., 2014), or reduced groove ratings in musicians (Hurley et al., 2014). However, these studies defined musicianship less strictly, thus perhaps attenuating the effects of training-based internal models or expectancies on the sensation of groove.

There were differing results depending on whether musicianship was tested as a continuous regressor with the whole sample or in a group comparison with a subset of the sample. This was despite the fact that both analyses used hours of weekly practice and years formal training as determinants. We originally hypothesized that the effect of harmonic complexity on groove would be greater for musicians, however, we only saw this in the main analysis and not in the group comparison. There are several possible reasons for this. First, the continuous regressor approach is more likely to reveal small effects that are distributed in a population, which likely applies to the interaction between musicianship and harmonic complexity seen here. Secondly, the characteristics that define the musician group compared to others in the sample are many years of formal training, and active current practice. This suggests that the effect of musicianship on sensitivity to rhythmic complexity is less normally distributed or present only at the extremes. Together, these results highlight that the inverted U effect for both rhythm and harmony is sensitive to musicianship. Importantly, these results also provide further evidence that both the statistical approach used, and the way musicianship is defined, are important when testing the effects of musical training (Daly & Hall, 2018).

In conclusion, we have shown that rhythm and harmony interact to afford the sensation of groove. While rhythmic complexity is the primary driver, harmony both modulates the effect of rhythm and makes a unique contribution via its effect on pleasure. Syncopated rhythms create the optimal level of tension between expectancy and violation which increases pleasure and the desire to move. Harmony also affects pleasure, and by influencing emotional valence, may alter the attentional and temporal prediction processes that underlie rhythm perception. These predictive processes are encoded in auditory-motor networks and are influenced by experience, which may account for the increased sensitivity to groove in those with strong associations between movement and music, such as musicians and those who enjoy dancing. In addition, greater sensitivity to harmonic manipulations as musicianship increases may enhance the affective component of groove. Taken together, this work provides important new information about how the predictive and entrainment processes involved in rhythm perception interact with musical pleasure.

Data Availability

The ratings and background data that support these findings are available in the Open Science Framework with identifier link: https://doi.org/10.17605/osf.io/76zwy

Supporting Information

Table S2.1. Musical Background.

	Full sample (n = 201, 96 F)	Musicians (n = 58, 15 F)	Non-Musicians (n = 51, 18 F)
Age	34.74 (13.24)	35.59 (13.55)	37.29 (14.60)
Years of formal training	6.68 (7.44)	14.5 (5.31)	0.21 (0.49)
Years playing an instrument	15.96 (13.81)	25.12 (11.35)	4.25 (8.29)
Age of start	10.18 (5.48)	7.93 (3.45)	7.96(6.43)
Weekly Practice (Hours)	3.39 (5.86)	6.52 (8.51)	0 (0)

```
Weights   0 -5 -4 -5 -3 -5 -4 -5 -2 -5 -4 -5 -3 -5 -4 -5 -1 -5 -4 -5 -3 -5 -4 -5 -2 -5 -4 -5 -3 -5 -4 -5 ||
Count     1···e···&···a···2···e···&···a···3···e···&···a···4···e···&···a···||
Hi-hat    x·······x·······x·······x·······x·······x·······x·······x·······||
Low 1     x···············x·······x·······x···············x···············||
Low 2     x·······x·······x···············x···············x···············||
Low 3     x·······x·······x···············x·······················x·······||
Medium 1  x···········x···········x···············x···············x·······||
Medium 2  x···········x···············x···········x···············x·······||
Medium 3  x···············x·······x···········x···················x·······||
High 1    x·····x···············x···················x···············x·····||
High 3    x·········x·······x···············x···················x·········||
High 7    x···········x·····x···················x···············x·········||
```

Figure S2.1. **Schematic representation of rhythms used to create the stimuli**.

Weights represent weights used to calculate the syncopation index. Medium 1 = Son clave, Medium 2 = Rumba clave.
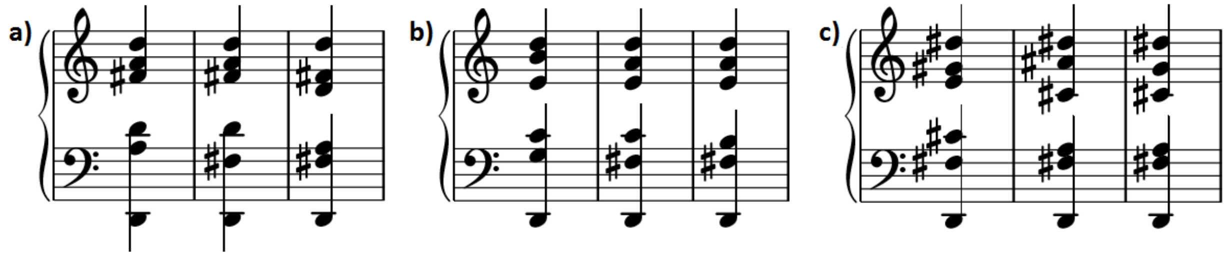
Figure S2.2. Chords used in the stimuli. a) low harmonic complexity, b) medium complexity chords, c) high complexity chords.

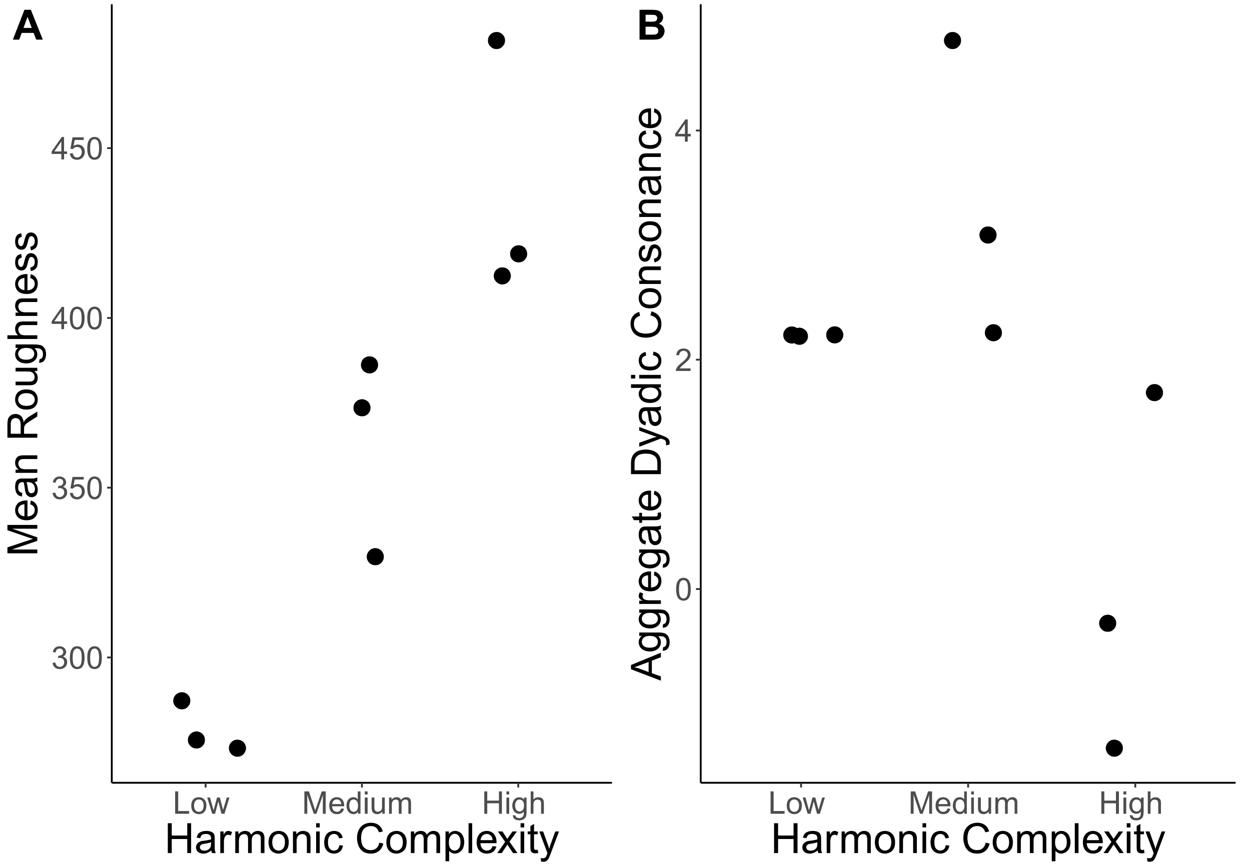

Figure S2.3. Indices for the chords used in the stimuli. A) Mean roughness, and B) Aggregate dyadic consonance.

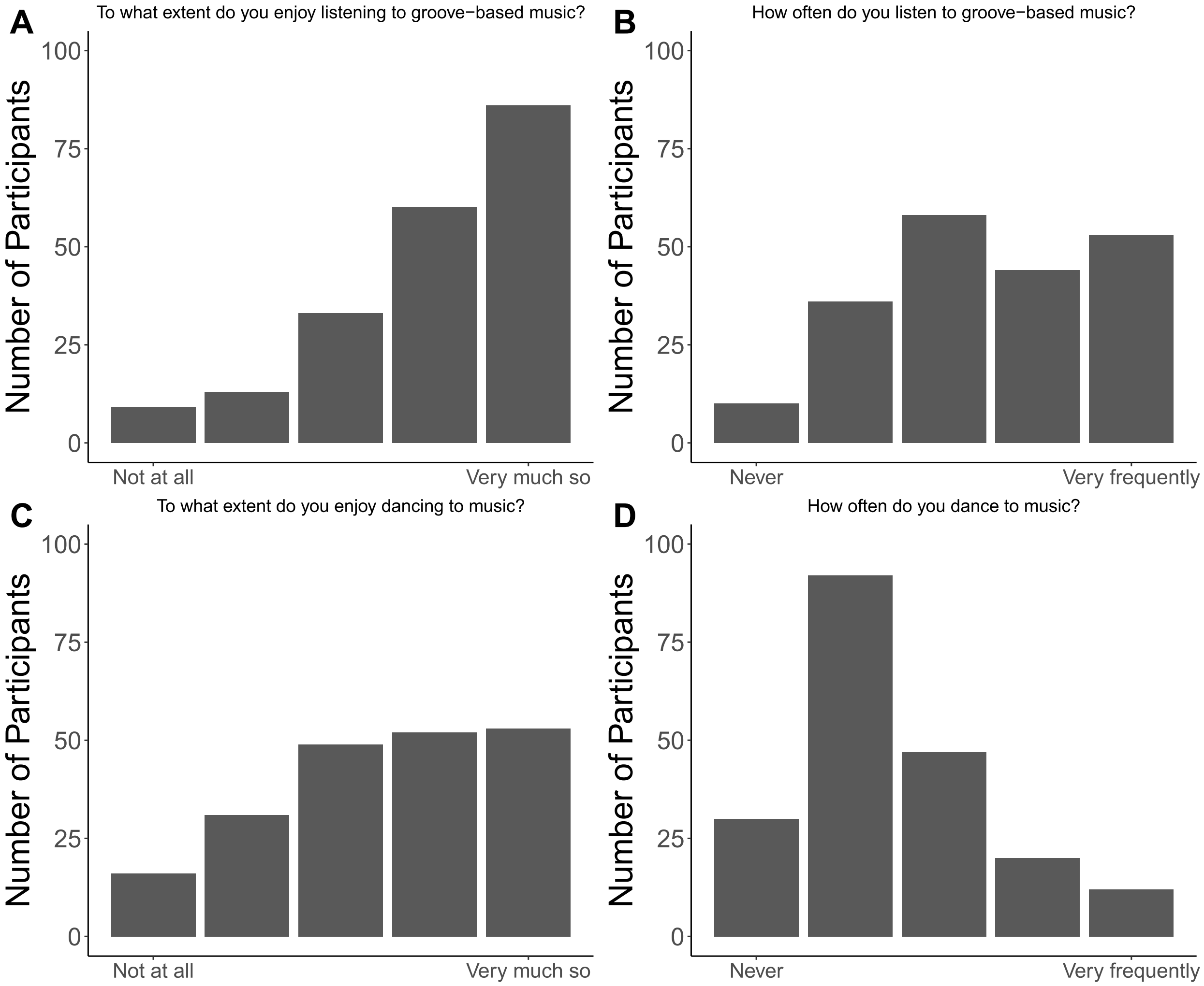

Figure S2.4. Counts for responses to groove and dance questions. A) Enjoyment of groove-based music, B) How often one listens to groove-based music, C) Enjoyment of dancing to music, and D) How often one dances to music.

CHAPTER THREE:
ARTICLE 2

Perceived motor synchrony with the beat is a stronger predictor of groove than measured synchrony

Matthews, T. E., Witek, M. A., Thibodeau, J. N. L., Vuust, P., & Penhune, V. B. (2021). Perceived motor synchrony with the beat is a stronger predictor of groove than measured synchrony**.** Under review at *Music Perception* (Article ID: MP-2021-0023).

Abstract

The sensation of groove is the pleasurable urge to move to music. Previous work has shown an inverted U-shaped relation between rhythmic complexity and groove, with medium levels of complexity leading to the highest groove ratings. Conversely, moving in synchrony with the beat of a rhythm becomes more difficult as the rhythms get more complex. This presents an interesting paradox. Why do we have an increased urge to synchronize our movements to medium compared to low complexity rhythms when it is more difficult to do so? One possibility is that perceived synchrony is more important in determining groove than actual (i.e., measured) synchrony. To test this hypothesis, we asked participants to rate the degree of groove of 50 drum breaks with varying rhythmic complexity then tap to the beat of the same drum breaks and rate how well they thought their taps synchronized with the beat. Supporting our hypothesis, perceived synchrony predicted groove ratings over and above measured synchrony and rhythm complexity. Additionally, the effect of perceived synchrony on groove was strongest for medium complexity rhythms. We interpret these results in the context of the beat bin hypothesis which suggests that the beat reflects a flexible window that expands and contracts depending on the rhythmic context. Applying this to beat synchronization suggests that medium complexity rhythms widen the beat bin thus increasing the number of movements that are perceived as synchronous and thus rewarded.

Introduction

Groove is the pleasurable urge to move to music (Janata et al., 2012; Witek et al., 2014). It is the impulse to bob our heads, tap our feet, or get up and dance. This pleasurable urge is largely driven by rhythmic complexity, with medium complexity rhythms creating a stronger sensation of groove than rhythms that are very simple or very complex (Matthews, Witek, Heggli, Penhune, & Vuust, 2019; Sioros, Mirron, Davies, Gouyon, & Madison, 2014; Witek et al., 2014). Conversely, moving in synchrony with the beat of a rhythm becomes more difficult as the rhythms get more complex (Fitch & Rosenfeld, 2007). This presents an interesting paradox. Why do we have an increased urge to synchronize our movements to medium compared to low complexity rhythms when it is in fact more difficult to do so? One possibility is that perceived synchrony is more important in determining groove than actual (i.e., measured) synchrony. Previous work has shown that tapping synchrony is greater for rhythms rated high in groove and that perceived difficulty in synchronizing is a strong predictor of groove (Janata et al., 2012). However, the relative impact of perceived and measured synchrony on groove has yet to be directly tested.

The urge to move to music, as well as our ability to do so, depends in large part on the beat. The beat is the perceived isochronous underlying pulse of a rhythm with which people typically synchronize their movements. The beat acts as a rhythmic anchor in that the timing of all other musical events are heard in relation to it, allowing us to form expectations or predictions about what will happen next. Therefore, the stronger the perceived beat, the more regular or predictable the rhythm. Metre is the pattern of strong and weak beats within a rhythm, for example, a waltz consists of a strong beat followed by two weak beats. Beat and metre can be perceived in rhythms that include syncopations – when no note falls on a strong beat but instead falls on a preceding, metrically weaker beat (Longuet-Higgins & Lee, 1984) – indicating that these structures reflect a combination of bottom-up sensory processes and top-down internal processes (Desain & Honing, 1999). Previous work has used the number of syncopations as a measure of rhythm complexity (Matthews et al., 2019; Matthews, Witek, Lund, Vuust, & Penhune, 2020; Sioros, Mirron, et al., 2014; Witek et al., 2014). For rhythms with a low or medium number of syncopations, the beat (and metre) can still be perceived and beat-based predictions can still be made, however, with less confidence or certainty as the number of syncopations increases. Beyond a moderate number of syncopations, the beat and metre become obscured, the sense of regularity is lost, it becomes difficult to predict future onsets, and therefore difficult or impossible to synchronize movements to the rhythm. Thus, the degree of syncopation can determine both the predictability (i.e., the ability to make predictions) and the certainty (i.e., the confidence in these predictions) of a rhythmic pattern or context.

The above description frames the beat as a discrete event occurring at a fixed timepoint within each rhythmic cycle, as is represented by a metronome. A different account is provided by the beat bin hypothesis. According to this view, individual beats are perceived, not as a single point in time, but rather as a temporal window that expands or contracts depending on the rhythmic context (Danielsen, 2010, 2019). For example, onsets falling consistently slightly early or late relative to the metronomic beat, widen the beat bin such that these onsets are still perceived as on the beat despite not being perfectly aligned. Although the beat bin hypothesis focuses on the influence of small perturbations in the form of microtiming deviations (Danielsen, 2010, 2019), the width of the beat bin may be affected by the rhythmic context more generally. For example, syncopations, particularly those that fall on a strong beat point, may create uncertainty about the timing of the next beat, thus widening the beat bin. There is evidence that a wider beat bin affects movement synchrony (Danielsen, Haugen, & Jensenius, 2015). Therefore, the beat bin may be analogous to a tolerance zone (Müller, Aschersleben, Koch, Freund, & Prinz, 1999): taps within the zone are perceived as synchronous whereas taps outside it are not, and will thus lead to adjustment of tap timing. In this way, the beat bin hypothesis provides a mechanism for the expansion and contraction of the beat bin/tolerance zone based on the rhythmic context. Thus, the width of the beat bin may not only determine which onsets are perceived as on the beat, but also whether movements are perceived as synchronized with the beat.

Moving to the beat of music, referred to here as beat synchronization allows for an explicit comparison between the internal representation of the beat, incoming auditory information and the sensory consequences of movement. Therefore, beat synchronization can be thought of as a way of testing temporal predictions (Patel & Iversen, 2014), with synchronous movements reflecting prediction confirmations. In addition, synchronization accuracy may reflect the certainty of beat-based predictions. For example, taps are more accurately aligned with the first beat in a phrase compared to other beats (Patel et al., 2005). That is, temporal predictions regarding the first beat are more certain as it represents the strongest beat within the metrical hierarchy (Fitch & Rosenfeld, 2007), and this increased certainty is reflected in higher tapping accuracy. Prediction confirmations provide positive feedback that the internal model of the beat or metre is correct (Huron, 2006; Zald & Zatorre, 2011). This positive feedback can therefore be thought of as a reward signal and thus may be one of the motivating factors underlying the urge to move. When tapping to an auditory pacing signal, participants consistently to the beat, a phenomenon call the negative mean asynchrony (Aschersleben, 2002). However, participants are unaware of this asynchrony, reporting that they tapped accurately, and thus overestimate their tapping synchrony (Franěk, Radil, Indra, & Lánsky, 1987). This suggests a discrepancy between perceived and measured synchrony, which can lead to greater positive feedback despite no change in, or even a reduction in, tapping accuracy. This discrepancy may be increased as the rhythmic context leads to a wider beat bin. That is, with a wider beat bin, more taps would be perceived as synchronous leading to more prediction confirmations and greater reward, even if synchrony measured in relation to the metronomic beat has not increased. In this way, as perceived synchrony increases, the pleasurable aspect of groove may increase, regardless of whether there is an increase in measured synchrony. This suggests that perceived synchrony may contribute to groove independently of measured synchrony.

The beat bin hypothesis corresponds well to both dynamic attending and predictive coding accounts of rhythm and beat perception because they emphasize temporal predictions and the precision or certainty with which these predictions are made. According to dynamic attending theory, rhythm perception is supported by endogenous attentional oscillations which are entrained by rhythmic stimuli such that windows of attentional focus are temporally aligned with the beat (Large & Jones, 1999; Large & Kolen, 1994). These windows of attentional focus or ‘expectancy regions’ expand or contract depending on the certainty of the rhythmic context (Large and Jones, 1999, pg. 130). A similar account is provided by the predictive coding framework in which beat and metre emerge from the interaction between bottom-up sensory regularity and top-down internal models. A mismatch between the internal model (i.e., the beat or metre) and the sensory input results in a prediction error, which depending on the certainty of the prediction, leads to an update in the model. The certainty (or precision) of beat-based temporal predictions is formalized as the variance of a probability distribution around the point estimate, with increased variance (i.e., width of the distribution or extension in time) as certainty decreases (Koelsch et al., 2019; Vuust et al., 2018). Therefore, under both frameworks, the beat bin can be conceptualized as a probability distribution, with a point estimate (i.e., the mean) reflecting the predicted beat and the spread of the distribution reflecting certainty of that prediction.

According to predictive coding, medium degrees of syncopation elicit the highest groove ratings because they trigger a moderate number of prediction errors resulting from moderately certain beat-based predictions (Koelsch et al., 2019; Vuust & Witek, 2014; Vuust et al., 2018). Within this framework, the certainty of a prediction determines the weight of the resulting prediction error, that is, the degree to which it leads to improvement of the internal model, and thus its gain as a learning signal (Friston, 2019). The higher the certainty of the prediction, the greater the weight of the prediction error. Therefore, medium degrees of syncopation create moderately certain predictions, which when violated, elicit prediction errors that drive the listener to reaffirm and test current predictions via movement. Extending this model to beat synchronization, when we move to a syncopated rhythm, a prediction confirmation is assigned more weight as certainty decreases. In this way, the reward derived from perceiving movements as synchronous may be weighted by prediction certainty. Applying the beat bin hypothesis to beat synchronization suggests that the number of movements perceived as synchronous will depend on the rhythmic context, in this case, the degree of syncopation. Therefore, combining the predictive coding and beat bin accounts leads to the hypothesis that the degree of syncopation will affect both the number and weight of movements perceived as prediction confirmations, and thus impact the amount of rewarding feedback. Accordingly, the role of perceived synchrony in determining groove is hypothesized to depend on the degree of syncopation. Again, this effect may occur regardless, or in spite, of a change in measured synchrony.

Musical expertise is likely to affect the degree to which perceived and measured synchrony contribute to the sensation of groove. Musicians and non-musicians have been shown to differ in their experience of groove, with musicians experiencing a greater urge to move for medium complexity rhythms (Matthews et al., 2019; Matthews et al., 2020). This suggests greater sensitivity to rhythmic complexity in musicians, possibly due to more developed beat-based predictive models leading to more certain predictions and thus more strongly weighted prediction errors. Musicians are also better at synchronizing their taps to rhythms (Matthews et al., 2016; Repp, 2010; Repp & Doggett, 2007) and show smaller temporal windows for integrating self-generated actions with the resulting sounds (van Vugt & Tillmann, 2014). Therefore, musicians’ perception of synchrony may be less susceptible to the uncertainty associated with syncopations and may be more aligned with measured synchrony, thus reducing the impact of perceived synchrony on groove.

In order to assess the contribution of perceived and measured synchrony to groove, we asked musicians and non-musicians to listen and then to tap in synchrony to a set of synthesized drum sequences that varied in rhythmic complexity based on the number of syncopations. First, they passively listened to the sequence and rated the degree of perceived groove. Then they tapped to the beat of each sequence and immediately afterward rated how well they thought their taps were synchronized to the beat. The relation between groove ratings, tap ratings, measures of tapping performance (accuracy and precision), and number of syncopations were compared to test whether 1) the perception of synchrony (tap ratings) predicts groove over and above measured tapping performance and the number of syncopations, and 2) the effect of perceived synchrony on groove ratings is greatest for moderately syncopated rhythms. Tapping performance was also expected to depend on syncopation and musical training. Based on previous results (Matthews et al., 2019; 2020), musicians were expected to show a stronger relation between syncopation and groove. Additional analyses examined whether the effect of perceived synchrony depends on musical training and tested the relative effects of tapping precision and accuracy on perceived synchrony.

Methods

Participants

Nineteen musicians (nine female) and twenty-four non-musicians were recruited to participate in this study. Musicians had an average age of 25.16 (SD = 3.86), had an average of 13.58 years of formal music training (SD = 3.59) and practiced on average 12.63 hours a week (SD = 9.67) at the time of testing. Data of seven non-musicians were excluded from analysis due to not having enough analyzable trials (see preprocessing section below). The final sample consisted 17 non-musicians (11 female) with an average of one year of formal music training (SD = 1.03) and an average age of 24.13 (SD = 6.04).

The protocol was approved by the Concordia University Human Research Ethics committee. Participants provided written informed consent in accordance with the Declaration of Helsinki and were compensated for their time.

Stimuli

The stimuli were created for a previous study (Witek et al., 2014) and consisted of 50 drum sequences generated using synthesized drum sounds (bass drum, snare drum, and hihat) in GarageBand 5.1 (Apple, Inc.). Thirty-four of these were derived from actual songs, 14 were experimenter-generated and two were templates from GarageBand. Each sequence consisted of a single pattern repeated four times in 4/4 time, had an inter-beat interval of 500 ms, and lasted 16 seconds. In all sequences, the hihat maintained an isochronous pattern at twice the beat rate (inter-onset interval 250 ms). Therefore, the unique sequences were generated by the snare and bass drum patterns.

Rhythmic complexity was quantified using a modified version of the syncopation index (Fitch & Rosenfeld, 2007; Longuet-Higgins and Lee, 1984; Witek et al., 2014) in which the degree of syncopation depends on both the metric position and the instrument (snare or bass drum; see Witek et al., 2014 for a detailed description). Each syncopation in a sequence is weighted based on its metric position and whether it involves a snare or bass drum. These weights are then summed within a sequence providing a syncopation index ranging from 1 (low syncopation) to 81 (high syncopation).

Procedure

Upon arrival participants filled out a musical experience questionnaire. Before starting the experiment, participants were given the definition of groove as the pleasurable desire to move to music. Participants then listened to all fifty drum sequences through headphones (type) in a randomized order and rated each sequence on the degree it elicited the sensation of groove on a scale from one to five. Participants then listened to the same drum sequences, in a different randomized order, and were asked to tap in synchrony with the beat. Participants were given a four-beat count-in at the start of each sequence. At the end of each sequence participants rated how well they felt they were able to synchronize their taps to the beat of the sequence on a scale from one to five.

Measurement Apparatus

Taps were measured using a force-sensitive resistor[1] (FSR) covered by a thin layer of foam, to dampen the tapping sound. The outgoing audio stimulus was re-captured alongside the incoming force measurement using an audio interface[2] controlled by the experiment software at a sampling rate of 44.1kHz. At this sampling rate, and with the response time of the FSR rated at less than three microseconds, we concluded that any errors in the time-alignment between the recorded stimuli and tap measurements were negligible. In the recorded force measurements, we defined a tap as the maximum force produced by the impact of the participant's finger on the sensor. Beats were extracted from the stimulus audio signal using a similar process, using the amplitude envelope of the stimulus signal to determine drum onsets.

Preprocessing of tapping data

Data from trials were removed if participants tapped twice per beat, tapped too fast (more than 25% of ITIs are less than .3 s), or did not have enough taps in the trial for analysis (less than eight of an expected 32 taps). Data from participants with more than five excluded trials (%10) based on the above criteria were removed from analysis. This led to removal of data of seven non-musicians. In addition, 19 trials (1.06% of all trials) were removed across seven non-musician participants for the same reasons.

Indices of tapping precision and accuracy were calculated using circular statistics (Fisher, 1993) by calculating a vector on the unit circle for each tapping trial. The mean resultant length of this vector (MRL) is determined by the spread of taps around the unit circle and thus corresponds to a measure of tapping precision. MRL varies from zero to one with values closer to one indicating low spread and thus high tapping precision. The angle of the vector is calculated relative to the beat point with which participants are synchronizing and is therefore a measure of tapping accuracy. The angle is measured in radians and thus ranges from zero to $2*\pi$. Subsequent analysis on the effect of tapping performance on tap ratings and groove ratings used the absolute value of the angle subtracted from π. This measure varies from zero to π with values closer to π indicating more accurate taps.

---

[1] Model 406 Square. *Interlink Electronics FSR Integration Guide.* Accessed 2021-02-15: https://cdn.sparkfun.com/assets/4/d/0/f/7/DS-9375-Force_Sensitive_Resistor_0.5in.pdf

[2] Lexicon Omega. Accessed 2021-02-15: https://lexiconpro.com/en/products/omega

Statistical Analysis

All analyses were carried out using linear mixed effects regression in R (version 4.0.3; R core team, 2020). This approach was used as it allows for analysis of trial-level data while accounting for within-subject grouping of this data. Therefore, this approach accounts for inter-individual differences in rating style and responses to the predictor variables. All analyses followed the same three steps; 1) determination of the random structure, 2) hierarchical regression analyses testing which predictor variables lead to significant increases in model fit using the likelihood ratio test 3) final models were estimated using restricted maximum likelihood and included the significant predictors from the hierarchical regression analyses to test parameter estimates against zero. For all analyses, Steps 1 and 2 were carried out using the lme4 package (Bates, Mächler, Bolker, & Walker, 2014). The optimal random effects structure that can be supported by the data were determined by iteratively reducing the maximal random structure (Bates, Kliegl, Vasishth, & Baayen, 2015; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017). Several final models showed non-normal and heteroscedastic residuals and were therefore re-estimated using robust linear mixed effects regression using the robustlmm package (Koller, 2016). These models are identical to the standard linear mixed effects models however, they automatically detect, and down-weight data points contaminated by the near-ceiling effects. The degree to which these data points are down-weighted can be tuned to prioritize robustness or efficiency of the parameter estimates. Results of models tuned for higher robustness are reported here. Results of the models tuned for maximum efficiency are reported in the supplementary material.

For final models estimated using the standard approach, bootstrapped confidence intervals around parameter estimates were calculated with 5000 iterations. For these models, R^2 values for the models and partial eta-squared (η_p^2) values and associated confidence intervals were calculated using the r2glmm package (Jaeger, 2017) using the standardized generalized variance approach. For models estimated using the robust approach, Wald confidence intervals were calculated for each parameter estimate. R^2 and η_p^2 could not be calculated for the robust models.

Previous work indicates that syncopation shows an inverted U-shaped relation with ratings of groove (Matthews et al., 2019; Witek et al., 2014) therefore, orthogonal polynomial (both linear and quadradic) effects of syncopation were tested in all models. Only linear effects were tested for all other variables.

Effects of syncopation and group on tapping performance

To test the effect of syncopation, group, and their interaction on tapping performance, we conducted two hierarchical regression analyses, one for tapping precision (MRL) and one for tapping accuracy (absolute angle). Diagnostic plots of the final regression models showed non-normal and heteroskedastic residuals, likely because musicians exhibited a ceiling in performance, with mean absolute angles close to π and MRLs close to one (see Figure 3.2). Therefore, results of the models fitted with the robust approach and tuned for higher robustness are reported here.

Effects of tapping performance, syncopation, and group on tap ratings

To test the effect of tapping performance, syncopation, and group, as well as their interactions, on perceived synchrony, we used hierarchical regression analysis. Diagnostic plots of the final model showed non-normal and heteroskedastic residuals due to the fact that musicians frequently rated their tapping performance maximally (i.e., with a rating of five; see Figure 3.3A). Data with many points at the upper (or lower) limit of a scale are referred to as censored. Therefore, in addition to estimating a robust model, this data was analyzed using the lme4cens package which accounts for this censoring (Kuhn & Roeder, 2018). This approach does not allow for random slopes, therefore, only by-participant random intercepts were included in this model. Results of the final model tuned for higher robustness are reported here. Results of the final models tuned for higher efficiency and using lme4cens are reported in the supplemental material. Finally, because musicians' tap ratings and tap performance were near ceiling, confirmatory analyses were implemented on the non-musicians' data only.

Effects of tap ratings, tapping performance, syncopation and group on groove ratings

Hierarchical regression was used to test the effects of tap ratings, tapping performance, syncopation, and group, as well as the relevant interactions, on groove rating. In order to assess whether tap ratings accounted for variance in groove ratings over and above that accounted for by tapping performance, variables were entered in the model in the following order: group, syncopation, tapping accuracy, tapping precision, then tap ratings, then the relevant interactions following the same order. In the final model, standardized (z-scored) versions of the significant variables from the hierarchical analysis were used to allow for comparison between the effects of tap ratings and tapping performance on groove ratings. The standardized variables also served to reduce multicollinearity between the main effects and interactions involving the polynomial terms.

Diagnostic plots of the final model showed no violations of assumptions, therefore only the results from standard linear mixed effect models are reported. However, because musicians' tap ratings and tap performance were near ceiling and may therefore have affected the relationship to groove ratings, confirmatory analyses were implemented on the non-musicians' data only.

Results

Effects of syncopation and group on tapping performance

Figure 3.1 shows raw tapping data from musicians and non-musicians, showing that both groups clustered their taps just before the beat showing the expected negative mean asynchrony (Ascherleben, 2002). Figures 3.1 and 3.2 also indicate that musicians were precise and more accurate in their tapping than non-musicians, with more taps close to the beat.

Hierarchical regression was used to test the effects of group and syncopation, and the interaction between the two, on tapping accuracy (absolute angle) and precision (MRL). The analysis on tapping accuracy showed that the main effects of group ($\chi^2(1) = 12.33$, $p < .001$) as well as the linear ($\chi^2(1) = 27.67$, $p < .001$) and quadratic ($\chi^2(1) = 25.42$, $p < .001$) effects of syncopation, improved model fit. The interaction between group and the linear effect of syncopation improved model fit ($\chi^2(1) = 6.23$, $p = .013$), but the interaction between group and the quadratic effect did not ($\chi^2(1) = 1.02$, $p = .314$). The final model tuned for higher robustness showed a significant negative quadratic effect of syncopation (b = -1.11, 95% CI[-1.474, -0.752]). This effect can be seen in Figure 3.2A, where both groups show relatively similar degrees of tapping accuracy for low and medium complexity, with a drop-off in accuracy for high complexity rhythms. A steeper drop-off for non-musicians resulted in a significant interaction between groove and the linear effect of syncopation (b = 2.338, 95% CI[0.837, 3.840]). A second model with the same predictors but tuned to produce higher efficiency estimates produced similar results (see supplementary materials).

The analyses on tapping precision showed similar results. Hierarchical regression showed that main effects of group significantly improved model fit ($\chi^2(1) = 13.63$, $p < .001$) as did linear ($\chi^2(1) = 33.13$, $p < .001$) and quadratic effects ($\chi^2(1) = 26.42$, $p < .001$) of syncopation. The interaction between group and the linear effect of syncopation improved model fit ($\chi^2(1) = 8.64$, $p = .003$), but the interaction between group and the quadratic effect did not ($\chi^2(1) = 1.53$, $p = .217$). The final model, tuned for higher robustness, showed a significant negative quadratic effect of syncopation (*b* = -1.236, 95% CI[-1.724, -0.759]). As with tapping accuracy, both groups showed a similar degree of tapping precision for low and medium complexity rhythms and a drop-off for high complexity rhythms (see Figure 3.2B). Non-musicians showed a steeper drop-off in tapping precision compared to musicians, resulting in a significant group by syncopation (linear) interaction (*b* = 2.896, 95% CI[1.204, 4.587]). A second model with the same predictors but tuned to produce higher efficiency estimates produced similar results (see supplementary materials).

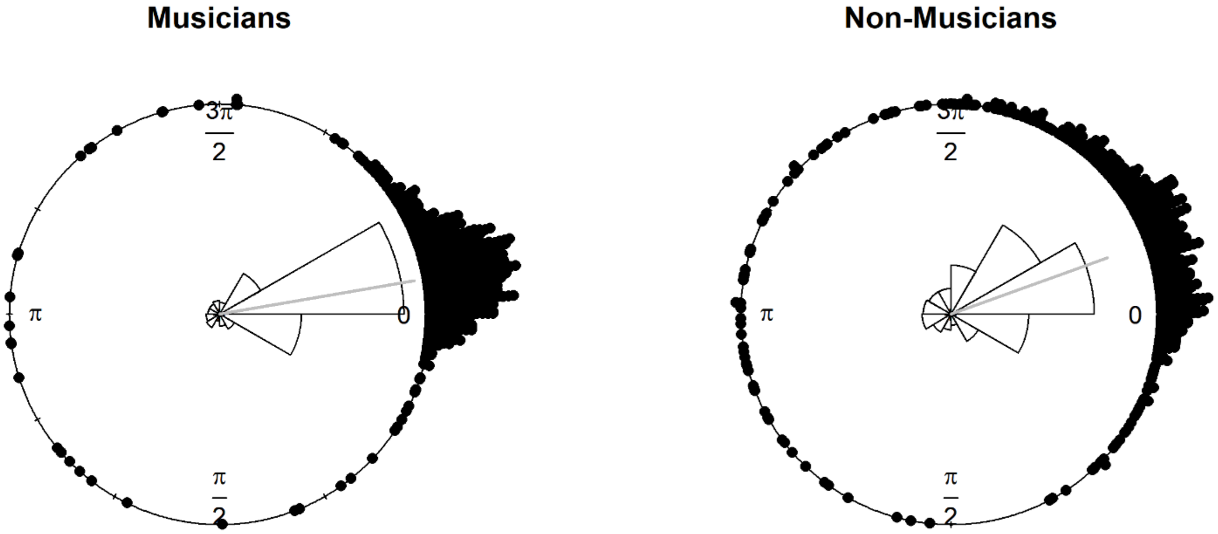

Figure 3.1. Circular plots of tapping data. A circular plot for each group showing every tap plotted on the circumference of the unit circle. The rose diagram in the centre shows the relative number of taps falling in each of 12 bins. The beat is represented by zero and taps counterclockwise to zero were early relative to the beat and taps clockwise to zero were late relative to the beat. Gray lines represent the mean vector, with the angle representing mean group accuracy and the length representing mean group precision.

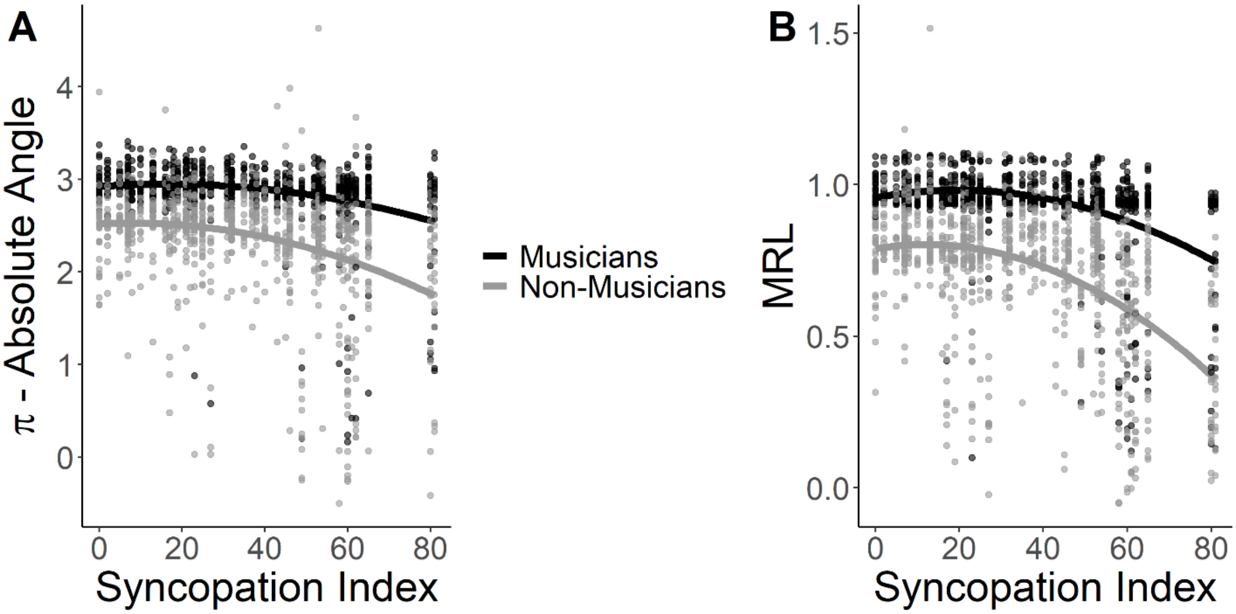

Figure 3.2. Relation between syncopation, A) tapping accuracy, and B) tapping precision. Grey lines represent the second polynomial function for each participant. The lines represent estimated effects from the final model. Points represent partial residuals which are the observed values while accounting for the other predictors.

Effects of tapping performance, syncopation, and group on tap ratings

Hierarchical regression was used to test the effects of tapping performance, syncopation and group, as well as the interactions between these variables, on tap ratings. This analysis showed that model fit was significantly improved by main effects of group ($\chi^2(1) = 21.19$, $p < .001$), tapping precision ($\chi^2(1) = 32.17$, $p < .001$), and both linear ($\chi^2(1) = 20.11$, $p < .001$) and quadratic effects ($\chi^2(1) = 23.62$, $p < .001$) of syncopation index. The main effect of tapping accuracy did not improve model fit ($\chi^2(1) = 2.55$, $p = .110$), however, the interaction between group and tapping accuracy did ($\chi^2(1) = 10.75$, $p = .001$). In addition, the interaction between tapping precision and the linear effect of syncopation ($\chi^2(1) = 11.04$, $p < .001$), and the interaction between group and the linear effect of syncopation ($\chi^2(1) = 12.38$, $p < .001$) improved model fit. Finally, a three-way interaction between group, tapping precision and the linear effect of syncopation improved model fit ($\chi^2(1) = 4.17$, $p = .041$).

In the final model, tuned for higher robustness, syncopation showed a negative quadratic effect in both groups ($\beta = -3.544$, 95% CI[-4.689, -2.400]), while non-musicians showed a steeper drop off leading to significant group by syncopation (linear) interaction ($\beta = 3.197$, 95%

CI[1.000, 5.394]; see Figure 3.3A). As can be seen in Figure 3.3C both groups showed a strong positive effect of tapping precision on tap ratings, however, this effect was stronger in musicians leading to a significant group by tapping precision interaction ($\beta = 0.089$, 95% CI[0.014, 0.165]). Unexpectedly, a significant group by tapping accuracy interaction indicated that musicians showed a negative effect of tapping accuracy on tap ratings while non-musicians showed a small positive effect ($\beta = -1.08$, 95% CI[-0.156, -0.060]). However, this result appears to be driven by the relative lack of variability in the musicians' tapping accuracy due to their near-ceiling performance (see Figure 3.3B).

Analysis of the non-Musicians' data only were generally consistent with the results of the analysis on the full sample (see supplementary material). The only difference was that the non-musicians analysis showed an interaction between tapping precision and both linear ($\beta = -3.317$, 95% CI[-5.550, -1.063]) and quadratic ($\beta = -1.548$, 95% CI[-3.083, -0.025]) effects of syncopation, suggesting that the effect of tapping precision on tap ratings is weaker for rhythms with higher degrees of syncopation. This effect was also shown in the analysis that modeled the censored nature of both group's data (see supplementary material).

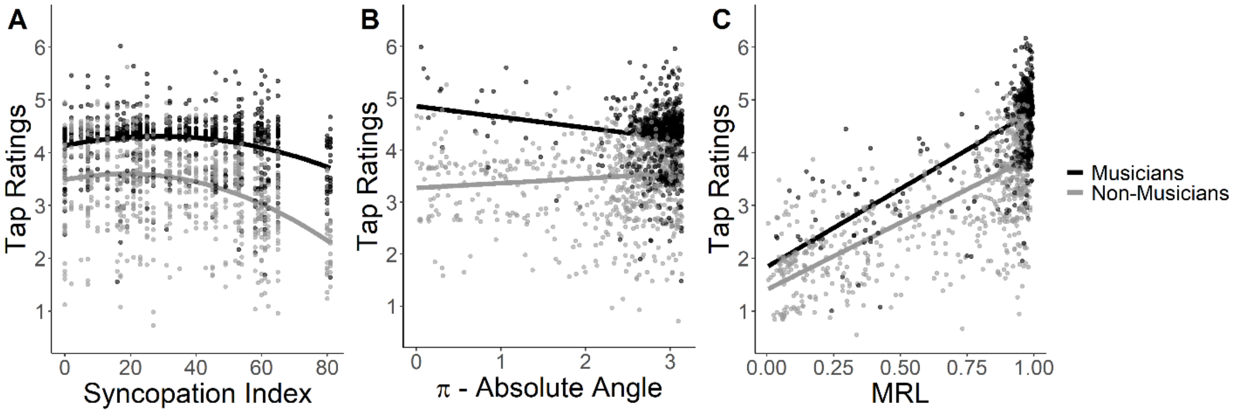

Figure 3.3. Relation between tap ratings, A) syncopation index, B) tapping accuracy, and C) tapping precision, for musicians and non-musicians. The lines represent estimated effects from the final model. The points represent partial residuals which are the observed values while accounting for the other predictors.

Effects of tap ratings, tapping performance, syncopation and group on groove ratings

Hierarchical regression was used to test the effects of tap ratings, tapping performance, syncopation and group, as well the relevant interactions on groove ratings. This analysis showed that group ($\chi^2(1) = 12.03$, $p < .001$) improved model fit and as did both the linear ($\chi^2(1) = 11.51$, $p < .001$) and quadratic effect ($\chi^2(1) = 132.03$, $p < .001$) of syncopation. In addition, the interaction between group and the quadratic effect of syncopation improved model fit ($\chi^2(1) = 5.23$, $p = .022$), but the interaction with the linear effect of syncopation did not ($\chi^2(1) = 1.51$, $p = .220$). This analysis also showed main effects of tapping precision ($\chi^2(1) = 31.85$, $p < .001$), but not tapping accuracy ($\chi^2(1) = 3.43$, $p = .064$). Crucially, tap ratings improved model fit over and above syncopation and tap performance measures ($\chi^2(1) = 100.38$, $p < .001$). This suggests that tap ratings account for additional variance in groove ratings that was not accounted for by the other predictors. The interaction between tap ratings and the quadratic effect of syncopation led to significantly improved model fit ($\chi^2(1) = 9.38$, $p = .002$) but the interaction with the linear effect of syncopation did not ($\chi^2(1) = 0.81$, $p = .368$). Finally, the interaction between group and tap ratings did not improve model fit ($\chi^2(1) = 2.38$, $p = .123$) nor did the three-way interactions with group, tap ratings, and the linear ($\chi^2(1) = 0.41$, $p = .520$) and quadratic ($\chi^2(1) = 0.48$, $p = .487$) effects of syncopation.

Results of the final model estimated using standard linear mixed effects with standardized predictor and outcome variables are shown in Table 3.1. Although tapping accuracy did not improve model fit in the hierarchical regression, it was included in the final model for comparison. The model accounted for 26.6% of the variability in groove ratings (95% CI[0.236, 0.301)]. As can be seen in Figure 3.4, both groups showed a significant negative quadratic effect of syncopation on groove. Although the interaction between the quadratic effect of syncopation and group improved model fit, this effect was not significant in the final model, suggesting that both groups showed a similar inverted U relation between syncopation and groove. Comparing standardized regression coefficients (β) s in Table 3.1 shows that tap ratings was a stronger predictor of groove ratings compared to both measures of tapping performance, indicating that perceived synchrony has a stronger influence on the sensation of groove than measured synchrony. Due to the scaling involved in making the linear and quadratic polynomials of syncopation orthogonal to each other, the standardized regression coefficients for these variables cannot be compared to those of the other variables. However, comparing the partial eta squared values (η_p^2) shows that tap ratings were strongest contributor to the model followed by the quadratic effect of syncopation. Finally, Figure 3.5 shows that the interaction between tap ratings and the quadratic effect of syncopation is due to a stronger effect of tap ratings on groove ratings for rhythms with medium levels of syncopation compared to those with low or high levels of syncopation.

Table 3.1

Standardized Parameter Estimates from Regression Model Predicting Groove Ratings

Effect	*β*	95% CI	η_p^2	95% CI
Group	-0.071	-0.197, 0.047	0.004	0.000, 0.013
Syncopation Index (Linear)	-5.445	-7.891, -2.985	0.016	0.007, 0.030
Syncopation Index (Quadratic)	-9.671	-11.448, -7.880	0.052	0.034, 0.073
Tap Ratings	0.327	0.267, 0.389	0.071	0.050, 0.096
Absolute Angle	0.003	-0.056, 0.063	0.000	0.000, 0.003
MRL	0.167	0.090, 0.244	0.015	0.006, 0.027
Group:Syncopation Index (Linear)	2.022	-0.542, 4.499	0.002	0.000, 0.009
Group:Syncopation Index (Quadratic)	-0.270	-2.053, 1.554	0.000	0.000, 0.003
Tap Ratings:Syncopation Index (Linear)	-0.623	-2.698, 1.412	0.000	0.000, 0.004
Tap Ratings:Syncopation Index (Quadratic)	-2.910	-4.635, -1.135	0.005	0.001, 0.014

Note: due to the scaling effect of the orthogonal polynomial on syncopation index, the parameter estimates for this variable and its interaction with group cannot be compared to the parameter estimates for the other effects.

Analyses of the non-musicians' data only showed very similar results to those carried out on the full data set. Importantly, the hierarchical regression showed that tap ratings improved model fit over and above syncopation and both measures of tap performance ($\chi^2(1) = 77.02$, $p < .001$). Further, the final model showed that tap ratings ($\beta = 0.343$, 95% CI[0.268,0.419]) had a stronger effect on groove than both tapping precision ($\beta = 0.182$, 95% CI[0.079, 0.285]) and tapping accuracy ($\beta = 0.009$, 95% CI[-0.075, 0.090]).

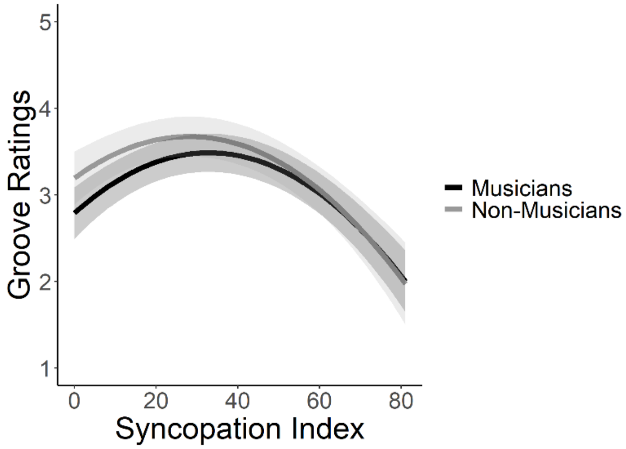

Figure 3.4. Relation between syncopation index and groove ratings in musicians and non-musicians. The lines represent estimated effects from the final model. Ribbons represent 95% confidence intervals.

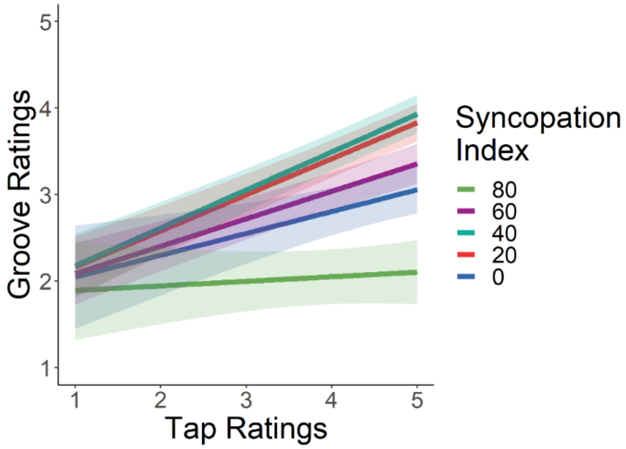

Figure 3.5. Relation between tap ratings, syncopation index, and groove ratings. The lines represent estimated effects from the final model at representative levels of syncopation index. Ribbons represent 95% confidence intervals.

Discussion

In this study we investigated the relation between perceived and measured synchrony and the sensation of groove. To do this musicians and non-musicians rated the groove of rhythms that varied in degree of syncopation, and then tapped to the beat of those rhythms and rated how well they synchronized. First, we showed that syncopation and groove ratings showed an inverted U-shaped relation for both musicians and non-musicians, replicating previous work (Matthews et al., 2019; Witek et al., 2014). Supporting our hypothesis, perceived synchrony showed a stronger relation with groove ratings than tapping precision, tapping accuracy, or syncopation. Perceived synchrony also accounted for unique variance in groove ratings over and above that accounted for by measured synchrony and syncopation. This latter result is important as it suggests that perceived synchrony has a unique effect on groove that goes beyond the effects of tapping performance and syncopation despite the relation among these variables. The result that perceived synchrony outweighed syncopation is particularly interesting given that syncopation has consistently shown a strong relation with groove across different stimuli and is intentionally used by musicians to engender groove (Madison et al., 2011; Matthews et al., 2019; Matthews et al., 2020; Sioros, Mirron, et al., 2014; Witek et al., 2014). However, these prior studies focused on the effect of syncopation on groove when listening without movement. When moving to music, the self-perception of how you are engaging with the music may become as important in determining your affective experience as specific features of the music itself. Crucially, the relation between perceived synchrony and groove was strongest for rhythms with a medium number of syncopations, thus extending work showing an inverted U-shaped relation between rhythmic complexity and groove. Finally, although musicians were close to ceiling for tapping performance and tap ratings, results were generally similar across groups suggesting that musical training does not have a strong influence on the relation between perceived synchrony and groove.

Together, these results suggest that when moving to music, ‘feeling in sync’ is a strong driver of the sensation of groove. These results also provide indirect support for the hypothesis that prediction confirmations during beat synchronization contribute to the reward associated with moving to music. Based on the beat-bin hypothesis (Danielsen, 2010, 2019), which aligns with both dynamic attending (Large & Jones, 1999) and predictive coding (Vuust & Witek, 2014) treatments of rhythm perception and groove, we propose that rhythmic context affects the strength and certainty of beat-based temporal predictions and in turn, the perception of synchrony. Movements that are perceived as synchronous confirm beat-based temporal predictions, leading to greater reward and an increased sensation of groove. Therefore, perceived synchrony may contribute to the rewarding experience of moving to music, regardless of true accuracy.

Perceived vs. Measured synchrony

Our results showed a stronger relation between perceived synchrony and groove compared to measured synchrony. This suggests that there is a divergence between what is perceived and actual performance accuracy, with perception having a stronger role in determining our affective experience. In other words, overestimating how synchronous our movements are to music may contribute positively to the sensation of groove. Overestimation of synchrony is also seen during simple synchronization with a metronome where participants are unaware that they are consistently tapping early relative to the pacing signal (Franěk et al., 1987). This lack of access to our degree of synchrony has been attributed to an asymmetric error tolerance zone where early taps are tolerated or go unnoticed, while late taps tend to be noticed and lead to correction (Müller et al., 1999). Corroborating this, Figure 3.1 shows that both musicians and non-musicians generally tapped early relative to the beat. We suggest that in the current context, the overestimation of synchrony increases the reward associated with groove as more taps perceived as synchronous increases the number of moderately-weighted prediction confirmations.

A relative lack of conscious access to tapping accuracy is supported here as tapping accuracy showed little or no relation to perceived synchrony or groove ratings. However, tapping precision, or variability, was positively related to both perceived synchrony and groove in both groups, suggesting that participants have better access to tapping precision than tapping accuracy. Tapping precision has been linked to the perceived difficulty of synchronizing taps (Baath & Madison, 2012), whereas, studies on the effect of accuracy on perceived synchrony are lacking. A relative lack of access to tapping (in)accuracy may relate to the different types of error correction that can occur during motor synchronization. Phase correction, where inaccuracies are minimized in the face of endogenous motor variance or perturbations in the stimuli, has been shown to be an automatic motor process that is not consciously accessible (Repp, 2005; Repp & Keller, 2004; Repp & Su, 2013). Studies relating motor synchronization performance and groove have shown mixed results with one showing a positive relation (Janata et al., 2012), while others have not shown this relation (Hurley et al., 2014), or have only shown a weak relation (Stupacher et al., 2016). However, these studies did not look at tapping precision and accuracy separately and involved different types of motor synchronization, including finger-tapping, hand-tapping, and head-bobbing. Therefore, further work is necessary to clarify which aspects of motor synchronization influence perceived synchrony and groove, and to assess whether conscious awareness mediates these relationships. In the current study, it is important to note that despite greater conscious access to tapping precision, perceived synchrony was still a stronger predictor of groove.

Perceived Synchrony and Syncopation

The effect of perceived synchrony on groove depended on the degree of syncopation, with a stronger effect for rhythms with medium/low-medium degrees of syncopation. We suggest that the overestimation of synchrony seen by Franěk et al., (1987) may increase as moderate uncertainty in the rhythmic context widens the tolerance zone (Müller et al., 1999), allowing more movements to be perceived as synchronous. Integrating across theoretical frameworks, we propose that the beat bin reflects prediction certainty (from predictive coding) or attentional focus (from dynamic attending) which not only determine the predicted beat location but also how one moves to the beat. Support for this comes from a study showing that the spread of movement asynchronies around the beat increases when phase mismatch between instrumental layers is introduced (Danielsen et al., 2015). The current study extends these results, providing evidence that not only does rhythmic context affect measured synchrony, but that it also affects perceived synchrony and moderates the relation between perceived synchrony and groove.

Rhythms with medium levels of syncopation combine moderate levels of predictability and certainty, thus leading to a relatively high number of moderately weighted prediction confirmations. For very simple rhythms, both predictability and certainty are high, leading to a narrow beat bin that allows only movements very close to the metronomic beat to be perceived as synchronous and be considered as prediction confirmations. Further, following the inversion of the predictive coding account, because certainty is high, the relative weight of prediction confirmations is low. In other words, it is not very rewarding to be correct when the task is easy. For high complexity rhythms with many syncopations, both predictability and certainty are low such that it might be difficult to perceive a beat and thus make predictions. Further, these predictions will be so uncertain as to be uninformative. Therefore, rhythms with medium levels of syncopation strike a balance between predictability and uncertainty, thus engendering more rewarding feedback. An increase in moderately weighted prediction confirmations may contribute to groove regardless of whether one is moving or not. Indeed, the effect of perceived synchrony on groove shows an inverted U-shaped relationship with syncopation similar to that observed between syncopation and groove here and in previous work (Matthews et al., 2019; Witek et al., 2014). However, externalizing beat-based predictions via movement provides additional sensory information regarding prediction confirmation or violation, thus potentially amplifying the gain of these prediction-based signals to further increase reward.

Neural resonance theory suggests that the attentional oscillations proposed by dynamic attending theory are the result of endogenous neural oscillations (Large & Snyder, 2009). That is, peaks of attention are thought to reflect peaks of neuronal excitability (Lakatos et al., 2008). The degree of neural entrainment has been positively linked with ratings of groove (Cameron et al., 2019), suggesting the possibility that the width of the beat bin is determined by the dynamics of entrained neural oscillations. In addition to coordinating attentional and perceptual resources with external rhythms, neural oscillations are thought to coordinate communication between brain regions (Buzsáki & Draguhn, 2004; Fries, 2015). In this way, oscillatory dynamics may determine the temporal windows within which there is perceptual binding of multisensory inputs resulting from the same stimulus (Bauer et al., 2020). In the current study, sounds and taps do not result from the same source. Instead, integration of auditory, motor and somatosensory information is necessary to determine whether movements are synchronous with the beat. Therefore, in addition to affecting attentional windows, rhythmic context may affect the temporal window for integration across sensory inputs, and thus affect the perception of synchrony (Occelli, Spence, & Zampini, 2011). A recent study showed that temporal windows for integrating keypress and the resulting auditory feedback are relatively large and that the width of this window is associated with tapping synchronization accuracy (van Vugt & Tillmann, 2014).

Since rhythmic context affects synchronization accuracy, as shown here, it could be that this integration window is also affected. In the current study, sensory feedback from movements is reduced as tapping does not result in a sound, which may further contribute to the discrepancy between perceived and measured tap timing (Ross & Balasubramaniam, 2014). Therefore, the match between perceived and measured synchrony may depend on the amount of sensory feedback the movements create. This is particularly relevant for dancing, where movements often lead to little or no auditory or tactile, feedback.

Musicianship

The effect of perceived synchrony on groove, and its interaction with syncopation was similar across groups, with no significant effect of musical training. We expected that musicians would show a closer match between perceived and measured synchrony, as experts tend to show a stronger correlation between perceived and measured performance on a variety of tasks (Zell & Krizan, 2014). Musicians did show a larger effect of tapping precision on tap ratings, however this effect was relatively small and both groups showed a similar pattern. The relative lack of variability in musicians' perceived and measured synchrony may have obscured group differences. Alternatively, even if musicians show a better match between perceived and measured synchrony, perceived synchrony may still be a stronger driver of groove. Further, it seems likely that rhythmic context would have a similar effect of widening the beat bin in musicians, even if their bin is narrower to start with. Future work should seek to replicate these results using a task with a level of difficulty optimized for musicians.

Conclusion

In this study we set out to investigate the relation between perceived and measured synchrony and the sensation of groove. We showed that perceived synchrony is a stronger predictor of groove than measured synchrony and even syncopation, and that this effect was strongest for medium complexity rhythms. This indicates that consciously accessible prediction confirmations contribute to the positive affective experience associated with moving to music over and above the fine-grained error correction mechanisms that determine measured synchrony. These results also support the application of the beat bin hypothesis to beat synchronization, suggesting that rhythmic context modulates the impact of movement-driven prediction confirmations on groove. These results align with previous work showing the primacy of medium complexity rhythms in eliciting groove, extending this relation to the role of perceived synchrony during beat synchronization. Further, we show that in the context of groove, both predictive coding and dynamic attending make similar predictions, which are supported here. Finally, the current results provide additional support that temporal predictions, and the certainty with which they are made, are integral to the sensation of groove. This study represents an early step in understanding why it feels good to move to music, with many questions yet to be answered. For example, although our results provide indirect evidence that overestimation of synchrony contributes to the pleasure of moving (and listening) to music, future work should test this directly.

Supplemental Material

Effects of syncopation and group on tapping performance in models tuned for high efficiency

The final model with tapping accuracy as the outcome variable and tuned for higher efficiency showed a significant negative quadratic effect of syncopation (*b* = -1.03, 95% CI[-1.485, -0.570]). A significant group by syncopation (linear) interaction indicated that non-musicians showed a stronger negative linear effect of syncopation than musicians (*b* = 1.62, 95% CI[0.029, 3.202]).

The final model with tapping precision as the outcome variable and tuned for higher efficiency showed a significant negative quadratic effect of syncopation (*b* = -1.38, 95% CI[-1.837, -0.925]). A significant group by syncopation (linear) interaction indicated that non-musicians showed a stronger negative linear effect of syncopation than musicians (*b* = 2.56, 95% CI[1.210, 3.917]).

Effects of tapping performance, syncopation, and group on tap ratings in a model tuned for high efficiency

In the final model with tap ratings as the outcome variable and tuned for higher efficiency, syncopation showed a negative quadratic effect in both groups (β = -3.68, 95% CI[-4.919, -2.444]), while non-musicians showed a steeper drop off leading to significant group by syncopation (linear) interaction (β = 3.046, 95% CI[0.675, 5.417]). Unlike the model tuned to high robustness, the model tuned for high efficiency did not show a significant group by tapping precision interaction (β = 0.066, 95% CI[-0.016, 0.147]). However, there was a significant main effect of tapping precision with tap ratings increasing as precision increased (β = 0.641, 95%

CI[0.556, 0.726). As in the high robustness model, the high efficiency model showed a significant group by tapping accuracy interaction indicating that musicians showed a negative effect (β = -1.07, 95% CI[-0.159, -0.056]).

Effects of tapping performance, syncopation, and group on tap ratings in a model accounting for the censored nature of the data

Using lme4cens package a model was estimated which accounted for the fact that a large number of tap ratings were at the upper limit of the ratings scale (a rating of 5). Note that due to limitations of the package, only by-participant random intercepts were estimated and only the linear effect of syncopation was included in the model. In addition, p values but not confidence intervals were estimated. Syncopation (z-scored) showed a significant main effect indicating a negative relation with tap ratings ($b = 0.205$, $p < .001$). The group by syncopation index was not significant ($b = 0.106$, $p = .12$). The group by tapping precision interaction was significant ($b = 0.516$, $p < .001$) as was the group by tapping accuracy interaction ($b = -0.198$, $p = .028$).

CHAPTER FOUR:

ARTICLE 3

The sensation of groove engages motor and reward networks

Matthews, T. E., Witek, M. A., Lund, T., Vuust, P., & Penhune, V. B. (2020). The sensation of groove engages motor and reward networks. *NeuroImage*, 214 (116768), 1-12. https://doi.org/10.1016/j.neuroimage.2020.116768

Abstract

The sensation of groove has been defined as the pleasurable desire to move to music, suggesting that both motor timing and reward processes are involved in this experience. Although many studies have investigated rhythmic timing and musical reward separately, none have examined whether the associated cortical and subcortical networks are engaged while participants listen to groove-based music. In the current study, musicians and non-musicians listened to and rated experimentally controlled groove-based stimuli while undergoing functional magnetic resonance imaging. Medium complexity rhythms elicited higher ratings of pleasure and wanting to move and were associated with activity in regions linked to beat perception and reward, as well as prefrontal and parietal regions implicated in generating and updating stimuli-based expectations. Activity in basal ganglia regions of interest, including the nucleus accumbens, caudate and putamen, was associated with ratings of pleasure and wanting to move, supporting their important role in the sensation of groove. We propose a model in which different cortico-striatal circuits interact to support the mechanisms underlying groove, including internal generation of the beat, beat-based expectations, and expectation-based affect. These results show that the sensation of groove is supported by motor and reward networks in the brain and, along with our proposed model, suggest that the basal ganglia are crucial nodes in networks that interact to generate this powerful response to music.

Introduction

The sensation of groove, defined as the pleasurable desire to move to music (Janata et al., 2012), is one of the most powerful sources of music-derived pleasure. One way in which music is thought to elicit pleasure is through the interplay between the violation and fulfillment of musical expectations (Cheung et al., 2019; Huron, 2006; Juslin & Västfjäll, 2008; Meyer, 1956; Salimpoor et al., 2015). Musicians and composers can manipulate the expectations of a listener by altering the complexity or predictability of the rhythms, melodies, harmonies, or other factors that make up a piece of music. For example, listeners prefer melodies that are moderately complex (i.e., moderately unpredictable) compared to very simple or very complex melodies (Pearce & Wiggins, 2012). Similarly, groove is thought to rely predominantly on rhythmic expectations, with moderately complex rhythms leading to greater pleasure and wanting to move (Matthews, Witek, Heggli, Penhune, & Vuust, 2019; Sioros, Mirron, Davies, Gouyon, & Madison, 2014; Witek et al., 2014).

Rhythmic expectations are closely tied to the metre, which is the pattern of alternating strong and weak beats (London, 2012; Vuust & Witek, 2014). For example, in a waltz metre which consists of a strong beat followed by two weak beats, listeners will expect a note to fall on the strong beat. When notes fall between beats, or on weak beats rather than strong beats, they create syncopations which violate expectations and challenge the metre (Fitch & Rosenfeld, 2007; Vuust & Witek, 2014). Very simple rhythms with no syncopations are highly predictable, but boring, as most, if not all rhythmic expectations are confirmed. Highly complex rhythms, with many syncopations, are unpredictable and hard to follow as it is difficult for the listener to perceive a metre, and thus generate rhythmic expectations. Medium complexity rhythms, with some syncopations, strike a balance allowing for both the formation and violation of rhythmic expectations. As the metre is challenged by syncopations, rhythmic expectations need to be assessed and updated. It has been proposed that this continuous engagement of rhythm expectation processes drives the pleasure associated with groove (Koelsch et al., 2019; Vuust & Witek, 2014; Vuust et al., 2018). One way of assessing rhythmic expectations is through movement (Patel & Iversen, 2014), which may account for the desire to move associated with groove (Koelsch et al., 2019).

The link between rhythmic expectations and wanting to move suggests that motor regions of the brain may be involved in processing groove-based music such as funk, Afro-Cuban, and hip-hop (Danielsen, 2006; Greenwald, 2002). There have been no previous neuroimaging studies investigating the brain regions involved in the sensation of groove. However, studies of beat perception show activity in brain networks associated with auditory-motor integration and motor timing (Araneda et al., 2016; Bengtsson et al., 2009; Burunat et al., 2017; Chapin et al., 2010; Chen et al., 2008; Grahn and Brett, 2007; Grahn and Rowe, 2013, 2009; Kung et al., 2013; Schubotz et al., 2000; Thaut et al., 2014). The basal ganglia (BG) seem to be particularly important for beat perception as they are crucial nodes in a core timing network proposed to underlie beat-based timing (Matell & Meck, 2004; Merchant et al., 2015; Teki et al., 2011). The BG also form distinct cortico-striatal circuits that may support different motor and motivational functions relevant to groove (Alexander, DeLong, & Strick, 1986; Haber, 2003). Recent studies have demonstrated that the putamen and supplementary motor area (SMA), which are parts of the cortico-striatal 'motor circuit', show selective responses to beat and metre (Araneda et al., 2016; Li et al., 2019). The caudate forms circuits with both prefrontal and parietal regions (Jarbo & Verstynen, 2015) and has been implicated in both rhythmic (Trost et al., 2014) and harmonic expectations (Seger et al., 2013).

Premotor, prefrontal, and parietal regions are also often activated in response to a strong beat (Bengtsson et al., 2009; Danielsen, Otnæss, Jensen, Williams, & Østberg, 2014; Grahn et al., 2011; Grahn & McAuley, 2009; Grahn & Rowe, 2009; Grahn & Schuit, 2012; McAuley, Henry, & Tkach, 2012; Schubotz et al., 2000; Schubotz & von Cramon, 2001). These regions are part of the dorsal auditory stream (Hickok & Poeppel, 2004; Rauschecker, 2011), while premotor and parietal regions together form the dorsal fronto-parietal network (Ptak et al., 2017). These networks are believed to underlie abstract motor representations that allow for integration of sensory information over time (Ptak et al., 2017; Rauschecker, 2011). Furthermore, rhythmic expectations can be thought of as temporal predictions which are thought to originate in the motor and premotor cortices (Morillon & Baillet, 2017; Rimmele et al., 2018) and may reflect covert action simulation (Arnal, 2012; Patel & Iversen, 2014; Ross, Iversen, & Balasubramaniam, 2016; Schubotz, 2007). Therefore, groove may activate motor regions of the brain via both the motor processes underlying rhythmic expectations and the overt or covert movement preparation purportedly involved in testing these expectations. Consistent with this, motor cortical excitability has been found to be greater for high compared to low groove music (Stupacher et al., 2013).

In addition to their role in beat-based timing, the BG, particularly the caudate and nucleus accumbens (NAcc), are associated with the anticipation and experience of music-derived pleasure (Blood & Zatorre, 2001; Blood, Zatorre, Bermudez, & Evans, 1999; Koelsch, 2014; Salimpoor et al., 2011, 2013). Activity in the NAcc has been associated with the experience of pleasure including from primary (e.g., food and sex) and secondary (e.g., money) rewards (Sescousse et al., 2013). During music-listening, the NAcc is active during moments of peak pleasure, while the caudate is active in the period just before peak pleasure, suggesting that the caudate is involved in the anticipation of pleasure (Salimpoor et al., 2011). The medial orbitofrontal cortex (mOFC) also plays a role in assigning, maintaining and monitoring the value of a stimulus (Kringelbach, 2005; O'Doherty, 2004), including music (Koelsch, 2014). A network formed by the NAcc, mOFC, and auditory cortex has been linked to the enjoyment of music as shown by both structural (Martinez-Molina et al., 2019) and functional (Salimpoor et al., 2013) connectivity measures.

Taken together, the sensation of groove can be framed as the intersection of reward processing and the motor processes that underlie beat perception, with rhythmic expectations as the driving mechanism. Therefore, to test the role of both reward and motor networks in the experience of groove, we asked participants to listen to rhythms with medium and high levels of complexity (i.e., degree of syncopation), and rate both their desire to move and pleasure while undergoing functional magnetic resonance imaging (fMRI). Stimuli were drawn from a previous behavioural study showing that medium complexity rhythms were rated as more pleasurable and elicited a greater desire to move compared to low and high complexity rhythms (Matthews et al., 2019). Because we also found that harmonic complexity modulated the affective component of groove, this factor was included here. Finally, we tested both musicians and non-musicians based on evidence that training can affect both the sensation of groove (Matthews et al., 2019; Senn et al., 2018) and neural processing in both auditory-motor (Alluri et al., 2017; Grahn & Brett, 2007; Grahn & Rowe, 2009) and reward networks (Alluri et al., 2015; Chapin et al., 2010).

We expected medium complexity stimuli to elicit activation in brain networks involved in the processing of musical beat, as well as in cortical and striatal regions linked to reward, with stronger effects in musicians than non-musicians. Given the roles of the putamen, caudate, and NAcc in beat-based timing and reward, we focused analysis on these regions of interest.

Material and Methods

Participants

Fifty-seven participants were recruited into two groups (musicians and non-musicians). Musicians had a minimum of eight years of training and were currently practicing. Non-musicians had less than one year of training and were not currently practicing. Informed consent was obtained, and the study was approved by the Central Denmark Region Committees on Health Research Ethics. Participants received 200 DKK remuneration. Two non-musicians were excluded from the scanning session due to technical problems. Another non-musician was excluded as their ratings showed no variability. Demographic data for the final sample are provided in Table 4.1.

Table 4.1. Participant Demographic Data

	Non-Musicians	**Musicians**
N (male/female)	25 (13/12)	29 (17/12)
Age (SD)	23.20 (2.46).	23.76 (2.84)
Years of musical training (SD)	0.16 (0.31)	11.5 (3.27)
Hours of music practice per week (SD)		11.67 (10.20)

Stimuli

The stimuli were a subset of those developed and validated in a previously reported online study (Matthews et al., 2019). The stimuli consisted of short musical sequences with two levels of both rhythmic and harmonic complexity. There were three rhythms and three chords for each level of complexity resulting in 36 unique stimuli of four different categories: medium rhythm/medium harmony (Mr-Mh), medium rhythm/high harmony (Mr-Hh), high rhythm/medium harmony (Hr-Mh), and high rhythm/high harmony (Hr-Hh). These levels of complexity were chosen since, in the previous study, medium levels of rhythmic and harmonic complexity elicited the highest ratings and showed the greatest difference in ratings compared to high complexity rhythms and chords. In addition, two rather than three levels of complexity were chosen in order to maximize the number of trials for each level. The stimuli were created using Cubase Pro version 8.0.30 (Steinberg Media Technologies).

The sequences consisted of piano chords organized into rhythmic chord patterns in a piano timbre presented at 96 beats per minute. Each sequence was 10 seconds long and contained four repeats of a five-onset rhythm pattern with a single chord repeating throughout each sequence plus an isochronous eighth-note hi-hat pattern (see Figure 4.1 for musical notation of a medium complexity rhythm and Figure S4.1 for a schematized representation of all rhythm patterns). The medium complexity rhythms consisted of two Afro-Cuban rhythms known as the son clave and rumba clave, and one experimenter-created rhythm. The high complexity rhythms had all but the first onsets shifted to be early or late relative to the medium complexity patterns, thus increasing their rhythmic complexity. Rhythmic complexity was quantified using the syncopation index (Fitch & Rosenfeld, 2007). As the hi-hat pattern was identical for all stimuli, it was not included when calculating the syncopation index. C-scores – a measure of counter-evidence to the metre – (Povel & Essens, 1985) were also calculated for each rhythm and were consistent with the syncopation index within each level of complexity (see Figure S4.2A and 3.2B).

All chords were in the key of D major and included six notes spanning four octaves (D2 to D#5; see Figure 4.1 for musical notation of a medium complexity chord and Table S4.1 for a list of notes and corresponding frequencies for all chords). In musical terms, the medium complexity chords consisted of four note chords with extensions. High complexity chords included a flat ninth interval between chord note and extension which is considered highly dissonant, when not specifically occurring as a flat 9th on a major 7th chord, according to contemporary harmonic theory (Freeman & Pease, 1989; Levine, 2011; Nettles & Ulanowsky, 1987). In lay terms, the high complexity chords contained notes with frequencies, or multiples of frequencies, that were very close to each other, thus creating an unpleasant sense of roughness or dissonance, while the medium complexity chords did not. Harmonic complexity was quantified using measures of peak roughness and inharmonicity, calculated using the MIRtoolbox version 1.6.1 (Lartillot et al., 2007; see Figure S4.1D and S4.1C;).

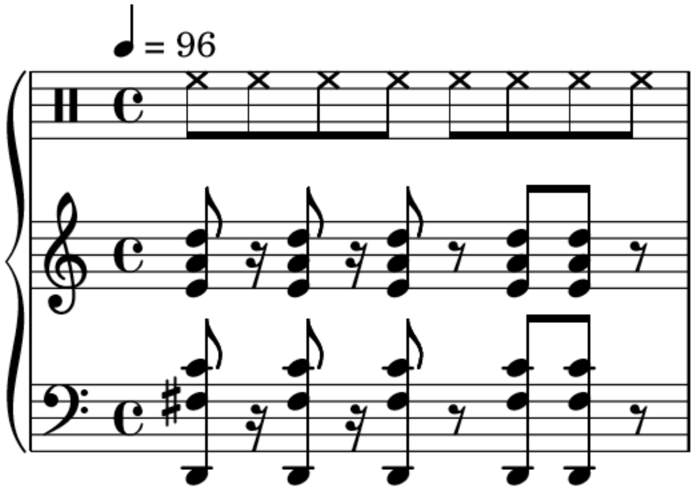

Figure 4.1. Example of a stimulus with medium levels of rhythmic and harmonic complexity.

Procedure

Before arriving for the study, participants filled out a questionnaire about their musical background and demographic information. Upon arrival, participants were familiarized with the stimuli and rating task with four familiarization trials using stimuli that were not included in the main study. There were two sessions during which participants listened to and rated all 36 stimuli, one inside the fMRI scanner and one outside the scanner. In order to avoid having ratings of wanting to move and pleasure influence each other, participants rated wanting to move in the scanner then pleasure and beat strength outside of the scanner, always in this order. Ratings of beat strength were collected in order to substantiate the rhythmic complexity manipulation and to investigate the association between the sensation of groove and perception of beat strength. In the scanning session, participants underwent three fMRI runs, each lasting around 11 minutes, during which they listened to all 36 stimuli in a pseudo-random order. A randomly selected subset of 12 stimuli were rated in each scanning run so that all 36 stimuli were rated over the three runs. Rating trials were randomly distributed within each run and participants were not aware that a given sequence would be rated until after it was presented, thus avoiding rating-specific activations. Participants selected their rating on a five-point visual scale by pressing two buttons on a button box to move a cursor right or left along the rating scale. Participants had seven seconds to make their rating and non-rated trials had inter-stimulus intervals of five, 7.5, or 10 seconds. Participants were instructed to look at a fixation cross while sequences were presented.

In order to reduce the effect of scanner noise, stimuli were presented with noise reduction headphones (Opto-Active, OptoAcoustics, Mazor, Israel, http://www.optoacoustics.com/medical/optoactive/features). In addition, participants wore earplugs inside the headphones. In order to compensate for the low-pass filter effect of the earplugs, the stimuli were compared with and without earplugs and then altered so that they subjectively matched. This resulted in a 10 to 20 decibel increase for frequencies greater than 1500 Hz. This adjustment was identical for all stimuli and participants.

After the scanning, participants listened to the stimuli again while seated at a computer. After each sequence participants had 10 seconds to rate the degree of pleasure they experienced and the beat strength of the sequence, both on a five-point visual scale, using a computer mouse to select their rating.

Behavioural data analysis

Correlations between rating types were tested on participants' averaged ratings (one value per participant). Confidence intervals around correlation coefficients were calculated via bootstrapping with 5000 iterations. Analysis of the effects of rhythmic and harmonic complexity and group on ratings of pleasure, wanting to move, and beat strength were conducted on trial-level ratings using linear mixed effects regression with the lme4 package (Bates, Mächler, Bolker, & Walker, 2014) in R (version 3.4.1, R core team, 2017). A linear mixed effects approach was used to account for inter-individual differences in ratings and in the effects of rhythmic and harmonic complexity as well as differences in effects across the three rhythms and chords (referred to as items) within each level of complexity. Starting with the maximal random structure, including by-participant and by-item random slopes and intercepts, this structure was then reduced to the optimal structure that could be supported by the data following the steps of Bates and colleagues (2015) and using their RePsychLing package. This led to by-participant random slopes and intercepts for rhythmic and harmonic complexity in all three models and by-item random intercepts for the models with wanting to move and beat ratings as outcome variables.

For the effects of interest, a forward hierarchical approach was used whereby regressors were added incrementally to an intercept-only model, then tested for increases in fit using the likelihood ratio test. Regressors that significantly contributed to model fit were included in a final model (fit with restricted maximum likelihood criterion) which was used to get parameter estimates of these regressors. For interactions, estimates of means and mean differences were calculated using emmeans (Lenth et al., 2018). Confidence intervals around the parameter estimates were calculated via parametric bootstrapping with 5000 iterations. Diagnostic plots of the residuals from all models were inspected for violations of the assumptions of normality and homoscedasticity. No violations were detected.

MRI data acquisition

Scanning took place at Aarhus University Hospital on a 3T Siemens TIM Trio scanner with a 32-channel coil. Each participant underwent three runs of whole-brain echo-planar imaging (EPI) using a multi-echo sequence which involved acquiring two whole brain volumes at two different echo times (TE1 = 12.4 ms, TE2 = 27.92 ms) per repetition time (TR = 2000 ms and voxel size = 2.35 x 2.53 x 2.50 mm, number of slices = 54, flip angle = 78 degrees). Using the multi-echo sequence reduces signal drop out in regions near sinuses such as the orbitofrontal cortex. The two EPI images within each TR were combined using a signal-to-noise ratio weighted average. This resulted in 326 images per run, with a total of 978 images per participant. T1 structural images were collected for each participant at the start of each session (TR = 2420 ms, TE = 3.7ms, voxel size = 1mm iso, flip angle = 9 degrees).

MRI preprocessing and statistical analysis

Statistical Parametric Mapping software (SPM12 Wellcome Trust Centre for Neuroimaging, University College London; www.fil.ion.ucl.ac.uk/spm/) was used for preprocessing and statistical analysis. Standard preprocessing steps were followed, including slice timing correction, unwarping, motion correction, coregistration to an MNI template, segmentation, spatial normalization, and spatial smoothing with an 8mm FWHM kernel.

First-level analysis used the general linear model with four condition regressors corresponding to the four types of stimuli (Mr-Mh, Mr-Hh, Hr-Mh, Hr-Hh) as well as twenty-four regressors accounting for motion parameters, and an additional regressor accounting for rating responses which were modeled as events time-locked to button presses. Silent inter-stimulus intervals were unmodeled, thus acting as an implicit baseline. All regressors were then convolved with a canonical hemodynamic response function. Four contrast images were calculated per participant, corresponding to the four stimuli conditions. These were then entered into a second level analysis where group-level contrasts for each main effect and interaction were generated. All results are reported at a false discovery rate (FDR; peak-level) corrected $p < .05$. In a mixed design, SPM uses the same error term and degrees of freedom for main effects of both within and between-subject factors (McLaren et al., 2011). Therefore, a confirmatory analysis was implemented in GLM Flex (http://mrtools.mgh.harvard.edu/index.php/GLM_Flex) with the same contrasts and FDR correction (see Tables S4.2-S4.4 for results).

Region of interest analyses

Parameter estimates (betas) for each participant, for each condition were extracted from the putamen and caudate (left and right combined) as well as the left and right nucleus accumbens using Marsbar (Brett et al., 2002; http://marsbar.sourceforge.net/) with anatomical masks from a probabilistic atlas (Hammers et al., 2003). Effects of rhythmic and harmonic complexity and musical training were then assessed using the same approach as the analysis of the ratings. Only by-participant random effects were included since parameter estimates were extracted from group level contrast images which did not contain item (i.e., trial) level activations.

An additional analysis was implemented to investigate the relation between subjective ratings and ROI activity. This analysis also used hierarchical linear mixed effects regression, with parameter estimates from the ROIs as outcome measures, and group, beat strength ratings, pleasure ratings, and wanting to move ratings, as well as interactions between group and the three types of ratings, as predictors. As in the above analysis, only by-participant random effects were included. In order to assess the degree of overlap in variance accounted for by pleasure and wanting to move ratings, and whether they accounted for variance over and above beat strength ratings and group differences, the hierarchical regression was implemented with two different orders: 1. Group, beat strength ratings, pleasure ratings, and wanting to move ratings, and 2. Group, beat strength ratings, wanting to move ratings, and pleasure ratings. The interactions between group and the ratings were entered after the main effects and followed the same orders. In addition to the final models including only the significant predictors from each hierarchical analysis, models with only pleasure ratings, only wanting to move ratings, and both together as predictors, were assessed.

Based on the findings of the whole brain analysis, a post hoc analysis was implemented to investigate the effect of rhythmic and harmonic complexity as well as the three ratings types on mOFC activity. The mOFC ROI was generated from the any effect whole brain F-contrast (thresholded at $p < 0.05$, FDR) and included two clusters on the left with peaks at $x = -18$, $y = 28$, $z = -18$ and $x = -14$, $y = 42$, $z = -20$ and one cluster on the right with two peaks at $x = 24$, $y = 32$, $z = -12$, and $x = 26$, $y = 32$, $z = -22$. The parameter estimates from this ROI were submitted to two analyses identical to those carried out on the BG ROIs.

The subjective ratings, background data, relevant t-maps, extracted ROI activations that support these findings, as well as the python code for generating stimuli orders, presenting stimuli, and recording responses, are available in the Open Science Framework with identifier link: https://doi.org/10.17605/osf.io/z2sy9

Results

Behavioural Results

All three types of ratings were strongly correlated yet independent enough to be analyzed separately: Pleasure and wanting to move ratings ($r = 0.62$, 95% CI[0.36, 0.81]); pleasure and beat strength ratings ($r = 0.55$, 95% CI[0.27, 0.77]); Wanting to move and beat strength ratings ($r = 0.42$, 95% CI[0.19, 0.61]).

For both musicians and non-musicians, pleasure ratings decreased as rhythmic and harmonic complexity increased (Figure 4.2A). However, a significant interaction between rhythmic and harmonic complexity ($\chi^2(1) = 8.98$, $p < .003$) showed that the difference in ratings between Mr-Mh and Mr-Hh (mean difference (MD) = 0.696) was greater than the difference between Hr-Mh and Hr-Hh (MD = 0.440; $b = 0.250$, 95% CI[0.090, 0.409]). This suggests that medium complexity chords increased pleasure to a greater degree when combined with medium complexity rhythms compared to high complexity rhythms. The rhythm by group interaction improved model fit ($\chi^2(1) = 4.69$, $p = .030$) and showed that the difference in ratings between medium and high complexity was greater for non-musicians (MD = 1.53) than musicians (MD = 1.17; $b = -0.364$, 95% CI[-0.679, -0.035]).

For wanting to move ratings, there was a three-way interaction with rhythm, harmony, and group ($\chi^2(1) = 5.84$, $p = .016$; Figure 4.2B). Musicians showed a greater difference in ratings between Mr-Mh and Mr-Hh (MD = 0.521) compared to Hr-Mh and Hr-Hh (MD = 0.226) whereas for non-musicians, the differences between Mr-Mh and Mr-Hh (MD = 0.116) and Hr-Mh and Hr-Hh (MD = 0.151) were similarly small (*b* = 0.331, 95% CI[0.062, 0.601]). This suggests that musicians' wanting to move ratings were increased by the combination of medium complexity rhythms and chords whereas non-musicians' ratings were increased by medium complexity rhythms alone.

For beat strength, the main effect of rhythmic complexity significantly improved model fit ($\chi^2(1) = 74.83$, $p < .001$), with medium complexity rhythms rated as having a stronger beat than high complexity rhythms (*b* = 1.672, 95% CI[1.408, 1.933]). The rhythm by harmony interaction also improved model fit ($\chi^2(1) = 4.08$, $p = .043$) showing that Hr-Mh were rated as having higher beat strength than Hr-Hh (MD = 0.207), whereas Mr-Mh and Mr-Hh were rated more similarly (MD = 0.077; *b* = -0.130, 95% CI[-0.254, 0.002]; Figure 4.2C). This suggests that high complexity rhythms combined with medium complexity chords are rated as having higher beat strength than high complexity rhythms with high complexity chords. However, the confidence interval contains zero suggesting that this effect may be unstable. There was no significant main effect of group nor a significant interaction between group and rhythmic and/or harmonic complexity.

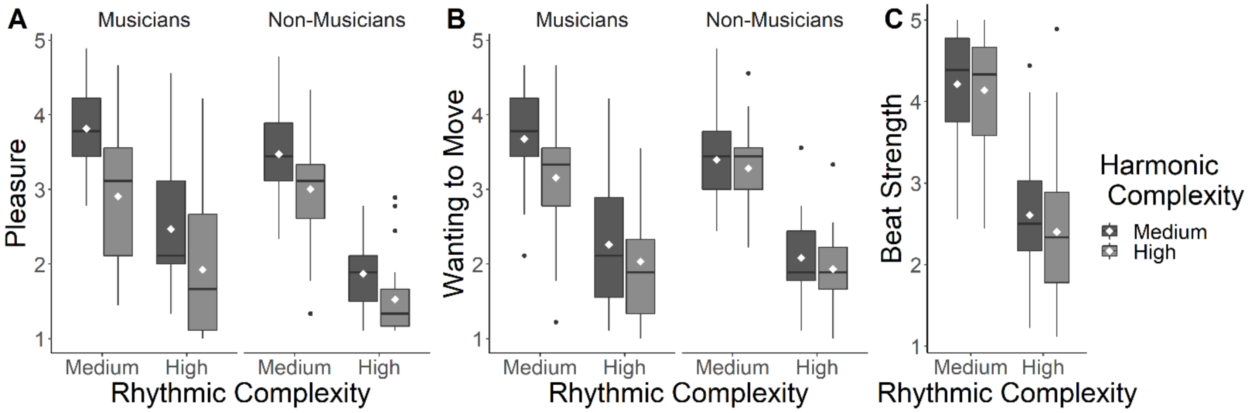

Figure 4.2. Subjective ratings as a function of rhythmic complexity, harmonic complexity and group. **A.** Pleasure ratings. **B.** Wanting to move ratings. **C.** Ratings of beat strength. Center line,

median; white dots, means; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; black dots, outliers.

Whole-Brain fMRI Results

Whole-brain contrast images were used to assess the effects of rhythm, harmony, and musical training (group). Contrasting medium versus high complexity rhythms (medium > high complexity) revealed activations in the bilateral BG including the putamen, caudate, and pallidum, with activation in the left BG bordering the NAcc. This contrast also revealed activation in a network of cortical regions associated with beat perception including the left SMA (including pre-SMA), bilateral dorsal premotor regions, and bilateral parietal regions (see Table 4.2 and Figure 4.3). In addition, this contrast revealed significant activation in the left prefrontal cortex, left mOFC, the bilateral inferior temporal cortex, and crus 1 in the right cerebellum. The opposite contrast (high > medium complexity rhythms) revealed no significant activations. Contrasting musicians versus non-musicians (musicians > non-musicians; averaging over all stimuli conditions) revealed activations in the bilateral caudate, bilateral motor cortex (extending into dorsal premotor cortices), bilateral SMA, right prefrontal cortex, right Heschl's gyrus, and left posterior superior temporal gyrus (see Table 4.3 and Figure 4.4). There were no significant activations in the reverse contrast (non-musicians > musicians), nor activations related to harmonic complexity, nor interactions between rhythmic and harmonic complexity or group.

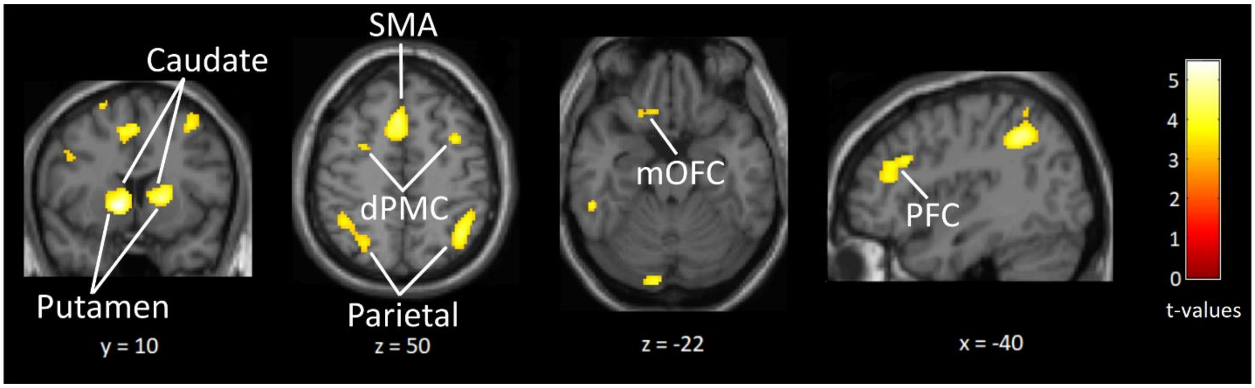

Figure 4.3. Results of the medium > high rhythmic complexity contrast. dPMC, dorsal premotor cortex; mOFC, medial orbitofrontal cortex; PFC, prefrontal cortex; SMA, supplementary motor area. Images are thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Table 4.2. Stereotaxic Locations of Peak Voxels in the Medium > High Rhythmic Complexity Contrast. Peak activations thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Brain region	Cluster size	t(208)	*p*FDR	x	y	z
L putamen	345	5.53	0.004	-14	10	-2
L thalamus		3.61	0.026	-2	-2	8
R putamen	344	5.32	0.004	22	4	8
L inferior parietal lobule	681	4.72	0.007	-42	-48	44
		4.57	0.008	-28	-58	40
		4.35	0.01	-36	-54	40
L SMA	321	4.57	0.008	-6	20	48
		4.31	0.01	-4	12	52
L inferior temporal gyrus	153	4.53	0.008	-58	-40	-18
R angular gyrus	557	4.34	0.01	38	-58	50
R superior parietal lobule		4.32	0.01	34	-66	56
R angular gyrus		4.16	0.011	36	-50	38
L superior frontal gyrus	59	4.32	0.01	-24	14	68
L SMA	210	4.27	0.01	-8	-10	60
R SMA		3.64	0.025	8	-4	68
R middle frontal gyrus	95	4.2	0.011	34	6	52
R inferior temporal	50	3.97	0.015	58	-36	-16
L cerebellum, Crus1	74	3.93	0.015	-14	-92	-22
L inferior frontal pars triangularis	272	3.87	0.017	-40	26	28
L middle frontal gyrus		3.81	0.019	-38	36	16
R cerebellum, Crus 2	22	3.71	0.022	38	-68	-46
R pons	1	3.57	0.028	6	-20	-44
Calcarine sulcus	18	3.54	0.029	0	-82	-12
L superior frontal gyrus	8	3.51	0.03	-20	64	0
L middle frontal gyrus	13	3.47	0.032	-28	0	50
L superior parietal lobule	16	3.46	0.032	-32	-60	62
L medial orbital gyrus	18	3.46	0.033	-14	26	-22
L anterior orbital gyrus		3.36	0.039	-22	24	-22
L anterior cingulum	3	3.41	0.036	-12	32	28
L precentral gyrus	8	3.4	0.036	-16	-18	72
R mid cingulum	21	3.34	0.039	4	-4	30
L precentral gyrus	31	3.34	0.04	-46	8	32
R cerebellum, Crus 2	5	3.33	0.04	12	-88	-28
L frontal superior gyrus	1	3.27	0.044	-16	66	2
R inferior temporal	2	3.27	0.044	42	-50	-8
L precentral gyrus	3	3.26	0.045	-36	6	46
L frontal operculum	1	3.21	0.048	-46	14	2

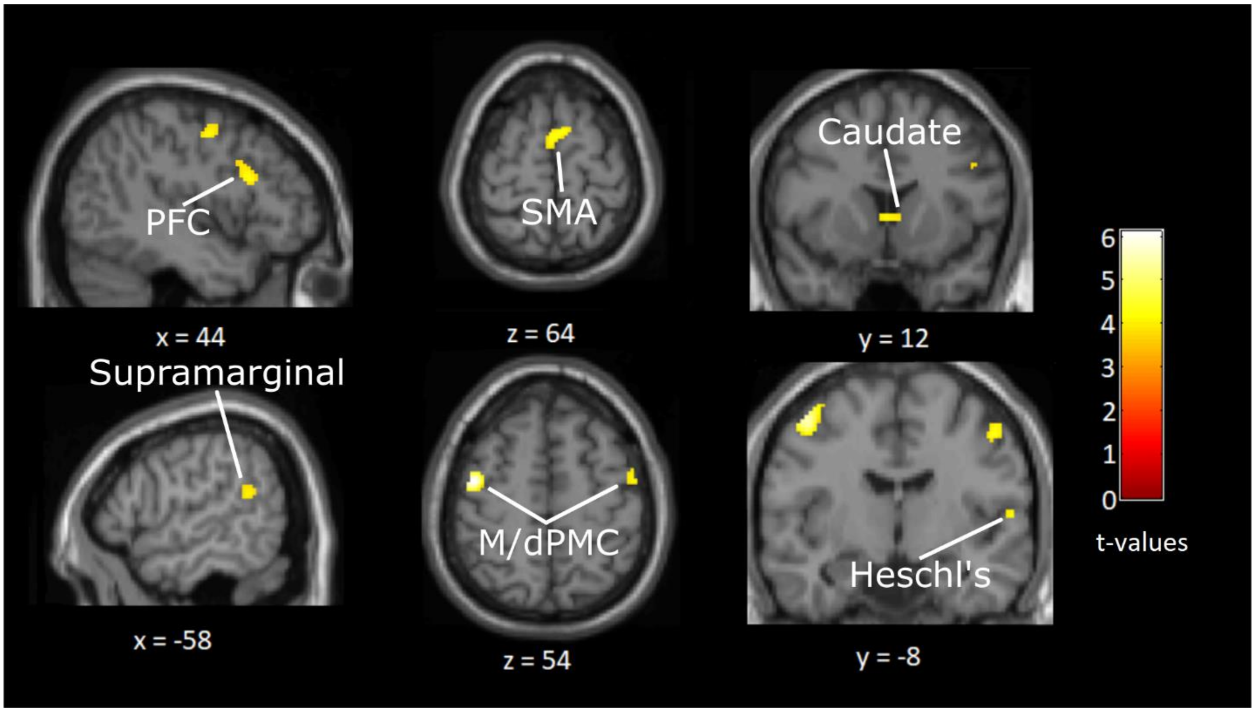

Figure 4.4. Results of the musician > non-musician contrast. M/dPMC, motor/dorsal premotor cortex; PFC, prefrontal cortex; SMA, supplementary motor area. Images are thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Table 4.3. Stereotaxic Locations of Peak Voxels in the Musicians > Non-Musicians Contrast. Peak activations thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Brain region	Cluster size	t(208)	*p*FDR	x	y	z
L precentral gyrus	162	6.1	0	-46	-4	54
White matter	89	4.84	0.004	-38	-42	20
White matter		4.44	0.015	-40	-44	12
R precentral gyrus	105	4.33	0.018	46	-6	48
L SMA	101	4.24	0.023	-2	2	64
R inferior frontal pars triangularis	63	4.19	0.024	44	18	24
R Heschl's gyrus	8	4.16	0.025	56	-8	6
L caudate	55	4.04	0.031	-4	12	4
L superior temporal gyrus	43	4.01	0.032	-58	-48	18
White matter	15	3.98	0.033	22	-12	32
R supramarginal gyrus	3	3.73	0.045	56	-36	26

ROI Results

Activity in the right NAcc showed a rhythm by harmony interaction ($\chi^2(1) = 6.50$, $p = .011$). The difference between activation for Mr-Mh versus Mr-Hh (MD = 0.132) was greater than Hr-Mh versus Hr-Hh (MD= -0.063; $b = 0.195$, 95% CI[0.048, 0.343]; Figure 4.5B) showing that the largest activation was for stimuli with medium complexity rhythms combined with medium complexity chords. Activity in the left NAcc showed a main effect of rhythmic complexity ($\chi^2(1) = 3.99$, $p = .046$) with greater activation for medium compared to high complexity rhythms ($b = 0.074$, 95% CI[0.001, 0.148]; Figure 4.5C). Activity in the caudate showed main effects for both rhythmic complexity ($\chi^2(1) = 12.43$, $p < .001$) and group ($\chi^2(1) = 5.48$, $p = .019$), with greater activation for medium compared to high complexity rhythms ($b = 0.083$, 95% CI[0.038, 0.129]; Figure 4.5D) and greater activation in musicians compared to non-musicians ($b = 0.184$, 95% CI[0.030, 0.337]). Activity in the putamen also showed a main effect of rhythmic complexity ($\chi^2(1) = 5.93$, $p = .015$), with greater activation for medium compared to high complexity rhythms ($b = 0.073$, 95% CI[0.015, 0.129]; Figure 4.5E). In a post-hoc analysis, activity in the mOFC also showed a main effect of rhythmic complexity ($\chi^2(1) = 6.67$, $p = .01$), with greater activation for medium compared to high complexity rhythms ($b = 0.063$, 95% CI[0.015, 0.111]).

In order to assess the overlap in variance accounted for in the ROI activations by pleasure and wanting to move ratings, the hierarchical regression was implemented twice per ROI, once with pleasure added to the model first and once with wanting to move ratings added first (see Table 4.4 for results). In addition, final models with both the significant predictors from the hierarchical analyses as well as models with both wanting to move and pleasure as predictors, both alone and together, were assessed (see Table 4.5 for results and Figure 4.6 for summary).

Analyses on the right NAcc activations showed that pleasure and wanting to move ratings accounted for overlapping variance, but only pleasure ratings accounted for variance over and above that of beat strength ratings. For the left NAcc activations, both pleasure and wanting to move ratings accounted for variance over and above beat strength ratings, but the variance they accounted for was strongly overlapping. For activity in the caudate, wanting to move but not pleasure ratings, accounted for variance over and above beat strength ratings. A near-significant trend showed that wanting to move ratings accounted for marginally unique variance compared to pleasure ratings. Analyses on the putamen activations showed that wanting to move ratings accounted for unique variance over and above that accounted for by both beat strength and pleasure ratings. In addition, there was an interaction between group by beat strength ratings, however, due to overlapping variance accounted for, the nature of this interaction depended on the inclusion of wanting to move ratings. Finally, in the mOFC, results showed that wanting to move ratings accounted for variance over and above pleasure ratings. In the final models, wanting to move ratings accounted for unique variance, however, this affect only approached significance.

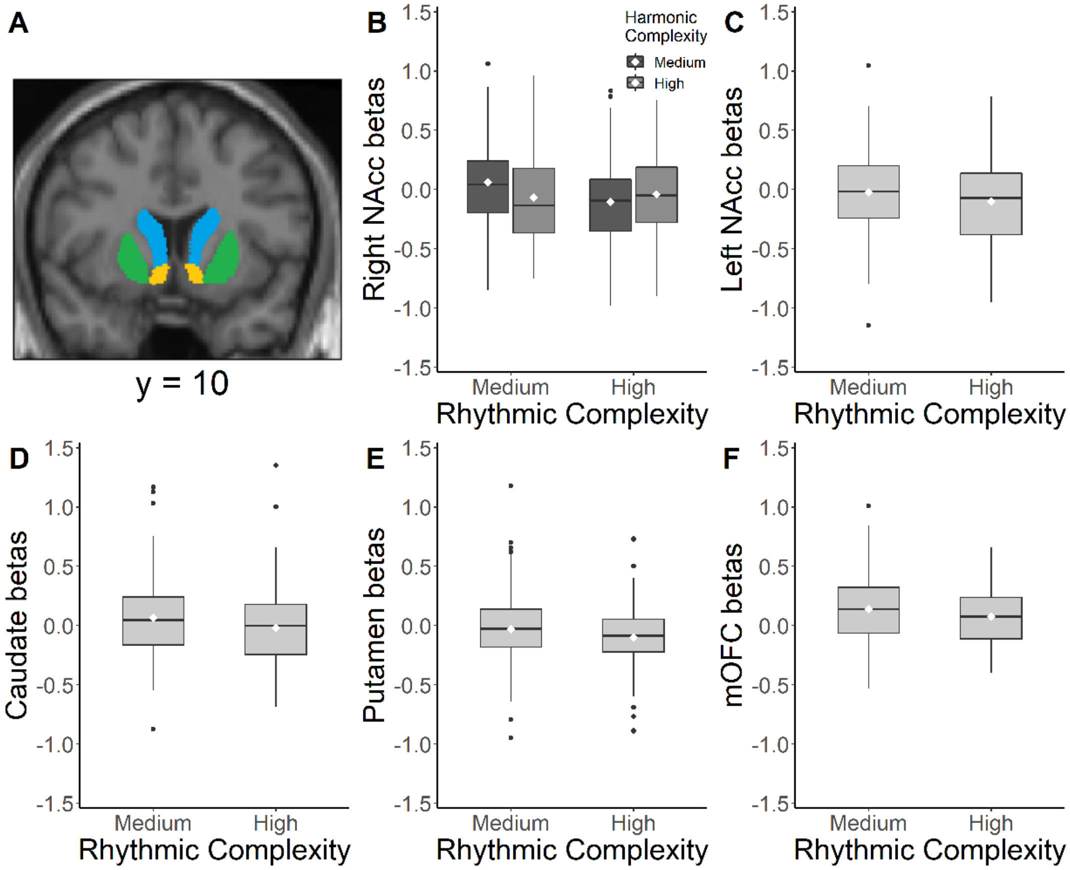

Figure 4.5. Results of ROI analysis. **A.** Coronal view of a single subject MNI template showing BG masks from probabilistic anatomical atlas used in region of interest analyses (Hammers et al., 2003). Blue, caudate; Green, putamen; Orange, nucleus accumbens. **B.** Right nucleus accumbens activation as a function of rhythmic and harmonic complexity. **C.** Left nucleus accumbens activation as a function rhythmic complexity. **D.** Caudate activation as a function of rhythmic complexity. **E.** Putamen activation as a function of rhythmic complexity. **F.** Medial

orbitofrontal cortex activation as a function of rhythmic complexity. NAcc, nucleus accumbens; mOFC, medial orbitofrontal. Center line, median; white dots, means; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; black dots, outliers.

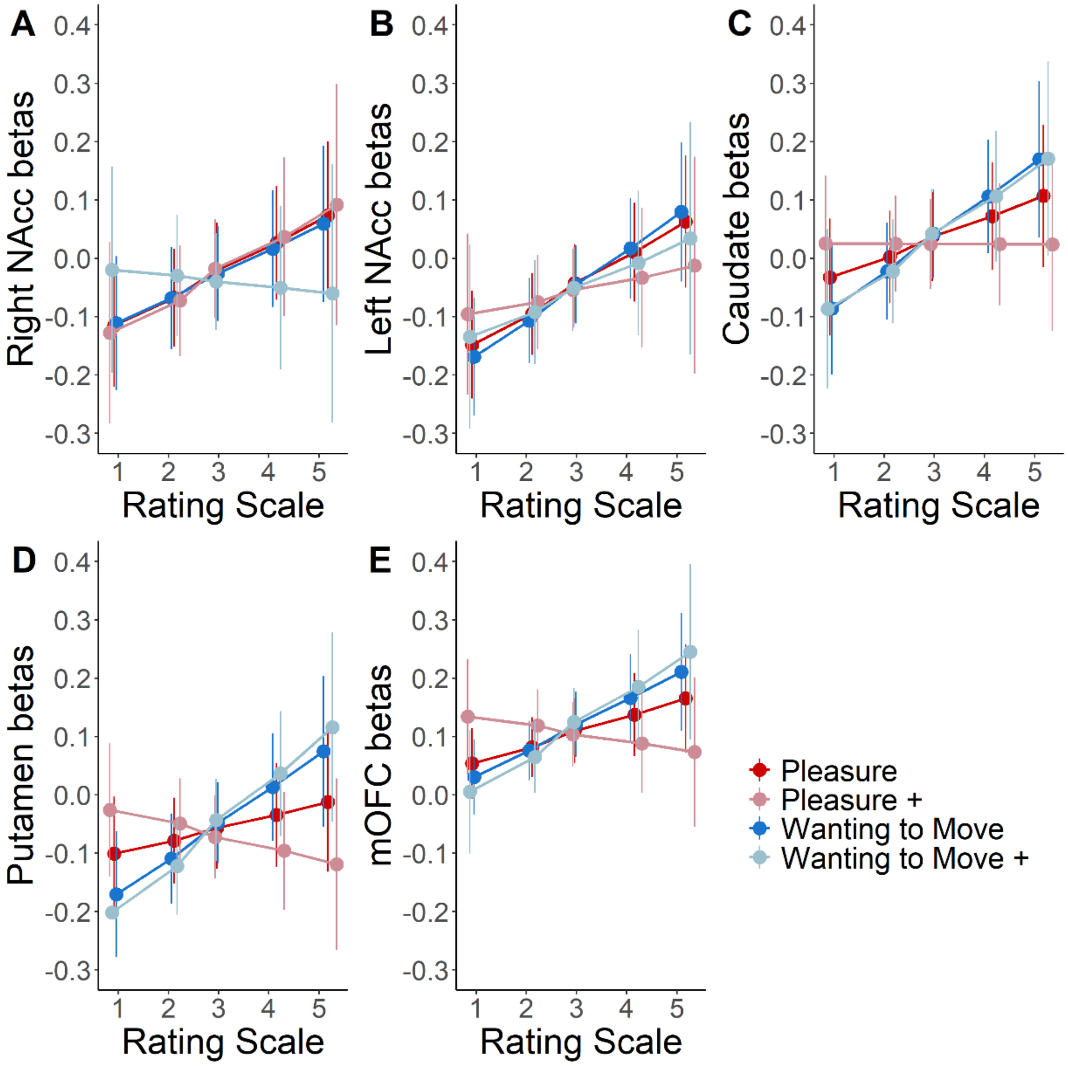

Figure 4.6. Estimated means from regression models testing the effects of pleasure and wanting to move ratings on activation in the regions of interest. Pleasure + denotes models that also include wanting to move ratings and Wanting to Move + denotes models that also include pleasure ratings. Points on the graphs represent estimated mean activations for each rating on the five-point scale of the indicated rating type, while holding the other effects constant at their means. **A.** Right nucleus accumbens. Pleasure and Wanting to Move denote estimated means

from models with only those predictors. **B.** Left nucleus accumbens. The models are identical to those in A. **C.** Caudate. All models also include group and beat strength ratings as predictors. **D.** Putamen. All models also include group and beat strength ratings as predictors, as well as an interaction between the two. **E.** Medial orbitofrontal cortex. The models are identical to those in A. NAcc, nucleus accumbens; mOFC, medial orbitofrontal cortex.

Table 4.4. Results of Hierarchical analysis Testing the Association between ROI Activations and Subjective Ratings.

Region	Order	Predictor	$\chi^2(1)$	*p* value
R NAcc				
		Group	2.165	0.141
		Beat	0.868	0.352
	Pleasure First	Pleasure	4.501	0.034
		Move	0.084	0.772
	Move first	Move	2.534	0.111
		Pleasure	2.050	0.152
L NAcc				
		Group	0.487	0.485
		Beat	2.649	0.104
	Pleasure First	Pleasure	4.172	0.041
		Move	1.751	0.186
	Move first	Move	5.389	0.020
		Pleasure	0.534	0.465
Caudate				
		Group	5.481	0.019
		Beat	4.956	0.026
	Pleasure First	Pleasure	2.812	0.094
		Move	3.636	0.057
	Move first	Move	6.448	0.011
		Pleasure	0.000	0.984
Putamen				
		Group	0.863	0.353
		Beat	1.607	0.205
	Pleasure First	Pleasure	3.499	0.061
		Move	3.913	0.048
		Group:beat	9.922	0.002
	Move first	Move	7.401	0.007
		Pleasure	0.011	0.917
mOFC				
		Group	2.510	0.113
		Beat	3.329	0.068
	Pleasure First	Pleasure	0.630	0.427

	Move	4.414	0.036
Move first	Move	4.499	0.034
	Pleasure	0.546	0.460

Beat, beat strength ratings; Move, wanting to move ratings; Pleasure, pleasure ratings; NAcc, nucleus accumbens; mOFC, medial orbitofrontal cortex.

Table 4.5. Final Models Testing the Association between ROI Activations and Subjective Ratings

Region	Model	Predictor	β	95% CI
R NAcc				
	Pleasure		0.047	[0.004, 0.089]
	Move		0.042	[-0.004, 0.090]
	Pleasure and Move	Pleasure	0.055	[-0.026, 0.137]
		Move	-0.010	[-0.104, 0.082]
L NAcc				
	Pleasure		0.053	[0.015, 0.092]
	Move		0.062	[0.018, 0.107]
	Pleasure and Move	Pleasure	0.021	[-0.053, 0.094]
		Move	0.042	[-0.040, 0.123]
Caudate				
	Group and Beat	Group	0.182	[0.035, 0.335]
		Beat	0.026	[0.003, 0.049]
	Group, Beat, and Pleasure	Pleasure	0.035	[-0.006, 0.075]
	Group, Beat, and Move	Move	0.064	[0.014, 0.113]
	Group, Beat, Pleasure, and Move	Pleasure	-0.001	[-0.056, 0.053
		Move	0.064	[-0.000, 0.132]
Putamen				
	Group*Beat		-0.073	[-0.120, -0.026]
	Group*Beat, and Pleasure	Pleasure	0.022	[-0.020, 0.063]

	Group*Beat, and Move	Move	0.061	[0.013, 0.109]
	Group*Beat, Pleasure, and Move	Pleasure	-0.023	[-0.080, 0.031]
		Move	0.079	[0.014, 0.145]
mOFC				
	Pleasure		0.028	[0.000, 0.057]
	Move		0.045	[0.016, 0.077]
	Pleasure and Move	Pleasure	-0.015	[-0.067, 0.036]
		Move	0.060	[-0.000, 0.119]

Beat, beat strength ratings; Move, wanting to move ratings; Pleasure, pleasure ratings; NAcc, nucleus accumbens; mOFC, medial orbitofrontal cortex. Group*Beat, a group by beat strength ratings interaction plus the main effect of each.

Discussion

In this study we set out to understand the brain networks involved in the sensation of groove. Consistent with previous findings, participants experienced a stronger sensation of groove for medium compared to high levels of both rhythmic and harmonic complexity, with higher ratings of pleasure and wanting to move (Matthews et al., 2019). This was coupled with greater activity for medium complexity rhythms in reward-related regions including the NAcc, caudate, and mOFC, and in regions associated with beat-based timing including the putamen, SMA, as well as prefrontal and parietal cortices. In addition, in both the left and right nucleus accumbens, pleasure and wanting to move ratings predicted activity to a similar degree, largely accounting for the same variance. In the mOFC, there was overlap in variance accounted for by wanting to move and pleasure, however, wanting to move was a stronger predictor. In the putamen, wanting to move ratings accounted for variance over and above that accounted for by both pleasure and beat strength ratings. In the caudate, wanting to move ratings and beat strength ratings accounted for overlapping variance. Finally, musicians showed overall greater activity in regions associated with beat perception.

Together, these findings suggest that the sensation of groove is driven by a combination of motor and reward regions in the brain. We interpret these results in the context of rhythmic expectations, suggesting that the generation of these expectations based on a regular beat, and their violation via syncopations, are core drivers of groove (Matthews et al., 2019; Vuust & Witek, 2014). Based on this formulation, we propose a theoretical model of the brain mechanisms underlying groove that is centered on the cortico-striatal circuits thought to underlie predictive timing and reward processing.

Medium complexity rhythms drive the sensation of groove

Behavioural results showed that medium complexity rhythms led to higher ratings of pleasure, wanting to move, and beat strength. Only the medium and high complexity conditions were included in order to maximize the number of trials per condition. Therefore, we could not confirm an inverted U-shaped pattern of ratings here. However, ratings for the medium and high complexity rhythms are consistent with those obtained in our previous study which included the low complexity condition (Matthews et al., 2019). Therefore, the current results provide further evidence that medium complexity rhythms strongly contribute to the sensation of groove.

Consistent with previous results, medium complexity chords in combination with medium complexity rhythms increased pleasure ratings, providing further evidence that harmony enhances the affective component of groove (Matthews et al., 2019). Intriguingly, ratings of beat strength were also enhanced by medium complexity chords, supporting previous work showing that beat and metre perception are not driven by rhythmic factors alone (Dawe et al., 1993; Hannon et al., 2004). Finally, for musicians, the combination of medium complexity rhythms and chords enhanced the desire to move, suggesting that for those with musical training, the sensation of groove is more affected by non-rhythmic factors.

The sensation of groove involves reward regions of the brain

fMRI results showed that medium complexity rhythms were associated with greater activity in the left NAcc and left mOFC. Converging evidence from neuroimaging studies suggests that the NAcc and mOFC are important for the experience of music-derived pleasure (Koelsch, 2014; Martinez-Molina et al., 2019; Martínez-Molina et al., 2016; Salimpoor et al., 2013). Here, activity in both left and right NAcc also showed a positive association with both pleasure and wanting to move ratings, suggesting an association with groove overall rather than the pleasure component alone. One explanation may be that the NAcc is not only involved in the experience of music-derived pleasure, but also in the processing of expectations that can lead to such pleasure (Gebauer et al., 2012; Koelsch, 2014; Salimpoor et al., 2015). For example, NAcc activation has recently been associated with musical uncertainty (Cheung et al., 2019) and musical surprise (Shany et al., 2019), and has also been shown to track reward prediction errors associated with harmonic violations (Gold, Mas-herrero, et al., 2019). In the current study, the right NAcc showed greater activation in response to the combination of medium complexity rhythms and chords, which was the condition that elicited the highest pleasure and wanting to move ratings. Interestingly, this was the only region to show an effect of harmonic complexity, which might relate to the right-dominance of regions involved in tonal processing (Zatorre, Belin, & Penhune, 2002).

Activity in the mOFC has been associated with assigning affective value to stimuli, including music (Zatorre & Salimpoor, 2013). However, in the current results mOFC activity showed a stronger association with wanting to move ratings than with pleasure ratings. A more recent hypothesis suggests that OFC involvement in value assignment is contingent on whether this process involves mental simulation of behavioural outcomes (Stalnaker, Cooch, & Schoenbaum, 2015). This is consistent with the current results as wanting to move ratings, in contrast to pleasure ratings, may involve action simulation. Therefore, one possibility is that the NAcc encodes the positive affective state of groove, while the mOFC encodes the association between the music and the desire to move.

The sensation of groove involves motor regions of the brain

Our results also showed greater activation in bilateral putamen and caudate as well as the SMA (including pre-SMA) and bilateral dorsal premotor cortices for medium complexity rhythms. The putamen and the SMA are part of the cortico-striatal ‘motor circuit’ (Alexander et al., 1986) and together with the caudate are suggested to be crucial nodes in both the striatal beat-frequency and pacemaker-accumulator models of timing (Coull et al., 2011; Matell & Meck, 2004; Merchant, Harrington, & Meck, 2013). In addition, recent theories suggest that temporal predictions are generated in the motor system via covert and unconscious action simulation (Arnal, 2012; Patel & Iversen, 2014; Rimmele et al., 2018; Ross et al., 2016; Schubotz, 2007). This is supported by a recent study showing that temporal predictions in the context of regular auditory stimuli are driven by motor signals to the auditory cortex (Morillon & Baillet, 2017). In the context of beat perception, the efferent signals of these covert actions may act as an internal representation of the beat, or 'pacing signal' (Kotz et al., 2016), informing beat-based expectations.

Converging evidence suggest that the putamen, SMA and dorsal premotor cortices are crucial for generating an internal representation of a beat (Araneda et al., 2016; Grahn & Brett, 2007; Grahn & Rowe, 2009; Merchant et al., 2015), with the putamen seeming particularly important (Grahn & Rowe, 2013). Studies with both Parkinson's disease (Grahn & Brett, 2009) and lesion patients (Nozaradan, Schwartze, et al., 2017) also support the importance of the BG in beat perception. Furthermore, oscillatory activity in the SMA and putamen has been shown to entrain to frequencies denoting the beat and metre, respectively (Li et al., 2019). However, two recent studies using transcranial magnetic stimulation (TMS) support the role of the dorsal premotor cortex (Ross et al., 2018a) but not the SMA (Ross et al., 2018b) in beat perception.

Interestingly, the caudate was the only region of interest whose activity showed a main effect of beat strength ratings. However, further analysis revealed strong overlap between the effects of beat strength and wanting to move ratings in this region. Beat strength ratings did show a relation to putamen activity via an interaction with group, the nature of which also depended on the inclusion of wanting to move ratings in the model. Together these results provide further evidence that beat perception and motor activation are strongly linked, both in terms of subjective experience and neural underpinnings.

The sensation of groove involves frontoparietal networks

Medium complexity rhythms also elicited increased activation in bilateral parietal (with peaks in inferior and superior parietal lobules) and left prefrontal cortical regions. Parietal and prefrontal regions are components of both the dorsal auditory (Hickok & Poeppel, 2004; Rauschecker, 2011) and the fronto-parietal networks (Ptak et al., 2017), which are thought to underlie the motor representations of stimuli allowing for the processing of sensory input that evolves over time (Ptak et al., 2017; Rauschecker, 2011). These regions have also been implicated in the cognitive aspects of temporal and rhythmic processing including temporal attention (Bolger et al., 2014; Coull & Nobre, 2008; Coull et al., 2011; Davranche et al., 2011; Nobre & van Ede, 2017), encoding and retrieval of beat-based time intervals (Konoike et al., 2015, 2012), and rhythmic deviant detection (Lappe, Lappe, & Pantev, 2016; Lappe, Steinsträter, et al., 2013). A recent TMS study showed that down-regulating parietal activity disrupts perception of phase shifts of the beat (Ross et al., 2018b). These results are consistent with the parietal cortices purported role as the interface between motor-driven temporal predictions and sensory input (Rauschecker, 2011; Rimmele et al., 2018).

Prefrontal activity during beat perception has been linked to precision of sensory predictions (Bengtsson et al., 2009) and working memory (Kung et al., 2013), consistent with its role in beat-based timing (Teki et al., 2011). Therefore, the dorsal prefrontal activity seen here may represent the generation of beat-based expectations and monitoring of their outcome. The caudate is strongly connected to prefrontal and parietal regions (Haber, 2016), and both whole-brain and ROI analyses showed greater caudate activation for medium complexity rhythms. A recent study using TMS suggests that a left dorsolateral prefrontal-caudate circuit determines music liking and wanting by coding musical expectancies based on structural properties (Mas-herrero, Dagher, & Zatorre, 2018). In the current context, prefrontal and parietal regions, along with the caudate, may generate and update beat-based expectations and compare these expectations to incoming stimuli.

Musicians show greater activation in regions associated with beat-based timing

Although the overall pattern of activity was similar for both groups, musicians showed greater activity in the caudate, right prefrontal cortex, SMA, primary and premotor cortex and primary and secondary auditory regions, compared to non-musicians, regardless of rhythm complexity. Musicians have shown greater activity in the SMA and premotor cortex (Grahn & Brett, 2007) and greater connectivity between SMA and auditory regions (Grahn & Rowe, 2009) during rhythm perception tasks. Together, these results suggest that musical training leads to greater engagement of regions involved in beat perception as well as stronger auditory-motor associations (Alluri et al., 2017; Zatorre, Chen, & Penhune, 2007). This is in line with the current behavioural findings, as well as those from a previous study showing that musicians are more sensitive to rhythmic and harmonic manipulations (Matthews et al., 2019), and with results showing greater neural responses to rhythmic deviants (Geiser, Sandmann, Jancke, & Meyer, 2010; Habibi, Wirantana, & Starr, 2014; Vuust et al., 2009).

A proposed model

We propose a theoretical model integrating the current results with previous work discussed above. According to this model, the putamen, along with the SMA and premotor cortices automatically generate an internal representation of the beat. These regions interact with the caudate, prefrontal, and parietal regions which use this beat representation to inform rhythmic expectations and compare them to incoming stimuli. These regions may also use this beat information to generate higher-level expectations regarding the way music will unfold over longer timescales (Salimpoor et al., 2015). Information from both the putamen and caudate networks may then be passed to the NAcc-mOFC circuit which generates a positive affective response, including both pleasure and the desire to move, and assigns value to both rhythmic and higher-level expectations. Medium complexity rhythms activate these networks as they are regular enough to allow for internal beat generation, but also contain syncopations that challenge this regularity and thus engage expectation processes leading to the pleasurable desire to move. In addition, the repetition of rhythmic patterns, used here in our stimuli and common in groove-based music (Danielsen, 2006), may engage processes involved in higher-level expectations. Furthermore, musical training may strengthen these expectations and the brain networks that support them. Finally, although rhythm appears to be the primary feature influencing groove, other factors, including harmony and familiarity also enhance pleasure (Matthews et al., 2019; Pereira et al., 2011; Senn, Bechtold, Hoesl, & Kilchenmann, 2019; van den Bosch, Salimpoor, & Zatorre, 2013).

Conclusion

The current study sought to investigate the brain networks underlying the pleasurable desire to move to music, known as the sensation of groove. Medium complexity rhythms led to greater activity in brain regions associated with both motor timing and reward. Subjective ratings of pleasure and wanting to move were associated with activity in BG regions of interest supporting their crucial role, not only in processing rhythmic complexity, but also in the subjective experience of groove. These results provide novel evidence supporting the formulation of groove as the intersection of motor timing and reward processes. Based on this formulation, we propose a model in which different cortico-striatal networks support the generation and affective valuation of beat-based expectations. Future studies will test the interactions between these networks, leading to a better understanding of how prediction and reward-based mechanisms work together.

Supporting Information

```
Weights    0 -5 -4 -5 -3 -5 -4 -5 -2 -5 -4 -5 -3 -5 -4 -5 -1 -5 -4 -5 -3 -5 -4 -5 -2 -5 -4 -5 -3 -5 -4 -5  ||
Count      1···e···&···a···2···e···&···a···3···e···&···a···4···e···&···a···||
Hi-hat     x·······x·······x·······x·······x·······x·······x·······x·······||
Son        x···········x···········x···············x···············x·······||
Rumba      x···········x···············x···········x···············x·······||
Mariato    x···············x·······x···········x···················x·······||
High 1     x·····x···············x···················x···············x·····||
High 3     x·········x·······x···············x···················x·········||
High 7     x···········x·····x···················x···············x·········||
```

Figure S4.1. Schematic representation of rhythms with onsets (‘x’) shown on a grid. Weights refer to those used to calculate the syncopation index. Count shows the musical counting (traditional American system) with numbers denoting the beat, ‘&’ denoting eighth notes, and ‘e’ and ‘a’ denoting sixteenth notes.

Table S4.1. Notes and corresponding frequencies for each chord

Chord Type	Notes	Frequencies (Hz)
Medium		
	D2, G3, C4, E4, B4, D5	73.416, 196.00, 261.60, 329.63, 493.88, 587.33
	D2, F#3, C4, E4, A4, D5	73.416, 185.00, 261.60, 329.63, 440.00, 587.33
	D2, F#3, B3, E4, A4, D5	73.416, 185.00, 246.94, 329.63, 440.00, 587.33
High		
	D2, F#3, A3, C#4, A#4, D#5	73.416, 185.00, 220.00, 277.18, 466.16, 622.25
	D2, F#3, A3, C#4, G4, D#5	73.416, 185.00, 220.00, 277.18, 392.00, 622.25
	D2, F#3, A3, G4, A#4, D#5	73.416, 185.00, 220.00, 392.00, 466.16, 622.25

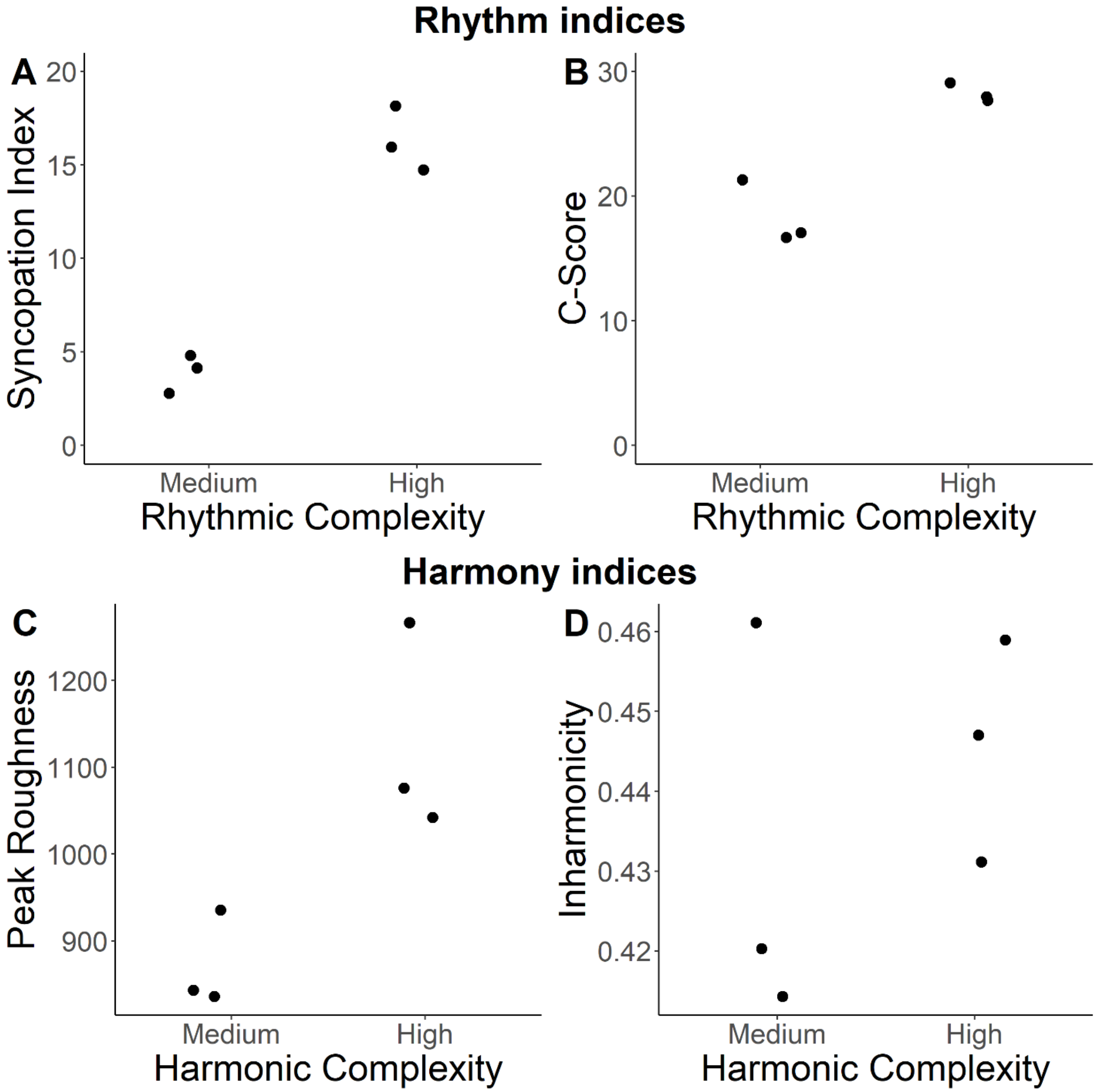

Figure S4.2. Indices of rhythmic and harmonic complexity for all stimuli. **A.** Syncopation indices. **B. C**-scores. **C.** Peak roughness. **D.** Inharmonicity. See main text for details.

Table S4.2 Stereotaxic Locations of Peak Voxels in the Medium > High Rhythmic Complexity Contrast using GLM Flex. Peak activations thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Brain region	cluster size	t(52)	x	y	z
L. Caudate	302	4.0071	-8	0	12
L. Caudate	302	3.868	-14	4	18
L. Pallidum	302	6.2786	-14	8	0
R. Caudate	244	4.3744	8	8	4
R. Pallidum	244	4.6245	16	8	2
R. Putamen	244	5.3596	22	4	8
L. Supplementary Motor Area	187	4.8392	-10	16	48
L. Supplementary Motor Area	187	4.3533	-4	12	52
L. Inferior Temporal Gyrus	117	4.6466	-56	-46	-16
R. Angular Gyrus	127	4.0359	38	-58	52
R. Superior Parietal Lobule	127	4.4686	36	-66	56
L. Inferior Parietal Lobule	126	4.0674	-40	-50	44
L. Inferior Parietal Lobule	126	3.9164	-28	-58	40
L. Superior Frontal Gyrus - Orbital Part	4	3.7934	-14	26	-22
R. Inferior Temporal Gyrus	6	3.7718	58	-34	-16
R. Supplementary Motor Area	6	3.7685	8	-4	70
L. Inferior Frontal Operculum	3	3.7425	-46	12	2
L. Supplementary Motor Area	2	3.6768	-14	-4	56
R. Cerebellum Crus II	2	3.6638	38	-68	-44
L. Superior Frontal Gyrus	1	3.6144	-20	16	68

Table S4.3. Stereotaxic Locations of Peak Voxels in the High > Medium Rhythmic Complexity Contrast using GLM Flex. Peak activations thresholded at $p < 0.05$, FDR corrected at the whole-brain level.

Brain region	Cluster size	t(52)	x	y	z
L. Middle Temporal Gyrus	282	-4.6228	-60	-20	-2
L. Middle Temporal Gyrus	282	-3.9921	-50	-34	8
L. Superior Temporal Gyrus	282	-4.804	-65	-34	10
L. Superior Temporal Gyrus	282	-4.5049	-66	-22	8
R. Superior Temporal Gyrus	42	-4.4466	60	-20	2

Table S4.4. Stereotaxic Locations of Peak Voxels in the Musicians > Non-Musicians Contrast using GLM Flex. Peak activations thresholded at $p < 0.001$, uncorrected at the whole-brain level.

Brain region	Cluster size	t(52)	x	y	z
undefined	125	-4.7278	22	-12	32
L. Precentral Gyrus	141	-4.6829	-46	-6	54
L. Caudate	217	-4.5725	-6	14	4
L. Caudate	217	-4.2379	0	6	2
R. Inferior Temporal Gyrus	27	-4.2699	42	-6	-26
R. Inferior Frontal Gyrus - pars triangulars	223	-4.0682	44	22	24
R. Inferior Frontal Operculum	223	-4.1822	44	14	30
R. Supplementary Motor Area	117	-4.0308	2	4	68
R. Middle Cingulate Cortex	9	-3.8583	18	-20	46
L. Middle Temporal Gyrus	10	-3.6997	-38	-46	10
R. SupraMarginal Gyrus	21	-3.689	48	-36	34
L. Insula	27	-3.6771	-22	30	12
R. Angular Gyrus	10	-3.5177	34	-50	32
R. Inferior Parietal Lobule	20	-3.5097	36	-50	46
R. Middle Cingulate Cortex	12	-3.5078	6	-4	28
L. Middle Frontal Gyrus	9	-3.4263	-46	22	32
R. Precentral Gyrus	7	-3.375	46	-10	46
L. Postcentral Gyrus	7	-3.352	-46	-16	48
L. Fusiform Gyrus	1	-3.3264	-32	-66	-18
R. Inferior Parietal Lobule	2	-3.2699	46	-46	48
L. Middle Frontal Gyrus	1	-3.2557	-26	34	22

CHAPTER FIVE:

GENERAL DISCUSSION

5.1 General Discussion

The work presented in this thesis sought to investigate the sensation of groove from three different angles: the interaction between rhythm and harmony, the perception of self-generated movement, and the brain regions implicated in the underlying processes. Results from Article 1 suggest that harmonic complexity affects the sensation of groove via its effect on pleasure and its interaction with rhythmic complexity. Article 2 provides evidence that the perception of synchrony between self-generated movements and a musical beat contributes to groove to a greater degree than measured synchrony. Finally, Article 3 suggests that the motor, limbic, and associative cortico-striatal networks implicated in beat perception and music-derived reward underlie the sensation of groove. The following sections will discuss these results in the context of predictive coding and dynamic attending frameworks (and their relatives), with temporal predictions as a common mechanism. In doing so, I will try to illustrate how groove provides a novel way to integrate these frameworks, and to study the interaction of the underlying processes.

5.2 Theoretical Frameworks of Rhythm Perception

The sensation of groove reflects the intrinsic link between perception, movement, and reward. Temporal predictions are a common element linking these processes. Predictive processes are ubiquitous in theories of perception. Two theoretical frameworks that have been applied to rhythm processing and groove are predictive coding (PC) and dynamic attending theory (DA). Both frameworks describe perception as an active process involving interactions between stimulus-driven and endogenous predictive processes. PC models perception as an inferential process in which predictions are generated based on internal models of the environment (or task/stimulus). Prediction errors, which reflect a mismatch between model and sensory input, lead to adjustments in the model depending on their weight, which is determined by the certainty (formalized as precision) of the antecedent prediction (Friston, 2019). DA suggests that perception is driven by ongoing, endogenous oscillations of attention, with peaks of attention aligning to salient components of the input. These frameworks are particularly well-suited to auditory perception in which temporally structured sequences, such as speech and music, allow for the extraction of temporal regularities to predict incoming stimuli and thus facilitate perception (Arnal & Giraud, 2012; Giraud & Poeppel, 2012). An isochronous rhythm provides an idealized example of these processes as the perfect temporal regularity allows for a highly precise and accurate internal representation, and thus highly accurate and precise temporal predictions. This allows for a near-optimal interaction between internal model, incoming stimuli, and behaviour. For example, participants show greater sensitivity and faster reaction times when detecting target sounds within isochronous or rhythmic compared to non-isochronous or random sequences (Ellis & Jones, 2010; ten Oever, Schroeder, Poeppel, van Atteveldt, & Zion-Golumbic, 2014; van Atteveldt et al., 2015; Wollman & Morillon, 2018). In addition, an isochronous beat facilitates motor reproduction of multi-second time intervals (Daikoku, Takahashi, Tarumoto, & Yasuda, 2018). In the context of music, the isochronous beat provides a stable bedrock on which immensely complex structures can be built. This bedrock, and the sensitivity to deviations that flow from it, allows composers and performers to manipulate listeners' temporal and content predictions with a granularity unparalleled in other auditory inputs (Barrett & Schulkin, 2017). It is this fine-grained and highly sophisticated manipulation of expectations that is thought to drive the affective responses to music (Huron, 2006; Meyer, 1956; Salimpoor et al., 2015), including the urge to move and pleasure associated with groove (Vuust & Witek, 2014).

In the context of rhythm perception, PC and DA can be seen as compatible frameworks together providing a comprehensive, systems-level account of the underlying processes. Based on this integrated view, a regular auditory rhythm engenders an internal model of the beat, as proposed by PC, consisting of an entrained attentional oscillator, as proposed by DA. Rhythms with hierarchical structures (i.e., metre), will entrain multiple endogenous oscillators with natural rates corresponding to the different levels of the metrical hierarchy. Therefore, attentional oscillations comprise not only the internal model of the beat but also the metre (Large & Jones, 1999). This sets up implicit temporal predictions regarding future musical events, which when violated lead to prediction errors which, if strong enough, will necessitate an update of the model (e.g., via phase correction). According to DA, the strength of the entrainment, that is, how strongly the internal oscillator is synchronized with the external rhythm, determines the strength of the model which corresponds to the degree to which a listener 'feels the beat'. In turn, stronger entrainment leads to more certain temporal predictions. In both PC and DA, this certainty is formalized as the width (i.e., extension in time) of the probability distribution around each temporal prediction. In PC, certainty determines the weight or strength of prediction error, that is, the degree to which it will lead to a correction to the model (Koelsch et al., 2019; Large

& Jones, 1999; Vuust et al., 2018). Similarly, in DA the width of the certainty window (or attentional focus) determines the threshold with which a temporal prediction necessitates a phase correction of the oscillator. The width of the certainty window is influenced by a number of endogenous and exogenous factors including attention, musical experience, and properties of the stimulus (i.e., the rhythmic context).

The effect of relatively high or low certainty, reflected by narrow or wide distributions, on temporal prediction errors is illustrated in Figure 5.1. In the context of a metronome (Figure 5.1, upper section), certainty is high and even a small temporally shifted onset will fall outside of the narrow probability window. This will lead to a strongly weighted prediction error which will thus be more likely to be propagated up the processing hierarchy, lead to a surprise response, and an update of the model. Conversely, the same temporal shift may have no impact if it occurs in a more complex, and therefore less certain, rhythmic context (Figure 5.1, lower section). In this case, the shifted note will fall into a wider window of temporal certainty and be registered as either a prediction confirmation or a weakly weighted prediction error. Within both PC and DA, prediction certainty can be thought of as a cyclic pulse that is phase-aligned to the beat. Additionally, global attention can also have influence on certainty. For example, focused listening may further increase prediction certainty whereas distracted listening would reduce certainty, even for a highly regular beat. A similar distinction can be made between global and local certainty reflecting the certainty of global or local internal models. For example, the temporal prediction of a beat directly following a perturbation may have reduced local certainty. Global uncertainty may result from a mix of syncopated and unsyncopated beats spread over many phrases and may therefore rely more heavily on working memory as predictions are monitored and adjusted over time.

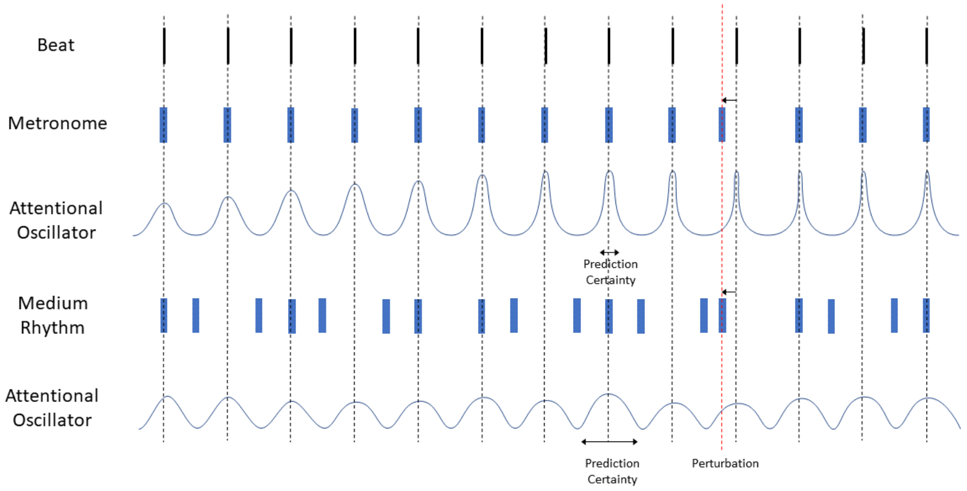

Figure 5.1. Beat-based predictions, prediction certainty, and prediction error in the context of an isochronous and non-isochronous rhythm. The underlying beat of both rhythms is represented by the solid and dashed black lines. Blue rectangles represent auditory onsets. The blue continuous lines represent the endogenous oscillators/internal models of the beat. An isochronous rhythm leads to highly certain predictions reflects in narrow pulses of attention. The non-isochronous rhythm leads to less certain predictions and thus wider windows. The same perturbation (red dashed line) engenders a strongly-weighted prediction error in the isochronous context, and a weakly-weighted prediction error (or a prediction confirmation) in the non-isochronous context.

Both PC and DA frameworks have relatives in active inference and active sensing models that account for the active nature of perception by linking it to overt or covert action. During overt action, motor effectors determine both the sensory input and the temporal context for this input. Efference copies of motor commands are sent to sensory and associative regions to temporally align perceptual processes to the input and to each other. This predictive alignment facilitates the selective processing of salient inputs as well as the synthesis of multimodal inputs into higher-level representations (Lakatos, Gross, & Thut, 2019). The same process also allows for attenuation of the sensory consequences of self-generated movements (Brown et al., 2013). This sensory attenuation is useful when the self-generated input, for example the sounds of one’s own footsteps, is not salient and thus to be ignored. According to active sensing, actions predictively align ongoing attentional oscillations to the sensory result of the movement, with the phase alignment determining whether there is amplification or attenuation of the sensory processing (Morillon & Schroeder, 2015; Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010). In active inference, actions are themselves predictions of their own sensory and kinematic consequences (Brown et al., 2013). Prediction error can therefore be minimized by changing the prediction, that is, adjusting the movement. Therefore, under both theories, motor commands provide temporal predictions to prepare sensory processes for an incoming signal and thus facilitate processing. Importantly, many motor processes are rhythmic (e.g., walking, breathing, chewing) which means the sensory input they generate is rhythmic. Therefore, there is an inherent rhythmicity and thus predictability to the link between action and perception.

In the case of passive auditory perception, our ears do not move to determine the auditory input. However, an implicit action-perception link is still thought to be in effect, with motor commands of covert actions providing the temporal prediction signal. Covert actions are those that are never carried out. Therefore, the associated motor computations are abstracted away from any specific motor effector (Cannon & Patel, 2020). However, the predictive spatio-temporal computations, for example, those necessary to clap your hands at a desired frequency and volume, still occur. The motor planning and timing functions underlying the vast repertoire of movements innate to humans, ranging from tens (e.g., speech) to hundreds of milliseconds (e.g., walking), are thus relied upon to organize sensory input (Schön & Morillon, 2019).

Rhythm perception is the ideal context for this action-perception contingency, allowing for the exploitation of innately rhythmic motor processes to predictively align perceptual (and other) processes to rhythmic input. This optimality is even more striking considering that the tempo of most music matches the rate of most natural movements, with both falling around 2 Hz on average (Ding et al., 2017; MacDougall & Moore, 2005). This suggests a predisposition to make and enjoy music that aligns to the natural rate of movement. That is, we tend to make music around this tempo because that is the tempo at which we naturally move. And, we enjoy listening to music at this tempo because it resonates with the natural frequency of our motor system. The reliance on motor commands of covert actions for temporal predictions has been proposed by several authors (Arnal, 2012; Morillon, Schroeder, Wyart, & Arnal, 2016; Morillon & Schroeder, 2015; Schubotz, 2007). An example of this theory within rhythm and beat perception is known as the action simulation for auditory perception (ASAP) hypothesis (Patel & Iversen, 2014).

5.3 Relating these Frameworks to Groove

The perception of groove has been consistently associated with a U-shaped relation between rhythmic complexity and ratings of the urge to move and pleasure. Further evidence of this relation is provided by Articles 1 and 2, which show this relation in separate samples and with different stimuli. In the context of PC, the inverted U is determined by a combination of the number of prediction errors, and the certainty or weight of these errors (Koelsch et al., 2019; Vuust & Witek, 2014; Vuust et al., 2018). By integrating this with DA, I suggest that the frequency and weight of these prediction errors is linked to the degree of entrainment of motor or attentional processes. As is shown in Figure 5.1 (upper section), a rhythm with few or no syncopations will strongly entrain attentional oscillators leading to highly certain predictions, which are generally confirmed, thus leading to very few prediction errors. Prediction errors lead to the refinement of internal models by engaging the motor processes generating the temporal predictions in the first place. I suggest that this automatic engagement of the motor system to reaffirm and test further temporal predictions leads to the urge to move.

Because refinement of the model based on prediction errors improves the match between model and environment, prediction errors constitute a learning signal. Since learning is adaptive, it is thought to be inherently rewarding (White, 1959). This in line with theories of intrinsic motivation which, in the context of learning, is the drive to get better at something as this improvement satisfies an innate need for competence and is thus inherently rewarding. Conversely, extrinsic motivation in learning is the drive to get better in order to receive an external, separable reward (e.g., a high grade; Ryan & Deci, 2000). This also aligns with the integration of concepts such as boredom and curiosity into models of learning (e.g., reinforcement learning), which are thought to affect a shift from exploitation to exploration (Dubey & Griffiths, 2020; Gomez-Ramirez & Costa, 2017). This shift is driven by the seeking of surprise (i.e., prediction error), novelty, or uncertainty in the form of more complex stimuli or environments. Therefore, if model refinement is a general goal, then seeking out moderately complex input that initially challenges model-based predictions via prediction errors, but is then incorporated into and accounted for by the model, will be intrinsically rewarding (Schmidhuber, 2010). In the context of groove, medium complexity rhythms lead to greater reward as they challenge internal predictive models, thus providing the opportunity to refine these models and resolve uncertainty by improving predictions and/or altering sensory input via movement (Vuust & Witek, 2014; Vuust et al., 2018).

The idea that learning in the context of intrinsic motivation is inherently rewarding has received support from both behavioural and neural studies. For example, a sudden insight or 'aha moment' (e.g., when an incoherent 'Mooney image' resolves into a coherent image), was associated with ratings of positive affect, particularly when it was self-generated rather than provoked by a cue (Kizilirmak, Galvao Gomes da Silva, Imamoglu, & Richardson-Klavehn, 2016). In other words, resolving uncertainty to gain new understanding of novel input led to reward, particularly when this new understanding was intrinsically driven. In an fMRI study, Ripollés et al (2014) showed that the intrinsic reward associated with learning new words was associated with activity in the ventral striatum. This activity matched that elicited by monetary gains (i.e., extrinsic rewards) in an independent gambling task. Crucially, they showed that ventral striatum activity was specifically related to the learning of novel words rather than the novelty itself. This indicates that the process of incorporating the novel input into an existing internal model of language elicited the reward-related activity.

Based on the above discussion, I suggest that rhythmic complexity determines the degree of engagement of motor and reward systems depending on the certainty and number of prediction errors. Rhythmic contexts that elicit no prediction errors preclude learning and thus do not engage the motor processes involved in updating temporal predictions nor the reward processes associated with learning. In uncertain contexts, prediction confirmations may also be rewarding as they reflect positive feedback regarding the model. That is, they are an indication that the model is indeed correct despite the uncertain context. Therefore, it may be that prediction confirmations, like prediction errors, are weighted depending on the certainty of the rhythmic context. However, given that prediction confirmations serve to resolve uncertainty, this would be an inverse relationship, with uncertain contexts leading to strongly weighted prediction confirmations. In the case of a very simple rhythm, there is no uncertainty and the likelihood of a prediction being incorrect is very low, so there is no chance for learning, therefore prediction confirmations would have very low weight, which leads to boredom (Zald & Zatorre, 2011).

Conversely, medium complexity rhythms lead to a moderate number of prediction errors which are weighted with a moderate degree of certainty. In this case, temporal predictions can be made, but they are less certain, as reflected by wider temporal windows around each beat. Here, perturbations such as syncopations both lead to prediction errors, and attenuate the certainty or weight of these prediction errors. This introduces just enough uncertainty to increase the engagement of motor-supported, temporal prediction processes necessary to maintain entrainment to the beat. Therefore, the urge to move increases as the motor system is engaged to reaffirm temporal predictions, along with the compulsion to test these temporal predictions via movement. In addition, moderately weighted prediction errors provide strong learning signals which increases reward. Further, there is now a non-zero probability of making an incorrect prediction, thus increasing the weight of prediction confirmations. Therefore, the combination of moderately weighted prediction errors and confirmations leads to an overall greater affective response. Finally, for highly complex rhythms with no discernible beat, entrainment is reduced or unstable, therefore predictions are uncertain thus prediction errors are given very low weights, while prediction confirmations are rare, resulting in reduced reward.

Recent studies on melodic and harmonic processing support the importance of both prediction errors and uncertainty in determining an affective response to music. For example, Gold et al. (2019) used information-theoretic models to quantify the degree of both predictability and uncertainty within monophonic melodic passages. They showed that both predictability, as indexed by information content (corresponding roughly to low prediction error), and uncertainty, as indexed by entropy, showed inverted U-shaped relations with liking ratings. Further, predictability and uncertainty interacted such that predictable events were rated more highly in melodies with more uncertain musical contexts. In other words, prediction confirmations elicited more reward as uncertainty increased. A similar result was shown in the context of chord progressions with higher pleasantness ratings for highly surprising chords in uncertain contexts, and relatively unsurprising chords in more certain contexts (Cheung et al., 2019). Although yet to be fully tested in the context of rhythm perception, these results support the suggestion that the degree to which a prediction error (or confirmation) leads to an affective response depends on the certainty of the rhythmic context. A salient example of this interaction is in electronic dance music, which often involves a highly regular metronome-like rhythmic pattern with relatively little deviation, and yet is highly successful in getting people on the dance floor. The highly regular beat, along with high volume and large low-frequency content, strongly entrains attentional oscillators thus leading to highly certain predictions and increased perceptual sensitivity. This allows for a somewhat minimal approach to composition, in which even the smallest change can have a large impact on affective responses and motor engagement.

5.4 Harmony and Temporal Predictions

Articles 1 and 3 also showed that rhythm and harmony work together to engender the sensation of groove. In Article 1, pleasure and urge to move ratings were highest for the combination of medium complexity rhythms and low and medium complexity chords. In Article 3, medium complexity chords enhanced pleasure, beat strength, and urge to move ratings, particularly in musicians. This suggests that pleasant harmonies may enhance attentional motor entrainment thus increasing the certainty of temporal predictions and thus the impact of prediction errors. Pleasant harmonies enhanced the effect of metre on reaction times in a visual detection task (Trost et al., 2014) and SMS is enhanced for pleasant versus unpleasant harmonies (Komeilipoor et al., 2015), suggesting that the modulatory effect of harmony extends to motor entrainment. This is in line with the mediation analysis in Article 1 which showed that harmony primarily affected pleasure which in turn affected the urge to move. In addition, recent work has shown that predictions regarding pitch dominate over temporal predictions, with temporal predictions increasing sensitivity and facilitating a motor response only when pitch predictions are confirmed (i.e., when the pitch of the standard tones is consistent from one trial to the next; Morillon, Schroeder, Wyart, & Arnal, 2016). Similarly, in both Articles 1 and 3, the chords were static within a trial. However, unlike the aforementioned study which dealt with individual pitches, Articles 1 and 3 involved chords. A highly dissonant chord is likely more surprising, at least initially, than an altered pitch as it violates implicit musical expectations. Therefore, the first onsets of such a chord may induce a prediction error which dissipates as the chord repeats. This paves the way for the temporal predictions to dominate, with the pleasantness of the chord playing a modulatory role.

Groove has also been associated with increased arousal. Both high-groove musical excerpts and syncopated synthesized rhythms increase arousal as measured by both physiological (pupil dilation) and subjective (ratings) measures (Bowling et al., 2019). Pupil dilation is specifically linked to the noradrenergic system, which is linked to greater sensorimotor activation associated with motor planning and auditory sensitivity (Bowling et al., 2019). Harmonic complexity affects other physiological indices of arousal, such as heart rate (Labbé &

Trost, 2020), and medium complexity chords may increase arousal by creating tension associated with a sense of suspended resolution (Huron, 2006; Lahdelma & Eerola, 2016). Thus, an increase in arousal may sharpen attention and activate motor preparatory processes, increasing the urge to move. Finally, arousal is known to affect time estimation, with higher arousal leading to an overestimation of durations, suggesting a faster internal clock (Droit-Volet & Meck, 2007). Together, these results along with our findings in Article 1 suggest that harmony can play a modulatory role on the sensation of groove by enhancing both attentional and motor entrainment and affecting arousal.

5.5 Temporal Predictions, Sensorimotor Synchronization, and Groove

According to PC, certainty weighted prediction errors are not only necessary for improving internal models and thus learning, but are themselves informative signals that are propagated up the processing hierarchy (Friston, 2005). The more certain the prediction, the more weight is applied to the prediction error, reflecting a greater impact on the internal model. In Article 2, I showed that perceived synchrony predicts groove over and above measured synchrony. Therefore, the focus is on synchrony rather than asynchrony. In this context, it is useful to invert the PC account. That is, prediction confirmations are given more weight as certainty decreases, such that a prediction confirmation is a stronger signal as it resolves more uncertainty. In the context of SMS, this means that a synchronous movement has more weight when the rhythmic context is relatively uncertain as it provides feedback that the internal model is correct despite the uncertain context. Accordingly, prediction confirmations should lead to greater learning and reward for relatively complex compared to simple rhythms. This is supported in Article 2, as the impact of perceived synchrony on groove was greatest for medium complexity rhythms. Further, compared to passive listening, SMS provides additional proprioceptive and tactile information with which to determine whether each movement reflects a confirmation or violation of the temporal prediction. This greater sensory feedback may further increase the weight of prediction confirmations, thus leading to greater impact on the affective response.

Many movements are themselves rhythmic, oscillatory processes. For example, when walking, oscillatory pattern generators send rhythmic signals to the leg muscles to generate movements (Damm, Varoqui, Cochen de Cock, Dalla Bella, & Bardy, 2020). This is generally an automatic process as we do not have to consciously move each leg, unless some change in the environment requires the engagement of top-down supervision. Similar processes are involved in SMS, where automatic oscillatory processes may generate rhythmic movements, which can be entrained to external rhythms. In this case, the entrainment of endogenous oscillations corresponding to the internal beat model, and the associated temporal predictions are externalized to the motor effector as the beat is represented physically by the movement. Therefore, beat-based temporal predictions are offloaded to the motor effectors and beat perception becomes embodied in a literal sense (Maes, 2016). In a highly regular rhythmic context, such as a low complexity rhythm, the motor system can fully take over without the necessity of supervision of conscious processes. In this case, only automatic, phase correction processes are necessary to account for the inherent variability in motor timing. When some uncertainty is introduced, such as in medium complexity rhythms, then top-down processes are engaged to update and maintain the internal beat. This relates to the distinction between internal and motor timing processes, with both as potential sources of timing variability (Wing and Kristoffersen,1973). However, in the context of DA and active sensing, internal and motor timing would be considered different expressions of the same oscillatory processes, rather than two processes working in parallel.

5.6 The Neuroanatomy of Temporal Predictions in the Context of Groove

In Article 3, I showed that both objective determinants (degree of syncopation) and subjective experience (ratings) of groove are associated with a network of brain regions linked to rhythm and beat perception, and to music-derived reward. Based on this, as well as previous neuroimaging work, I proposed a model in which different cortico-striatal circuits supporting distinct functions work together to generate the sensation of groove. Specifically, I suggested that a BG-PMC-SMA network encodes the beat percept and associated temporal predictions which are then compared with ongoing auditory input in the parietal cortices. In parallel, prefrontal regions provide context by holding metrical and other music-structural information in working memory. Beat-based predictions and contextual information are then integrated in the BG and assigned affective value in the NAcc and mOFC. The following sections expand on this model and integrate it within the PC and DA frameworks.

The proposed cortico-striatal network for groove overlaps with a network thought to underlie predictive processing more generally. A recent meta-analysis that included studies involving predictive processing in music, speech, and action perception found a network of regions including the BG, cerebellum, PMC, SMA/pre-SMA, parietal, posterior superior temporal cortex, and frontal prefrontal regions (Siman-Tov, Granot, Shany, Singer, & Gordon, 2019). In addition, they showed that both prediction formation and prediction errors related to timing, content, and spatial location are processed in this network. Similar networks have been shown in studies of beat perception (Araneda et al., 2016; Bengtsson et al., 2009; Burunat et al., 2017; Chapin et al., 2010; Chen et al., 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009, 2013; Kung et al., 2013; Schubotz et al., 2000; Thaut et al., 2014), and in studies of motor and perceptual timing with both visual and auditory, rhythmic and non-rhythmic stimuli (Chen et al., 2008a; Chen, Penhune, & Zatorre, 2008b; Coull & Nobre, 2008; Coull, Frith, Buchel, & Nobre, 2000; Coull, Cotti, & Vidal, 2016; Coull et al., 2011; Henry, Herrmann, & Obleser, 2015; Lewis, Wing, Pope, Praamstra, & Miall, 2004; Macar et al., 2002; Pecenka, Engel, & Keller, 2013; Wiener, Turkeltaub, & Coslett, 2010).

This prediction network also corresponds well to a theoretical network proposed to underlie learning in the context of PC (Friston et al., 2016). According to this proposal, the outcomes of behaviours are predicted in the parietal cortex, cerebellum, and dorsal striatum, and given value in the ventral prefrontal and ventral striatum (i.e., NAcc). Based on these predictions, dorsal striatal regions (putamen and caudate) select specific behaviours and determine the certainty (precision weighting) of the predicted outcomes via dopaminergic modulation. This information is then integrated into an internal model in dorsal prefrontal regions, which can then trigger actions via connections to motor cortices. This model has been extended beyond sensorimotor loops to include cognitive and affective processes by incorporating other parallel cortico-striatal circuits connecting BG regions to medial and lateral prefrontal regions (Friston, Parr, & de Vries, 2017) that correspond to those proposed by Alexander et al., (1985; see also Jahanshahi, Obeso, Rothwell, & Obeso, 2015).

My proposed model for groove perception fits well with this neurophysiological model linking prediction and learning. It also corresponds well with the ASAP hypothesis (Cannon & Patel, 2020; Patel & Iversen, 2014), which builds on work suggesting that the dorsal pathway is responsible for transforming auditory signals into abstract motor representations for predictive motor control (Hickok & Poeppel, 2007; Rauschecker, 2011). Echoing previous suggestions regarding motor involvement in temporal predictions (Arnal, 2012; Schubotz, 2007), the ASAP hypothesis (Cannon & Patel, 2020; Patel & Iversen, 2014) proposes that the endogenous component of the beat percept relies on covert motor processes within the BG, premotor, and motor regions. Building on this and other work, I suggest that the BG-SMA-PMC network implements the predictive timing computations necessary to temporally align movements to a regular sequence. In the context of 'passive' listening, these computations would never be sent to M1 and would therefore never be carried out. Instead they would establish regularly occurring temporal predictive signals which would be compared to the ongoing auditory input within the parietal cortex to maintain and update the predictive model. As these motor regions have evolved to generate rhythmic motor patterns, such as those involved in walking (Damm et al., 2020), they are the ideal candidates for generating these regularly timed predictive signals which provide the temporal context for perceptual and multisensory integration processes (Lakatos et al., 2019; Schroeder et al., 2010). Without inhibition to suppress overt actions, these motor computations may leak into M1, thus leading to synchronized movements such as unconsciously bobbing one's head or tapping one's foot to the beat. Therefore, within this model, the BG-SMA-PMC network is responsible for the combination of both the low-level regularity detection and top-down temporal prediction processes that result in the beat percept.

The relative engagement of bottom-up and top-down temporal prediction processes in the context of beat perception likely depends on the complexity of the rhythmic pattern and the degree to which a beat or metre is automatically or intentionally imposed on this pattern. In the context of a highly regular rhythm such as a metronome, only low-level regularity detection mya be necessary. That is, neural oscillations within the BG-SMA-PMC network may be automatically entrained to the stimulus without the necessity of top-down oversight. Conversely, for syncopated rhythms, in which there is reduced or no acoustic energy falling on a some of the beats, top-down processes may be engaged to maintain the beat percept, that is, to ensure that oscillatory processes continue to be aligned with the rhythmic pattern. This is consistent with work showing that beat perception, along with activity in the BG-SMA-PMC, during more complex rhythms requires greater attentional engagement (Chapin et al., 2010). However, top-down processes may be engaged even when listening to a metronome. For example, listeners may impose imagined accents on the metronome that lead to the perception of metre, which may result in the entrainment of oscillations at frequencies other than the stimulation frequency (Iversen et al., 2009; Nozaradan, Peretz, & Mouraux, 2012). This can also occur automatically, as is the case in the tick-tock illusion in which every second note of a metronome is perceived to be accented (Brochard, Abecasis, Potter, Ragot, & Drake, 2003). This may be due to the metronomic signal acting as an attractor, drawing in endogenous oscillations that have natural frequencies close to the harmonic frequencies of the stimulation rate. The automatic imposition of imagined accents has been deployed to interpret results showing greater activity for an unaccented isochronous rhythm (Grahn & Rowe, 2009). However, further works is necessary to test the role of the BG-SMA-PMC in imagining or imposing a beat.

Barring the imposition of imagined accents on very simple rhythms, the above discussion implies an inverted U-shaped relation between rhythm complexity and activity in the BG-SMA-PMC. That is, activity in this network should be relatively low for simple rhythms that require no top-down engagement and for highly complex rhythms that do not elicit a beat percept. Whereas, BG-SMA-PMC activity should be relatively high for medium complexity rhythms that are relatively regular but still require top-down engagement to maintain the beat and generate temporal predictions. This would possibly explain why several studies have shown a positive relation between BG-SMA-PMC activation and beat salience (Bengtsson et al., 2009; Grahn & Brett, 2007; Toiviainen, Burunat, Brattico, Vuust, & Alluri, 2019) while others have shown the opposite relation (Burunat et al., 2017). That is, depending on the stimuli used, these studies may be capturing different parts of the inverted U. Articles 1 and 2 also showed an inverted U-shaped relation between ratings of groove and rhythmic complexity, suggesting that the neural activity associated with beat perception covaries with the sensation of groove. The stimuli in Article 3 only capture the upper half of the inverted U, however, greater activity in BG-SMA-PMC for medium complexity rhythms as well as the link between BG activity and ratings is consistent with the inverted U hypothesis. Future studies combining a wide range of rhythmic complexity with subjective ratings could further clarify the relation between BG activity, the beat percept, and groove.

The necessity of low-level regularity detection or top-down internal beat maintenance may engage different subregions within the BG-SMA-PMC network. Functional and structural connections between the cortex and the BG shows an anterior-posterior organization (Lehericy et al., 2004; Postuma & Dagher, 2006). For example, the SMA can be divided into the pre-SMA and the SMA proper, with the more anterior pre-SMA connected to more anterior BG along with prefrontal regions, and the SMA proper connected to more posterior BG as well as to the PMC, M1, and motor part of the cerebellum (Johansen-Berg et al., 2004; Saga, Hoshi, & Tremblay, 2017). Therefore, syncopated rhythms eliciting a more top-down, internally generated beat percept may rely on a more frontal BG-SMA-PMC network including the pre-SMA. In Article 3, the medium > high complexity rhythm contrast elicited activity in both pre-SMA and SMA proper. This aligns with the above discussion as medium complexity rhythms are regular but include syncopations that necessitate top-down attentional processes to maintain the beat. Conversely, high complexity rhythms do not elicit a beat. Further, participants were not instructed to try and find or impose a beat on these rhythms. Therefore, these rhythms engage beat-based processes to a lesser degree or lead to a more global mode of listening, similar to listening to random or non-rhythmic stimuli. The musicians > non-musicians contrast elicited activity in the SMA proper. This, along with the more posterior premotor/primary motor cortical activation, may reflect reduced engagement of top-down processes in musicians compared to non-musicians.

Activity in the auditory cortex, along with functional connectivity with the BG, has also been shown to be modulated by rhythmic complexity (Grahn & Rowe, 2009; Kung et al., 2013). Early auditory processing involves the analysis of spectral (high frequency) and rhythmic (low frequency) components of complex sounds (Nozaradan, Mouraux, et al., 2017). Information from this processing step is passed to the dorsal pathway, including parietal, premotor and prefrontal regions, via the planum temporale (PT; Damm et al., 2020). This places the PT as a crucial node in the network that transforms complex acoustic signals into abstract motor representations. Indeed, this region has shown selective response to the beat frequency in syncopated rhythms (Nozaradan, Mouraux, et al., 2017), suggesting a specific role in detecting regularity at the beat frequency. In Article 3, the medium > high rhythmic complexity contrast did not elicit STG activity (neither primary auditory cortex nor PT), but rather activity in regions in the dorsal pathway downstream to these auditory regions. Both medium and high complexity rhythms were matched acoustically. Therefore, low-level auditory processing in the auditory cortices and the PT may be common to both rhythm types with the differentiation of these complexity levels occurring at later processing stages. Conversely, in our experiment musicians showed greater activity in both right primary auditory cortex (Heschl's gyrus) and left caudal temporal gyrus (adjacent to the PT). As this contrast averaged over levels of rhythmic complexity, this further supports the involvement of lower-level auditory processes across levels of complexity, and to a greater degree in those with musical training.

The cerebellum is thought to be crucial for various timing processes, particularly those involving overt motor timing on fast timescales (Bareš et al., 2019). Therefore, along with beat-based timing in the BG-SMA-PMC, SMS tasks, such as that used in Article 2, likely involve the cerebellum for computing the fine motor timing adjustments necessary to align each tap to the beat. Along these lines, Teki et al. (2012) proposed a theoretical framework, based on lesion and TMS studies, distinguishing beat-based and absolute timing processes relying on BG and cerebellar networks, respectively. Beat-based timing works at a longer timescale (hundreds of milliseconds) and thus is more likely to involve conscious, attention-driven processes (Bouwer, 2016; Chapin et al., 2010) such as those implicated in period correction during SMS (Repp & Keller, 2004). Conversely, absolute timing works on shorter timescales (tens of milliseconds), thus involving subconscious and automatic processes. This shorter timescale is crucial to making the fine-grained motor adjustments necessary to achieve the predicted sensory outcome (Krause et al., 2014; Pollok et al., 2008; 2017; Wolpert et al., 1998b; MacDonald and Paus, 1993; Ivry et al., 2002; Spencer et al., 2005; for a review, see Molinari et al., 2003). In SMS, these fine-grained adjustments take the form of automatic phase correction (Repp, 2005; Repp & Keller, 2004). This aligns with a model suggesting that the cerebellar pathway is involved in fast temporal processing while the BG and frontal regions represent a slow pathway focused on relational timing (Schwartze & Kotz, 2013). This is supported by recent data from non-human primates showing that although both caudate and cerebellum neurons tracked the regularity of visual stimuli, cerebellar neurons did so with greater temporal accuracy (Kameda, Ohmae, & Tanaka, 2019; Tanaka et al., 2020).

In Article 2, groove ratings showed a stronger association with perceived synchrony than measured synchrony. This may suggest an imbalanced contribution and mismatch between beat-based and absolute timing processes. That is, perceived synchrony may rely on conscious access to less accurate, beat-based timing mechanisms supported by the BG-SMA-PMC network. Conversely, measured synchrony was likely determined, to a large degree, by automatic fine-grained (more accurate) timing mechanisms supported by a cerebellar network which is less accessible to conscious awareness. This suggests that it is conscious access to beat-based timing mechanisms that interact with reward processes to generate groove. This proposal is particularly appealing given that both beat-based and reward processes are linked to the BG. Further, this may provide one explanation as to why fine-grained timing deviations (e.g., microtiming) have not consistently been linked to groove (Butterfield, 2010; Davies et al., 2013; Frühauf et al., 2013; Kilchenmann & Senn, 2015; Madison & Sioros, 2014). Parietal cortices are likely involved in both beat-based and absolute timing contexts and are particularly important in contexts requiring greater attention or cognitive control (e.g., tapping to polyrhythms; Vuust, Wallentin, Mouridsen, Ostergaard, & Roepstorff, 2011) or when temporal prediction errors are consciously detected (Bijsterbosch et al., 2011).

5.7 Temporal Prediction Errors in the Brain

The above discussion implicates the parietal cortex in matching temporal predictions to sensory inputs in the contexts of both fast and slow timescales and in both SMS and passive beat perception. This suggests that the parietal cortex encodes temporal prediction errors and may be involved in communicating these prediction errors to motor and reward regions to update beat-based models giving rise to an affective response. This places the parietal cortex as a crucial node in the network supporting the processes that underlie groove. Support for this comes from studies using an evoked neural response called the mismatched negativity (MMN), as measured by EEG or MEG, as a neural index of prediction error. MMNs related to rhythm-based temporal predictions are localized to the parietal and auditory cortices while melodic prediction errors are seen in frontal and auditory cortices, thus reflecting the dorsal and ventral auditory pathways, respectively (Lappe, Steinsträter, et al., 2013). Interestingly, the amplitude of the rhythm-based MMNs depends on the rhythmic context (Ladinig, Honing, Haden, & Winkler, 2009; Lappe et al., 2016; Lumaca et al., 2019). Similar context effects on MMNs have been shown for pitch deviants (Quiroga-Martinez et al., 2019). Therefore, MMNs within fronto-parietal and auditory regions may provide a neural index of both prediction error and certainty for both rhythmic and melodic contexts, particularly for consciously detected errors (Bijsterbosch et al., 2011).

According to the proposal from Article 3, rhythm-based errors are communicated to the BG and motor network to update and maintain the beat-based model. In parallel, these errors, along with the antecedent prediction, are assigned affective and motivational value in the ventral BG-mOFC network. The parietal cortex has also been shown to process action-reward associations (Dorris & Glimcher, 2004; Wisniewski, Reverberi, Momennejad, Kahnt, & Haynes, 2015) in a movement and effector-specific fashion (Kubanek & Snyder, 2015), suggesting that the parietal regions may be crucial for linking motor and reward processes. Functional and structural connectivity studies show that both parietal and frontal regions show connectivity with the BG. For example, resting-state fMRI reveals functional connectivity between the ventral (including NAcc) and dorsal striatum with parietal and motor-related regions (Cauda et al., 2011; Di Martino et al., 2008). Meanwhile MRI measures of white matter tracts show a convergence of neurons from the parietal cortex, OFC, and DLPFC in the caudate and putamen, along with their well-established connections with motor regions such as the SMA and PMC (Jarbo & Verstynen, 2015). Therefore, although direct evidence is lacking, the above pathways may provide the anatomical basis for the convergence of beat-based predictions (from the motor circuit) and consciously detected temporal prediction errors (from the frontoparietal network) on the BG. These signals may then be integrated in the BG to inform beat-based internal models as well as affective and motivational responses.

Within the BG, the NAcc has been implicated in computing reward prediction errors which reflect the value, rather than the timing or content, of the sensory input and are thought to be driven by dopaminergic signalling (Chase, Kumar, Eickhoff, & Dombrovski, 2015; Schultz, 2016). Work on reward prediction associated with rhythms is lacking, however, a recent study showed a link between reward prediction errors related to chord progressions and NAcc activity (Gold et al., 2019). However, prediction errors related to musical content, particularly those considered pleasant, have also been linked to both NAcc activity and connectivity between NAcc and auditory cortex (Shany et al., 2019). Conversely, another recent study showed that the certainty of harmonic predictions, but not prediction error, was positively associated with NAcc activation (Cheung et al., 2019). This latter result aligns with the proposed role of dopamine within the BG, as framed within PC, as determining prediction certainty, particularly for sensorimotor predictions (Friston et al., 2014; Owens, Allen, Ondobaka, & Friston, 2018). In this model, dopamine in the BG may encode prediction certainty for predictions about content, timing, or affective value, as long as it informs behavioural selection. This is in contrast with prediction certainty regarding interoceptive input, which is thought to be coded by noradrenergic signals in the amygdala (Owens et al., 2018). This suggests that contextual information regarding predictions relating to multiple musical structures (melody, harmony, rhythm) are integrated in the BG to inform behaviour. In addition, prediction certainty likely affects the recruitment of attentional and cognitive resources supported by frontoparietal networks, with engagement of this network increasing as uncertainty increases (Koch et al., 2008). Taken together, the BG is seen as a crucial hub in which the errors, confirmations, and uncertainty of temporal predictions are integrated with the valuation of these predictions to inform the motor and affective responses to rhythmic music.

5.8 Neural Oscillations and PC

According to the neural resonance theory, neural oscillations are the mechanism underlying the attentional oscillations that, according to DA, are entrained by rhythmic auditory stimuli. Therefore, neural entrainment at beat and metre frequencies may provide the substrate for the internal models associated with beat and metre proposed by PC. However, due to a focus on different analytical methods and neural correlates (e.g., evoked potentials versus neural oscillations), the PC and DA frameworks have rarely been considered together. This has changed in recent years with theoretical and experimental work suggesting that these frameworks are not only compatible but convergent. For example, Arnal and Giraud (2012) proposed that neural oscillations provide a mechanism for PC in the context of auditory perception, suggesting that predictions about content and timing are encoded in high and low frequency oscillations, respectively. Specifically, they suggest that oscillations in the beta range (12-30 Hz) represent predictions of content (i.e., ‘what’) while low frequency oscillations (e.g., in the delta range, 0.5 - 4 Hz) reflect temporal (‘when’) predictions by automatically entraining to a regular signal. And finally, gamma-band oscillations (> 30 Hz) are thought to encode prediction errors. Similar proposals have been made for language comprehension (Lewis & Bastiaansen, 2015; Lewis, Schoffelen, Schriefers, & Bastlaansen, 2016) and visual perception (Bastos et al., 2012; Friston, Bastos, Pinotsis, & Litvak, 2015), therefore the role of these frequency bands in predictive processes is thought to be domain general. However, as discussed below, more recent work indicates that the links between predictive processes and neural oscillations in specific frequency bands may not be quite so clear.

Contradicting the idea that beta carries only ‘what’ information, there is mounting evidence that beta oscillations also encode temporal predictions (Arnal, 2012; Morillon & Baillet, 2017; Teki, 2014). In addition, modulations in the power of beta oscillations, which indicate more or less neural synchrony in the beta range, have been linked to beat perception (Fujioka et al., 2015; Fujioka et al., 2012; Iversen et al., 2009). Crucially, beta modulations are similar for acoustic and imagined beats (Iversen et al., 2009), are larger for strong compared to weak beats (Fujioka et al., 2015), and, in the context of SMS, are stronger when participants tap on every fourth beat compared to tapping on every beat (Gompf, Pflug, Laufs, & Kell, 2017). Together, these studies strongly implicate beta oscillations in top-down temporal predictions based on both beat and metre rather than simply tracking temporal regularity in an auditory stimulus. That is, beta activity may be particularly engaged in situations requiring internal generation of the beat, for example during syncopated rhythms or when imposing metre on a metronome. This aligns with work linking beta to top-down processing more generally (Spitzer & Haegens, 2017).

Beta oscillations have also been associated with sensorimotor processes (Engel & Fries, 2010) as well as with communication between sensorimotor and other regions (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013) including directed communication from motor to auditory regions (Abbasi & Gross, 2019; Morillon & Baillet, 2017). Consistent with this evidence, beta modulations associated with rhythm and beat perception are found in motor and auditory regions as well as other regions in the dorsal pathway. For example, beat-based beta activity has been localized to auditory, motor, and frontoparietal networks (Fujioka et al., 2015), while beta activity in the putamen of monkeys has been linked to self-paced tapping (Bartolo & Merchant, 2015; Bartolo, Prado, & Merchant, 2014). Therefore, in the context of passive listening, beta activity may reflect the covert motor computations that act as beat-based temporal predictions, as suggested by the ASAP hypothesis (Patel & Iversen, 2014). Going further, I suggest that these predictive beta signals are generated within the BG-SMA-PMC and relayed to other brain regions, such as the parietal and auditory cortices where they influence perception and are compared against auditory input. However, as proposed by Arnal and Giraud (2012), beta activity has also been linked to predictions of content (i.e., pitch) in the context of auditory perception (Chang, Bosnyak, & Trainor, 2016, 2018). According to active inference, movements are themselves predictions of the timing and content of the sensory consequences of these movements, that is, both the consequent sound and the timing of that sound. Therefore, within music listening, beta oscillations may provide a general-purpose, top-down prediction mechanism, generating expectations regarding both when an event will occur and what that event will be.

In most music the beat occurs within the 0.5 – 4 Hz delta frequency range (Ding et al., 2017), therefore, neural oscillations in this range, entrained to the beat, may reflect the low-level processing associated with detecting and tracking regularity (Doelling & Poeppel, 2015). By doing so, delta oscillations are thought to segment the auditory input into useful units (e.g., words or beats; Lakatos, Gross, & Thut, 2019) while also providing the time windows in which various perceptual (e.g., multisensory binding) and cognitive (higher level predictions) processes are synchronized (Morillon, Arnal, Schroeder, & Keitel, 2019). Therefore, in music perception, just as the beat can be thought of as the fundamental temporal unit, delta oscillations likely provide a temporal context for the synchronization, and thus integration, of both low level and higher-level predictive processes. The work from Nozaradan and colleagues provides evidence of entrainment of neural oscillations to the beat and metre which naturally fall in the delta range (Lenc, Keller, Varlet, & Nozaradan, 2018; Nozaradan et al., 2012).

Functionally speaking, entrainment of delta oscillations has been linked to low-level perceptual sensitivity. For example, the phase of delta oscillations, that is, the alignment of periods of high neural excitability to predicted time points, is linked to rhythm-based temporal judgements (Arnal, Doelling, & Poeppel, 2015; Arnal & Kleinschmidt, 2017) as well as behavioural adjustments in response to movement timing errors (Barne et al., 2017). The behavioural relevance of delta phase has also been shown in non-rhythmic, but temporally predictable contexts, linking it to target detection and reaction times (Stefanics et al., 2010). This link between delta phase and perceptual sensitivity suggests that delta oscillations may provide the neural substrate for the attentional entrainment proposed in the DA framework. Conversely, beta activity seems to be more engaged when top-down processes are necessary, for example by providing the motor-driven, endogenous component of the beat percept during medium complexity rhythms.

During rhythm perception beta power fluctuates at a frequency matching the musical beat, that is, in the delta range (Fujioka et al., 2012; Iversen et al., 2009). This, along with the evidence described above, suggests that delta and beta oscillations are coupled in the context of rhythm perception, with the phase of delta oscillations modulating the power of beta oscillations (Morillon & Baillet, 2017). Indeed, delta-beta coupling has been linked to the accuracy of temporal judgements and rhythm-based temporal predictions (Arnal et al., 2015; Morillon & Baillet, 2017). Therefore, given the role of beta in top-down processing and communication across auditory and motor regions, delta activity may serve to optimally align these processes to relevant (i.e., predicted) timepoints. In addition, low frequency neural oscillations may synchronize activity across distant brain regions while higher frequency activity may reflect local synchronization (Buzsáki & Draguhn, 2004). This supports the role of delta oscillations in coordinating the more local beta-band activity across a wide network of regions, thus allowing for the integration of predictive, attentional, motor, and reward processes within beat-based time windows.

Top-down beta activity may also act on delta oscillations to influence perception. Recent studies have shown that, in the context of both rhythmic and non-rhythmic auditory stimulation, delta-beta coupling is directional, with beta activity in dorsal and motor regions influencing delta activity in auditory cortices (Abbasi & Gross, 2019; Morillon & Baillet, 2017). In the context of overt movement, this directed beta activity has been linked to the attenuation of the sensory consequences of self-generated movements (Abbasi & Gross, 2019). That is, beta reflects efference copies of motor commands which are sent to auditory regions to predictively suppress the processing of the resulting auditory input. These top-down beta signals may influence delta activity by phase resetting ongoing oscillations, realigning them with the auditory input when there is drift or a perturbation (Rimmele et al., 2018). This would be particularly important in more complex rhythms where top-down input is necessary to monitor and maintain entrainment to the beat. Therefore, in the context of beat perception, delta and beta oscillations may be interdependent, representing a recurrent network formed between auditory and motor (BG-SMA-PMC) regions and thus reflecting different stages in the processing hierarchy. In this way, a loop is formed in which low level, auditory-driven delta sets the temporal context for top-down, motor-generated predictions which are fed back to auditory cortices to influence low-level auditory perception.

Arnal and Giraud (2012) proposed that prediction errors are encoded in gamma oscillations based on evidence demonstrating a link between gamma modulations and mis-match signals (MMNs). As discussed above, MMNs have been shown to index prediction errors and their certainty in the context of both rhythmic timing and pitch deviations (Lappe et al., 2016; Lumaca et al., 2019; Quiroga-Martinez et al., 2019). MMNs in response to content prediction errors have been linked to increases in gamma power (Arnal & Giraud, 2012). However, studies linking neural oscillations to temporal prediction errors are lacking. Fujioka et al. (2009) showed that omitting a note within an isochronous sequence leads to gamma followed by beta power modulations (Fujioka et al., 2009), which they interpreted as reflecting a prediction error followed by adjustment of the predictive model. However, omissions represent both a content and temporal prediction error, whereas syncopations, in which the note does occur but earlier than expected, violate temporal predictions but confirm content predictions (e.g., Lappe, et al., 2013; Lappe et al., 2016). Therefore, work using syncopations could allow us to uncover the neural oscillations related specifically to temporal prediction errors.

There is a similar lack of clarity in relating neural oscillations to the certainty of temporal predictions. The certainty of pitch predictions has been linked to alpha oscillations (Sedley et al., 2016) and beta oscillations have been linked to sensorimotor prediction certainty in a visuomotor task (Palmer, Auksztulewicz, Ondobaka, & Kilner, 2019). Given that delta amplitude is modulated by rhythmic context (Nozaradan et al., 2012) and beta power modulations are affected by accent strength (Fujioka et al., 2015), temporal prediction certainty may be reflected in the neural oscillations that encode the predictions themselves. Therefore, the certainty of higher-level temporal predictions (e.g., based on metre or musical schemas) may be reflected in the magnitude of beta power modulations. Conversely, the certainty of low-level temporal predictions (e.g., whether an onset will occur on or off the beat) may be reflected in the amplitude of delta oscillations. Given the purported role of beta in top-down predictive processes, it may be linked to the certainty of beat-based predictions that are available to conscious awareness while delta activity reflects more automatic, subconscious timing processes. Indirect support for this is provided by work showing that beta activity is involved in both the generation and self-evaluation of non-rhythmic time intervals (Kononowicz, Roger, & Van Wassenhove, 2019), suggesting that beta signaling allows for conscious access to timing performance. However, in more complex rhythmic contexts, rhythm perception involves a combination of both lower- and higher-level temporal predictions, thus necessitating the coupling between delta and beta oscillations. In this context, temporal predictions, and their certainty, may be reflected in the strength of the delta-beta coupling rather than one frequency band on its own.

5.8 Reward, the Urge to Move, and Neural Oscillations

The link between the urge to move and affective responses associated with groove, observed across all of the studies in this thesis, can also be interpreted in terms of motivation: the reward-based drive to action. In the broader literature on reward processing, the experience of pleasure has been divided into wanting and liking. Wanting is described as an active, or motivational response, and liking as a more passive, (self-)reflective response (Berridge & Kringelbach, 2015). Beta activity in sensorimotor regions is sensitive to reward value during the decision phase of a decision-making task requiring a motor output (Go/NoGo task; Chen, McCarthy, & Kwak, 2019). In addition, beta activity in dorsal prefrontal regions is sensitive to reward feedback and therefore involved in strengthening stimulus-action associations (Hosseini & Holroyd, 2015). Studies combining EEG and fMRI have shown that positive (i.e., rewarding) feedback leads to beta activation in the NAcc and frontal regions (Andreou et al., 2017; Mas-Herrero, Ripollés, HajiHosseini, Rodríguez-Fornells, & Marco-Pallarés, 2015). This reward-based beta activity has been associated with dopaminergic signalling in the BG (Marco-Pallarés, Münte, & Rodríguez-Fornells, 2015; Mas-Herrero et al., 2015) suggesting a common function of beta activity and dopamine signaling in integrating predictive errors and their certainty to determine (i.e., motivate) behaviour. Therefore, beta activity may form the link between the internal endogenous beat, sensorimotor activation, and affective responses that characterize the sensation of groove.

Studies relating neural oscillations to music-derived reward are sparse, however, several theoretical proposals have suggested strong links between neural and motor entrainment to music, and affective responses (Trost & Vuilleumier, 2013; Vuilleumier & Trost, 2015). One recent study showed a positive association between phase coherence of neural oscillations in the delta range and ratings of groove while participants listened to rhythmic stimuli (Cameron et al., 2019). These results are in line with the application of neural resonance theory to music-induced affect (Flaig & Large, 2014). According to this proposal, entrainment of neural oscillations to musical components (e.g., low frequencies to rhythm, high frequencies to pitch) support the affective responses to music. For example, affective contagion, where listeners are thought to 'catch' the emotion in an expressive performance, relies on the degree to which neural oscillations entrain to the various musical components. In this way, music does not lead us to internally mimic emotions (Juslin & Västfjäll, 2008), but directly engages these emotions by ‘speaking to the brain in its own language’ (Flaig & Large, 2014, pg. 7). A similar hypothesis proposes that entrainment of neural, physiological (e.g., heart rate), social (moving in synchrony with someone else) and other oscillatory processes to music is itself rewarding (Trost et al., 2017; Trost & Vuilleumier, 2013; Vuilleumier & Trost, 2015). Neural evidence for this is lacking, however, subjective reports of visceral (i.e., physiological) and motor (urge to move) entrainment were linked to a positive affective response (Labbé & Grandjean, 2014). Therefore, according to these accounts, the music that elicits the strongest sensation of groove is that which resonates with the natural frequencies of motor and affective systems.

5.9 Tying it all Together

The work in my thesis and the literature reviewed in this discussion suggest possible neural substrates for the processes underlying the sensation of groove, particularly the temporal prediction processes involved in rhythm perception. The following section attempts to tie all of this together with the theoretical model proposed in the Article 3.

The first step towards a pleasurable urge to move is beat induction, that is perceiving or extracting a beat from rhythmic music, which then provides a temporal scaffold on which higher level processes are built upon. Beat induction may be driven by the entrainment of neural oscillations in the delta range to the stream of auditory input. This delta activity would interact with beta oscillations that represent predictions to generate percepts corresponding to the beat and metre. Delta entrainment would provide temporal alignment to the beat while beta oscillations would use this temporal context to form top-down temporal (and content) predictions, possibly in the form of efference copies of covert motor computations. The coupling of delta and beta activity may establish bidirectional communication between the BG-SMA-PMC network and auditory regions, forming a loop. I propose that this loop is the neural substrate for the attentional oscillations that form the beat percept. That is, low-level regularity tracking in auditory cortices may drive motor-generated temporal predictions which in turn focuses auditory perception to those timepoints.

Once a beat percept is established, beat-based predictions and on-going auditory input may be compared within parietal and prefrontal cortices. If a mismatch is detected, the prediction error would be passed back to the BG-SMA-PMC, possibly via gamma oscillations to refine the model. Depending on the size and nature of the perturbation and the degree to which it engages attention, the associated prediction error may contribute to the uncertainty of future predictions. For larger perturbations, such as a tempo change, top-down beta activity may affect period correction of the delta oscillations representing the internally generated beat via repeated phase resetting. In addition, frontoparietal networks may be engaged, reflecting the necessity of top-down, conscious mechanisms to realign perceptual processes to the beat. Small perturbations, such as microtiming deviations, would engage fine-grained processes such as those involved in phase correction and which rely on cerebellar networks. During SMS, the same processes would take place, with greater engagement of the fine-grained, cerebellar processes necessary for accurate and precise motor control. The greater degree of explicit feedback during SMS also allows for greater refinement of the predictive models representing the beat and metre.

Rhythm complexity, dictated by the size and number of perturbations, would determine the engagement of top-down mechanisms. Medium-sized perturbations such as syncopations, falling between tempo changes and microtiming, may engage conscious, attentional processes in frontoparietal networks as well as delta-beta coupling in order to update and maintain the current beat model. That is, only when comparisons between predictions and input are necessary is the motor system and the affective valuation of these prediction engaged. Conversely, for a highly regular rhythm or one with only very small timing perturbations, delta entrainment and the associated prediction processes can go on ‘autopilot’ (assuming that the listener is not imposing a beat or metre). In this case, when high certainty predictions are continuously confirmed, higher level processes can disengage, pending any new information. Whereas, if there is a syncopation, the predictive system would be activated to check whether the model and the associated predictions are still valid. This check would engage both the motor and reward system, via beta oscillations in the BG, to either reinforce or punish the current state of the oscillatory model. This information would then determine whether the delta phase reflecting the internal beat is maintained, refined, or requires a phase reset. This provides a potential mechanism by which both temporal prediction errors and prediction confirmations lead to reward, particularly in the context of medium complexity rhythms.

Rhythmic complexity, along with other factors such as global attention, would also determine the global uncertainty of the rhythmic context, thus affecting the confidence with which predictions are made. I propose the degree of uncertainty is reflected in the modulations of delta-coupled beta oscillations. That is, the specific pattern of beta power fluctuations within the delta rate may set the width of the temporal window that determines the precision of the temporal prediction. Therefore, during SMS, a medium degree of certainty would be reflected in a relatively wide beta modulation window which increases the number of movements that fall within that window (or beat bin) and are considered synchronous. This would permit movements (and onsets) to be further away from the predicted beat point without affecting the ongoing delta entrainment representing the internal beat. Thus, I suggest that it is the interaction between low-level, delta-driven processes and the effect of uncertainty on beta modulations that leads to a disparity between perceived and measured synchrony and the greater influence of the former on groove.

Repetitions of rhythmic patterns within a composition, along with familiarity with the composition or genre, may afford higher level predictions about the occurrence of perturbations such as syncopations. In other words, the perturbations may be incorporated into the model such that the syncopations themselves are predicted and no longer register as prediction errors. This might further free up resources for higher level processing including the interaction of melodic, harmonic, and rhythmic components on longer timescales. This information may be maintained and contextualized within frontoparietal networks via working memory processes to generate an overall percept of the musical input. Beta oscillations have been implicated in both content and temporal predictions as well as the maintenance (Engel and Fries, 2010) and reactivation (Spitzer & Haegens, 2017) of cognitive and sensory representations. Therefore, beta oscillations are likely involved in this high-level processing. It follows then that beta activity would underlie the processing stage at which harmonic and rhythmic complexity combine to influence the sensation of groove. As predictions shift towards higher level processes representing the overall percept and its longer timescale structure, these higher-level processes may become stronger drivers of affective responses. However, delta oscillations entrained to low-frequency musical components would still be necessary to maintain the temporal context and synchronization of these processes across the levels of the processing hierarchy. This delta engagement, as well as coupling with beta oscillations, would thus continue to resonate in the motor system preventing the attenuation of the urge to move even after repeated listens.

5.10 Conclusion

This thesis presents three research articles focusing on the sensation of groove viewed through three different lenses representing the perceptual, behavioural, and the neural, while framing groove as the integration of perceptual, motor, and reward processes. I have emphasized the role of temporal predictions, as the linking mechanism between these processes in the context of groove. The high degree of temporal regularity, and thus predictability, inherent to rhythmic music makes it a uniquely powerful tool for studying the role of predictions, and their certainty, on behaviour and the brain. This inherent predictability, as well as the capacity for controlled manipulation of this predictability, makes musical rhythm an ideal test bed for theoretical treatments of temporal prediction. Although, there are many other relevant theoretical frameworks, I have focused on dynamic attending and predictive coding as they are highly influential and have been explicitly applied to musical rhythm. Within the idealized context of rhythmic music and the sensation of groove, I show how these frameworks, and their relatives, can be integrated. Focusing this integrated framework on temporal predictions also highlights the importance of the motor system in the low-level, perceptual, and high-level, cognitive processes, thus placing groove as a thoroughly embodied process. Finally, rhythmic music, and groove in particular, provides a platform on which to build the links between elemental processes such as prediction, motor-learning and motivation. Therefore, if nothing else, I hope I have made clear that groove is not some frivolous phenomenon relegated to pop music, but an essential part of the human experience. Or at least, one of the good parts.

References

Abbasi, O., & Gross, J. (2019). Beta-band oscillations play an essential role in motor–auditory interactions. *Human Brain Mapping*, (October), 1–10. https://doi.org/10.1002/hbm.24830

Alexander, G., DeLong, M. R., & Strick, P. L. (1986). Parallel Organization of Functionally Segregated Circuits Linking Basal Ganglia and Cortex. *Annual Review of Neuroscience*, *9*(1), 357–381. https://doi.org/10.1146/annurev.neuro.9.1.357

Alluri, V., Brattico, E., Toiviainen, P., Burunat, I., Bogert, B., Numminen, J., & Kliuchko, M. (2015). Musical expertise modulates functional connectivity of limbic regions during continuous music listening. *Psychomusicology*, *25*(4), 443–454.

Alluri, V., Toiviainen, P., Burunat, I., Kliuchko, M., Vuust, P., & Brattico, E. (2017). Connectivity patterns during music listening: Evidence for action-based processing in musicians. *Human Brain Mapping*, *38*(6), 2955–2970. https://doi.org/10.1002/hbm.23565

Andreou, C., Frielinghaus, H., Rauh, J., Mußmann, M., Vauth, S., Braun, P., … Mulert, C. (2017). Theta and high-beta networks for feedback processing: A simultaneous EEG-fMRI study in healthy male subjects. *Translational Psychiatry*, *7*(1). https://doi.org/10.1038/tp.2016.287

Araneda, R., Renier, L., Ebner-Karestinos, D., Dricot, L., & De Volder, A. G. (2016). Hearing, feeling or seeing a beat recruits a supramodal network in the auditory dorsal stream. *European Journal of Neuroscience*, *45*, 1439–1450. https://doi.org/10.1017/CBO9781107415324.004

Arnal, L. H. (2012). Predicting “when” using the motor system’s beta-band oscillations. *Frontiers in Human Neuroscience*, *6*, 1–3. https://doi.org/10.3389/fnhum.2012.00225

Arnal, L. H., Doelling, K. B., & Poeppel, D. (2015). Delta-beta coupled oscillations underlie temporal prediction accuracy. *Cerebral Cortex*, *25*(9), 3077–3085. https://doi.org/10.1093/cercor/bhu103

Arnal, L. H., & Giraud, A.-L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, *16*(7), 390–398. https://doi.org/10.1016/j.tics.2012.05.003

Arnal, L. H., & Kleinschmidt, A. K. (2017). Entrained delta oscillations reflect the subjective tracking of time. *Communicative and Integrative Biology*, *0889*. https://doi.org/10.1080/19420889.2017.1349583

Arthurs, Y., Beeston, A. V., & Timmers, R. (2017). Perception of Isolated Chords: Examining Frequency of Occurrence, Instrumental Timbre, Acoustic Descriptors and Muiscal Training. *Psychology of Music*, *26*(1), 1–23. https://doi.org/10.1177/ToBeAssigned

Aschersleben, G. (2002). Temporal control of movements in sensorimotor synchronization. *Brain and Cognition*, *48*(1), 66–79. https://doi.org/10.1006/brcg.2001.1304

Auksztulewicz, R., Myers, N., Schnupp, J., & Nobre, A. (2019). Rhythmic temporal expectation boosts neural activity by increasing neural gain. *Journal of Neuroscience*, *39*(49), 9806–9817.

Baath, R., & Madison, G. S. (2012). The subjective difficulty of tapping to a slow beat. In *Proceedings of the 12th International Conference on Music Perception adn Cognition and the 8th Triennial Conference of the European Society fo the Cognitive Sciences of Music* (pp. 82–85). https://doi.org/10.1017/CBO9781107415324.004

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Baker, S. N. (2007). Oscillatory interactions between sensorimotor cortex and the periphery.

Current Opinion in Neurobiology, *17*(6), 649–655. https://doi.org/10.1016/j.conb.2008.01.007

Bareš, M., Apps, R., Avanzino, L., Breska, A., D'Angelo, E., Filip, P., … Petter, E. A. (2019). Consensus paper: Decoding the Contributions of the Cerebellum as a Time Machine. From Neurons to Clinical Applications. *The Cerebellum*, *18*(2), 266–286. https://doi.org/10.1007/s12311-018-0979-5

Barne, L. C., Maurice, P., Claessens, E., Reyes, M. B., Caetano, M. S., & Cravo, A. M. (2017). Low-frequency cortical oscillations are modulated by temporal prediction and temporal error coding. *NeuroImage*, *146*(November 2016), 40–46. https://doi.org/10.1016/j.neuroimage.2016.11.028

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Barrett, N. F., & Schulkin, J. (2017). A neurodynamic perspective on musical enjoyment: The role of emotional granularity. *Frontiers in Psychology*, *8*, 1–6. https://doi.org/10.3389/fpsyg.2017.02187

Bartolo, R., & Merchant, H. (2015). β Oscillations Are Linked to the Initiation of Sensory-Cued Movement Sequences and the Internal Guidance of Regular Tapping in the Monkey. *The Journal of Neuroscience*, *35*(11), 4635–4640. https://doi.org/10.1523/JNEUROSCI.4570-14.2015

Bartolo, R., Prado, L., & Merchant, H. (2014). Information processing in the primate basal ganglia during sensory-guided and internally driven rhythmic tapping. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *34*(11), 3910–3923. https://doi.org/10.1523/JNEUROSCI.2679-13.2014

Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J. (2012). Canonical Microcircuits for Predictive Coding. *Neuron*, *76*(4), 695–711. https://doi.org/10.1016/j.neuron.2012.10.038

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious Mixed Models. *ArXiv Preprint*. Retrieved from http://arxiv.org/abs/1506.04967

Bates, D. M. (2010). lme4: Mixed-effects modeling with R, 1–145. https://doi.org/10.1177/009286150103500418

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *Eprint ArXiv:1406.5823*, 51. https://doi.org/10.18637/jss.v067.i01

Bauer, A. K. R., Debener, S., & Nobre, A. C. (2020). Synchronisation of Neural Oscillations and Cross-modal Influences. *Trends in Cognitive Sciences*, *24*(6), 481–495. https://doi.org/10.1016/j.tics.2020.03.003

Bengtsson, S. L., Ullen, F., Henrik Ehrsson, H., Hashimoto, T., Kito, T., Naito, E., … Sadato, N. (2009). Listening to rhythms activates motor and premotor cortices. *Cortex*, *45*(1), 62–71. https://doi.org/10.1016/j.cortex.2008.07.002

Berlyne, D. E. (1971). *Aesthetics and Psychobiology*. East Norwalk, CT: Appleton-Century-Crofts.

Berridge, K. C., & Kringelbach, M. L. (2015). Pleasure Systems in the Brain. *Neuron*, *86*(3), 646–664. https://doi.org/10.1016/j.neuron.2015.02.018

Bijsterbosch, J. D., Lee, K., Hunter, M. D., Tsoi, D. T., Lankappa, S., Wilkinson, I. D., … Woodruff, P. W. R. (2011). The Role of the Cerebellum in Sub- and Supraliminal Error Correction during Sensorimotor Synchronization : Evidence from fMRI and TMS. *Journal* *of Cognitive Neuroscience*, *23*(5), 1100–1112.

Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(20), 11818–11823. https://doi.org/10.1073/pnas.191355898

Blood, A. J., Zatorre, R. J., Bermudez, P., & Evans, A. C. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience*, *2*(4), 382–387.

Bolger, D., Coull, J. T., & Schon, D. (2014). Metrical Rhythm Implicitly Orients Attention in Time as Indexed by Improved Target Detection and Left Inferior Parietal Activation. *Journal of Cognitive Neuroscience*, *26*(3), 593–605. https://doi.org/10.1162/jocn

Bouwer, F. L. (2016). *What do we need to hear a beat? The influence of attention, musical abilities, and accents on the perception of metrical rhythm*. https://doi.org/10.1177/1745691612459060.

Bowling, D. L., Ancochea, P. G., Hove, M. J., Fitch, W. T., & Madison, G. (2019). Pupillometry of Groove : Evidence for Noradrenergic Arousal in the Link Between Music and Movement. *Frontiers in Neuroscience*, *12*, 1–12. https://doi.org/10.3389/fnins.2018.01039

Brattico, E., Pallesen, K. J., Varyagina, O., Bailey, C., Anourova, I., Jarvenpaa, M., … Tervaniemi, M. (2008). Neural Discrimination of Nonprototypical Chords in Music Experts and Laymen: An MEG Study. *Journal of Cognitive Neuroscience*, *21*(11), 2230–2244.

Breska, A., & Ivry, R. B. (2018). Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson ' s disease. *PNAS*, 1–6. https://doi.org/10.1073/pnas.1810596115

Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. (2002). Region of interest analysis using an SPM toolbox. In *8th International Conferance on Functional Mapping of the Human Brain*. https://doi.org/10.1007/978-3-540-75387-2_17

Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "Ticktock" of Our Internal Clock: Direct Brain Evidence of Subjective Accents in Isochronous Sequences. *Psychological Science*, *14*(4), 362–366. https://doi.org/10.1111/1467-9280.24441

Brown, H., Adams, R. A., Parees, I., Edwards, M., & Friston, K. (2013). Active inference, sensory attenuation and illusions. *Cognitive Processing*, *14*(4), 411–427. https://doi.org/10.1007/s10339-013-0571-3

Bundt, C., Abrahamse, E. L., Braem, S., Brass, M., & Notebaert, W. (2016). Reward anticipation modulates primary motor cortex excitability during task preparation. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2016.07.013

Burger, B., Thompson, M. R., Luck, G., Saarikallio, S., & Toiviainen, P. (2013). Influences of rhythm- and timbre-related musical features on characteristics of music-induced movement. *Frontiers in Psychology*, *4*(183), 1–10. https://doi.org/10.3389/fpsyg.2013.00183

Burunat, I., Tsatsishvili, V., Brattico, E., & Toiviainen, P. (2017). Coupling of Action-Perception Brain Networks during Musical Pulse Processing: Evidence from Region-of-Interest-Based Independent Component Analysis. *Frontiers in Human Neuroscience*, *11*(230), 1–14. https://doi.org/10.3389/fnhum.2017.00230

Butterfield, M. (2010). Participatory discrepancies and the perception of beats in Jazz. *Music Perception*, *27*(3), 157–175. https://doi.org/10.1525/mp.2010.27.3.157

Buzsáki, G. (2006). *Rhythms of the Brain*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195301069.001.0001

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science*, *304*(5679), 1926–1929. https://doi.org/10.1126/science.1099745

Cameron, D. J., Stewart, L., Pearce, M. T., Grube, M., & Muggleton, N. G. (2012). Modulation of motor excitability by metricality of tone sequences. *Psychomusicology: Music, Mind, and Brain*, *22*(2), 122–128. https://doi.org/10.1037/a0031229

Cameron, D. J., Zioga, I., Lindsen, J. P., Pearce, M. T., Wiggins, G. A., Potter, K., & Bhattacharya, J. (2019). Neural entrainment is associated with subjective groove and complexity for performed but not mechanical musical rhythms. *Experimental Brain Research*, *237*(8), 1981–1991. https://doi.org/10.1007/s00221-019-05557-4

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

Cannon, P. R., Hayes, A. E., & Tipper, S. P. (2010). Sensorimotor fluency influences affect: Evidence from electromyography. *Cognition and Emotion*, *24*(4), 681–691. https://doi.org/10.1080/02699930902927698

Cauda, F., Cavanna, A. E., Federico, D., Sacco, K., Duca, S., & Geminiani, G. C. (2011). Functional Connectivity and Coactivation of the Nucleus Accumbens: A Combined Functional Connectivity. *Journal of Cognitive Neuroscience*, *23*(10), 2864–2877.

Chang, A., Bosnyak, D. J., & Trainor, L. J. (2016). Unpredicted pitch modulates beta oscillatory power during rhythmic entrainment to a tone sequence. *Frontiers in Psychology*, *7*(327), 1–13. https://doi.org/10.3389/fpsyg.2016.00327

Chang, A., Bosnyak, D. J., & Trainor, L. J. (2018). Beta oscillatory power modulation reflects the predictability of pitch change. *Cortex*, (July), 1–13. https://doi.org/10.1016/J.CORTEX.2018.06.008

Chapin, H., Jantzen, K., Kelso, J. A. S., Steinberg, F., & Large, E. (2010). Dynamic emotional and neural responses to music depend on performance expression and listener experience. *PloS One*, *5*(12), 1–14. https://doi.org/10.1371/journal.pone.0013812

Chapin, H. L., Zanto, T., Jantzen, K. J., Kelso, S. J. a, Steinberg, F., & Large, E. W. (2010). Neural responses to complex auditory rhythms: the role of attending. *Frontiers in Psychology*, *1*(December), 224. https://doi.org/10.3389/fpsyg.2010.00224

Chase, H. W., Kumar, P., Eickhoff, S. B., & Dombrovski, A. Y. (2015). Reinforcement learning models and their neural correlates: An activation likelihood estimation meta-analysis. *Cognitive, Affective & Behavioral Neuroscience*, *15*(2), 435–459. https://doi.org/10.3758/s13415-015-0338-7

Chemin, B., Mouraux, A., & Nozaradan, S. (2014). Body Movement Selectively Shapes the Neural Representation of Musical Rhythms. *Psychological Science*, (October). https://doi.org/10.1177/0956797614551161

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008a). Listening to musical rhythms recruits motor regions of the brain. *Cerebral Cortex*, *18*(12), 2844–2854. https://doi.org/10.1093/cercor/bhn042

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008b). Moving on time: brain network for auditory-motor synchronization is modulated by rhythm complexity and musical training. *Journal of Cognitive Neuroscience*, *20*(2), 226–239. https://doi.org/10.1162/jocn.2008.20018

Chen, J. L., Zatorre, R. J., & Penhune, V. B. (2006). Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms. *NeuroImage*, *32*, 1771–1781. https://doi.org/10.1016/j.neuroimage.2006.04.207

Chen, X. J., McCarthy, M., & Kwak, Y. (2019). Contribution of sensorimotor beta oscillations during value-based action selection. *Behavioural Brain Research*, *368*(March), 111907. https://doi.org/10.1016/j.bbr.2019.111907

Cheung, V. K. M., Harrison, P. M. C., Meyer, L., Pearce, M. T., Haynes, J.-D., & Koelsch, S. (2019). Uncertainty and Surprise Jointly Predict Musical Pleasure and Amygdala, Hippocampus, and Auditory Cortex Activity. *Current Biology*, 1–9. https://doi.org/10.1016/j.cub.2019.09.067

Christensen, R. (2015). Analysis of ordinal data with cumulative link models—estimation with the R-package ordinal. *R-Package Version*, 1–31. Retrieved from http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Analysis+of+ordinal+data+with+cumulative+link+models+—+estimation+with+the+R+-package+ordinal#0

Coull, J. T., Cheng, R.-K., & Meck, W. H. (2011). Neuroanatomical and neurochemical substrates of timing. *Neuropsychopharmacology*, *36*(1), 3–25. https://doi.org/10.1038/npp.2010.113

Coull, J. T., Cotti, J., & Vidal, F. (2016). Differential roles for parietal and frontal cortices in fixed versus evolving temporal expectations: Dissociating prior from posterior temporal probabilities with fMRI. *NeuroImage*, *141*, 40–51. https://doi.org/10.1016/j.neuroimage.2016.07.036

Coull, J. T., Frith, C. D., Buchel, C., & Nobre, A. C. (2000). Orienting attention in time: behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia*, *38*, 808–819. Retrieved from papers3://publication/uuid/34613EAB-F00B-444C-8E33-7510A0565977

Coull, J. T., & Nobre, A. C. (2008). Dissociating explicit timing from temporal expectation with fMRI. *Current Opinion in Neurobiology*, *18*(2), 137–144. https://doi.org/10.1016/j.conb.2008.07.011

Daikoku, T., Takahashi, Y., Tarumoto, N., & Yasuda, H. (2018). Motor Reproduction of Time Interval Depends on Internal Temporal Cues in the Brain : Sensorimotor Imagery in Rhythm. *Fontiers in Psychology*, *9*(1873), 1–11. https://doi.org/10.3389/fpsyg.2018.01873

Daly, H. R., & Hall, M. D. (2018). Not All Musicians Are Created Equal: Statistical Concerns Regarding the Categorization of Participants. *Psychomusicology: Music, Mind, and Brain*, *28*(2), 117–126.

Damm, L., Varoqui, D., Cochen de Cock, V., Dalla Bella, S., & Bardy, B. G. (2020). Why do we move to the beat? A multi-scale approach, from physical principles to brain dynamics. *Neuroscience & Biobehavioral Reviews*, *112*, 553–584. https://doi.org/10.1016/j.eplepsyres.2019.106192

Danielsen, A. (2006). *Presence and Pleasure. The Funk Grooves of James Brown and Parliament*. Middletown, CT: Wesleyan University Press.

Danielsen, A. (2010). Here, there and everywhere: Three accounts of pulse in D'Angelo's "left and right." In *Musical Rhythm in the Age of Digital Reproduction* (pp. 19–34).

Danielsen, A. (2019). Pulse as dynamic attending: Anlysing beat bin metre in neo soul grooves. In C. Scotto, K. Smith, & J. Brackett (Eds.), *The Routledge Companion to Popular Music Analysis: Expanding Approaches* (1st ed., pp. 179–189). New York, New York, USA: Routledge.

Danielsen, A., Haugen, M. R., & Jensenius, A. R. (2015). Moving to the Beat: Studying Entrainment to Micro-Rhythmic Changes in Pulse by Motion Capture. *Timing and Time Perception*, *3*(1–2), 133–154. https://doi.org/10.1163/22134468-00002043

Danielsen, A., Otnæss, M. K., Jensen, J., Williams, S. C. R., & Østberg, B. C. (2014). Investigating repetition and change in musical rhythm by functional MRI. *Neuroscience*, *275*, 469–476. https://doi.org/10.1016/j.neuroscience.2014.06.029

Davies, M., Madison, G., Silva, P., & Gouyon, F. (2013). The Effect of Microtiming Deviations on the Perception of Groove in Short Rhythms. *Music Perception: An Interdisciplinary Journal*, *30*(5), 497–510.

Davranche, K., Nazarian, B., Vidal, F., & Coull, J. (2011). Orienting Attention in Time Activates Left Intraparietal Sulcus for Both Perceptual and Motor Task Goals. *Journal of Cognitive Neuroscience*, *23*(11), 3318–3330.

Dawe, L. A., Platf, J. R., & Racine, R. J. (1993). Harmonic accents in inference of metrical structure and perception of rhythm patterns. *Perception & Psychophysics*, *54*(6), 794–807. https://doi.org/10.3758/BF03211804

Desain, P., & Honing, H. (1999). Computational models of beat induction: The rule-based approach. *Journal of New Music Research*, *28*(1), 29–42. https://doi.org/10.1076/jnmr.28.1.29.3123

Di Martino, A., Scheres, A., Margulies, D. S., Kelly, A. M. C., Uddin, L. Q., Shehzad, Z., … Milham, M. P. (2008). Functional Connectivity of Human Striatum: A Resting State fMRI Study. *Cerebral Cortex*, *18*(12), 2735–2747. https://doi.org/10.1093/cercor/bhn041

Ding, N., Patel, A. D., Chen, L., Butler, H., Luo, C., & Poeppel, D. (2017). Temporal modulations in speech and music. *Neuroscience and Biobehavioral Reviews*, *81*, 181–187. https://doi.org/10.1016/j.neubiorev.2017.02.011

Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, 1–10. https://doi.org/10.1073/pnas.1508431112

Dorris, M. C., & Glimcher, P. W. (2004). Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron*, *44*(2), 365–378. https://doi.org/10.1016/j.neuron.2004.09.009

Droit-Volet, S., & Meck, W. H. (2007). How emotions colour our perception of time. *Trends in Cognitive Sciences*, *11*(12), 504–513. https://doi.org/10.1016/j.tics.2007.09.008

Dubey, R., & Griffiths, T. L. (2020). Reconciling Novelty and Complexity through a Rational Analysis of Curiosity. *Psychological Research*, *127*(3), 455. https://doi.org/10.3917/cm.102.021

Ellis, R. J., & Jones, M. R. (2010). Rhythmic context modulates foreperiod effects ROBERT. *Attention, Perception, & Psychophysics*, *72*(8), 2274–2288. https://doi.org/10.3758/APP

Engel, A. K., & Fries, P. (2010). Beta-band oscillations-signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Etzel, J. A., Cole, M. W., Zacks, J. M., Kay, K. N., & Braver, T. S. (2016). Reward Motivation Enhances Task Coding in Frontoparietal Cortex. *Cerebral Cortex*, *26*(4), 1647–1659. https://doi.org/10.1093/cercor/bhu327

Ferreri, L., Mas-herrero, E., Zatorre, R. J., Ripollés, P., Gomez-andres, A., & Alicart, H. (2018). Dopamine modulates the reward experiences elicited by music. *PNAS*, 1–6. https://doi.org/10.1073/pnas.1811878116

Fitch, W. T., & Rosenfeld, A. J. (2007). Perception and production of syncopated rhythms. *Music Perception: An Interdisciplinary Journal*, *25*(1), 43–58.

Flaig, N. K., & Large, E. W. (2014). Dynamic musical communication of core affect. *Frontiers in Psychology*, *5*(March), 72. https://doi.org/10.3389/fpsyg.2014.00072

Foster, N. E. V, Halpern, A. R., & Zatorre, R. J. (2013). Common parietal activation in musical mental transformations across pitch and time. *NeuroImage*, *75*, 27–35.

Franěk, M., Radil, T., Indra, M., & Lánsky, P. (1987). Following complex rhythmical acoustical patterns by tapping. *International Journal of Psychophysiology*, *5*(3), 187–192. https://doi.org/10.1016/0167-8760(87)90005-5

Freeman, B., & Pease, T. (1989). *Arranging 2 Workbook*. Boston, MA: Berklee College of Music.

Fries, P. (2015). Rhythms for Cognition: Communication through Coherence. *Neuron*, *88*(1), 220–235. https://doi.org/10.1016/j.neuron.2015.09.034

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 815–836. https://doi.org/10.1098/rstb.2005.1622

Friston, K. J. (2019). Waves of prediction. *PLOS Biology*, *17*(10), 1–7.

Friston, K. J., Bastos, A. M., Pinotsis, D., & Litvak, V. (2015). LFP and oscillations-what do they tell us? *Current Opinion in Neurobiology*, *31*, 1–6. https://doi.org/10.1016/j.conb.2014.05.004

Friston, K. J., Parr, T., & de Vries, B. (2017). The graphical brain: Belief propagation and active inference. *Network Neuroscience*, *1*(4), 381–414. https://doi.org/10.1162/NETN

Friston, Karl, FitzGerald, T., Rigoli, F., Schwartenbeck, P., O'Doherty, J., & Pezzulo, G. (2016). Active inference and learning. *Neuroscience and Biobehavioral Reviews*, *68*, 862–879. https://doi.org/10.1016/j.neubiorev.2016.06.022

Friston, Karl, Schwartenbeck, P., FitzGerald, T., Moutoussis, M., Behrens, T., & Dolan, R. J. (2014). The anatomy of choice: Dopamine and decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1655). https://doi.org/10.1098/rstb.2013.0481

Frühauf, J., Kopiez, R., & Platz, F. (2013). Music on the timing grid: The influence of microtiming on the perceived groove quality of a simple drum pattern performance. *Musicae Scientiae*, *17*(2), 246–260. https://doi.org/10.1177/1029864913486793

Fujioka, T., Fidali, B. C., & Ross, B. (2014). Neural correlates of intentional switching from ternary to binary meter in a musical hemiola pattern. *Frontiers in Psychology*, *5*(NOV), 1–15. https://doi.org/10.3389/fpsyg.2014.01257

Fujioka, T., Ross, B., & Trainor, L. J. (2015). Beta-Band Oscillations Represent Auditory Beat and Its Metrical Hierarchy in Perception and Imagery. *Journal of Neuroscience*, *35*(45), 15187–15198. https://doi.org/10.1523/JNEUROSCI.2397-15.2015

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2009). Beta and gamma rhythms in human auditory cortex during musical beat processing. *Annals of the New York Academy of Sciences*, *1169*, 89–92. https://doi.org/10.1111/j.1749-6632.2009.04779.x

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic β oscillations. *The Journal of Neuroscience*, *32*(5), 1791–1802. https://doi.org/10.1523/JNEUROSCI.4107-11.2012

Galaro, J., Celink, P., Chib, V. S., Galaro, J., Celink, P., & Chib, V. S. (2018). Motor Cortex Excitability Reflects the Subjective Value of Reward and Mediates its Effects on Incentive Motivated Performance Motor Cortex Excitability Reflects the Subjective Value of Reward and Mediates its Effects on Incentive Motivated Performance MD. *The Journal of Neuroscience*.

Gebauer, L., Kringelbach, M. L., & Vuust, P. (2012). Ever-changing cycles of musical pleasure: The role of dopamine and anticipation. *Psychomusicology: Music, Mind, and Brain*, *22*(2), 152–167. https://doi.org/10.1037/a0031126

Geiser, E., Sandmann, P., Jancke, L., & Meyer, M. (2010). Refinement of metre perception – training increases hierarchical metre processing. *European Journal of Neuroscience*, *32*, 1979–1985. https://doi.org/10.1111/j.1460-9568.2010.07462.x

Giovannelli, F., Innocenti, I., Rossi, S., Borgheresi, A., Ragazzoni, A., Zaccara, G., … Cincotta, M. (2014). Role of the dorsal premotor cortex in rhythmic auditory-motor entrainment: a perturbational approach by rTMS. *Cerebral Cortex (New York, N.Y. : 1991)*, *24*(4), 1009–1016. https://doi.org/10.1093/cercor/bhs386

Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nature Neuroscience*, *15*(4), 511–517. https://doi.org/10.1038/nn.3063

Gold, B. P., Mas-herrero, E., Zeighami, Y., Benovoy, M., & Dagher, A. (2019). Musical reward prediction errors engage the nucleus accumbens and motivate learning. *PNAS*, 1–6. https://doi.org/10.1073/pnas.1809855116

Gold, B. P., Pearce, M. T., Mas-Herrero, E., Dagher, A., & Zatorre, R. J. (2019). Predictability and uncertainty in the pleasure of music: a reward for learning? *The Journal of Neuroscience*, *39*(47), 9397–9409.

Gomez-Ramirez, J., & Costa, T. (2017). Boredom begets creativity: A solution to the exploitation–exploration trade-off in predictive coding. *BioSystems*, *162*, 168–176. https://doi.org/10.1016/j.biosystems.2017.04.006

Gompf, F., Pflug, A., Laufs, H., & Kell, C. A. (2017). Non-linear Relationship between BOLD Activation and Amplitude of Beta Oscillations in the Supplementary Motor Area during Rhythmic Finger Tapping and Internal Timing. *Frontiers in Human Neuroscience*, *11*(November), 1–11. https://doi.org/10.3389/fnhum.2017.00582

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

Grahn, J. A., & Brett, M. (2009). Impairment of beat-based rhythm discrimination in Parkinson’s disease. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *45*(1), 54–61. https://doi.org/10.1016/j.cortex.2008.01.005

Grahn, J. A., Henry, M. J., & McAuley, J. D. (2011). FMRI investigation of cross-modal interactions in beat perception: Audition primes vision, but not vice versa. *NeuroImage*, *54*(2), 1231–1243. https://doi.org/10.1016/j.neuroimage.2010.09.033

Grahn, J. A., & McAuley, J. D. (2009). Neural bases of individual differences in beat perception. *NeuroImage*, *47*(4), 1894–1903. https://doi.org/10.1016/j.neuroimage.2009.04.039

Grahn, J. A., & Rowe, J. B. (2009). Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. *The Journal of Neuroscience*, *29*(23), 7540–7548. https://doi.org/10.1523/JNEUROSCI.2018-08.2009

Grahn, J. A., & Rowe, J. B. (2013). Finding and feeling the musical beat: striatal dissociations between detection and prediction of regularity. *Cerebral Cortex (New York, N.Y. : 1991)*, *23*(4), 913–921. https://doi.org/10.1093/cercor/bhs083

Grahn, J. A., & Schuit, D. (2012). Individual differences in rhythmic ability: Behavioral and neuroimaging investigations. *Psychomusicology: Music, Mind, and Brain*, *22*(2), 105–121. https://doi.org/10.1037/a0031188

Graybiel, A. M. (2008). Habits, rituals, and the evaluative brain. *Annual Review of Neuroscience*, *31*, 359–387. https://doi.org/10.1146/annurev.neuro.29.051605.112851

Graybiel, A. M., & Grafton, S. T. (2015). The striatum: where skills and habits meet. *Cold Spring Harbor Perspectives in Biology*, *7*(8), 1–14. https://doi.org/10.1101/cshperspect.a021691

Greenwald, J. (2002). Hip-Hop drumming: The rhyme may define, but the groove makes you move. *Black Music Research Journal*, *22*(2), 259–271.

Grube, M., Cooper, F. E., Chinnery, P. F., & Griffiths, T. D. (2010). Dissociation of duration-based and beat-based auditory timing in cerebellar degeneration. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(25), 11597–11601. https://doi.org/10.1073/pnas.0910473107

Grube, M., Lee, K. H., Griffiths, T. D., Barker, A. T., & Woodruff, P. W. (2010). Transcranial magnetic theta-burst stimulation of the human cerebellum distinguishes absolute, duration-based from relative, beat-based perception of subsecond time intervals. *Frontiers in Psychology*, *1*(OCT), 1–8. https://doi.org/10.3389/fpsyg.2010.00171

Haber, S. (2016). Perspective on basal ganglia connections as described by Nauta and Mehler in 1966: Where we were and how this paper effected where we are now. *Brain Research*. https://doi.org/10.1016/j.brainres.2016.04.016

Haber, S. N. (2003). The primate basal ganglia: parallel and integrative networks. *Journal of Chemical Neuroanatomy*, *26*(4), 317–330. https://doi.org/10.1016/j.jchemneu.2003.10.003

Habibi, A., Wirantana, V., & Starr, A. (2014). Cortical Activity during Perception of Musical Rhythm; Comparing Musicians and Non-musicians. *Psychomusicology*, *24*(2), 125–135. https://doi.org/10.1037/pmu0000046.Cortical

Hammers, A., Allom, R., Koepp, M. J., Free, S. L., Myers, R., Lemieux, L., … Duncan, J. S. (2003). Three-dimensional maximum probability atlas of the human brain, with particular reference to the temporal lobe. *Human Brain Mapping*, *19*(4), 224–247. https://doi.org/10.1002/hbm.10123

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

Hartcher-O'Brien, J., Brighouse, C., & Levitan, C. A. (2016). A single mechanism account of duration and rate processing via the pacemaker-accumulator and beat frequency models. *Current Opinion in Behavioral Sciences*, *8*, 268–275. https://doi.org/10.1016/j.cobeha.2016.02.026

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

Henry, M. J., Herrmann, B., & Obleser, J. (2015). Selective attention to temporal features on nested time scales. *Cerebral Cortex*, *25*(2), 450–459. https://doi.org/10.1093/cercor/bht240

Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(49), 20095–20100. https://doi.org/10.1073/pnas.1213390109

Heyduk, R. G. (1975). Rated preference for musical compositions as it relates to complexity and exposure frequency. *Perception & Psychophysics*, *17*(1), 84–90. https://doi.org/10.3758/BF03204003

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams : a framework for understanding aspects of the functional anatomy of language. *Cognition*, *92*, 67–99. https://doi.org/10.1016/j.cognition.2003.10.011

Hickok, G., & Poeppel, D. (2007). The Cortical Organization of Speech Processing. *Nature Reviews Neuroscience*, *8*, 393–402. https://doi.org/10.1038/nrn2113

Hickok, G., & Poeppel, D. (2016). Neural Basis of Speech Perception. In *Neurobiology of Language* (pp. 299–310). Elsevier Inc. https://doi.org/10.1016/B978-0-12-407794-2.00025-0

Hollerman, J. R., & Schultz, W. (1998). Dopamine neurons report an error in the temporal prediction of reward during learning. *Nature Neuroscience*, *1*(4), 304–309. https://doi.org/10.1038/1124

Hosseini, A. H., & Holroyd, C. B. (2015). Reward feedback stimuli elicit high-beta EEG oscillations in human dorsolateral prefrontal cortex. *Scientific Reports*, *5*(July), 1–8. https://doi.org/10.1038/srep13021

Hurley, B. K., Martens, P. A., & Janata, P. (2014). Spontaneous sensorimotor coupling with multipart music. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(4), 1679–1696. https://doi.org/10.1037/a0037154

Huron, D. (1994). Interval-Class Content in Equally Tempered Sets: Common Scales Exhibit Optimum Tonal Consonance. *Music Perception: An Interdisciplinary Journal*, *11*(3), 289–305.

Huron, D. (2006). *Sweet Anticipation: Music and the Psychology of Expectation*. *MIT Press*. Cambridge, MA. https://doi.org/10.1525/mp.2007.24.5.511

Iversen, J. R., Repp, B. H., & Patel, A. D. (2009). Top-down control of rhythm perception modulates early auditory responses. *Annals of the New York Academy of Sciences*, *1169*, 58–73. https://doi.org/10.1111/j.1749-6632.2009.04579.x

Jaeger, B. C. (2017). Package ‘r2glmm.’ *Package ‘R2glmm,’* 12. https://doi.org/10.1002/sim.3429>is

Jahanshahi, M., Obeso, I., Rothwell, J. C., & Obeso, J. a. (2015). A fronto–striato–subthalamic–pallidal network for goal-directed and habitual inhibition. *Nature Reviews Neuroscience*, (November). https://doi.org/10.1038/nrn4038

Jamieson, S. (2004). Likert scales: how to (ab)use them. *Medical Education*, *38*, 1212–1218. https://doi.org/10.1111/j.1365-2929.2004.02012.x

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

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

Jarbo, K., & Verstynen, T. D. (2015). Converging Structural and Functional Connectivity of Orbitofrontal, Dorsolateral Prefrontal, and Posterior Parietal Cortex in the Human Striatum. *The Journal of Neuroscience*, *35*(9), 3865–3878. https://doi.org/10.1523/JNEUROSCI.2636-14.2015

Johansen-Berg, H., Behrens, T. E. J., Robson, M. D., Drobnjak, I., Rushworth, M. F. S., Brady, J. M., … Matthews, P. M. (2004). Changes in connectivity profiles define functionally distinct regions in human medial frontal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(36), 13335–13340. https://doi.org/10.1073/pnas.0403743101

Juslin, P. N., & Västfjäll, D. (2008). Emotional responses to music: the need to consider underlying mechanisms. *The Behavioral and Brain Sciences*, *31*(5), 559–621. https://doi.org/10.1017/S0140525X08005293

Kameda, M., Ohmae, S., & Tanaka, M. (2019). Entrained neuronal activity to periodic visual stimuli in the primate striatum compared with the cerebellum. *ELife*, *8*, 1–18. https://doi.org/10.7554/elife.48702

Kammann, R. (1966). Verbal complexity and preferences in poetry. *Journal of Verbal Learning and Verbal Behavior*, *5*(6), 536–540. https://doi.org/10.1016/S0022-5371(66)80088-9

Karabanov, A., Blom, O., Forsman, L., & Ullén, F. (2009). The dorsal auditory pathway is involved in performance of both visual and auditory rhythms. *NeuroImage*, *44*(2), 480–488. https://doi.org/10.1016/j.neuroimage.2008.08.047

Keller, P., & Schubert, E. (2011). Cognitive and affective judgements of syncopated musical themes. *Advances in Cognitive Psychology*, *7*(1), 142–156. https://doi.org/10.2478/v10053-008-0094-0

Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. a, & Riehle, A. (2013). The ups and downs of β oscillations in sensorimotor cortex. *Experimental Neurology*, *245*, 15–26. https://doi.org/10.1016/j.expneurol.2012.09.014

Kilchenmann, L., & Senn, O. (2015). Microtiming in Swing and Funk affects the body movement behavior of music expert listeners. *Frontiers in Psychology*, *6*(1232), 1–14. https://doi.org/10.3389/fpsyg.2015.01232

Kizach, J. (2014). Analyzing Likert-scale data with mixed-effects linear models - a simulation study. *Poster Presented at Linguistic Evidence,Tübingen, Germany*.

Kizilirmak, J. M., Galvao Gomes da Silva, J., Imamoglu, F., & Richardson-Klavehn, A. (2016). Generation and the subjective feeling of "aha!" are independently related to learning from insight. *Psychological Research*, *80*(6), 1059–1074. https://doi.org/10.1007/s00426-015-0697-2

Koch, K., Schachtzabel, C., Wagner, G., Reichenbach, J. R., Sauer, H., & Schlösser, R. (2008). The neural correlates of reward-related trial-and-error learning: An fMRI study with a probabilistic learning task. *Learning and Memory*, *15*(10), 728–732. https://doi.org/10.1101/lm.1106408

Koelsch, S. (2014). Brain correlates of music-evoked emotions. *Nature Reviews. Neuroscience*, *15*(3), 170–180. https://doi.org/10.1038/nrn3666

Koelsch, S., & Skouras, S. (2014). Functional centrality of amygdala, striatum and hypothalamus in a "small-world" network underlying joy: An fMRI study with music. *Human Brain Mapping*, *35*(7), 3485–3498. https://doi.org/10.1002/hbm.22416

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

Koller, M. (2016). Robustlmm: An R package for Robust estimation of linear Mixed-Effects models. *Journal of Statistical Software*, *75*(1). https://doi.org/10.18637/jss.v075.i06

Komeilipoor, N., Rodger, M. W. M., Craig, C. M., & Cesari, P. (2015). (Dis-)Harmony in movement: effects of musical dissonance on movement timing and form. *Experimental Brain Research*, *233*(5), 1585–1595. https://doi.org/10.1007/s00221-015-4233-9

Konoike, N., Kotozaki, Y., Jeong, H., Miyazaki, A., Sakaki, K., Shinada, T., … Nakamura, K. (2015). Temporal and motor representation of rhythm in fronto-parietal cortical areas: An fMRI study. *PLoS ONE*, *10*(6), 1–19. https://doi.org/10.1371/journal.pone.0130120

Konoike, N., Kotozaki, Y., Miyachi, S., Miyauchi, C. M., Yomogida, Y., Akimoto, Y., … Nakamura, K. (2012). Rhythm information represented in the fronto-parieto-cerebellar motor system. *NeuroImage*, *63*(1), 328–338. https://doi.org/10.1016/j.neuroimage.2012.07.002

Kononowicz, T. W., Roger, C., & Van Wassenhove, V. (2019). Temporal Metacognition as the Decoding of Self-Generated Brain Dynamics. *Cerebral Cortex*, *29*(10), 4366–4380. https://doi.org/10.1093/cercor/bhy318

Kornysheva, K., & Schubotz, R. I. (2011). Impairment of auditory-motor timing and compensatory reorganization after ventral premotor cortex stimulation. *PloS One*, *6*(6), e21421. https://doi.org/10.1371/journal.pone.0021421

Koshimori, Y., Strafella, A. P., Valli, M., Sharma, V., Cho, S., Houle, S., & Thaut, M. H. (2019). Motor Synchronization to Rhythmic Auditory Stimulation (RAS) Attenuates Dopaminergic Responses in Ventral Striatum in Young Healthy Adults : [11 C] - (+) -PHNO PET Study. *Frontiers in Neuroscience*, *13*, 1–10. https://doi.org/10.3389/fnins.2019.00106

Kotz, S. A., Brown, R. M., & Schwartze, M. (2016). Cortico-striatal circuits and the timing of action and perception. *Current Opinion in Behavioral Sciences*, 8–11. https://doi.org/10.1016/j.cobeha.2016.01.010

Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Nature Reviews Neuroscience*, *6*, 691–702. https://doi.org/10.1038/nrn1748

Kubanek, J., & Snyder, L. H. (2015). Reward-based decision signals in parietal cortex are partially embodied. *Journal of Neuroscience*, *35*(12), 4869–4881. https://doi.org/10.1523/JNEUROSCI.4618-14.2015

Kuhn, M., & Roeder, I. (2018). lme4cens: Linear Mixed Models with Censored Observations (Vol. 67, p. 18637).

Kung, S.-J., Chen, J. L., Zatorre, R. J., & Penhune, V. B. (2013). Interacting cortical and basal ganglia networks underlying finding and tapping to the musical beat. *Journal of Cognitive Neuroscience*, *25*(3), 401–420. https://doi.org/10.1162/jocn_a_00325

Labbé, C, & Grandjean, D. (2014). Musical emotions predicted by feelings of entrainment. *Music Perception*, *32*(2), 170–185.

Labbé, Carolina, & Trost, W. (2020). Affective experiences to chords are modulated by mode, meter, tempo, and subjective entrainment. *Psychology of Music*, 1–16. https://doi.org/10.1177/0305735620906887

Ladinig, O., Honing, H., Haden, G., & Winkler, I. (2009). Probing attentive and preattentive emergent meter in adult listeners without extensive music training. *Music Perception*, *26*(4), 377–386.

Lahdelma, I., & Eerola, T. (2014). Single chords convey distinct emotional qualities to both naive and expert listeners. *Psychology of Music*, *44*(1), 37–54. https://doi.org/10.1177/0305735614552006

Lahdelma, I., & Eerola, T. (2016). Mild Dissonance Preferred Over Consonance in Single Chord Perception. *I-Perception*, *7*(3), 1–21. https://doi.org/10.1177/2041669516655812

Lakatos, P., Gross, J., & Thut, G. (2019). A new unifying account of the roles of neuronal entrainment. *Current Biology*, *29*(18), 1–16. https://doi.org/10.1016/j.cub.2019.07.075

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, *320*(5872), 110–113. https://doi.org/10.1126/science.1154735

Lappe, C., Lappe, C., Steinsträter, O., Lappe, C., Steinsträter, O., & Pantev, C. (2013). A rhythmic deviation within a musical sequence induces neural activation in inferior parietal regions after short-term multisensory training. *Multisensory Research*, *26*(0), 164. https://doi.org/10.1163/22134808-000s0121

Lappe, C., Lappe, M., & Pantev, C. (2016). Differential processing of melodic, rhythmic and simple tone deviations in musicians -an MEG study. *NeuroImage*, *124*, 898–905. https://doi.org/10.1016/j.neuroimage.2015.09.059

Lappe, C., Steinsträter, O., & Pantev, C. (2013). Rhythmic and melodic deviations in musical sequences recruit different cortical areas for mismatch detection. *Frontiers in Human Neuroscience*, *7*(June), 260. https://doi.org/10.3389/fnhum.2013.00260

Large, E. W., & Jones, M. R. (1999). The Dynamics of Attending: How People Track Time-Varying Events. *Psychological Review*, *106*(1), 119–159.

Large, E. W., & Kolen, J. F. (1994). Resonance and the perception of musical meter. *Connection Science*, *6*(1), 177–208. https://doi.org/10.1080/09540099408915723

Large, E. W., & Palmer, C. (2002). Perceiving temporal regularity in music. *Cognitive Science*, *26*(1), 1–37. https://doi.org/10.1207/s15516709cog2601_1

Large, E. W., & Snyder, J. S. (2009). Pulse and meter as neural resonance. *Annals of the New York Academy of Sciences*, *1169*, 46–57. https://doi.org/10.1111/j.1749-6632.2009.04550.x

Lartillot, O., Toiviainen, P., & Eerola, T. (2007). A Matlab Toolbox for Music Information Retrieval. *Data Analysis, Machine Learning and Applications*, 261–268. https://doi.org/10.1007/978-3-540-78246-9_31

Lehericy, S., Ducros, M., Krainik, A., Francois, C., Van De Moortele, P. F., Ugurbil, K., & Kim, D. S. (2004). 3-D diffusion tensor axonal tracking shows distinct SMA and pre-SMA projections to the human striatum. *Cerebral Cortex*, *14*(12), 1302–1309. https://doi.org/10.1093/cercor/bhh091

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

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2018). Package “emmeans.” https://doi.org/10.1080/00031305.1980.10483031>.License

Levine, M. (2011). *The Jazz Theory Book*. O’Reilly Media, Inc.

Lewis, A. G., & Bastiaansen, M. (2015). A predictive coding framework for rapid neural dynamics during sentence-level language comprehension. *Cortex*, *68*, 155–168. https://doi.org/10.1016/j.cortex.2015.02.014

Lewis, A. G., Schoffelen, J. M., Schriefers, H., & Bastlaansen, M. (2016). A predictive coding perspective on beta oscillations during sentence-level language comprehension. *Frontiers in Human Neuroscience*, *10*(MAR2016), 1–6. https://doi.org/10.3389/fnhum.2016.00085

Lewis, P. A., Wing, A. M., Pope, P. A., Praamstra, P., & Miall, R. C. (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. *Neuropsychologia*, *42*(10), 1301–1312. https://doi.org/10.1016/j.neuropsychologia.2004.03.001

Li, Q., Liu, G., Wei, D., Liu, Y., Yuan, G., & Wang, G. (2019). Distinct neuronal entrainment to beat and meter: Revealed by simultaneous EEG-fMRI. *NeuroImage*, *194*(March), 128–135. https://doi.org/10.1016/j.neuroimage.2019.03.039

London, J. (2012). *Hearing in Time*. New York: Oxford University Press.

Longuet-Higgins, H. C., & Lee, C. S. (1984). The Rhythmic Interpretation of Monophonic

Music. *Music Perception: An Interdisciplinary Journal*, *1*(4), 424–441.

Lumaca, M., Haumann, N. T., Brattico, E., Grube, M., & Vuust, P. (2019). Weighting of neural prediction error by rhythmic complexity: a predictive coding account using Mismatch Negativity. *European Journal of Neuroscience*, *49*, 1597–1609. https://doi.org/10.1111/ejn.14329

Macar, F., Lejeune, H., Bonnet, M., Ferrara, A., V., P., Vidal, F., & Maquet, P. (2002). Activation of the supplementary motor area and of attentional networks during temporal processing. *Experimental Brain Research*, *142*(4), 475–485. https://doi.org/10.1007/s00221-001-0953-0

MacDougall, H. G., & Moore, S. T. (2005). Marching to the beat of the same drummer: The spontaneous tempo of human locomotion. *Journal of Applied Physiology*, *99*(3), 1164–1173. https://doi.org/10.1152/japplphysiol.00138.2005

Madison, G. (2006). Experiencing Groove Induced by Music: Consistency and Phenomenology. *Music Perception*, *24*(2), 201–208. https://doi.org/10.1525/mp.2006.24.2.201

Madison, G., Gouyon, F., & Ullen, F. (2009). Musical groove is correlated with properties of the audio signal as revealed by computational modelling, depending on musical style. In *Proceedings of the SMC 2009 - 6th Sound and Music Computing Conference* (pp. 239–240).

Madison, G., Gouyon, F., Ullén, F., & Hörnström, K. (2011). Modeling the tendency for music to induce movement in humans: First correlations with low-level audio descriptors across music genres. *J. Exp. Psychol. Hum. Percept. Perform*, *37*, 1578–1594.

Madison, G., & Sioros, G. (2014). What musicians do to induce the sensation of groove in simple and complex melodies, and how listeners perceive it. *Frontiers in Psychology Auditory Cognitive Neuroscience*, *5*(894), 1–14. https://doi.org/10.3389/fpsyg.2014.00894

Maes, P. J. (2016). Sensorimotor grounding of musical embodiment and the role of prediction: A review. *Frontiers in Psychology*, *7*, 1–10. https://doi.org/10.3389/fpsyg.2016.00308

Marco-Pallarés, J., Münte, T. F., & Rodríguez-Fornells, A. (2015). The role of high-frequency oscillatory activity in reward processing and learning. *Neuroscience and Biobehavioral Reviews*, *49*, 1–7. https://doi.org/10.1016/j.neubiorev.2014.11.014

Martinez-Molina, N., Mas-Herrero, E., Rodríguez-fornells, A., Zatorre, R. J., & Marco-pallarés, J. (2019). White matter microstructure reflects individual differences in music reward sensitivity. *The Journal of Neuroscience*, *39*(25), 5018–5027.

Martínez-Molina, N., Mas-Herrero, E., Rodríguez-Fornells, A., Zatorre, R. J., & Marco-Pallarés, J. (2016). Neural correlates of specific musical anhedonia. *Proceedings of the National Academy of Sciences*, E7337–E7345. https://doi.org/10.1073/PNAS.1611211113

Mas-herrero, E., Dagher, A., & Zatorre, R. J. (2018). Modulating musical reward sensitivity up and down with transcranial magnetic stimulation. *Nature Human Behaviour*, *2*, 27–32. https://doi.org/10.1038/s41562-017-0241-z

Mas-Herrero, E., Ripollés, P., HajiHosseini, A., Rodríguez-Fornells, A., & Marco-Pallarés, J. (2015). Beta oscillations and reward processing: Coupling oscillatory activity and hemodynamic responses. *NeuroImage*, *119*(May 2016), 13–19. https://doi.org/10.1016/j.neuroimage.2015.05.095

Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: coincidence detection of oscillatory processes. *Cognitive Brain Research*, *21*(2), 139–170. https://doi.org/10.1016/j.cogbrainres.2004.06.012

Matthews, T. E., Thibodeau, J. L. N., Gunther, B. P., & Penhune, V. B. (2016). The Impact of

Instrument-Specific Musical Training on Rhythm Perception and Production. *Frontiers in Psychology*, *7*(February), 69. https://doi.org/10.3389/fpsyg.2016.00069

Matthews, T. E., Witek, M. A. G., Heggli, O. A., Penhune, V. B., & Vuust, P. (2019). The sensation of groove is affected by the interaction of rhythmic and harmonic complexity. *PLoS ONE*, *14*(1). https://doi.org/10.1371/journal.pone.0204539

Matthews, T. E., Witek, M. A. G., Lund, T., Vuust, P., & Penhune, V. B. (2020). The sensation of groove engages motor and reward networks. *NeuroImage*, *214*(116768), 1–12. https://doi.org/10.1016/j.neuroimage.2020.116768

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing Type I error and power in linear mixed models. *Journal of Memory and Language*, *94*, 305–315. https://doi.org/10.1016/j.jml.2017.01.001

McAuley, J. D., Henry, M. J., & Tkach, J. (2012). Tempo mediates the involvement of motor areas in beat perception. *Annals of the New York Academy of Sciences*, *1252*, 77–84. https://doi.org/10.1111/j.1749-6632.2011.06433.x

Menon, V., & Levitin, D. J. (2005). The rewards of music listening : Response and physiological connectivity of the mesolimbic system. *NeuroImage*, *28*, 175–184. https://doi.org/10.1016/j.neuroimage.2005.05.053

Merchant, H., Grahn, J., Trainor, L., Rohrmeier, M., Fitch, W. T., & Merchant, H. (2015). Finding the beat: a neural perspective across humans and non-human primates. *Philosophical Transactions of the Royal Society*, *370*, 1–16.

Merchant, H., Harrington, D. L., & Meck, W. H. (2013). Neural Basis of the Perception and Estimation of Time. *Annual Review of Neuroscience*, *36*(1), 313–336. https://doi.org/10.1146/annurev-neuro-062012-170349

Merchant, H., Pérez, O., Zarco, W., & Gámez, J. (2013). Behavioral/Cognitive Interval Tuning in the Primate Medial Premotor Cortex as a General Timing Mechanism. *The Journal of Neuroscience*, *33*(21), 90-=82-9096. https://doi.org/10.1523/JNEUROSCI.5513-12.2013

Meyer, L. B. (1956). *Emotion and Meaning in Music*. Chicago: University of Chicago Press.

Michaelis, K., Wiener, M., & Thompson, J. C. (2014). Passive listening to preferred motor tempo modulates corticospinal excitability. *Frontiers in Human Neuroscience*, *8*(1 APR), 1–10. https://doi.org/10.3389/fnhum.2014.00252

Morillon, B., Arnal, L. H., Schroeder, C. E., & Keitel, A. (2019). Prominence of delta oscillatory rhythms in the motor cortex and their relevance for auditory and speech perception. *Neuroscience and Biobehavioral Reviews*, *107*, 136–142. https://doi.org/10.1016/j.neubiorev.2019.09.012

Morillon, B., & Schroeder, C. E. (2015). Neuronal oscillations as a mechanistic substrate of auditory temporal prediction. *Annals of the New York Academy of Sciences*, *1337*, 26–31. https://doi.org/10.1111/nyas.12629

Morillon, B., Schroeder, C. E., Wyart, V., & Arnal, L. H. (2016). Temporal Prediction in lieu of Periodic Stimulation. *Journal of Neuroscience*, *36*(8), 2342–2347. https://doi.org/10.1523/JNEUROSCI.0836-15.2016

Morillon, Benjamin, & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences*, *114*(42), E8913–E8921. https://doi.org/10.1073/pnas.1705373114

Müller, K., Aschersleben, G., Koch, R., Freund, H. J., & Prinz, W. (1999). Action timing in an isochronous tapping task. Evidence from behavioral studies and neuroimaging. *Advances in Psychology*, *129*(C), 233–250. https://doi.org/10.1016/S0166-4115(99)80023-5

Nettles, B., & Ulanowsky, A. (1987). *Harmony 1-4*. Boston, MA: Berklee College of Music.

Nobre, A. C., & van Ede, F. (2017). Anticipated moments: temporal structure in attention. *Nature Reviews Neuroscience*, *19*(1), 34–48. https://doi.org/10.1038/nrn.2017.141

Norman, G. (2010). Likert scales, levels of measurement and the '"laws"' of statistics. *Advances in Health Sciences Education*, *15*(5), 625–632. https://doi.org/10.1007/s10459-010-9222-y

North, A. C., & Hargreaves, D. J. (1997). Liking, arousal potential, and the emotions expressed by music. *Scandinavian Journal of Psychology*, *38*(1), 45–53. https://doi.org/10.1111/1467-9450.00008

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

Nozaradan, S., Mouraux, A., Jonas, J., Colnat-Coulbois, S., Rossion, B., & Maillard, L. (2017). Intracerebral evidence of rhythm transform in the human auditory cortex. *Brain Structure and Function*, *222*, 2389–2404. https://doi.org/10.1007/s00429-016-1348-0

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

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

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

O'Doherty, J. P. (2004). Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Current Opinion in Neurobiology*, *14*(6), 769–776. https://doi.org/10.1016/j.conb.2004.10.016

Obleser, J., Henry, M. J., & Lakatos, P. (2017). What do we talk about when we talk about rhythm? *PLoS Biology*, *15*(9), 1–5. https://doi.org/10.1371/journal.pbio.2002794

Occelli, V., Spence, C., & Zampini, M. (2011). Audiotactile interactions in temporal perception. *Psychonomic Bulletin and Review*, *18*(3), 429–454. https://doi.org/10.3758/s13423-011-0070-4

Orr, M. G., & Ohlsson, S. (2005). Relationship between complexity and liking as a function of expertise. *Music Perception: An Interdisciplinary Journal*, *22*(4), 583–611.

Owens, A. P., Allen, M., Ondobaka, S., & Friston, K. J. (2018). Interoceptive inference: From computational neuroscience to clinic. *Neuroscience and Biobehavioral Reviews*, *90*(May 2017), 174–183. https://doi.org/10.1016/j.neubiorev.2018.04.017

Pallesen, K. J., Brattico, E., Bailey, C., Korvenoja, A., Koivisto, J., Gjedde, A., & Carlson, S. (2005). Emotion processing of major, minor, and dissonant chords: A functional magnetic resonance imaging study. *Annals of the New York Academy of Sciences*, *1060*, 450–453. https://doi.org/10.1196/annals.1360.047

Palmer, C. E., Auksztulewicz, R., Ondobaka, S., & Kilner, J. M. (2019). Sensorimotor beta power reflects the precision-weighting afforded to sensory prediction errors. *NeuroImage*, *200*(May), 59–71. https://doi.org/10.1016/j.neuroimage.2019.06.034

Patel, A. D., & Iversen, J. R. (2014). The evolutionary neuroscience of musical beat perception: The Action Simulation for Auditory Prediction (ASAP) hypothesis. *Frontiers in Systems*

Neuroscience, *8*(57), 1–14. https://doi.org/10.3389/fnsys.2014.00057

Patel, A. D., Iversen, J. R., Chen, Y., & Repp, B. H. (2005). The influence of metricality and modality on synchronization with a beat. *Experimental Brain Research*, *163*(2), 226–238. https://doi.org/10.1007/s00221-004-2159-8

Pearce, M. T., & Wiggins, G. A. (2012). Auditory expectation: the information dynamics of music perception and cognition. *Topics in Cognitive Science*, *4*(4), 625–652. https://doi.org/10.1111/j.1756-8765.2012.01214.x

Pecenka, N., Engel, A., & Keller, P. E. (2013). Neural correlates of auditory temporal predictions during sensorimotor synchronization. *Frontiers in Human Neuroscience*, *7*(380), 1–16. https://doi.org/10.3389/fnhum.2013.00380

Pereira, C. S., Teixeira, J., Figueiredo, P., Xavier, J., Castro, S. L., & Brattico, E. (2011). Music and Emotions in the Brain: Familiarity Matters. *PLoS ONE*, *6*(11), e27241. https://doi.org/10.1371/journal.pone.0027241

Plomp, R., & Levelt, J. M. (1965). Tonal consonance and critical bandwidth. *The Journal of the Acoustical Society of America*, *38*(4), 548–560. https://doi.org/10.1063/1.3033202

Postuma, R. B., & Dagher, A. (2006). Basal Ganglia Functional Connectivity Based on a Meta-Analysis of 126 Positron Emission Tomography and Functional Magnetic Resonance Imaging Publications. *Cerebral Cortex*, *16*(10), 1508–1521. https://doi.org/10.1093/cercor/bhj088

Povel, D., & Essens, P. (1985). Perception of Temporal Patterns. *JSTOR*, *2*(4), 411–440.

Pressing, J. (2002). Black atlantic rhythm: Its computational and transcultural foundations. *Music Perception*, *19*(3), 285–310. https://doi.org/10.1525/jams.2009.62.1.145.

Ptak, R., Schnider, A., & Fellrath, J. (2017). The Dorsal Frontoparietal Network: A Core System for Emulated Action. *Trends in Cognitive Sciences*, *21*(8), 589–599. https://doi.org/10.1016/j.tics.2017.05.002

Putkinen, V., Makkonen, T., & Eerola, T. (2017). Music-induced positive mood broadens the scope of auditory attention. *Social Cognitive and Affective Neuroscience*, *12*(7), 1159–1168. https://doi.org/10.1093/scan/nsx038

Quiroga-Martinez, D. R., Hansen, N. C., Højlund, A., Pearce, M. T., Brattico, E., & Vuust, P. (2019). Reduced prediction error responses in high-as compared to low-uncertainty musical contexts. *Cortex*, *120*, 181–200. https://doi.org/10.1016/j.cortex.2019.06.010

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*(1), 79–87. https://doi.org/10.1038/4580

Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hearing Research*, *271*(1–2), 16–25. https://doi.org/10.1016/j.heares.2010.09.001

Repp, B. H. (2000). Compensation for subliminal timing perturbations in perceptual-motor synchronization. *Psychological Research*, *63*, 106–128.

Repp, B. H. (2001). Phase correction, phase resetting, and phase shifts after subliminal timing perturbations in sensorimotor synchronization. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(3), 600–621.

Repp, B. H. (2002). Automaticity and voluntary control of phase correction following event onset shifts in sensorimotor synchronization. *Journal of Experimental Psychology: Human Perception and Performance*, *28*(2), 410–430.

Repp, B. H. (2005). Sensorimotor synchronization: a review of the tapping literature.

Psychonomic Bulletin & Review, *12*(6), 969–992. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16615317

Repp, B. H. (2010). Sensorimotor synchronization and perception of timing: Effects of music training and task experience. *Human Movement Science*. https://doi.org/10.1016/j.humov.2009.08.002

Repp, B. H., & Doggett, R. (2007). Tapping to a very slow beat: A comparison of musicians and nonmusicians. *Music Perception: An Interdisciplinary Journal*, *24*(4), 367–376.

Repp, B. H., & Keller, P. E. (2004). Adaptation to tempo changes in sensorimotor synchronization: Effects of intention, attention, and awareness. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, *57*(3), 499–521. https://doi.org/10.1080/02724980343000369

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

Rimmele, J. M., Morillon, B., Poeppel, D., & Arnal, L. H. (2018). Proactive Sensing of Periodic and Aperiodic Auditory Patterns. *Trends in Cognitive Sciences*, *22*(10), 870–882. https://doi.org/10.1016/j.tics.2018.08.003

Ripollés, P., Marco-Pallarés, J., Hielscher, U., Mestres-Missé, A., Tempelmann, C., Heinze, H. J., … Noesselt, T. (2014). The role of reward in word learning and its implications for language acquisition. *Current Biology*, *24*(21), 2606–2611. https://doi.org/10.1016/j.cub.2014.09.044

Ross, J. M., & Balasubramaniam, R. (2014). Physical and neural entrainment to rhythm: human sensorimotor coordination across tasks and effector systems. *Frontiers in Human Neuroscience*, *8*(August), 576. https://doi.org/10.3389/fnhum.2014.00576

Ross, J. M., Iversen, J. R., & Balasubramaniam, R. (2016). Motor Simulation Theories of Musical Beat. *Neurocase*, (September).

Ross, J. M., Iversen, J. R., & Balasubramaniam, R. (2018a). Dorsal Premotor Contributions to Auditory Rhythm Perception: Causal Transcranial Magnetic Stimulation Studies of Interval, Tempo, and Phase. *BioRxiv*, 1–16. Retrieved from https://www.sciencedirect.com/science/article/pii/S1877065718300551

Ross, J. M., Iversen, J. R., & Balasubramaniam, R. (2018b). The Role of Posterior Parietal Cortex in Beat-based Timing Perception: A Continuous Theta Burst Stimulation Study. *Journal of Cognitive Neuroscience*, 1–10. https://doi.org/10.1162/jocn

Rump, E. E. (1968). Relative preference as a function of the number of elements in Abstract Designs. *Australian Journal of Psychology*, *20*(1), 39–48. https://doi.org/10.1080/00049536808255737

Ryan, R. M., & Deci, E. L. (2000). Intrinsic and Extrinsic Motivations: Classic Definitions and New Directions. *Contemporary Educational Psychology*, *25*(1), 54–67. https://doi.org/10.1006/ceps.1999.1020

Saga, Y., Hoshi, E., & Tremblay, L. (2017). Roles of multiple globus pallidus territories of monkeys and humans in motivation, cognition and action: An anatomical, physiological and pathophysiological review. *Frontiers in Neuroanatomy*, *11*(April). https://doi.org/10.3389/FNANA.2017.00030

Salimpoor, V. N., Benovoy, M., Larcher, K., Dagher, A., & Zatorre, R. J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature Neuroscience*, *14*(2), 257–262. https://doi.org/10.1038/nn.2726

Salimpoor, V. N., van den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science (New York, N.Y.)*, *340*(6129), 216–219. https://doi.org/10.1126/science.1231059

Salimpoor, V. N., Zald, D. H., Zatorre, R. J., Dagher, A., & McIntosh, A. R. (2015). Predictions and the brain: how musical sounds become rewarding. *Trends in Cognitive Sciences*, *19*(2), 86–91. https://doi.org/10.1016/j.tics.2014.12.001

Samiee, S., & Baillet, S. (2017). Time-resolved phase-amplitude coupling in neural oscillations. *NeuroImage*, *159*(February), 270–279. https://doi.org/10.1016/j.neuroimage.2017.07.051

Schmidhuber, J. (2010). Formal Theory of Creativity & Intrinsic Motivation (1990-2010). *IEEE TRANSACTIONS ON AUTONOMOUS MENTAL DEVELOPMENT*, *2*(3), 1–18.

Schön, D., & Morillon, B. (2019). Music and Language. In *The Oxford Handbook of Music and the Brain* (pp. 1–31). https://doi.org/10.1093/oxfordhb/9780198804123.013.16

Schroeder, C. E., Wilson, D. A., Radman, T., Scharfman, H., & Lakatos, P. (2010). Dynamics of Active Sensing and Perceptual Selection. *Current Opinion in Neurobiology*, *20*(2), 172–176. https://doi.org/10.1016/j.conb.2010.02.010.Dynamics

Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences*, *11*(5), 211–218. https://doi.org/10.1016/j.tics.2007.02.006

Schubotz, R. I., Friederici, A. ., & von Cramon, D. Y. (2000). Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI. *NeuroImage*, *11*(1), 1–12. https://doi.org/10.1006/nimg.1999.0514

Schubotz, R. I., & von Cramon, D. Y. (2001). Interval and ordinal properties of sequences are associated with distinct premotor areas. *Cerebral Cortex (New York, N.Y. : 1991)*, *11*(3), 210–222. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11230093

Schultz, W. (2016). Dopamine reward prediction- error signalling: a two-component response. *Nature Reviews Neuroscience*.

Schwartze, M., & Kotz, S. a. (2013). A dual-pathway neural architecture for specific temporal prediction. *Neuroscience and Biobehavioral Reviews*, *37*(10 Pt 2), 2587–2596. https://doi.org/10.1016/j.neubiorev.2013.08.005

Sedley, W., Gander, P. E., Kumar, S., Kovach, C. K., Oya, H., Kawasaki, H., … Griffiths, T. D. (2016). Neural signatures of perceptual inference. *ELife*, *5*(MARCH2016), 1–13. https://doi.org/10.7554/eLife.11476

Seger, C. A., Spiering, B. J., Sares, A. G., Quraini, S. I., Alpeter, C., David, J., & Thaut, M. H. (2013). Corticostriatal contributions to musical expectancy perception. *Journal of Cognitive Neuroscience*, *25*(7), 1062–1077. https://doi.org/10.1162/jocn_a_00371

Senn, O., Bechtold, T. A., Hoesl, F., & Kilchenmann, L. (2019). Taste and familiarity affect the experience of groove in popular music. *Musicae Scientiae*. https://doi.org/10.1177/1029864919839172

Senn, O., Kilchenmann, L., Bechtold, T., & Hoesl, F. (2018). Groove in drum patterns as a function of both rhythmic properties and listeners ’ attitudes. *PLoS ONE*, *13*(6), 1–33.

Sescousse, G., Caldú, X., Segura, B., & Dreher, J. (2013). Processing of primary and secondary rewards : a quantitative meta-analysis and review of human functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews*, *37*(4), 681–696.

Sethares, W. A. (2004). *Tuning , Timbre , Spectrum , Scale*. Springer Science and Business Media.

Shany, O., Singer, N., Gold, B. P., Jacoby, N., Tarrasch, R., Hendler, T., & Granot, R. (2019). Surprise-related activation in the nucleus accumbens interacts with music-induced pleasantness. *Social Cognitive and Affective Neuroscience*, 1–12. https://doi.org/10.1093/scan/nsz019

Siman-Tov, T., Granot, R. Y., Shany, O., Singer, N., & Gordon, C. R. (2019). Is there a prediction network? Meta-analytic evidence for a cortical-subcortical network likely subserving prediction. *Neuroscience and Biobehavioral Reviews*, *105*, 262–275. https://doi.org/10.1016/j.neubiorev.2019.08.012

Sioros, G., Miron, M., Davies, M., Gouyon, F., & Madison, G. (2014). Syncopation creates the sensation of groove in synthesized music examples. *Frontiers in Psychology*, *5*(SEP), 1–10. https://doi.org/10.3389/fpsyg.2014.01036

Sioros, G., Mirron, M., Davies, M., Gouyon, F., & Madison, G. (2014). Syncopation creates the sensation of groove in synthesized music examples. *Frontiers in Psychology*, *5*(1036), 1–10. https://doi.org/10.3389/fpsyg.2014.01036

Spitzer, B., & Haegens, S. (2017). Beyond the Status Quo: A Role for Beta Oscillations in Endogenous Content (Re) Activation. *Eneuro*, *4*(4), 1–15.

Stalnaker, T. A., Cooch, N. K., & Schoenbaum, G. (2015). What the orbitofrontal cortex does not do. *Nature Neuroscience*, *18*(5), 620–627. https://doi.org/10.1038/nn.3982

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

Stupacher, J. (2019). The experience of flow during sensorimotor synchronization to musical rhythms. *Musicae Scientiae*, *23*(3), 348–361. https://doi.org/10.1177/1029864919836720

Stupacher, J., Hove, M. J., & Janata, P. (2016). Audio features underlying perceived groove and sensorimotor synchronization in music. *Music Perception*, *33*(5), 571–589.

Stupacher, J., Hove, M. J., Novembre, G., Schütz-Bosbach, S., & Keller, P. E. (2013). Musical groove modulates motor cortex excitability: A TMS investigation. *Brain and Cognition*, *82*, 127–136.

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

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

Tanaka, M., Kunimatsu, J., Suzuki, T. W., Kameda, M., Ohmae, S., Uematsu, A., & Takeya, R. (2020). Roles of the cerebellum in motor preparation and prediction of timing. *Neuroscience*. https://doi.org/10.1016/j.neuroscience.2020.04.039

Teki, S. (2014). Beta drives brain beats. *Frontiers in Systems Neuroscience*, *8*(155), 1–2. https://doi.org/10.1038/nrn1764

Teki, S., Grube, M., & Griffiths, T. D. (2012). A unified model of time perception accounts for duration-based and beat-based timing mechanisms. *Frontiers in Integrative Neuroscience*, *5*(January), 90. https://doi.org/10.3389/fnint.2011.00090

Teki, S., Grube, M., Kumar, S., & Griffiths, T. D. (2011). Distinct neural substrates of duration-based and beat-based auditory timing. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(10), 3805–3812.

https://doi.org/10.1523/JNEUROSCI.5561-10.2011

Teki, S., & Kononowicz, T. W. (2016). Commentary: Beta-Band Oscillations Represent Auditory Beat and Its Metrical Hierarchy in Perception and Imagery. *Frontiers in Neuroscience*, *10*(389), 1–3. https://doi.org/10.3389/fnins.2016.00389

ten Oever, S., Schroeder, C. E., Poeppel, D., van Atteveldt, N., & Zion-Golumbic, E. (2014). Rhythmicity and cross-modal temporal cues facilitate detection. *Neuropsychologia*, *63*, 43–50. https://doi.org/10.1016/j.neuropsychologia.2014.08.008.Rhythmicity

Thaut, M., Trimarchi, P., & Parsons, L. (2014). Human Brain Basis of Musical Rhythm Perception: Common and Distinct Neural Substrates for Meter, Tempo, and Pattern. *Brain Sciences*, *4*(2), 428–452. https://doi.org/10.3390/brainsci4020428

Tingley, D., Yamamoto, T., Hirose, K., Keele, L., & Kosuke, I. (2014). mediation : R Package for Causal Mediation Analysis. *Journal of Statistical Software*, *59*(5), 1–38.

Toiviainen, P., Burunat, I., Brattico, E., Vuust, P., & Alluri, V. (2019). The chronnectome of musical beat. *NeuroImage*, *216*, 1–13. https://doi.org/10.1016/j.neuroimage.2019.116191

Toiviainen, P., & Snyder, J. S. (2003). Tapping to Bach. *Music Perception*, *21*(1), 43–80.

Trost, W., Frühholz, S., Schön, D., Labbé, C., Pichon, S., Grandjean, D., & Vuilleumier, P. (2014). Getting the beat: Entrainment of brain activity by musical rhythm and pleasantness. *NeuroImage*, *103*, 55–64. https://doi.org/10.1016/j.neuroimage.2014.09.009

Trost, W. J., Labbé, C., & Grandjean, D. (2017). Rhythmic entrainment as a musical affect induction mechanism. *Neuropsychologia*, *96*(February 2016), 96–110. https://doi.org/10.1016/j.neuropsychologia.2017.01.004

Trost, W., & Vuilleumier, P. (2013). Rhythmic entrainment as a mechanism for emotion induction by music. In *The Emotional Power of Music: Multidisciplinary perspectives on musical arousal, expression, and social control*. https://doi.org/10.1093/acprof

van Atteveldt, N., Musacchia, G., Zion-Golumbic, E., Sehatpour, P., Javitt, D. C., & Schroeder, C. (2015). Complementary fMRI and EEG evidence for more efficient neural processing of rhythmic vs. unpredictably timed sounds. *Frontiers in Psychology*, *6*(OCT), 1–11. https://doi.org/10.3389/fpsyg.2015.01663

van den Bosch, I., Salimpoor, V. N., & Zatorre, R. J. (2013). Familiarity mediates the relationship between emotional arousal and pleasure during music listening. *Frontiers in Human Neuroscience*, *7*(September), 534. https://doi.org/10.3389/fnhum.2013.00534

van Vugt, F. T., & Tillmann, B. (2014). Thresholds of auditory-motor coupling measured with a simple task in musicians and non-musicians: was the sound simultaneous to the key press? *PloS One*, *9*(2), e87176. https://doi.org/10.1371/journal.pone.0087176

Vuilleumier, P., & Trost, W. (2015). Music and emotions: from enchantment to entrainment. *Annals of the New York Academy of Sciences*, *1337*, 212–222. https://doi.org/10.1111/nyas.12676

Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music -Brain responses to rhythmic incongruity. *Cortex*, *45*(1), 80–92. https://doi.org/10.1016/j.cortex.2008.05.014

Vuust, P., Wallentin, M., Mouridsen, K., Ostergaard, L., & Roepstorff, A. (2011). Tapping polyrhythms in music activates language areas. *Neuroscience Letters*, *494*(3), 211–216. https://doi.org/10.1016/j.neulet.2011.03.015

Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, *5*(1111), 1–14. https://doi.org/10.3389/fpsyg.2014.01111.

Vuust, P., Witek, M., Dietz, M., & Kringelbach, M. L. (2018). Now You Hear It: A novel predictive coding model for understanding rhythmic incongruity. *Annals of the New York Academy of Sciences*, 1–11. https://doi.org/10.1111/nyas.13622

White, R. W. (1959). Motivation reconsidered: The concept of competence. *Psychological Review*, *66*(5), 297–333. https://doi.org/10.1037/h0040934

Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010). The image of time: a voxel-wise meta-analysis. *NeuroImage*, *49*(2), 1728–1740. https://doi.org/10.1016/j.neuroimage.2009.09.064

Wing, A. M., & Kristofferson, A. B. (1973). Response delays and the timing of discrete motor responses. *Perception & Psychophysics*, *14*(1), 5–12. https://doi.org/10.3758/BF03198607

Wisniewski, D., Reverberi, C., Momennejad, I., Kahnt, T., & Haynes, J. D. (2015). The role of the parietal cortex in the representation of task–reward associations. *Journal of Neuroscience*, *35*(36), 12355–12365. https://doi.org/10.1523/JNEUROSCI.4882-14.2015

Witek, M. A. G. (2009). Groove experience: Emotional and physiological responses to groove-based music. In *Proceedings of the 7th Triennial Conference of European Society for the Cognitive Sciences of Music (ESCOM 2009) Jyväskylä, Finland* (pp. 573–582).

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

Witek, M. A. G., Clarke, E. F., Wallentin, M., Kringelbach, M. L., & Vuust, P. (2014). Syncopation, body-movement and pleasure in groove music. *PloS One*, *9*(4), 1–12. https://doi.org/10.1371/journal.pone.0094446

Wollman, I., & Morillon, B. (2018). Organizational principles of multidimensional predictions in human auditory attention. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-31878-5

Zald, D. H., & Zatorre, R. J. (2011). On music and reward. In J. Gottfried (Ed.), *The neurobiology of Sensation and Reward*. Taylor & Francis.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: music and speech. *Trends in Cognitive Sciences*, *6*(1), 37–46.

Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: Auditory-motor interactions in music perception and production. *Nature Reviews Neuroscience*, *8*(7), 547–558. https://doi.org/10.1038/nrn2152

Zatorre, R. J., & Salimpoor, V. N. (2013). From perception to pleasure: music and its neural substrates. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 10430–10437. https://doi.org/10.1073/pnas.1301228110

Zell, E., & Krizan, Z. (2014). Do People Have Insight Into Their Abilities? A Metasynthesis. *Perspectives on Psychological Science*, *9*(2), 111–125. https://doi.org/10.1177/1745691613518075