Behavioral and Neural Mechanisms Supporting Rate Flexibility of Auditory-Motor Synchronization

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Abstract

This dissertation investigates the behavioral and neural mechanisms underlying rate flexibility of auditory-motor synchronization. The first hypothesis tested in this dissertation states that musical training enhances the flexibility with which individuals can coordinate at rates different from their Spontaneous Production Rates (natural movement rates). The second hypothesis states that this enhanced flexibility is characterized behaviorally by less repetitive, predictable, and mathematically stable patterns of synchronization. The third hypothesis states that neural signatures of flexibility are characterized by more deterministic and mathematically stable oscillatory neural activity at the rate with which an individual is synchronizing. Chapter 2 describes two behavioral studies in which a novel musical task is validated and then implemented with musicians and nonmusicians to show greater synchronization accuracy in musicians than nonmusicians as synchronization rates move farther from individuals' Spontaneous Production Rates. Chapter 3 describes a behavioral study extending the results from the first two studies to show that musicians adapt more quickly and accurately to unexpected rate perturbations than nonmusicians; more efficient adaptation is reflected by differences in parameters of a damped harmonic oscillator model, suggesting underlying nonlinear mechanisms. Chapter 4 describes a novel application of a nonlinear time series analysis method to electroencephalography (EEG) data for measuring neural signatures of rate flexibility. Chapter 5 describes a study in which this novel implementation is applied to EEG measured from musicians and nonmusicians during auditory-motor synchronization at different rates. The findings from this study show 1) greater synchronization accuracy at slower rates and greater overall synchronization consistency in musicians than nonmusicians; 2) greater neural predictability at slower rates than faster rates; 3) greater neural stability in musicians than nonmusicians; and 4) a relationship between neural predictability and stability and behavioral synchronization consistency such that as predictability and stability increase, so does synchronization consistency. This dissertation provides further insight into how musical training interacts with Spontaneous Production Rates to influence rate flexibility of behavior, develops a novel method for examining neural flexibility, suggests a neural signature of enhanced flexibility with musical training, and gives future avenues of exploration for both behavioral and neural research on flexibility of auditory-motor synchronization.

Résumé

Cette thèse étudie les mécanismes comportementaux et neuraux qui sous-tendent la flexibilité de la synchronisation auditive-motrice. La première hypothèse testée dans cette thèse stipule que l'entraînement musical améliore la flexibilité avec laquelle les individus peuvent se coordonner à des taux différents de leurs Taux de Production Spontanée (taux de mouvement naturel). La deuxième hypothèse stipule que cette flexibilité accrue se caractérise sur le plan comportemental par des modèles de synchronisation moins répétitifs, prévisibles et stables sur le plan mathématique. La troisième hypothèse stipule que les signatures neuronales de la flexibilité sont caractérisées par une activité neuronale oscillatoire plus déterministe et mathématiquement stable au rythme auquel un individu se synchronise. Le chapitre 2 décrit deux études comportementales dans lesquelles une nouvelle tâche musicale est validée puis testée avec des musiciens et des non-musiciens, révélant une plus grande précision de synchronisation chez les musiciens que chez les non-musiciens à mesure que les taux de synchronisation s'éloignent des Taux de Production Spontanée des individus. Le chapitre 3 décrit une étude comportementale qui étend les résultats des deux premières études, montrant que les musiciens s'adaptent plus rapidement et plus précisément aux perturbations inattendues du taux de production que les non-musiciens ; une adaptation plus efficace est reflétée par des différences dans les paramètres d'un modèle d'oscillateur harmonique amorti, suggérant des mécanismes non linéaires sous-jacents. Le chapitre 4 décrit une nouvelle application d'une méthode d'analyse de séries temporelles non linéaires aux données d'électroencéphalographie (EEG) pour mesurer les signatures neurales de la flexibilité de synchronisation. Le chapitre 5 décrit une étude dans laquelle cette nouvelle mise en œuvre est appliquée à des données EEG récoltées chez des musiciens et des non-musiciens pendant la synchronisation auditive-motrice à différents rythmes. Les résultats de cette étude montrent 1) une plus grande précision de la synchronisation à des rythmes plus lents et une plus grande cohérence globale de la synchronisation chez les musiciens que chez les non-musiciens ; 2) une plus grande prévisibilité neuronale à des rythmes plus lents que rapides ; 3) une plus grande stabilité neuronale chez les musiciens que chez les non-musiciens ; et 4) une relation entre la prévisibilité et la stabilité neuronales et la cohérence de la synchronisation comportementale, telle que la cohérence de la synchronisation augmente avec la prévisibilité et la stabilité. Cette thèse permet de mieux comprendre comment la formation musicale interagit avec les Taux de Production Spontanée pour influencer la flexibilité du comportement, développe une nouvelle méthode pour examiner la flexibilité neuronale, suggère une signature neuronale de la flexibilité accrue avec la formation musicale, et donne des pistes d'explorations futures pour la recherche comportementale et neuronale sur la flexibilité de la synchronisation auditive-motrice.

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I am so fortunate to have had the opportunity to follow my passions and attend graduate school. I would like to take a final moment to acknowledge the many women who were not able to have this same opportunity. I dedicate this dissertation to you and to all other women who will follow behind me. The world needs to see and hear all of us. I hope that this dissertation will inspire others to not ever be afraid to make their voices heard.

Preface

Contribution to Original Knowledge

This dissertation is organized according to McGill University's guidelines for manuscript-based theses. It contains a General Introduction (Chapter 1), four manuscripts presenting original and distinct contributions to knowledge (Chapters 2-5), text connecting the overarching focus and goals of the manuscripts, and a General Discussion (Chapter 6).

The first manuscript, presented in Chapter 2, is published in *Frontiers in Psychology* and describes two studies. The first study validates a novel musical task that allows for the investigation of the interactive effects of musical training and Spontaneous Production Rates on rate flexibility for the first time in broader populations. The second study implements the novel task with musicians and nonmusicians to show that musical training can reduce constraints of Spontaneous Production Rates specifically when synchronizing at slower rates. Furthermore, this study applies Recurrence Quantification analysis, a non-linear analytical technique, to show that inflexibility of synchronization can be characterized by more recurrent, deterministic, and mathematically stable behaviour.

The second manuscript, presented in Chapter 3, is published in *Experimental Brain Research*. The study described in this manuscript extends the findings from Chapter 2 by modelling musicians' and nonmusicians' adaptation to rate perturbations away from and toward their Spontaneous Production Rates. This study first shows that musical training enhances rate adaptation. Importantly, this study also shows that nonlinear models both best capture and differentiate between rate adaptation of musicians and nonmusicians.

The third manuscript, presented in Chapter 4, is published in *Proceedings of the 41st Annual Meeting of the Cognitive Science Society*. The study described in this manuscript develops a novel implementation of Recurrence Quantification Analysis for neurophysiological data. This study shows that Recurrence Quantification Analysis can capture subtle changes in neurophysiological dynamics that occur with changing task demands.

Finally, the fourth manuscript, presented in Chapter 5, is in preparation. The study described in this manuscript implements the novel application of Recurrence Quantification Analysis from Chapter 4 to examine the neurophysiological mechanisms underlying enhanced rate flexibility with musical training. Most importantly, this study shows greater neural stability in musicians than in nonmusicians during synchronization at participants' Spontaneous Production Rates and slower rates. This greater neural stability is related to greater synchronization consistency at slower rates. Unlike previous work, this study controlled for possible differences in inhibitory control between musicians and nonmusicians which may result in better synchronization performance.

Contribution of Authors

Chapter 1. General Introduction

Authors: Rebecca Scheurich

I, Rebecca Scheurich, am the only author of the content in this chapter. Caroline Palmer suggested revisions of the content.

Chapter 2. Tapping into rate flexibility: Musical training facilitates synchronization around spontaneous production rates (published in *Frontiers in Psychology,* 2018, Volume 9, 458)

Authors: Rebecca Scheurich, Anna Zamm, and Caroline Palmer

All authors contributed to the design and implementation of the experiments. I, Rebecca Scheurich, performed the data analysis and wrote drafts of the manuscript. Anna Zamm contributed to data analysis and editing the manuscript. Caroline Palmer contributed to data analysis as well as writing and editing the manuscript.

Chapter 3. Musical training enhances temporal adaptation of auditory-motor synchronization (published in *Experimental Brain Research*, 2019, Volume 238, 81-92)

Authors: Rebecca Scheurich, Peter Q. Pfordresher, and Caroline Palmer

I, Rebecca Scheurich, contributed to the design and implementation of the experiment, performed the data analysis, and wrote drafts of the manuscript. Peter Q. Pfordresher contributed to data analysis and editing the manuscript. Caroline Palmer contributed to the design and implementation of the experiment, data analysis, and editing the manuscript.

Chapter 4. Capturing intra- and inter-brain dynamics with recurrence quantification analysis (published in *Proceedings of the 41st Annual Meeting of the Cognitive Science Society*, 2019, 2748-2754)

Authors: Rebecca Scheurich, Alexander P. Demos, Anna Zamm, Brian Mathias, and Caroline Palmer

I, Rebecca Scheurich, contributed to the design and implementation of the experiment, performed the data analysis, and wrote drafts of the manuscript. Alexander P. Demos contributed to data analysis and editing the manuscript. Anna Zamm contributed to the design and implementation of the experiment, to data analysis, and editing the manuscript. Brian Mathias contributed to the designed and implementation of the experiment as well as editing the manuscript. Caroline Palmer contributed to the design and implementation of the experiment as well as editing the manuscript.

Chapter 5. Stability of neural oscillations supports enhanced auditory-motor synchronization with musical training (in preparation)

Authors: Rebecca Scheurich, Ella Sahlas, and Caroline Palmer

I, Rebecca Scheurich, contributed to the design and implementation of the experiment, performed the data analysis, and wrote drafts of the manuscript. Ella Sahlas contributed to implementation and programming of the experiment as well as data analysis. Caroline Palmer contributed to the design and implementation of the experiment, data analysis, and editing the manuscript.

Chapter 6. General Discussion

Authors: Rebecca Scheurich

I, Rebecca Scheurich, am the only author of the content in this chapter. Caroline Palmer suggested revisions of the content.

Chapter 1

General Introduction and Literature Review

The accurate and precise timing of actions with sound is ubiquitous in human society. It can be observed in the spontaneous synchronization of hand clapping among audience members (Néda, Ravasz, Brechet, Vicsek, & Barabási, 2000), in the synchronization of neonates' body movements with adult speech rhythms (Condon & Sander, 1974), or in the synchronization of tone onsets between pianists performing a musical duet (cf. Loehr & Palmer, 2011; Zamm, Pfordresher, & Palmer, 2015; Zamm, Wellman, & Palmer, 2016). Auditory-motor synchronization's ubiquitous nature may stem from its ability to act as a social glue, promoting pro-social behavior and affiliation among members of a group (cf. Cirelli, Einarson, & Trainor, 2014; Hove & Risen, 2009; Kirschner & Tomasello, 2010; Rabinowitch & Knafo-Noam, 2015; Rabinowitch & Meltzoff, 2017). Although the ability to coordinate actions with sound may not be unique to humans, one key feature of human auditory-motor synchronization is the flexibility with which it occurs. Unlike non-human animals (Cook, Rouse, Wilson, & Reichmuth, 2013; Hasegawa, Okanoya, Hasegawa, & Seki, 2011; Patel, Iversen, Bregman, & Schulz, 2009), humans can quickly and accurately adapt the rate of planned actions to match changes in the auditory environment, a key component of flexibility (MacKay, 1982). An open question in the field of auditory cognitive neuroscience asks what mechanisms afford humans rate flexibility of auditory-motor synchronization. The current dissertation investigates this question, providing both behavioral and neural insights into the factors that influence rate flexibility within individuals.

1. Theories of Auditory-Motor Synchronization

Multiple theoretical frameworks have been proposed for explaining how individuals coordinate their actions with sound, both in single- and multi-person behaviors. Many theories propose mental models that encode actions, sound, and time to support action planning and adaptation for achieving auditory-motor synchronization (Patel, 2006; Sebanz, Bekkering, & Knoblich, 2006; Vorberg & Schulze, 2002; Wing & Kristofferson, 1973). In contrast, another theory proposes systems of nonlinear coupled oscillators (Haken, Kelso, & Bunz, 1985), commonly observed in biological systems (cf. Michaels, Matyas, & Jalife, 1987; Mirollo & Strogatz, 1990), to support auditory-motor synchronization. When two oscillators share information, as in two pendulum clocks or metronomes placed on the same surface, synchronization can occur (Pantaleone, 2002; Pikovsky, Rosenblum, & Kurths, 2001; Strogatz & Stewart, 1993).

There are two primary perspectives that pertain to auditory-motor synchronization in single-person behaviors. These perspectives propose linear timekeeper models (Vorberg & Schulze, 2002; Wing & Kristofferson, 1973) and nonlinear dynamical systems models (Large & Jones, 1999; Large & Palmer, 2002). According to linear timekeeper models, an internal clock tracks auditory rhythms and triggers motor responses; any error between motor responses and auditory rhythms is corrected linearly as a proportion of the temporal difference between the two (Vorberg & Schulze, 2002; Wing & Kristofferson, 1973). In contrast, nonlinear dynamical systems models propose that ongoing internal oscillations entrain with auditory rhythms (Large & Jones, 1999; Large & Palmer, 2002). When auditory rhythms occur at predictable time intervals, these oscillations generate temporal expectancies via a temporal receptive field which guide motor responses. Any error between temporal expectancies and the timing of auditory rhythms is corrected by both phase and period adjustments of these oscillations.

More recent linear models (Mates, 1994; Vorberg & Schulze, 2002) and nonlinear models (Large, Fink, & Kelso, 2002) make similar predictions for how individuals adapt to changes in the *phase* (changes in the timing of a single onset) of an auditory sequence. Importantly, differences in error correction mechanisms between these two model types result in different predictions for how individuals adapt to changes in the *period* (inter-stimulus interval) of an auditory sequence. Whereas linear models predict that adaptation to period changes will be equal in magnitude regardless of their direction (i.e., speeding or slowing), nonlinear models predict better adaptation to slowing than to speeding period changes (Loehr, Large, & Palmer, 2011). Furthermore, in contrast to linear models, the magnitude of adaptation predicted by nonlinear models does not increase linearly with the magnitude of change in an auditory stimulus.

The plausibility of these model predictions has typically been studied through the perturbation task paradigm (cf. Large, Fink, & Kelso, 2002; Palmer, Lidji, & Peretz, 2014; Repp, 2010; Thaut, Miller, & Schauer, 1998). In this task, participants synchronize motor behavior (e.g., finger-tapping) with an auditory stimulus that unexpectedly changes its phase (position of a single stimulus onset in time) or period. Thaut, Miller, and Schauer (1998) examined how individuals adapted finger-tapping to unexpected period changes in a regular auditory stimulus. The period was allowed to change by 2%, 4%, or 10% of the initial stimulus period. Participants displayed different patterns of adaptation to period changes of different magnitudes: overcorrection was observed in response to large period changes, but not in response to small period changes. Participants also showed faster adaptation to slowing than to speeding period changes, an effect that has been replicated in later studies implementing similar tapping paradigms (cf. Large, Fink, & Kelso, 2002; Palmer, Lidji, & Peretz, 2014). Also consistent with a nonlinear approach, model fits to the data required different constant parameter values to capture adaptation to period changes of different magnitudes.

Loehr, Large, and Palmer (2011) directly tested the different predictions of linear and nonlinear models for slowing and speeding period changes. Pianists performed simple melodies with a metronome that linearly changed its period (i.e., increased or decreased its period by the same amount each beat) at the beginning or end of the melodic phrase. The period was allowed to change by 1% or 3% of the initial stimulus period. Like Thaut, Miller, and Schauer (1998), participants showed faster adaptation to slowing than to speeding period changes. Both a linear timekeeper model (Vorberg & Schulze, 2002) and a nonlinear oscillator model (Glass & Mackey, 1988; Pikovsky, Rosenblum, & Kurths, 2001) were fit to pianists' performances; the nonlinear oscillator model was better able to account for pianists' adaptation to period changes than the linear timekeeper model.

The plausibility of linear and nonlinear models can also be tested by examining model fits to adaptation behavior in which an underlying component of each model is either periodic (nonlinear models) or non-periodic (linear models). Palmer, Lidji, and Peretz (2014) examined adaptation of finger-tapping of beat-deaf and control participants to unexpected phase and period changes in an auditory stimulus. Fits of a damped harmonic oscillator model (Large, Fink, & Kelso, 2002) and an exponential decay model (Pfrodresher & Kulpa, 2011), containing a similar damping parameter but no periodic component, to adaptation measures were compared. The damped harmonic oscillator model provided significant fits to adaptation measures for both control and beat-deaf individuals. In contrast, the exponential decay model only provided significant fits for approximately half of the control individuals; this model could not account for adaptation behavior of beat-deaf individuals.

To summarize, literature to date supports the nonlinear nature of period adaptation, one key component to rate flexibility of auditory-motor synchronization. Adaptation occurs asymmetrically in a few important ways predicted by a nonlinear framework: 1) with more efficient adaptation at slower rates (Large, Fink, & Kelso, 2002; Loehr, Large, & Palmer, 2011; Palmer, Lidji, & Peretz, 2014; Thaut, Miller, & Schauer, 1998); and 2) requiring different strategies depending on the magnitude of change (Thaut, Miller, & Schauer, 1998). Given the evidence for systems of nonlinear coupled oscillators supporting auditory-motor synchronization, this dissertation proposal will adopt a nonlinear dynamical systems approach to examine rate flexibility.

2. Role of Neural Oscillations in Auditory-Motor Synchronization

A neurobiological extension of dynamical systems models for auditory-motor synchronization is neural resonance theory. This theory describes auditory-motor synchronization as resulting from neural oscillations that couple with auditory rhythms (Large & Snyder, 2009). It is grounded in the principle of neural resonance in which sustained oscillations of neural activity have greatest magnitude at a resonant or natural frequency of stimulation (Izhikevich, 2007). In a system of nonlinear neural oscillators with different natural frequencies, locking of integer ratios between cycles of a neural oscillator and cycles of an auditory rhythm, called mode-locking or entrainment, can occur. Entrainment allows for perception of and synchronization with multiple hierarchical levels of auditory rhythms (Large, Herrera, & Velasco, 2015).

Magnetoencephalography (MEG) is one neuroimaging tool that has been used to examine the role of neural oscillations in auditory-motor behaviors. MEG measures neural activity via magnetic fields that are generated by electrical brain activity; one advantage of using MEG over other tools is its favorable temporal and spatial resolution, allowing researchers to investigate both temporal and spatial questions (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Fujioka, Trainor, Large, and Ross (2009) used MEG to investigate how cortical oscillations may support rhythmic beat perception in auditory sequences in which the beat is not always present in the acoustic signal. Participants passively listened to a sequence of pure tones while MEG was recorded; occasionally, a tone was omitted from the sequence. Results showed oscillatory modulations of power in β and γ frequency bands: Power decreased in the β-band immediately following tones whereas power increased in the γ-band immediately following tones. When tones were omitted, there was no response in the β-band but there continued to be a peak in power in the γ-band following the omitted tone.

Extending these findings, Fujioka, Ross, and Trainor (2015) used MEG to examine neural responses in the β-band to both perceived and imagined metrical structures. Participants listened to pure tone sequences with an accented tone every two or three tones corresponding to the meter of a march or waltz, respectively. Pure tone sequences were also presented to participants without accented tones, and participants were instructed to imagine the meter of a march or waltz for these sequences. Results showed that both perception and imagery of a musical meter influenced β-band activity: the typical decrease in power following tone onsets was greater for both accented and imagined downbeats. Furthermore, source localization revealed involvement of auditory and motor brain regions, as well as regions typically involved in integration of information for higher order functions (e.g., frontal and parietal lobes); similar evidence comes from Morillon and Baillet (2017) who showed oscillatory neural activity in sensorimotor cortex involved in temporal prediction. Taken together, these findings suggest a role of neural oscillations in encoding the temporal information necessary for beat and meter perception, as well as for preparing motor responses.

Another popular means by which researchers have examined the role of cortical oscillations, specifically, in auditory perception and auditory-motor synchronization is electroencephalography (EEG). EEG measures electrical brain activity via electrodes placed on the scalp (Berger, 1929). Although EEG has poor spatial resolution, its excellent temporal resolution allows researchers to precisely investigate the temporal evolution of cortical oscillations in response to external stimuli. This is particularly useful for investigating brain responses to auditory stimuli, which requires fine temporal precision.

Nozaradan, Zerouali, Peretz, and Mouraux (2013) used EEG to examine ongoing cortical oscillations during auditory perception and auditory-motor synchronization tasks. Participants passively listened to and synchronized tapping with every other beat of an amplitude-modulated tone while EEG was recorded. To examine whether ongoing cortical oscillations represented the auditory stimulus and tapping frequencies, the researchers transformed the EEG signal to the frequency domain. To do so, the signal is treated as a sum of component frequencies and, using the discrete Fourier transform, gives the amplitude of the signal at each component frequency (Frigo & Johnson, 1998). Using this method, the researchers showed a peak in amplitude of neural activity at the auditory beat and tapping frequencies in the synchronization task. Furthermore, the latency of neural oscillations at both the auditory beat and tapping frequencies correlated with tapping latency.

Extending these findings, Nozaradan, Peretz, and Keller (2016) used EEG to examine the relationship between the amplitude of neural activity at a beat frequency and auditory-motor synchronization accuracy. The amplitude of neural activity at the beat frequency was correlated with synchronization accuracy: as power at the beat frequency increased, synchronization accuracy increased. By examining neural activity during auditory-motor synchronization tasks, these studies more directly suggest a role of neural oscillations in supporting auditory-motor synchronization.

3. Dynamical Systems Principles in Action: Spontaneous Production Rates

Neural resonance theory offers key predictions for rate flexibility. Both the directionality and strength of coupling between neural oscillations and external stimuli depends on the sign and magnitude of the difference in their frequencies (Large & Snyder, 2009). When the natural frequency of neural oscillators is faster than the stimulus frequency, neural oscillations should anticipate the stimulus; when the natural frequency is slower, neural oscillations should lag the stimulus. When the magnitude of difference between the natural frequency of neural oscillators and the stimulus frequency is large, neural oscillations should have a large phase offset from the stimulus; when the difference is small, the phase offset should be small. In other words, neural oscillations will tend to be pulled toward the natural frequency when coupling with other frequencies (Winfree, 1987). These predictions about the directionality and strength of coupling can also be extended to behavioral performance. Thus, individuals should tend to anticipate at slower frequencies and lag at faster frequencies relative to a natural frequency. Furthermore, synchronization accuracy should be greatest (i.e., phase offset smallest) when the magnitude of difference between a natural frequency and the stimulus frequency is small.

These predictions have been observed in studies of simple physical systems in which the magnitude of the difference between natural frequencies and external frequencies was manipulated. When the difference in natural frequencies between two rocking chairs was increased by adding weights to one chair, synchronization between individuals rocking side-by-side was less accurate (Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007). Lopresti-Goodman, Richardson, Silva, and Schmidt (2008) similarly manipulated the difference between the natural frequency of a pendulum and the frequency of an oscillatory visual stimulus. When the difference was large, there were fewer occurrences of spontaneous synchronization between pendulum-swinging and the visual stimulus. This effect has also been replicated for spontaneous synchronization of pendulum-swinging with an auditory stimulus: spontaneous synchronization occurred least often when there was a larger difference between the natural frequency of pendulum-swinging and the frequency of the auditory stimulus (Varlet, Williams, & Keller, 2018).

Natural frequencies have been measured for more complex auditory-motor behaviors as Spontaneous Production Rates (SPRs), defined as the rates at which individuals perform rhythmic auditory sequences in the absence of external cues (Loehr & Palmer, 2011; Zamm, Pfordresher, & Palmer, 2015; Zamm, Wang, & Palmer, 2018; Zamm, Wellman, & Palmer, 2016). Similar evidence exists for SPRs as representing natural frequencies of internal oscillations that constrain auditory-motor synchronization performance. Musicians perform least variably at and tend to drift back toward their SPRs when performing simple melodies at a different rate (Zamm, Wang, & Palmer, 2018). Furthermore, SPRs constrain synchronization between musicians performing musical duets together such that partners with different SPRs synchronize less accurately than partners with similar SPRs (Loehr & Palmer, 2011; Zamm, Pfordresher, & Palmer, 2015; Zamm, Wellman, & Palmer, 2016).

Despite existing evidence for SPRs as representing natural frequencies of internal oscillations, the effects of SPRs on auditory-motor synchronization observed to date in musicians tend to be quite small. Although pairs of pianists with different SPRs synchronize less accurately than those with similar SPRs, they still achieve a level of synchronization performance typical of highly trained musicians (Loehr & Palmer, 2011; Zamm, Pfordresher, & Palmer, 2015; Zamm, Wellman, & Palmer, 2016). Musical skill may promote accuracy, helping to overcome constraining factors of auditory-motor synchronization (MacKay, 1982). Therefore, SPRs may constrain auditory-motor synchronization to a larger extent in less skilled individuals (i.e., nonmusicians). One limitation of previous work is that SPRs have typically been measured only in musically skilled individuals. This may not represent the full range of constraints that SPRs place on auditory-motor synchronization.

4. Musical Training as a Model for Rate Flexibility

Action control has been proposed to consist of a competition between two components: the persistence of a particular strategy and the flexibility to adopt new strategies (Hommel, 2015). Different actions require a different balance between these components to ensure behaviors are not too rigid or too loosely constrained. Changes in the auditory environment can occur at a sub-second timescale, and so to achieve auditory-motor synchrony flexibility is required to allow for the appropriate corresponding changes in the motor output. In this case, persistence of previous synchronization strategies may prove sub-optimal, resulting in poorer performance.

Previous experience and learning, including musical training, may be one critical factor that allows individuals to adopt more flexible synchronization strategies. There is an extensive body of literature comparing auditory-motor synchronization accuracy between musicians and nonmusicians. To facilitate comparison, researchers have examined synchronization of simple finger-tapping with auditory sequences ranging from a regular metronome to complex music. Musicians show greater synchronization accuracy than nonmusicians in synchronized finger-tapping with a regular auditory metronome (Aschersleben, 2002). This difference becomes more pronounced when synchronizing with a regular auditory metronome set to increasingly slower rates (Repp & Doggett, 2007). Chen, Penhune, and Zatorre (2008b) examined the role of musical training in synchronization with more complex auditory stimuli. Musicians and nonmusicians listened to increasingly complex metrical and non-metrical rhythms, and then produced them in synchrony with the auditory stimulus. Both musicians and nonmusicians produced rhythms with the same accuracy, but musicians showed greater synchronization accuracy with the auditory stimulus than nonmusicians. Further increasing stimulus complexity, Drake, Penel, and Bigand (2000) examined the role of musical training in synchronization with musical pieces. Musicians synchronized more accurately and were able to synchronize with a wider hierarchy of the musical meter compared with nonmusicians. Consistent with Repp and Doggett (2007) showing greater differences between groups at slower rates, musicians also synchronized with higher (slower) metrical levels more often than nonmusicians. These findings suggest that musical training enhances auditory-motor synchronization accuracy with both simple and complex auditory sequences. Furthermore, musical training may enhance rate flexibility specifically when coordinating at slower rates.

Why might musical training affect rate flexibility asymmetrically for slower and faster rates? Research suggests different systems governing movement at different timescales, with faster timescales drawing on an automatic system and slower timescales requiring cognitive control (Lewis & Miall, 2003). Thus, musical training may provide certain cognitive benefits that emerge specifically during synchronization with slower rates. One possibility is that enhanced auditory working memory may play a role in musicians’ greater flexibility. However, research suggests enhanced auditory temporal processing with musical training in the absence of greater auditory working memory (Rammsayer & Altenmüller, 2006). Another possibility is that musical training affords greater executive control, an effect that has been shown in multiple studies (cf. Bialystok & DePape, 2009; Bugos, Perlstein, McCrae, Brophy, & Bedenbaugh, 2007; Moreno, Bialystok, Barac, Schellenberg, Cepeda, & Chau, 2011). Differences in executive control should generate an asymmetrical effect for slower and faster rates; poorer response inhibition of nonmusicians, for example, should produce greater differences in synchronization accuracy between groups at slower than faster rates. Several studies have shown impaired motor timing and synchronization abilities in populations with known deficits in executive function, as in children and adults with Attention Deficit Hyperactivity Disorder (cf. Puyjarinet, Bégel, Lopez, Dellacherie, & Dalla Bella, 2017; Rubia, Taylor, Taylor, & Sergeant, 1999). Importantly, Puyjarinet, Bégel, Lopez, Dellacherie, and Dalla Bella (2017) showed that these timing deficits appear to be linked to key executive functions such as inhibition and flexibility but not short-term memory function, making this a promising avenue for further research.

Researchers have also examined how musicians and nonmusicians respond and adapt to sudden temporal changes in auditory stimuli. Madison and Merker (2004) examined adaptation of musicians and nonmusicians to perceptible and imperceptible perturbations in the period of an auditory stimulus. Participants synchronized drum hits with an auditory stimulus that increased and decreased its period throughout each trial. The magnitude of perturbations was manipulated to be perceptible or imperceptible to participants. When changes in the auditory stimulus were perceptible, musicians adapted more to those changes than nonmusicians. Repp (2010) further examined adaptation of musicians and nonmusicians to both phase and period perturbations in an auditory stimulus. Participants synchronized tapping with sequences that contained either a single phase perturbation or a linear increase or decrease in period at the end of the sequence. Whereas adaptation to phase changes was similar across groups, musicians adapted more quickly to period changes than nonmusicians.

Although a musicians' advantage has been consistently demonstrated across a wide range of auditory-motor synchronization tasks, evidence for enhanced rate flexibility with musical training is constrained by a few critical limitations. These include limited sample sizes, differences in task experience across populations, and inconsistent criteria for qualifying individuals as musicians or nonmusicians across studies. Furthermore, other factors that may influence rate flexibility such as SPRs were not considered in these studies. Thus, the full scope of influence of musical training on rate flexibility remains an open question needing further research.

5. Mechanisms of Rate Flexibility: Auditory and Motor Contributions

What underlying mechanisms result in poorer auditory-motor synchronization performance and perhaps rate flexibility in nonmusicians? The roles of perceptual mechanisms, production mechanisms, and a combination of the two have been investigated. Early research attempted to isolate perceptual and motor mechanisms by presenting participants with auditory discrimination or motor production tasks. Rammsayer and Altenmüller (2006) investigated differences in auditory perception between musicians and nonmusicians. Participants were presented with temporal discrimination, temporal generalization, rhythm perception, and auditory fusion tasks. These tasks required participants to discriminate between temporal interval durations, identify stimulus durations as the same as or different from a memorized duration, categorize rhythms as regular or irregular, and indicate whether they perceived sounds as one unified or two separate sounds, respectively. Musicians showed enhanced performance on temporal discrimination, rhythm perception, and auditory fusion tasks compared with nonmusicians. These findings suggest enhancement of auditory temporal information processing with musical training independent of auditory memory processes as there were no differences between groups in temporal generalization tasks. Baer, Thibodeau, Gralnick, Li, & Penhune (2013) investigated timing variability of motor responses in musicians and nonmusicians for discrete and continuous timing tasks. Musicians and nonmusicians performed finger-tapping (discrete timing) and circle drawing (continuous timing) tasks in which they had to continue at the pace of a metronome after the auditory feedback of the metronome was removed. Musicians showed less temporal variability than nonmusicians in the finger tapping task, suggesting enhancement of motor production with musical training.

It is possible that these enhancements of auditory perception and motor production with musical training may be the mechanisms underlying musicians' superior auditory-motor synchronization abilities. However, musical training may also result in enhancements of auditory-motor coupling because actions in music performance often serve important acoustic goals (for a review, see Palmer & Scheurich, 2019). In support of this idea, source localization of EEG activity has shown greater activation of motor cortex in pianists when listening to previously performed compared with previously perceived musical pieces (Mathias, Palmer, Perrin, & Tillmann, 2015). Furthermore, Bangert and Altenmüller (2003) engaged nonmusicians in short-term musical training and examined changes after training in neural responses to auditory and motor probes. Following training, distribution of neural activity on the scalp reflected auditory-motor network co-activation in response to these probes. Similar changes in auditory-motor networks following musical training have also been observed using functional magnetic resonance imaging (fMRI; Lahav, Saltzman, & Schlaug 2007). Interestingly, although musical training may enhance auditory-motor coupling, it may not be a requirement for coupling to occur between these networks (Keele, Pokorny, Corco, & Ivry, 1985). Similar co-activation of auditory and motor networks has been shown without providing participants musical training, suggesting a natural integration of auditory and motor processes that may strengthen with training (Chen, Penhune, & Zatorre, 2008a).

Several behavioral studies support the important role of auditory-motor integration processes in auditory-motor tasks. Franěk, Mates, Radil, Beck, & Pöppel (1991) investigated differences in rhythm production between musicians and nonmusicians. Participants were presented with regular auditory sequences and reproduced the sequences with auditory feedback. Musicians reproduced sequence intervals with greater accuracy than nonmusicians, suggesting enhanced auditory-motor integration with musical training. However, this study could not rule out the possibility that enhanced auditory perception or motor production alone accounted for these differences. Pfordresher and Brown (2007) examined both pitch perception abilities and errors made in musical sequence production in accurate and poor-pitch singers. Poor-pitch singers showed no pitch perception deficits and a limited vocal range only during imitation of musical sequences but not during simple production of vocal sweeps. These findings suggest that poor-pitch singers’ difficulties lie in auditory-motor integration rather than auditory perception or motor production in isolation. Sowiński and Dalla Bella (2013) investigated auditory and motor production difficulties in poor synchronizers. These individuals demonstrated difficulty synchronizing finger-tapping accurately or consistently with a regular auditory sequence or music. Of ten total poor synchronizers, eight showed impairments in rhythm perception, pitch perception, or both; none presented impairments in motor production as shown by similar consistency in self-paced tapping as compared with normal controls. This left two poor synchronizers who showed deficits in auditory-motor synchronization in the absence of deficits in auditory perception or motor production. These individuals instead presented difficulties with auditory-motor integration.

Taken together, this research suggests that enhanced integration of auditory and motor processes may support musicians' superior performance in auditory-motor synchronization tasks. It is still unknown whether similar mechanisms may be responsible for group differences in flexibility of auditory-motor synchronization. However, the finding from Pfordresher and Brown (2007) that poor-pitch singers show a more limited vocal production range in the absence of perception or production deficits suggests that auditory-motor integration processes may also play a key role in flexibility.

6. Challenges to Measuring Rate Flexibility

There are a few measurement challenges that must be overcome to be able to examine influences of SPRs and musical training on rate flexibility of auditory-motor synchronization. First, SPRs have traditionally been measured by asking participants to perform musical sequences on an instrument at a comfortable and regular rate (cf. Loehr & Palmer, 2011; Zamm, Pfordresher, & Palmer, 2015; Zamm, Wang, & Palmer, 2018; Zamm, Wellman, & Palmer, 2016). However, nonmusicians do not have the training required to be able to perform this type of task. This raises the need for development of a novel auditory-motor task that could be easily performed by both populations while measuring the same construct as music performance.

A second more complex challenge relates to how entrainment of neural oscillations with auditory rhythms can be examined over time to characterize flexibility. This dissertation will focus on measuring neural entrainment using EEG because of its excellent resolution for examining activity over time. A technique that has become increasingly popular over the past decade for examining entrainment of neural activity as measured through EEG with auditory rhythms is a frequency-tagging approach, described earlier (cf. Nozaradan, Peretz, Missal, Mouraux, 2011). This technique has led to an increasing body of literature examining how the frequencies of perceived, imagined, and produced auditory rhythms are represented in the neural signal in a variety of simple to complex tasks (cf. Henry, Herrmann, & Obleser, 2014; Nozaradan, 2014; Nozaradan, Peretz, & Keller, 2016; Nozaradan, Peretz, Missal, Mouraux, 2011; Nozaradan, Peretz, & Mouraux, 2012; Nozaradan, Zerouali, Peretz, & Mouraux, 2013; Zamm, Palmer, Bauer, Bleichner, Demos, & Debener, 2017).

Although a fruitful technique, there are important limitations for using a frequency-tagging approach to examine flexibility of neural entrainment. First, this approach assumes stationarity of the signal being analyzed, and thus non-stationarity (often characteristic of physiological data) can lead to difficulties with interpretation of the results (Kantz & Schreiber, 2004). Second, when the signal is transformed to the frequency domain, all information about the temporal domain is lost. Therefore, this technique cannot speak to the time-dependent characteristics of neural entrainment critical to studying neural flexibility. For example, when and how often neural oscillations come in and out of phase with a rhythmic auditory stimulus cannot be captured with a frequency-tagging approach.

How can we capture the time-dependent characteristics of neural entrainment to auditory rhythms? Recurrence Quantification Analysis (RQA) is a nonlinear time series analysis technique for examining recurrences of one or more systems over time as they move through a phase space representing all possible states of the system(s) (Marwan, Romano, Thiel, & Kurths, 2007; Marwan & Webber, 2015). For auto-recurrence, these recurrences represent when in time a system returns to a state it was previously in; for cross-recurrence, these recurrences represent when in time two systems visit similar states in the same space (Marwan, Romano, Thiel, & Kurths, 2007; Marwan & Webber, 2015). These quantifications are computed from and represented through Recurrence Plots (RPs), displaying points at the times when a system recurs with itself or with another system (Eckmann, Kamphorst, & Ruelle, 1987). To demonstrate how this technique works, take for example the measurement of action potentials of a single neuron. To record when action potentials occur in a neuron, imagine that changes in the membrane potential of the neuron are measured over time. At rest, the neuron's membrane potential would be negative; when the neuron receives external input, it may fire an action potential, showing a sharp depolarization (i.e., increase in membrane potential; Bean, 2007; Hodgkin & Huxley, 1952). Other measurements could also have been taken to examine the timing of action potentials in the neuron. The membrane potential at any point in time determines its conductance for different ions: as the neuron becomes depolarized, sodium conductance increases; as it becomes repolarized (i.e., as the resting membrane potential is restored), sodium conductance decreases (Hodgkin & Huxley, 1952).

Often only a single state of the system, where the system in this example is a single neuron, is measured even though other interdependent states may exist. In this example, the neuron's membrane potential (one state of the system) was measured to capture the timing of action potentials. The membrane potential determines its ion conductance, a second state that could also have been measured. Imagine we now wish to examine recurrences within this system to see the points in time at which action potentials are repeatedly fired by the neuron. To examine these recurrences within the system's phase space, all states of the system are needed but, as is illustrated by this example, are not always measured. How is this challenge overcome? Phase Space Reconstruction (PSR) recovers (reconstructs) all states of the system (i.e., the phase space) assuming that at least a single state of the system has been measured. PSR relies on the demonstrated interdependency of different states within a system. According to Takens' Embedding Theorem, other states can be recovered from the single measured state by taking time-delayed copies of the measured state to reconstruct the higher-dimensional phase space of the system; this results in a reconstructed phase space that is isomorphic (similar in form) to the original phase space of the system (Sauer, Yorke, & Casdagli, 1991; Takens, 1981). Because of the isomorphism, inferences can be made about the original system by examining the relationships among points on the trajectory or movement over time in reconstructed phase space. Figure 1 (adapted from Paxton, Silva, Richardson, & Riley's Complex Dynamics Workshop, 2019) shows a sample time series, its trajectory in reconstructed phase space, and how the relationships among points on the trajectory over time in this reconstructed phase space are depicted on the recurrence plot.

Insert Figure 1 Here

Once the phase space of a system has been reconstructed, the relationships among points *within* a system can be examined using auto-recurrence in which a system's return to its previous states is quantified. These quantifications can reveal critical characteristics about the time evolution of a system's behavior: the stationarity of a system, whether a system returns to previous states in a periodic manner, and when in time abrupt changes occur in the behavior of the system, to name a few. Although numerous quantifications can be made about the system, this dissertation focuses on a few most relevant to the study of rate flexibility: recurrence rate, determinism, maxline, and meanline (Schmit, Regis, & Riley, 2005; Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006). Recurrence rate describes the density of recurrent points on the RP, or how often a system returns to its previous states; determinism describes the proportion of recurrent points that fall on diagonal lines, a measure of the system's predictability; maxline and meanline describe the longest and mean diagonal line lengths, respectively, both related to mathematical stability representing how the system will respond to changes in initial conditions (Marwan, Romano, Thiel, & Kurths, 2007). Although maxline is most directly related to mathematical stability via the largest positive Lyapunov exponent (Eckmann, Kamphorst, & Ruelle, 1987; Marwan & Webber, 2015), meanline will be of primary focus in this dissertation given its robustness for noisy systems and its previous use as an index for mathematical stability (e.g., Rosen, Epstein, & Van Orden, 2013).

Also considered in this dissertation is the relationship among points *between* different systems. These systems could be, for example, movement patterns of two individuals performing a joint-action task or the activity recorded from two brain networks. In these cases, cross-recurrence is used to quantify the trajectories of the two systems in the same phase space, providing critical information about how these systems interact with one another. These quantifications allow for the investigation of the times at which two systems occupy the same space, travel along similar trajectories, or at which the dynamics between the systems diverge. Of primary interest in this dissertation are the quantifications of recurrence rate, determinism, and meanline. In the context of cross-recurrence, recurrence rate represents how often two systems are in the same state, determinism represents how often two systems travel along similar trajectories, and meanline represents the average amount of time that the trajectories of the two systems are stable with one another (Marwan, Romano, Thiel, & Kurths, 2007).

Behaviorally, a flexible system can be characterized through auto-recurrence by relatively low recurrence rate, determinism, maxline, and meanline: a mathematical system with more noise (less predictability) indicates greater capacity to change behavior and reduced disturbance to changes in initial conditions such as perturbations (Schmit, Regis, & Riley, 2005;

Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006). Neurally, the markers of a flexible system as measured using RQA has yet to be explored. Previous work with other techniques such as inter-trial phase locking to examine consistency of neural responses to auditory stimuli suggests that increased neural consistency is linked to better synchronization performance (Tierney & Kraus, 2013). Thus, neural markers of auditory-motor synchronization flexibility using RQA may reflect less noisy and more predictable oscillatory neural activity in contrast to the expected behavioral markers of flexibility. RQA is used in the dissertation studies described in the following section to examine both behavioral and neural flexibility during auditory-motor tasks.

7. Overview of Research

This dissertation contains four manuscript-based chapters describing five studies. **Chapter 2** describes two behavioral studies that validate and subsequently implement a novel musical tapping task with musicians and nonmusicians to examine rate flexibility of auditory-motor synchronization. **Chapter 3** extends this work by implementing a modified version of the novel task with musicians and nonmusicians to examine rate adaptation in real time. **Chapter 4** then develops a novel application of RQA for EEG data to characterize the temporal dynamics of oscillatory neural activity during auditory-motor synchronization. Finally, **Chapter 5** implements this novel application of RQA with EEG data recorded from musicians and nonmusicians during an auditory-motor synchronization task to examine neural signatures of rate flexibility.

More specifically, the first two behavioral studies in this dissertation, described in **Chapter 2**, test the hypothesis that flexibility to synchronize at rates that are not the Spontaneous Production Rate is enhanced with musical training. To examine this, it was first necessary to develop and validate a novel musical task that could be performed by both musicians and nonmusicians to measure individual SPRs. In the novel task, participants tap the rhythm of a familiar melody while hearing the corresponding melody tones controlled by the experimenter; controlling the auditory feedback allows participants of different musical skill levels to perform the task. Pianists' SPRs were measured as they tapped and performed familiar melodies. It was expected that, if the novel task captures the same construct as music performance, SPRs measured through these two tasks should not differ. SPRs measured through the novel task were indeed highly correlated with and not different from SPRs measured through piano performance, validating use of the task in broader populations. With this validation, the novel task was then implemented with musicians and nonmusicians in the second study. Participants tapped a familiar melody at their SPRs, and subsequently synchronized their tapping of the same familiar melody with a metronome set at, slower than, and faster than their SPRs. All participants were expected to show constraints of SPRs such that they would tend to anticipate more at slower rates and lag more at faster rates relative to their SPRs. Furthermore, musicians were expected to show greater flexibility such that they would synchronize more accurately than nonmusicians as rates became farther from their SPRs. Finally, applying RQA to synchronization accuracy measures was expected to show greater recurrence rate, determinism, and maxline for nonmusicians, indicative of greater inflexibility compared with musicians (Schmit, Regis, & Riley, 2005).

The third behavioral study in this dissertation, described in **Chapter 3**, investigates the nonlinear mechanisms underlying enhancements in rate flexibility with musical training. More specifically, this study tests the hypothesis that musicians should show more efficient adaptation than nonmusicians when responding to unexpected rate perturbations; this should be reflected in specific parameters of a nonlinear damped harmonic oscillator model (Large, Fink, & Kelso, 2002; Palmer, Lidji, & Peretz, 2014). In this study, a version of the novel task was implemented in which participants tapped an isochronous (regular) version of a familiar melody while hearing isochronous melody feedback. Participants first tapped the isochronous melody at their SPRs, and subsequently synchronized their tapping of the isochronous melody with a metronome set at, slower than, and faster than their SPRs, and which unexpectedly changed its rate. Based on previous research, all participants were expected to adapt more quickly to slowing than to speeding perturbations (Large, Fink, & Kelso, 2002; Palmer, Lidji, & Peretz, 2014). Furthermore, all participants were expected to adapt more quickly to rate perturbations that moved toward their SPRs than those that moved away from their SPRs. Finally, musicians were expected to adapt more quickly and more accurately than nonmusicians, as shown by the *b* and *c* parameters of the damped harmonic oscillator model reflecting adaptation time and return to baseline synchronization, respectively. This study sheds further light on the underlying mechanisms of enhanced rate flexibility with musical training described in Chapter 2.

Chapter 4 describes the first EEG study in this dissertation in which a novel implementation of RQA to EEG data is validated to investigate neural signatures of flexibility. This implementation was designed to capture subtle changes in the temporal dynamics of neural oscillations as two partners synchronized at different integer ratios. Neural oscillations at one partner’s tapping rate were expected to be more recurrent and mathematically stable (related to flexibility) when that rate was dominant (i.e., more feedback at that rate) relative to the second partner’s tapping rate. Because one partner’s tapping rate was always held constant, it allowed for the investigation of subtle changes in neural entrainment at the constant rate with changes in the pair’s integer ratio of synchronization that are more readily detectable by RQA than traditional linear methods.

Finally, **Chapter 5** describes an EEG study in which the validated implementation of RQA is applied to investigate neural signatures of flexibility in musicians and nonmusicians during auditory-motor synchronization. The aim of this study is to test the hypothesis that more predictable and stable neural oscillations at the synchronization rate should relate to enhanced synchronization performance. Therefore, musicians should show both more deterministic and mathematically stable neural oscillations as well as more accurate and consistent synchronization than nonmusicians, reflecting their enhanced rate flexibility. Due to the ongoing COVID-19 public health crisis, this study focused on two primary tasks performed by musicians and nonmusicians to explore this hypothesis: 1) tapping the rhythm of a familiar melody while hearing the corresponding melody tones (the previously validated task) to measure participants’ SPRs; and 2) synchronizing their performance of the validated task with a metronome at their SPRs and rates slower than their SPRs to measure rate flexibility. This study focused on slower rates given that musical training appears to provide a specific advantage when synchronizing at slower rates (e.g., Repp & Doggett, 2007). Behaviorally, it was expected that musicians would synchronize more accurately and consistently than nonmusicians as the rate became slower. Neurally, it was expected that RQA on EEG activity reflecting auditory-motor network interactions would show more deterministic and mathematically stable neural oscillations in musicians than nonmusicians. Furthermore, a brain-behavior correspondence was expected such that the more deterministic and mathematically stable the oscillatory neural activity, the greater the synchronization consistency.

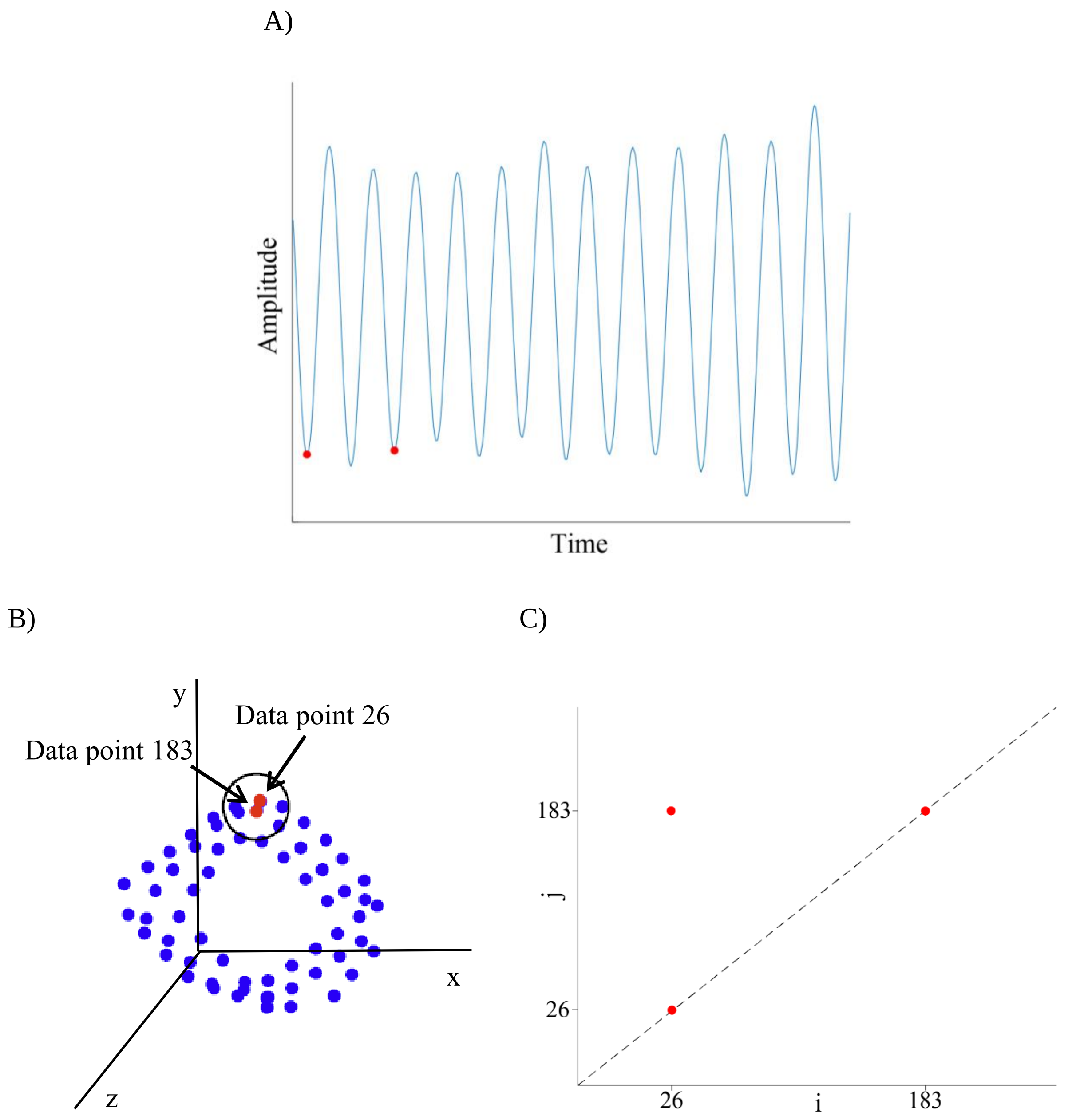

Figure 1. Depiction of a time series (A) in its reconstructed three-dimensional phase space (B). Red points show time points at which the time series returns to the same state in the reconstructed phase space, which become recurrent points on the two-dimensional recurrence plot (C). Note that the diagonal line is perfectly recurrent because it represents each point compared to itself.

Chapter 2

Tapping into Rate Flexibility:
Musical Training Facilitates Synchronization Around Spontaneous Production Rates

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Abstract

The ability to flexibly adapt one's behavior is critical for social tasks such as speech and music performance, in which individuals must coordinate the timing of their actions with others. Natural movement frequencies, also called spontaneous rates, constrain synchronization accuracy between partners during duet music performance, whereas musical training enhances synchronization accuracy. We investigated the combined influences of these factors on the flexibility with which individuals can synchronize their actions with sequences at different rates. First, we developed a novel musical task capable of measuring spontaneous rates in both musicians and non-musicians in which participants tapped the rhythm of a familiar melody while hearing the corresponding melody tones. The novel task was validated by similar measures of spontaneous rates generated by piano performance and by the tapping task from the same pianists. We then implemented the novel task with musicians and non-musicians as they synchronized tapping of a familiar melody with a metronome at their spontaneous rates, and at rates proportionally slower and faster than their spontaneous rates. Musicians synchronized more flexibly across rates than non-musicians, indicated by greater synchronization accuracy. Additionally, musicians showed greater engagement of error correction mechanisms than non-musicians. Finally, differences in flexibility were characterized by more recurrent (repetitive) and patterned synchronization in non-musicians, indicative of greater temporal rigidity.

1. Introduction

Auditory-motor synchronization occurs when individuals coordinate their actions in time with external auditory events, as in conversational speech or joint music-making. Music performance is an ideal model for the study of flexibility in auditory-motor synchronization. Musical sequences are typically produced at a wide range of rates, and musicians are expected to flexibly change their production rates to achieve precise synchronization with one another (Palmer, 1997; Repp, 2005). Musical synchronization is not restricted to highly trained individuals, but also occurs in individuals with little to no musical training. For example, individuals without musical training can clap along with a musical beat at a concert. Several studies have examined differences in auditory-motor synchronization accuracy between trained and untrained individuals (Aschersleben, 2002; Repp and Doggett, 2007; Chen et al., 2008; Repp, 2010). Little is known about how extensive training alters the flexibility with which individuals coordinate their actions at different rates. We investigate here the underlying variables that influence rate flexibility across musical skill levels.

A dynamical systems perspective proposes that biological and physical systems have internal rhythms or oscillators that entrain or couple with quasi-periodic rhythms in the environment; synchronization occurs via changes in the intrinsic or natural frequency (rate) and the relative phase of these internal oscillators (Strogatz and Stewart, 1993; Large and Jones, 1999). Natural frequencies in rhythmic (periodic) tasks such as walking, speaking, and performing music have been measured in terms of the rates at which individuals naturally or spontaneously produce rhythmic sequences in the absence of external cues (Murray et al., 1964; Loehr and Palmer, 2011; Zamm et al., 2015, 2016). Spontaneous rates measured in isochronous (regular) finger-tapping tasks, usually collected in the absence of auditory feedback, are referred to as spontaneous motor tempi (SMT) (Drake et al., 2000a,b; McAuley et al., 2006). SMT reflect biases toward particular rates which change from faster in early childhood to slower in adulthood, (McAuley et al., 2006), and are slower in musicians than in non-musicians (Drake et al., 2000a). Spontaneous rates at which musicians perform naturally (in the presence of auditory feedback), referred to as spontaneous production rates (SPRs), similarly reflect biases toward performing at a particular rate, and have been proposed to represent natural frequencies of underlying oscillations that place constraints on synchronization accuracy. Partners who have similar natural frequencies, reflected by SPRs of solo performance, are more synchronous in duet performance than partners who have different SPRs (Loehr and Palmer, 2011; Palmer et al., 2013; Zamm et al., 2015, 2016), consistent with predictions of a dynamical system in which natural frequencies that are more similar couple with each other more strongly.

The natural frequency represented by an individual’s spontaneous rate may act as an attractor, or state that requires less energy expenditure and toward which a system’s behavior will converge over time (Strogatz and Stewart, 1993). According to this perspective, individuals should be pulled toward their spontaneous rates during tasks in which they are required to move at other rates. When the difference between an individual’s spontaneous rate and the external rate is too great, coupling between the individual’s internal oscillations and the external rate cannot occur (Strogatz and Stewart, 1993). Much research that has investigated spontaneous rates as attractors has focused on skilled individuals such as musicians (Loehr and Palmer, 2011; Zamm et al., 2015, 2016) who receive intensive training that is assumed to enhance their flexibility to perform at a large range of rates (MacKay, 1982). Untrained individuals might be expected to show greater constraints of an attractor on synchronization due to less flexibility in coordinating actions across a range of rates (Drake et al., 2000a,b). Thus, it is unknown whether spontaneous rates act as an attractor frequency that is stronger for less skilled (non-musicians) compared with more skilled individuals (musicians).

Different perspectives have been offered for the mechanisms that contribute to SPRs. In one perspective, spontaneous rates may be driven primarily by central timing mechanisms such as central pattern generators (Latash, 1992). Another perspective suggests that spontaneous rates arise primarily from peripheral (anatomical and biomechanical) properties of the body (Goodman et al., 2000). Investigations into contributions of central and peripheral mechanisms to SPRs have shown mixed results. Whereas spontaneous rates appear to be consistent across similar limbs in music performance (Zamm et al., 2015, 2016), evidence also suggests that the joints at which oscillatory movements are initiated influence spontaneous rates (Peckel et al., 2014). For example, leg swinging occurs at a slower frequency when initiated from the hip than from the knee (Peckel et al., 2014). Despite mixed results about contributions to spontaneous rates, synchronization-continuation tasks have shown that participants tend to drift back over time toward their spontaneous rates when initially cued to perform at other rates (Yu et al., 2003; McAuley et al., 2006).

Comparisons of musicians and non-musicians in tapping tasks suggest that synchronization accuracy is influenced both by musical training and spontaneous rates (Drake et al., 2000a,b). Drake et al. (2000a) compared the SMT of children and adults, both musically trained and untrained, as well as their synchronization with different auditory sequences. Musicians successfully synchronized more often than non-musicians across age groups, particularly for isochronous (regular intervals) and rhythmic sequences. Participants with slower SMT tended to synchronize with higher hierarchical levels (slower rates); this correlation was stronger for non-musicians than for musicians, suggesting that non-musicians were less able to synchronize with rates less similar to their SMT than musicians. These findings are consistent with those from Drake et al. (2000b), who showed that musicians were better able than non-musicians to synchronize their tapping with a musical excerpt at both higher and lower hierarchical levels of the meter than the level with which they naturally synchronized. Overall, musical training and spontaneous rates show different effects on synchronization such that musical training enhances flexibility across rates, whereas spontaneous rates cause a bias in synchronization with an attraction toward a natural frequency.

2. Current Research

The current research examines the influences of spontaneous rates and musical training on rate flexibility in a synchronization task. To date, no studies have directly compared musicians' and non-musicians' synchronization accuracy in music production tasks, for the obvious reason that non-musicians cannot perform the same musical tasks as musicians. To compare synchronization abilities of musicians and non-musicians, we developed a novel musical task capable of measuring SPRs that could be implemented with individuals with limited or no musical expertise. Experiment 1 validated the novel musical tapping task by comparing pianists' performances while tapping melody rhythms with normal piano performances of the same melodies. If the novel task elicits an experience similar to music performance, then SPRs across tasks should be similar. We also investigated contributions of peripheral mechanisms to SPRs by measuring pianists' hand sizes (Yu et al., 2013). If peripheral mechanisms contribute to SPRs, then pianists with larger hands might be expected to show slower SPRs (Goodman et al., 2000).

Experiment 2 implemented the novel task with musician and non-musician participants to investigate the influences of spontaneous rates and musical training on rate flexibility of synchronization. Participants tapped a familiar melody at a comfortable and regular rate to assess their SPRs. They then synchronized their tapping of the same familiar melody with a metronome set to their SPRs as well as to rates proportionally faster and slower than their SPRs. We predicted that non-musicians would show faster SPRs than musicians, consistent with previous research on SMT (Drake et al., 2000a). We applied linear (lag-1 autocorrelation) and non-linear (recurrence quantification analysis) time series analyses to investigate rate flexibility as a function of temporal error correction as well as dynamic patterns of behavior across longer timescales. Finally, individuals' hand measurements were collected to further explore potential contributions of peripheral mechanisms to SPRs. If spontaneous rates represent attractor states within the space of possible production rates, then biases in synchronization accuracy should center around an individual's spontaneous rate. We hypothesize that this will be shown by lagging at faster rates and anticipating at slower rates relative to the spontaneous rate. In addition, we hypothesize that spontaneous rates should act as a weaker attractor for musicians than for non-musicians, resulting in greater synchronization accuracy for musicians across rates.

3. Experiment 1

3.1 Methods

3.1.1 Participants

Twenty pianists (mean years old = 21, SD = 3; 14 females) with at least 6 years of private piano instruction (mean years private instruction = 12 years; SD = 3) were recruited to participate in this study. Only right-handed pianists were included. Handedness was confirmed using the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were right-handed (16 pianists) or had indeterminate handedness with a tendency toward righthandedness (4 pianists), as determined by their scores (ranging from 33.33 to 100). All participants exhibited normal hearing in the frequency range of stimuli used in the experiment (<30 dB HL threshold for 125–750 Hz), as determined by an audiometry screening. Although there were no neurological or speech disorder exclusion criteria, we report the neurological histories here of the participants: Two participants reported a history of concussions, and one participant reported a lisp. These participants met all of the inclusion criteria and their data yielded the same patterns of results as the other participants.

3.1.2 Equipment and Stimuli

Hearing screenings were administered with a Maico MA 40 audiometer. Hand measurements were taken from tracings of participants' right (dominant) hands with a 12-inch Capri digital caliper. Participants performed and tapped melodies on a Yamaha PSR-500M electronic keyboard. Auditory feedback from the keyboard was delivered to participants in a piano timbre via a Roland Studio Canvas SD-50 through Bose QC 20 noise-canceling headphones. FTAP (Finney, 2001) was used to generate auditory feedback and record MIDI tap timing on a computer (Dell T3600) running Linux (Fedora 16).

Stimulus melodies were chosen for their familiarity among participants and their simple rhythms. Practice melodies were chosen for the purpose of teaching participants the novel task, and consisted of "London Bridge is Falling Down," "If You're Happy and You Know It Clap Your Hands," and "Happy Birthday to You," all composed in D Major. Experimental melodies used in the actual trials after participants were comfortable with the novel task consisted of "Twinkle, Twinkle Little Star," composed in G Major (Stimulus 1), and "Mary Had a Little Lamb," composed in F Major (Stimulus 2). Each melody consisted of a 8–12 measure tune of binary (4/4) meter, performed by the right hand, which was notated with suggested fingerings.

Questionnaires included the Edinburgh Handedness Inventory (Oldfield, 1971), which assessed the degree to which an individual was right- or left-handed, and a musical background questionnaire that assessed participants’ age, level of education, musical training background, musical experience (i.e., listening and performance), as well as any hearing, speech, or neurological problems.

3.1.3 Design

The experiment used a within-subjects design with two independent variables of Melody (Stimulus 1 and Stimulus 2) and Task (Piano Performance and Tapping). The dependent variable was the SPR (see section “Data Analysis”). Participants always completed the Piano Performance task first to ensure that they learned the correct rhythm of each melody for the Tapping task. Melodies were blocked within task; melody order within task was randomized for each participant, and this order was held constant across tasks.

3.1.4 Procedure

All participants gave informed consent upon arrival at the lab. In the first part of the experiment, participants completed an audiometry screening. Participants were then given the names of the practice and experimental melodies to assess their familiarity with these melodies. Participants who passed the audiometry screening and were familiar with at least one practice melody and both experimental melodies upon hearing only the melody names were eligible to participate. Tracings were then taken of each participant’s right (dominant) hand, marking the first crease of the wrist. Hand measurements were taken from these tracings from the radius to the ulna at the wrist (wrist width), from the first crease of the wrist to the tip of the third digit (middle finger), and from the ulna at the wrist to the tip of the first digit (thumb).

Next, participants were given music notation for the first experimental melody and were asked to practice the melody until it was memorized. Participants were instructed to write their chosen fingering on the notation if it differed from the suggested fingering. Once the melody was memorized, the notation was removed and participants completed one practice trial in which they played the melody four times through without stopping to ensure that the melody was memorized without pitch errors. Following the practice trial, participants completed three test trials in which they performed the same melody four times through without stopping between melody repetitions at a comfortable and steady rate. This procedure was then repeated for the second experimental melody. Both practice and test trials were checked for pitch errors by computer comparison with the notated score (described in section “Data Analysis”) (Large, 1993; Rankin et al., 2009).

Participants next completed the musical background questionnaire and the Edinburgh Handedness Inventory (Oldfield, 1971), lasting approximately 5–10 min, which created a short break between the piano performance and tapping tasks to reduce the likelihood that consistency in SPRs across tasks could be explained by recent exposure to the piano performance rate. During this break, a blanket was placed over the entire keyboard except for the ends of the white keys for the tapping task to reduce associations with music performance that might be primed by visual exposure to the keyboard.

Participants next performed the tapping task in which they were instructed to tap the rhythm of the familiar melody on a single key of the keyboard with the index finger of their dominant (right) hand. They were told that each time they tapped, a melody tone would sound. Participants first completed a practice trial with one of the practice melodies, during which they tapped the melody four times continuously. Once participants felt comfortable with the tapping task, they moved on to the experimental trials. Participants completed a practice trial with the first experimental melody. Then participants completed three test trials in which they tapped the melody four times without stopping between melody repetitions at a comfortable and steady rate. This procedure was then repeated for the second experimental melody.

3.1.5 Data Analysis

Participants' SPRs were computed as the mean inter-onset interval (IOI) across the middle two repetitions of the melody in each test trial to capture participants' maximally stable behavior (Loehr and Palmer, 2011; Zamm et al., 2015, 2016). In piano performances, pitch errors were identified by computer comparison of the performance with the pitch contents based on the music notation for that melody using the MIDI Matcher program in Matlab (Large, 1993; Rankin et al., 2009). Melody repetitions that contained pitch errors (added or deleted tones) were excluded from analysis (2.1% of all repetitions). Tapping trials did not contain pitch errors because pitches were produced by a computer. Half notes in the melodies were interpolated to extract the quarter note pulse for calculation of the mean IOI and the final (whole) note in each melody repetition was excluded to avoid bias in quarter note pulse estimation. Outlier IOIs defined as values more than three standard deviations away from the mean were excluded from analysis (piano performance trials = 1.0% of all IOIs; tapping trials = 1.1% of all IOIs).

3.2 Results

We first assessed the consistency of SPRs across the two Melodies within each Task. Simple correlations showed that SPRs were consistent across Melodies for both the Piano Performance Task, $r(18) = 0.71$, $p < 0.001$ and the Tapping Task, $r(18) = 0.89$, $p < 0.001$, shown in Figure 1. SPRs were then collapsed across Melodies within Tasks for each individual to compare each individual's Piano Performance SPR with their Tapping SPR. The simple correlation of individual SPRs from Piano Performance and Tapping Tasks, shown in Figure 2, yielded highly consistent SPRs across Tasks, $r(18) = 0.91$, $p < 0.001$.

Insert Figure 1 Here

Insert Figure 2 Here

Next, we tested whether SPRs differed across Tasks and Trials. A two-way analysis of variance (ANOVA) conducted on the mean IOI of each performance by Task (Piano Performance and Tapping) and Trial (1, 2, and 3) showed that there was no main effect of Task, $F(1,19) = 0.52$, $p = 0.48$, indicating that the mean SPRs for Piano Performance (mean = 391 ms) and Tapping (mean = 398 ms) did not differ significantly. A main effect of Trial, $F(2,38) = 19.94$, $p < 0.001$ indicated small but slightly faster rates across Trials (Trial 1 mean = 402 ms; Trial 2 mean = 394 ms; Trial 3 mean = 388 ms; Tukey's HSD = 5.21, $p < 0.05$). There was no interaction between Task and Trial, $F(2,38) = 1.39$, $p = 0.26$.

We next investigated the relationship between SPRs and hand measurements to test whether hand size contributed to individual differences. Piano Performance SPR did not correlate significantly with any of the hand measurements (Wrist to Digit 3: $r(18) = 0.02$, $p = 0.93$; Wrist Width: $r(18) = 0.31$, $p = 0.18$; Wrist to Digit 1: $r(18) = 0.13$, $p = 0.59$). The relationship between Tapping SPR and the Wrist Width measurement was marginally significant following Bonferroni correction for multiple comparisons, $r(18) = 0.49$, $p = 0.09$. There were no other correlations between Tapping SPR and hand measurements (Wrist to Digit 3: $r(18) = 0.16$, $p = 0.51$; Wrist to Digit 1: $r(18) = 0.28$, $p = 0.23$).

To further investigate the independent contributions of Piano Performance SPR and Wrist Width to Tapping SPR, a multiple regression was conducted to predict Tapping SPR from Piano Performance SPR and Wrist Width. Piano Performance SPR and Wrist Width provided a significant fit as predictors of Tapping SPR ($R = 0.94$, $p < 0.001$; Figure 3). Together, the variables accounted for 88% of the variance. Semi-partial correlation coefficients were significant both for Piano Performance SPR, $b = 0.84$, $t(17) = 9.50$, $p < 0.001$, and Wrist Width, $b = 0.23$, $t(17) = 2.55$, $p < 0.05$, indicating significant contributions of each variable to Tapping SPR.

Insert Figure 3 Here

3.3 Discussion

Experiment 1 demonstrated the consistency of spontaneous rates across piano performance and tapping, two tasks that differ in their motor complexity due to differences in the number of fingers used to execute each task (the tapping task required single-finger movement; the piano performance task required 5-finger movement) and the number of spatial dimensions of movement (the tapping task required up/down movement; the piano performance task required lateral (left/right) movement in addition to up/down movement). The consistency of SPRs across tasks provides validation of the tapping task as eliciting a rate-specific experience similar to piano performance. One benefit of the novel task is that it can be used with any participant who needs only to be familiar with the rhythm of a melody to be able to produce the melody. Another benefit is that the task is equally novel to musicians and non-musicians.

These findings also provide further support for the SPR as reflecting a preferred coordination mode at which movement is optimized. Biomechanical views that predict movement rates as reflecting task-specific motor demands (Goodman et al., 2000) are not consistent with the similarities we observed in SPRs for 5-finger lateral movements typical of piano performance and 1-finger vertical movements typical of tapping. Instead, these results suggest at least some contribution to these rates from central timing mechanisms (Latash, 1992).

We also found significant contributions of both wrist width and piano performance SPR to tapping SPR, consistent with previous research showing that wrist movements contribute most to freestyle single-finger tapping (Dennerlein et al., 2007). Wrist width is an anatomical (rather than kinematic) measurement; specifically, wrist width has been shown to provide an accurate measure of frame size (Himes and Bouchard, 1985). Wrist width as a predictor of tapping SPR may therefore reflect the additional influence of body frame (i.e., larger body frame, slower tapping SPR) in the tapping task. We pursue this finding further in Experiment 2 to better understand contributions of wrist size to SPRs.

4. Experiment 2

Experiment 2 implemented the novel musical tapping task with musicians and non-musicians to examine the effects of spontaneous rates and musical training on rate flexibility of synchronization. While previous research has independently shown that spontaneous rates constrain synchronization (Loehr and Palmer, 2011; Palmer et al., 2013; Zamm et al., 2015, 2016) whereas musical training enhances it (Drake et al., 2000a,b; Aschersleben, 2002), little is known about how musical training influences the flexibility with which individuals can move away from their spontaneous rates. Musicians and non-musicians tapped a familiar melody at a comfortable and regular rate as a measure of their SPRs. They then synchronized their tapping of the same melody with a metronome cue calibrated to a range of rates centered around each individual's SPR. Additionally, participants' wrist width measurements were taken to further examine the relationship between wrist width and tapping SPR.

4.1 Methods

4.1.1 Participants

Twenty musicians (mean years old = 21; SD = 2; 17 females) and 20 non-musicians (mean years old = 23; SD = 4; 17 females) participated in the experiment. None of the musicians had participated in the previous experiment. Musicians had at least 6 years of private instrumental music instruction (mean years private instruction = 10; SD = 3). Percussionists were excluded because they have been shown to have superior synchronization abilities compared with other musicians (Krause et al., 2010). Non-musicians had no private music instruction in the past 6 years, and had less than 2 years of private music instruction overall (mean years private instruction = 0.4; SD = 0.6). Most musicians (18) and non-musicians (19) were right-handed; one musician had indeterminate handedness with a tendency toward right-handedness, one non-musician had indeterminate handedness with a tendency toward left-handedness, and one musician was left-handed as determined by their scores (ranging from -50 to 100) on the Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal hearing in the frequency range of stimuli used in the experiment (<30 dB HL threshold for 125–750 Hz), as determined by an audiometry screening, and stated being familiar with the melodies used in the experiment. Additionally, all participants had normal pitch perception as determined by the Montreal Battery of Evaluation of Amusia (MBEA) scale subtest (Peretz et al., 2003). Although there were no neurological or speech disorder exclusion criteria, we report the neurological histories here of the participants: One participant reported a history of concussions, three participants reported a history of epilepsy (one in childhood), and one participant reported a lisp. These participants met all of the inclusion criteria and their data yielded the same patterns as the other participants. Participants included in the experiment showed successful synchronization in at least one trial in all rate conditions, as determined by the Rayleigh test (see section "Data Analysis"); 8 additional non-musicians were excluded due to failure to synchronize in one or more rate conditions. Groups did not differ significantly in age (musicians = 20.80; non-musicians = 22.50; $t(1) = 3.41$, $p = 0.07$) or years of education (musicians = 14.93; non-musicians = 16.13; $t(1) = 2.81$, $p = 0.10$).

4.1.2 Equipment and Stimuli

Participants' hearing thresholds were tested with a Maico MA 40 audiometer. Hand measurements were taken with a 12-inch Capri digital caliper. Participants tapped the rhythms of melodies on a force-sensitive resistor (FSR) of an Arduino connected via a MIDI cable to a computer (Dell T3600) running FTAP (Finney, 2001) on Linux (Fedora 16). Based on timing tests conducted with a Tektronix TDS 2002 oscilloscope, the time from the start of the tap on the FSR to the start of the MIDI signal sent from the Arduino averaged 1.0 millisecond (SD = 0.035; see Supplementary Figures 1, 2). Auditory feedback consisted of a familiar melody in a piano timbre and a metronome in a woodblock timbre, delivered to participants via a Roland mobile studio canvas SD-50 through AKG headphones at a comfortable listening level.

Stimuli consisted of a subset of the melodies from Experiment 1: "Happy Birthday to You" and "Mary Had a Little Lamb." These melodies were chosen for their familiarity among participants from the previous experiment as well as for their simple rhythms. "Happy Birthday to You," composed in D Major, was used as a practice melody to teach participants the tapping task. "Mary Had a Little Lamb," composed in F Major, was used as the experimental melody.

4.1.3 Design

The experiment consisted of three main tasks: a SPR task, a rate flexibility task, and a maximal rate task, performed in that order. During the SPR task, participants tapped the experimental melody at a comfortable and steady rate. Performances from this task were used to calculate the SPR (see section "Data Analysis"). In the rate flexibility task, participants synchronized their tapping of the experimental melody with a metronome at five different rates: 30% slower than the SPR, 15% slower than the SPR, the SPR, 15% faster than the SPR, and 30% faster than the SPR. The rate flexibility task had a mixed design with a between-subject variable of Group (Musician and Non-musician) and within-subject variable of Metronome Rate (30% Slower, 15% Slower, the SPR, 15% Faster, and 30% Faster). The order of rates was pseudo-randomized such that participants never received rates in order from either slowest to fastest or fastest to slowest. Finally, participants completed the maximal rate task in which they tapped the experimental melody as fast as possible while maintaining the rhythm of the melody; the goal of this task was to assess participants' motor limits.

4.1.4 Procedure

All participants gave informed consent upon arrival at the lab. First, participants completed an audiometry screening and a familiar melody assessment to confirm normal hearing and familiarity with the stimulus melodies. Participants who did not pass these assessments were excluded from the experiment. Next, the hand measurement from the radius to the ulna at the wrist (wrist width) was taken of each participant's dominant hand using a digital caliper.

Participants were next taught how to perform the tapping task using the familiar practice melody. Participants were seated next to a table on which the Arduino was placed at a comfortable height such that participants could rest their arm while tapping. Participants were instructed to tap the rhythm of the melody with the index finger of their dominant hand in the middle of the FSR, and that each time they tapped, a tone of the melody would sound. Participants practiced the task with a practice melody until they were comfortable with the task.

Participants then completed the SPR task with the experimental melody. Participants first completed a practice trial in which they tapped the melody at a comfortable and steady rate. Participants were instructed that they should continue tapping the melody four times through without stopping between melody repetitions until they no longer heard the melody tones, a signal that the trial was over. After completing one practice trial, the experimenter gave participants extra practice as was necessary and participants completed three experimental trials. At the end of the SPR task, participants' SPRs were calculated (see section "Data Analysis") to determine the rate conditions for the rate flexibility task. During this time, participants completed a musical background questionnaire and the Edinburgh Handedness Inventory (Oldfield, 1971).

At the beginning of the rate flexibility task, participants were instructed that they would hear a metronome, and that they should start synchronizing their tapping of the same experimental melody with the metronome within the first eight metronome clicks. Participants were instructed to synchronize each tap with a metronome click and to continue synchronizing their tapping of the melody with the metronome for four melody repetitions without stopping between repetitions until they no longer heard the melody tones, which would signal the end of a trial. Participants first completed a practice trial in which they synchronized with the metronome at one of the 5 metronome rates. The experimenter gave participants extra practice as was necessary. Next, participants completed three test trials. Extra trials were given if participants made mistakes, such as not tapping on the FSR. This procedure was repeated for the remaining rate conditions.

Participants then completed the maximal rate task. Participants were instructed that they would tap the same experimental melody as fast as possible (without a metronome) while maintaining the rhythm of the melody. Participants were instructed to tap the melody only once through. Participants completed one practice trial and one test trial.

Finally, participants completed the scale subtest from the MBEA (Peretz et al., 2003). In each trial, two short melodies were presented over headphones and participants indicated whether the two melodies were the same or different in pitch.

4.1.5 Data Analysis

Participants' SPRs were calculated from the SPR task as before: the mean IOI across the middle two repetitions of each trial. Outlier IOIs more than three standard deviations from the mean were excluded (% of total IOIs per group: musicians = 0.8%; non-musicians = 1%). Participants' maximal rates were calculated in the same way; calculations were based on only one repetition because participants only completed one test trial in which they tapped the melody once through.

Synchronization trials were analyzed by aligning taps and metronome clicks in each trial using a nearest neighbor approach, similar to Pecenka and Keller (2011). The signed asynchronies were calculated as the tap minus metronome onset, such that a negative value indicates that a tap preceded the metronome and a positive value that a tap lagged the metronome. For each participant, asynchrony outliers more than 3 standard deviations from their mean were removed from analysis (% of total asynchronies per group: musicians = 0.6%; nonmusicians = 0.8%). Taps that did not align with a metronome onset were discarded, as participants were instructed to synchronize each tap with a metronome click. Given that the non-musician group showed a wide range of synchronization abilities, the Rayleigh test for circular non-uniformity was first implemented to determine trials containing a unimodal synchronization pattern (Fisher, 1993). This test is implemented by computing relative phase (asynchrony divided by the metronome IOI), and then converting to degrees. This test is sensitive to unimodal departures from uniformity, with a significant result indicating a unimodal distribution. Following previous synchronization measures (Kirschner and Tomasello, 2009; Pecenka and Keller, 2011; Sowiński and Dalla Bella, 2013; Dalla Bella and Sowiński, 2015), trials in which the null hypothesis of circular uniformity could not be rejected (i.e., the distribution was not unimodal) at $p < 0.05$ were excluded from further analysis (musicians: 0% of trials excluded; non-musicians: 9% of trials excluded).

Finally, adjusted synchronization accuracy measures for each individual were defined as mean asynchrony in each individual's rate condition minus the mean asynchrony in that individual's SPR rate condition. The adjusted synchronization measures allowed us to examine the pattern of synchronization relative to the SPR, and to compare synchronization accuracy across musician and non-musician participants with different baseline synchronization abilities.

4.2 Results

4.2.1 Spontaneous Production Rates

We first investigated whether SPRs differed between Musicians and Non-musicians, and whether SPRs were stable across Trials. Figure 4 shows the distribution of SPRs. A mixed analysis of variance (ANOVA) by Group (Musician and Non-musician) and Trial (1, 2, and 3) showed a significant main effect of Group, $F(1,38) = 14.48$, $p < 0.01$; Musicians' SPRs (mean =

405 ms) were slower on average than Non-musicians' SPRs (mean = 306 ms). There was also a significant main effect of Trial, $F(2,76) = 13.71$, $p < 0.001$. Post hoc comparisons revealed that Trial 1 (mean = 363 ms) was slightly slower than Trials 2 and 3 (mean Trial 2 = 353 ms; Trial 3 = 350 ms) (Tukey's HSD = 5.84, $p < 0.05$), likely reflecting an adjustment to the task during Trial 1. There was no significant interaction between Group and Trial, $F(2,76) = 1.15$, $p = 0.32$.

Insert Figure 4 Here

We also investigated the stability of the SPR, measured by the coefficient of variation (CV; standard deviation of the IOIs divided by the mean IOI). The same ANOVA repeated on the CVs in the SPR task showed a significant main effect of Group, $F(1,38) = 11.08$, $p < 0.01$; Musicians were less variable at their SPR (mean = 0.05) than Non-musicians (mean = 0.06). There was no main effect of Trial, $F(2,76) = 0.77$, $p = 0.47$, or interaction between Group and Trial, $F(2,76) = 0.50$, $p = 0.61$, suggesting that SPRs were stable across time for all participants.

4.2.2 Synchronization Accuracy

Next, we examined the adjusted synchronization accuracy by Group and Metronome Rate, shown in Figure 5. A mixed ANOVA indicated a significant main effect of Group, $F(1,38) = 6.99$, $p < 0.05$, a significant main effect of Metronome Rate, $F(3,114) = 37.01$, $p < 0.001$, and a significant interaction between Group and Metronome Rate, $F(3,114) = 4.43$, $p < 0.01$. Post hoc comparisons revealed that Non-musicians anticipated more at the 30% Slower than at 15% and 30% Faster rates, and at the 15% Slower than at 15% and 30% Faster rates (Tukey's HSD = 12.41, $p < 0.05$). Musicians anticipated more at the 30% Slower than at 15% and 30% Faster rates, and at the 15% Slower than 30% Faster rate. Finally, Musicians synchronized more accurately than Non-musicians at both 15% and 30% Slower rates.

Insert Figure 5 Here

We also examined which Metronome Rate conditions in Figure 5 differed from 0, where 0 is participants' synchronization accuracy at the SPR. *T*-tests (Bonferroni-adjusted) of mean values at each Metronome Rate against 0 indicated that Musicians lagged significantly at 15% and 30% Faster rates relative to 0 (p's < 0.01). Non-musicians lagged significantly at 15% ($p = 0.01$) and 30% ($p < 0.01$) Faster rates and also anticipated significantly at 15% and 30% Slower rates (p's < 0.01) relative to 0.

To compare Musicians' and Non-musicians' synchronization accuracy across rates, the slope of each individual's adjusted mean signed asynchronies was computed by predicting the adjusted mean signed asynchronies shown in Figure 5 from the prescribed metronome IOI (ms) for each rate condition. A one-way ANOVA on each participant's slope values from these regression fits indicated a significant main effect of Group, $F(1,38) = 8.90$, $p < 0.01$. Musicians had shallower slopes (mean = -0.08) than Non-musicians (mean = -0.19), indicating greater synchronization accuracy across rates.

4.2.3 Maximal Rates

To ensure that observed effects of Group and Metronome Rate on synchronization were not driven by biomechanical limits at participants' fastest metronome rates, maximal rates were compared across Groups and were also compared with participants' fastest metronome rate (30% Faster rate). A one-way ANOVA on maximal rates showed no significant main effect of Group,

$F(1,38) = 0.37$, $p = 0.55$ (Musicians' mean maximal rate = 172 ms; Non-musicians' mean maximal rate = 164 ms). A one-way ANOVA on CV of maximal rates also showed no significant main effect of Group, $F(1,38) = 1.79$, $p = 0.19$ (Musicians' mean CV = 0.06; Non-musicians' mean CV = 0.07).

Participants' maximal rates were then compared with the fastest synchronization condition (30% Faster) to ensure that participants did not reach ceiling on their possible movement rates. Thirty-eight of the 40 participants showed maximal tapping rates faster than their 30% Faster prescribed (metronome-determined) rate. For the two exceptions (both Non-musicians), participants' maximal rates were then compared with their 30% Faster observed (tapping) rate to ensure that their maximal rates reflected their fastest tapping rate. These comparisons showed that both participants had faster 30% Faster observed rates than maximal rates. These findings suggest that no participant reached ceiling on their possible movement rates during the rate flexibility task.

4.2.4 Lag-1 Autocorrelation

To investigate Musicians' enhanced synchronization across the range of rates, we ran a lag-1 autocorrelation on the IOIs in each rate condition to test the potential role of error correction (Wing and Kristofferson, 1973). Similar to error correction analyses of poor synchronizers (Sowiński and Dalla Bella, 2013), the analysis included the first melody repetition in each trial with the fewest IOI outliers. A mixed ANOVA on the lag-1 autocorrelation coefficients per trial by Group and Metronome Rate showed a significant main effect of Group, $F(1,38) = 11.16$, $p < 0.01$, such that Musicians showed more negative lag-1 autocorrelations (mean = -0.18) than Non-musicians (mean = -0.03). Results also showed a significant main effect of Metronome Rate, $F(4,152) = 5.19$, $p < 0.01$; the lag-1 autocorrelation coefficients are shown by Metronome Rate in Figure 6. Post hoc comparisons revealed larger negative values in the 30% Slower than 30% Faster rate, 15% Slower than SPR and 30% Faster rates, and 15% Faster than 30% Faster rate. There was no interaction between Group and Metronome Rate, $F(4,152) = 1.03$, $p = 0.39$. Thus, Musicians showed more error correction than Non-musicians and both Groups showed more error correction at slower rates.

Insert Figure 6 Here

4.2.5 Recurrence Quantification Analyses

To further investigate differentiating characteristics of coordination between Musicians and Non-musicians across a longer timescale, we ran autorecurrence quantification analyses (RQA) on the asynchrony time series. Whereas the lag-1 autocorrelation investigates error correction at a local timescale (Sowiński and Dalla Bella, 2013), RQA measures provide information about recurring behavioral patterns across longer timescales (Schmit et al., 2005, 2006; Richardson et al., 2008). Because we were interested in comparing optimal performances of Musicians and Non-musicians, RQA was applied to the SPR Metronome Rate condition, a conservative test between Groups because the SPR condition was tailored to be most comfortable for all participants. If Non-musicians show RQA patterns that indicate temporal rigidity in synchronization, this could provide a possible mechanism for their reduced flexibility in synchronizing with other rates. The RQA analysis was applied to all data (including outliers) to preserve the time series, and to asynchronies (rather than IOIs) to allow that Non-musicians did not always tap the melody rhythm as expected, and thus the asynchrony measures provided longer uninterrupted time series for analysis.

Consistent with previous RQA implementations, (Schmit et al., 2005, 2006; Richardson et al., 2008), we examined the outcome measures of percent recurrence (how often a data point is repeated in a time series, related to regularity), percent determinism (how often recurrent points form lines, an inverse measure of randomness), and maxline (measure of the response of a system to changes in initial conditions, also known as mathematical stability). Based on tests of a wider range of parameter values that generated similar patterns of results, final parameter settings for the analysis were: time delay = 14 samples (which coincided with approximately half of the stimulus melody cycle), embedding dimensions = 7, radius = 60% of the mean distance between data points in the reconstructed phase space. The number of successive points required to form a line was set to 2. These parameters were selected to obtain percent recurrence of at least 1% for each trial without reaching a ceiling of 100% determinism (Schmit et al., 2005).

The mean values for percent recurrence, percent determinism, and maxline per Group are shown in Table 1. ANOVAs conducted by Group for each measure showed a main effect of Group on percent recurrence, $F(1,38) = 15.70$, $p < 0.001$, percent determinism, $F(1,38) = 24.94$, $p < 0.001$, and maxline, $F(1,38) = 31.05$, $p < 0.001$. Non-musicians had significantly higher recurrence (Non-musicians = 6.83%; Musicians = 4.48%), higher determinism (Non-musicians = 36.03%; Musicians = 12.99%), and higher maxline (Non-musicians = 2.18; Musicians = 0.73) than Musicians. Thus, Non-musicians showed more regularly patterned behavior than Musicians. Exemplar plots for a single trial by a Musician and a Non-musician are shown in Figure 7.

Insert Table 1 Here

Insert Figure 7 Here

4.2.6 Individual Differences in Rate Flexibility

We examined the relationship between each performer's rate flexibility in synchronization (represented by the slope value for the asynchronies across rates in Figure 5), and the measures of temporal variability in spontaneous production (CV), feedback correction (mean lag-1 autocorrelation of IOIs across rates), and recurrence patterns during synchronization at the SPR (% determinism). These measures were chosen because they showed group differences between Musicians and Non-musicians. Multiple regressions were conducted separately for each group with CV, lag-1 autocorrelation, and % determinism as predictors for asynchrony slope (larger asynchronies across rates were represented by a more negative slope value); two participants were excluded due to outlier values for the measures of CV (1 Non-musician) and lag-1 autocorrelation (1 Non-musician). The multiple regression analysis indicated a significant fit for Musicians ($R = 0.79$, $p < 0.001$). Semi-partial correlation coefficients indicated that only the CV values predicted the asynchrony slope values above and beyond other variables, $\beta = -0.73$, $t(16) = 3.41$, $p < 0.01$ (lag-1 autocorrelation, $\beta = -0.09$, $p = 0.64$; % determinism, $\beta = -0.03$, $p = 0.87$). In contrast, the multiple regression model did not provide a significant fit for Non-musicians' slope values ($R = 0.21$, $p = 0.88$). Thus, individual differences in Musicians' temporal variability in unpaced (spontaneous) performance was predictive of rate flexibility; the more regular their unpaced performance (CV closer to 0), the closer to 0 (less negative) their slope value.

4.2.7 Wrist Width

Finally, we examined the relationship between participants' wrist width measures and their SPRs. An ANOVA on wrist width measures by Group showed no significant differences, $F(1,38) = 0.56$, $p = 0.46$. Next, a correlation conducted across Groups indicated that wrist width was not significantly correlated with the SPR, $r(38) = -0.18$, $p = 0.26$. As well, wrist width was not significantly correlated with the SPR within either Group: for Musicians, $r(18) = -0.26$, $p = 0.27$, or Non-musicians, $r(18) = 0.04$, $p = 0.88$. Nor was wrist width correlated with the slope values from participants' adjusted mean asynchronies across rates ($r = 0.03$, $p = 0.87$). These findings suggest that biomechanical factors alone did not account for Group differences in SPR.

4.3 Discussion

The second experiment implemented the novel musical tapping task validated in the first experiment with musicians and non-musicians to investigate the effects of musical training and spontaneous rates on rate flexibility of synchronization. Participants' SPRs were measured as they tapped the rhythm of a familiar melody at a comfortable and steady rate. Participants then synchronized their tapping of the melody with a metronome set at their SPRs and rates proportionally slower and faster than their SPRs.

First, musicians' SPRs were significantly slower than non-musicians' SPRs. This finding is consistent with previous research on SMT in which musicians show slower tapping rates than non-musicians (Drake et al., 2000a). Additionally, musicians were less variable than non-musicians during self-paced performances at their SPRs. Given that the SPR task required participants to produce the rhythm in accordance with the corresponding melody tones, non-musicians' increased variability in this task may arise from weaker auditory-motor integration (Pfordresher and Brown, 2007; Sowiński and Dalla Bella, 2013).

Second, both musicians and non-musicians anticipated more at slower rates and lagged more at faster rates relative to their SPRs in the synchronization task. This finding indicates a constraint placed on rate flexibility by the SPR for all participants, consistent with results from studies on duet synchronization (Loehr and Palmer, 2011; Zamm et al., 2015, 2016). Interestingly, non-musicians synchronized less accurately than musicians at slower rates, whereas both groups performed similarly at faster rates. This finding, together with non-musicians' faster SPRs, suggests that non-musicians may have a bias toward faster rates. This bias may indicate that non-musicians are more restricted in their ability to track events over longer timescales compared with musicians (Drake et al., 2000b). Importantly, musicians synchronized more flexibly across rates than non-musicians, as indicated by their similar synchronization accuracy between rates close to their SPRs (i.e., 15% slower and faster rates) and by their smaller slope values (less change across rates) of the adjusted asynchronies. Additionally, the temporal regularity of unpaced performance significantly predicted synchronization performance across rates for musicians but not for non-musicians, suggesting different mechanisms driving rate flexibility across groups.

Third, musicians demonstrated larger negative lag-1 autocorrelations of IOIs compared with non-musicians. These findings suggest that musicians engage in more error correction than non-musicians, which may contribute to their enhanced synchronization accuracy across rates (Sowiński and Dalla Bella, 2013). Additionally, RQA indicated that non-musicians had higher recurrence (repetition), determinism (lower randomness), and maxline (mathematical stability) than musicians, suggesting more rigidity in their synchronization behaviors than musicians.

5. General Discussion

The current experiments investigated the roles of spontaneous rates and musical training on rate flexibility of synchronization. Experiment 1 introduced a novel musical tapping task appropriate for measuring spontaneous rates in both musicians and non-musicians; that experiment showed that pianists produced familiar melodies at highly consistent rates across 5-finger piano performance and 1-finger tapping. Experiment 2 implemented the novel task to show that musicians synchronized more flexibly across rates than non-musicians, and group differences in rate flexibility could be characterized both by differences in error correction and in dynamic patterns of synchronization over time.

Notably, all participants showed some constraint of SPRs on synchronization accuracy at other rates, indicated by the tendency to anticipate more at slower rates and lag more at faster rates relative to each individual's SPR. Musicians' temporal stability of performances at the SPR were correlated with their synchronization flexibility across rates: the less variable musicians were in unpaced performance, the more synchronous their paced performances were across rates. This finding of increased temporal stability for performances at the SPR as an indicator of synchronization flexibility across rates is consistent with the interpretation of the spontaneous rate as a natural frequency at which minimum energy expenditure is required to coordinate movement across the parts of a system (Von Holst, 1937; Haken et al., 1985; Kelso, 1997), such as finger and wrist joints in tapping.

Musicians and non-musicians differed on several performance measures. First, musicians synchronized more accurately across rates than non-musicians, suggesting that rate flexibility is enhanced by musical training. Furthermore, musicians showed larger negative lag-1 autocorrelations than non-musicians during the synchronization task, indicative of greater error correction (Wing and Kristofferson, 1973; Sowiński and Dalla Bella, 2013). Finally, recurrence quantification analyses revealed more repetitive, patterned, and mathematically stable synchronization behavior for non-musicians than for musicians. These findings are consistent with postural sway differences between patients with Parkinson's Disease (PD) and control participants (Schmit et al., 2006), and between track athletes and expert ballet dancers (Schmit et al., 2005). In both studies, the less skilled group (i.e., PD patients and track athletes) demonstrated more repetitive and patterned postural sway; our findings show a similar pattern of behavior in non-musicians during a synchronization task. The decreased noise observed in non-musicians' synchronization behavior is consistent with a dynamical systems perspective that a system with less noise should also be less flexible (Schmit et al., 2005). Indeed, we provide evidence that non-musicians synchronize less flexibly across rates than musicians.

The current experiments also examined the contributions of peripheral timing mechanisms to spontaneous rates. In Experiment 1, wrist width and piano performance SPR significantly predicted SPR: Participants with wider wrists tended to have slower SPRs. In Experiment 2, no relationship was observed between participants' wrist widths and SPRs. These conflicting results may have arisen due to differences in the tapping task across the two experiments. In the first experiment, participants tapped on a piano keyboard without arm support. In the second experiment, participants tapped on a FSR positioned on a table where they could rest their arm. Therefore, while the tapping motion in the first experiment likely came primarily from the wrist (Dennerlein et al., 2007), this may not have been true for the second experiment. Further research is needed to investigate how changes in movement execution influence peripheral contributions to spontaneous rates.

One limitation of the findings is their use of a small number of simple melodies to ensure musicians' and non-musicians' equivalent familiarity with the stimulus materials. Future studies should investigate a wider range of complex melodies to see whether the same results hold. Additionally, maximal rate measures from the second experiment indicated that some participants may not have tapped at their true maximal rates. The maximal rate task may have reflected cognitive as well as motor constraints. Future measurements of maximal rates may utilize isochronous tasks without the presence of auditory feedback to get a purer measure of biomechanical constraints.

In sum, both spontaneous rates and musical training modulated the degree to which individuals flexibly performed a synchronization task across rates. Consistent with the view that spontaneous rates act as an attractor in well-learned tasks, both musicians and non-musicians show biases in synchronization toward a natural frequency that cannot be explained solely by musical training or biomechanical hand differences. Finally, we show that musical training enhances performers' flexibility in moving away from this attractor. This enhanced flexibility is characterized by greater engagement of error correction mechanisms as well as less patterned (noisier) synchronization behaviors that may facilitate rate adaptation. Predictors of rate flexibility included tapping regularity at the spontaneous rate in the absence of a pacing cue; individual differences in this temporal regularity predicted rate flexibility for musicians, but not for non-musicians. Future research may investigate the neural mechanisms underlying musicians' enhanced flexibility around spontaneous rates, with an emphasis on treating musical training as a continuum.

6. Ethics Statement

This study was carried out in accordance with the recommendations of the McGill University Policy on the Ethical Conduct of Research Involving Human Participants and the Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans, McGill University Research Ethics Board with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was reviewed by the McGill University Research Ethics Board.

7. Funding

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8. Acknowledgements

We are grateful to Ashley Brown-Notargiacomo, Jamie Dunkle, and Frances Spidle for their assistance.

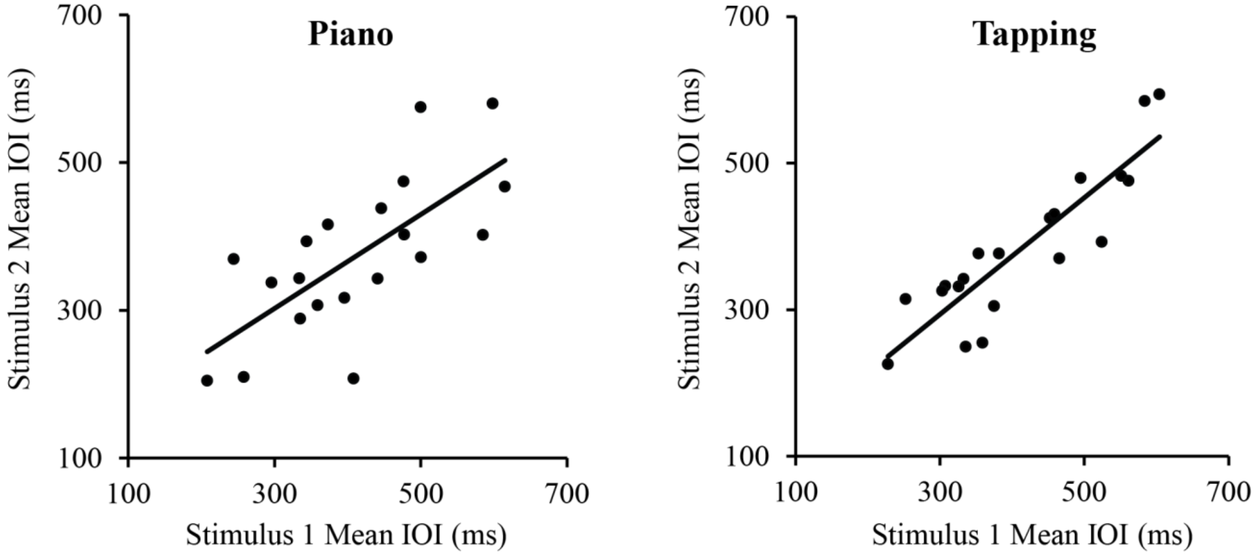


Figure 1. Correlations between pianists' Spontaneous Rate values (mean IOIs) for stimulus melodies 1 and 2. Left panel: piano performance task; Right panel: tapping task. Each point represents a single participant.

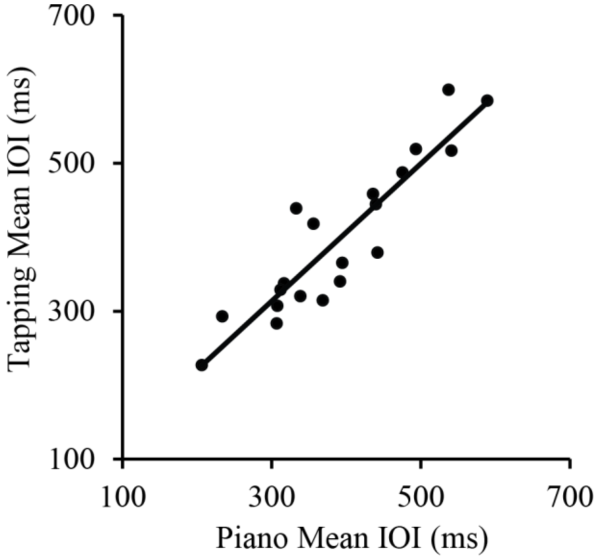


Figure 2. Correlations between pianists' Spontaneous Rate values (mean IOI across melodies) for the piano performance task and tapping task. Each point represents a single participant.

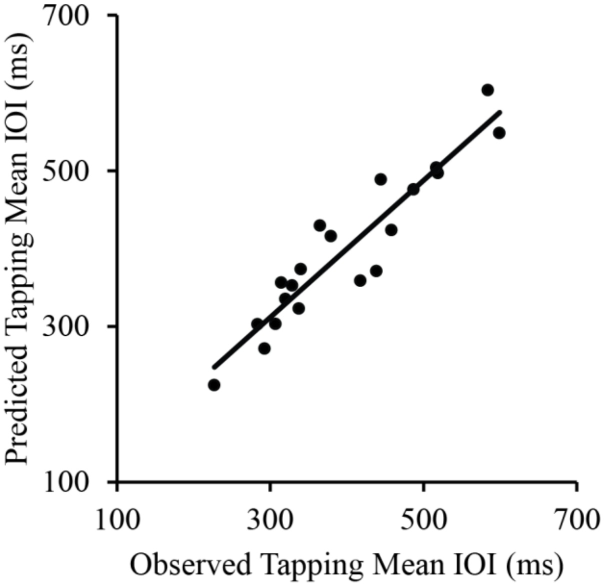


Figure 3. Correlations between pianists' observed tapping mean IOI and their predicted tapping IOI based on their piano performance SPR (mean IOI) and wrist width. Each point represents a single participant.

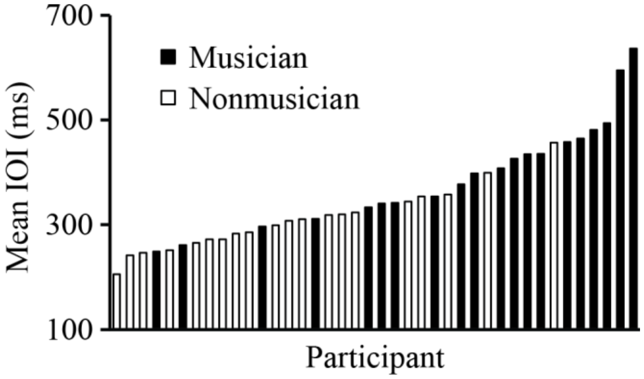


Figure 4. Distribution of SPR values (mean IOI) across participants. Each bar represents the SPR of a single participant; black bars are musicians (group mean = 405 ms) and white bars are non-musicians (group mean = 306 ms).

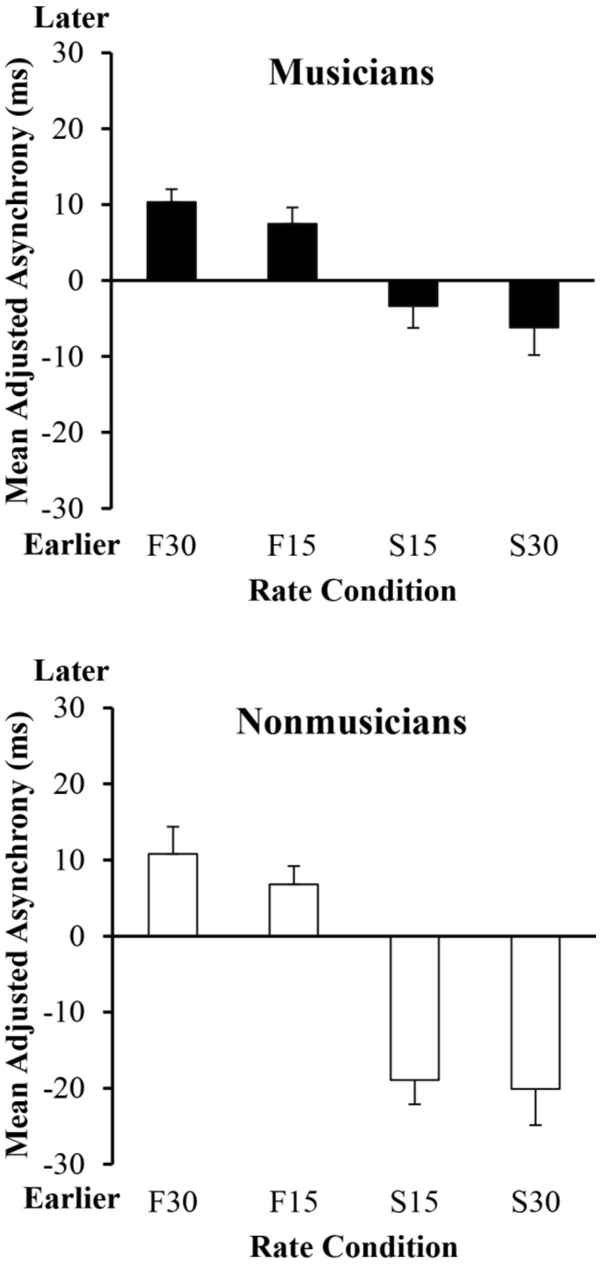


Figure 5. Mean adjusted signed asynchronies (each participant's rate condition mean asynchrony minus SPR condition mean asynchrony) by rate condition and group. Error bars show standard error. Positive values (earlier) indicate asynchrony values for which the participant tapped sooner and negative values indicate asynchrony values for which the participant tapped later relative to their performance in the SPR condition.

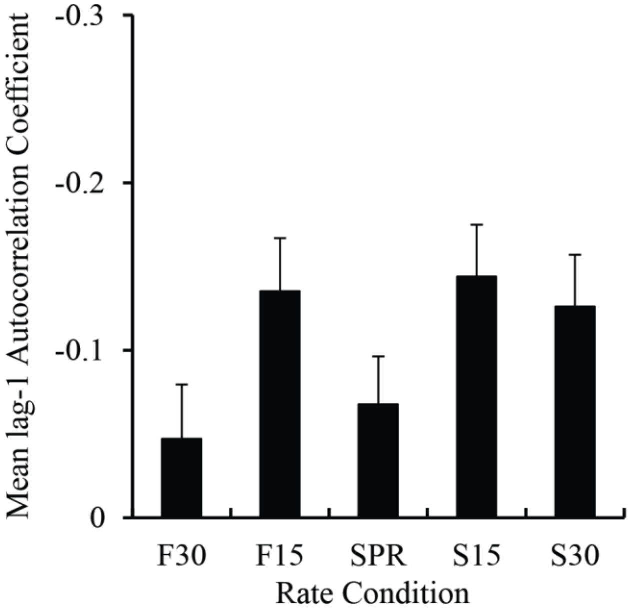


Figure 6. Mean lag-1 autocorrelation coefficients computed on the tapping IOI sequences by rate condition. Negative values are plotted upward. Error bars show standard error.

Table 1. Group comparisons of RQA outcomes.

RQA Measure	**Musicians**	**Non-musicians**
% Recurrence	4.48%	6.83%
% Determinism	12.99%	36.03%
Maxline	0.73	2.18

p’s < 0.001.

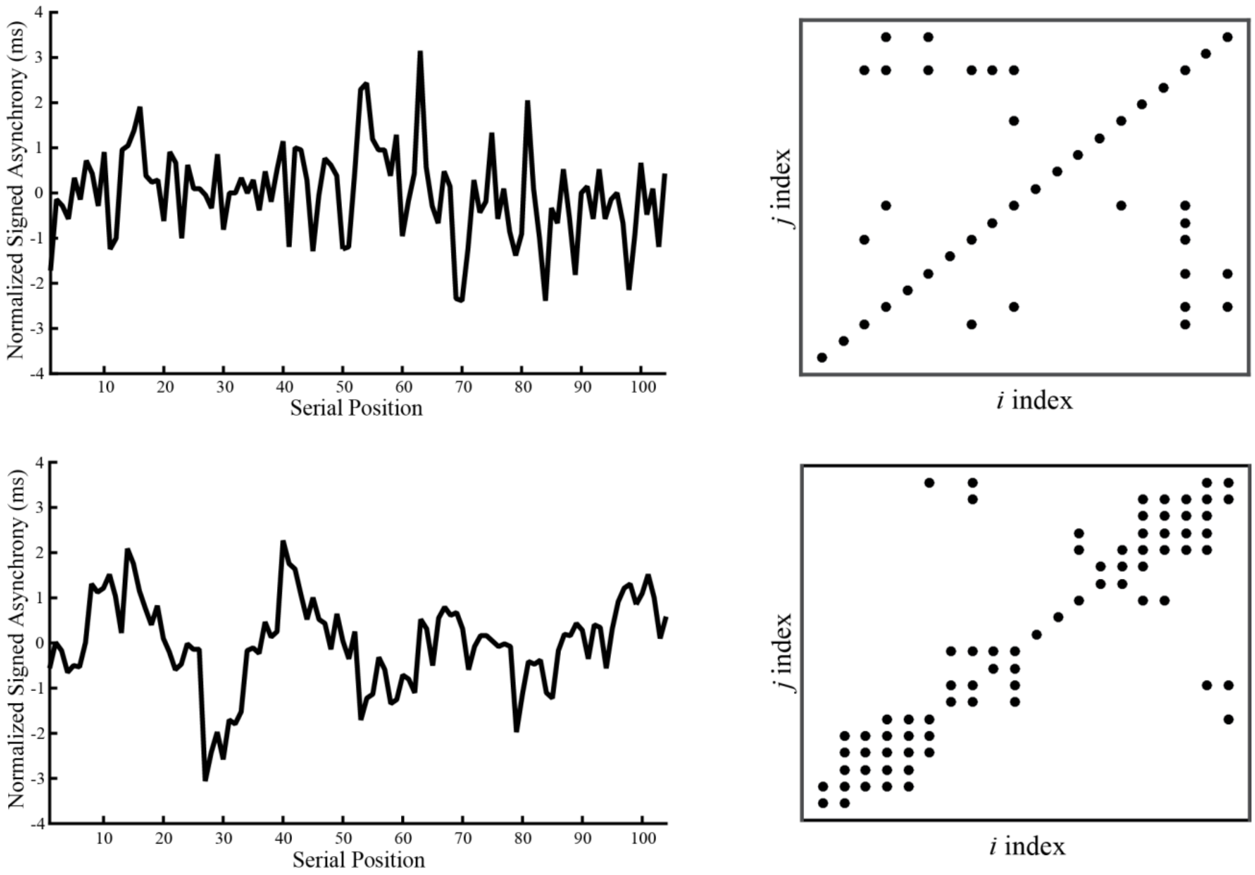
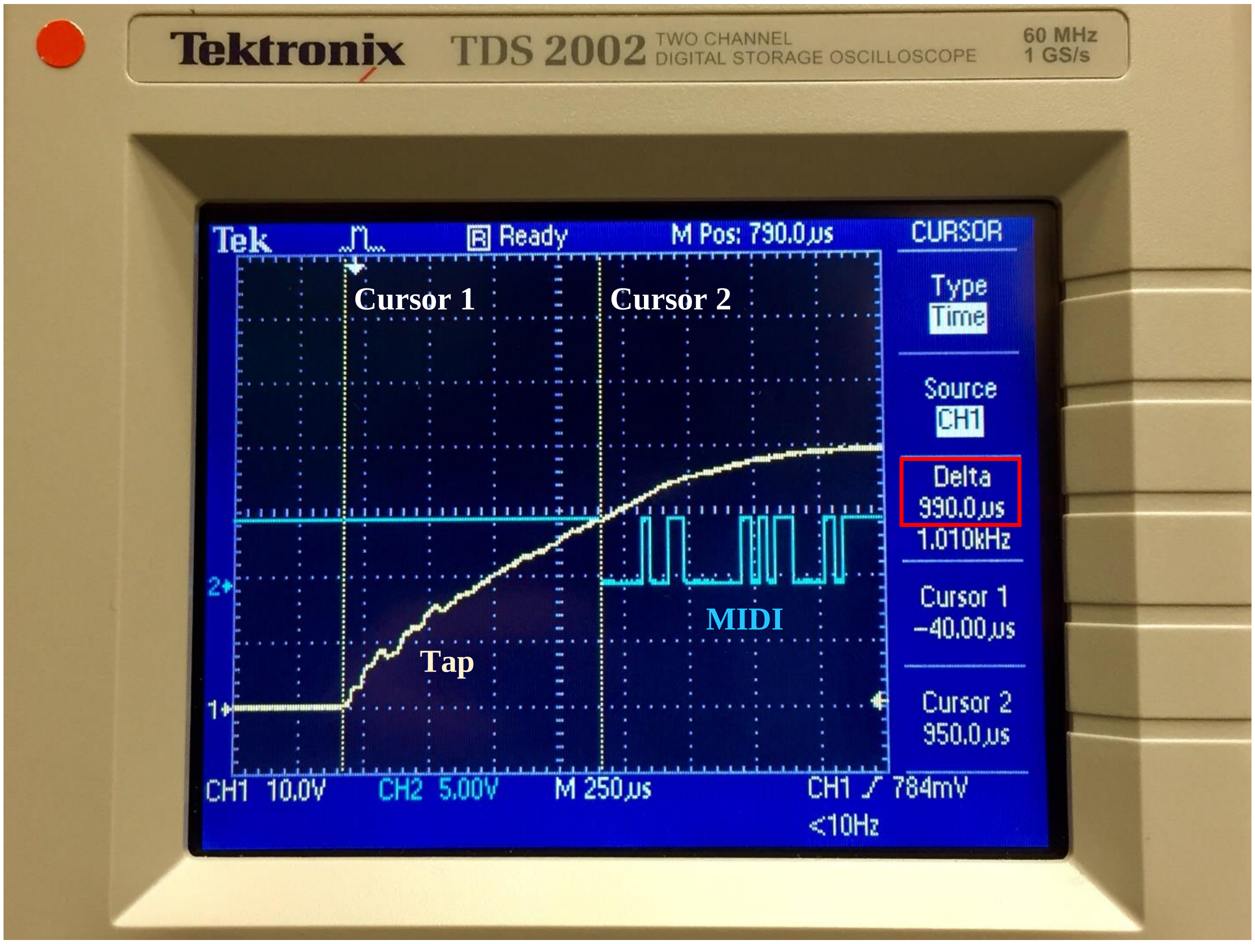


Figure 7. Sample normalized signed asynchronies (left graphs) and recurrence plots (right) for a single trial for one musician (top row) and one non-musician (bottom row).

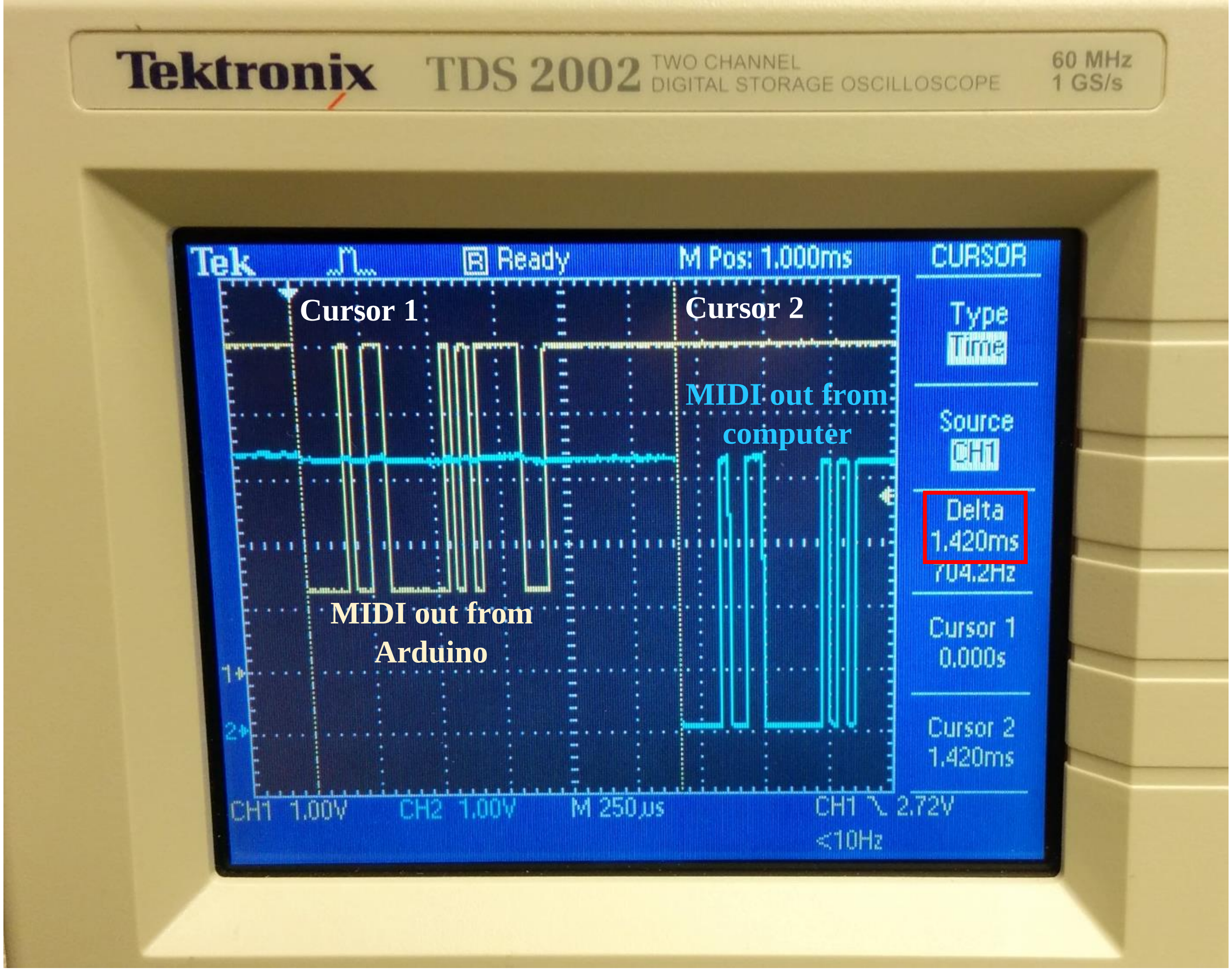
9. Supplementary Figures

The time from the start of the tap on the force sensitive resistor (FSR) to the start of the MIDI signal sent from the Arduino was measured with a Tektronix TDS 2002 oscilloscope. Data was recorded from 100 taps on the FSR and showed that this duration averaged 1.0 millisecond (SD = 0.035; see Supplementary Figure 1).

A MIDI signal was generated from the Arduino in response to a tap on the FSR and was sent via an M-Audio UNO MIDI-USB connector to a Linux computer running FTAP (Finney, 2001). FTAP processed the incoming MIDI signal from the Arduino and sent an outgoing MIDI signal. The time from the start of the MIDI signal sent from the Arduino to the start of the MIDI signal sent from the computer was measured with a Tektronix TDS 2002 oscilloscope. Data was recorded from 100 taps on the FSR and showed that this duration averaged 1.4 milliseconds (SD = 0.13; see Supplementary Figure 2).



Supplementary Figure 1. Sample trial measuring the time from the start of the tap on the FSR (yellow trace) to the time at which the MIDI signal (blue trace) is sent from the Arduino. Cursor 1 is aligned to the start of the tap on the FSR, and cursor 2 is aligned to the start of the MIDI signal sent from the Arduino. Delta (0.99 milliseconds) calculates the difference between cursors 1 and 2.



Supplementary Figure 2. Sample trial measuring the time from the start of the MIDI signal sent from the Arduino (yellow trace) to the time of the start of the MIDI signal sent from the computer (blue trace). Cursor 1 is aligned to the start of the MIDI signal sent from the Arduino, and cursor 2 is aligned to the start of the MIDI signal sent from the computer. Delta (1.42 milliseconds) calculates the difference between the signal onsets marked by cursors 1 and 2.

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Chapter 3

Musical Training Enhances Rate Flexibility of Synchronization

The first study presented in Chapter 2 validated the use of a novel musical tapping task to measure Spontaneous Production Rates by showing that musicians produced familiar melodies at similar rates across piano performance and tapping tasks. The second study in Chapter 2 then implemented the novel task to examine whether rate flexibility of auditory-motor synchronization is enhanced in individuals with musical training. Results showed first that all participants tended to anticipate more at slower rates and lag more at faster rates relative to their SPRs, suggesting a constraint of SPRs on rate flexibility in both musicians and nonmusicians. Results further showed that musicians synchronized more accurately, engaged in more error correction, and showed less recurrent and patterned synchronization behavior than nonmusicians, all indicative of greater flexibility. These results suggest that, even in the presence of SPR constraints, musical training may enhance rate flexibility.

The next study in this dissertation further investigates how musical training may influence rate flexibility of auditory-motor synchronization, and the nonlinear mechanisms supporting rate flexibility. Musicians and nonmusicians tapped isochronous (regular) versions of familiar melodies with a metronome that unexpectedly changed its rate away from their SPRs, and rates faster and slower than their SPRs. Adaptation was measured following these rate perturbations, and two models which either did or did not contain nonlinear components were fit to adaptation curves following perturbations. All participants were expected to show constraints of SPRs such that adaptation would be slower to perturbations that moved away from their SPRs. Musicians were expected to adapt more quickly to rate perturbations overall than nonmusicians, indicative of their greater flexibility, consistent with the results from Chapter 2. Furthermore, a nonlinear damped harmonic oscillator model was expected to fit adaptation curves following rate perturbations better than an alternative exponential decay model which contained no periodic component. Figure 1 gives a depiction of the damped harmonic oscillator model and the three parameters of interest: *b*, damping coefficient inversely related to adaptation time; *c*, intercept related to where tappers return to following adaptation; and *f*, oscillation frequency. Musicians' enhanced flexibility was expected to be shown in the *b* and *c* parameters of this model, specifically, showing faster adaptation time and closer adaptation back to baseline synchronization following perturbations, respectively.

Insert Figure 1 Here

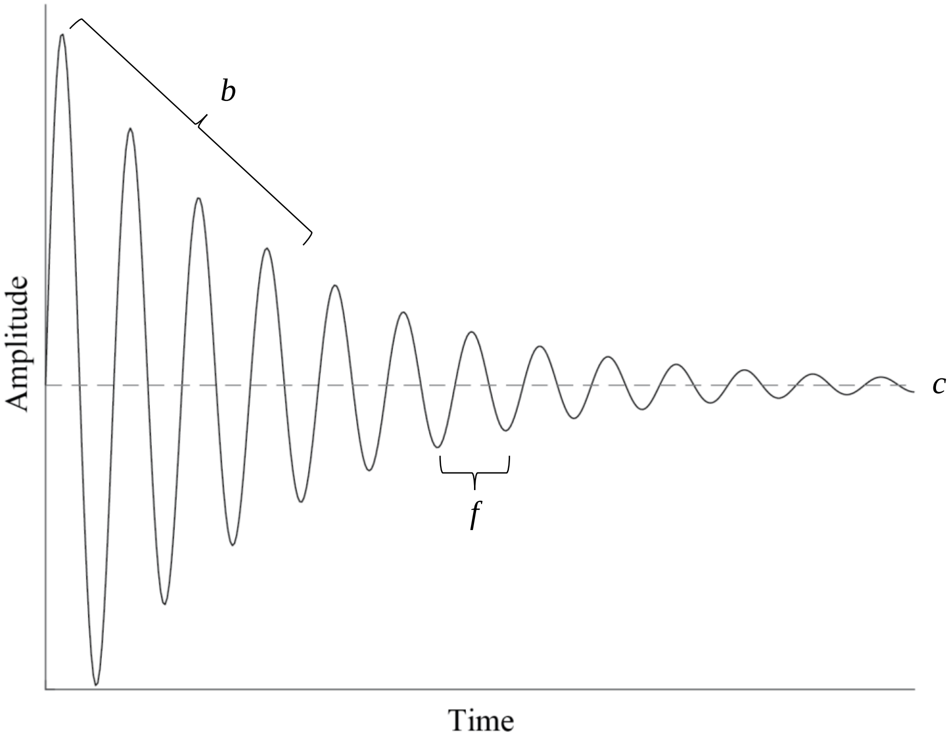

Figure 1. Depiction of the damped harmonic oscillator and the three parameters of interest: *b* (damping coefficient), *c* (intercept), and *f* (oscillation frequency).

Musical Training Enhances Temporal Adaptation of Auditory-Motor Synchronization

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Keywords: Flexibility, auditory-motor synchronization, temporal adaptation, musical training, spontaneous production rates

Abstract

To coordinate their actions successfully with auditory events, individuals must be able to adapt their behaviour flexibly to environmental changes. Previous work has shown that musical training enhances the flexibility to synchronize behaviour with a wide range of stimulus periods. The current experiment investigated whether musical training enhances temporal adaptation to period perturbations as listeners tapped with a metronome, and whether this enhancement is specific to individuals' Spontaneous Production Rates (SPRs; individuals' natural uncued rates). Both musicians and nonmusicians adapted more quickly to period perturbations that slowed down than to those that sped up. Importantly, musicians adapted more quickly to all period perturbations than nonmusicians. Fits of a damped harmonic oscillator model to the tapping measures confirmed musicians' faster adaptation and greater responsiveness to period perturbations. These results suggest that, even when the task is tailored to individual SPRs, musical training increases the flexibility with which individuals can adapt to changes in their environment during auditory-motor tasks.

1. Introduction

A key component of behavioural flexibility is the ability to adapt planned actions to achieve a specific goal (MacKay 1982). In conversational speech, rate adaptations help prevent interruptions. In joint music-making, rate adaptations help preserve synchronization. In each of these examples, individuals must quickly adapt the timing of their actions based on sensory feedback to achieve the desired outcome, a process called temporal adaptation. Music performance is a particularly good model of this process, as adaptation must occur at a very precise (millisecond-level) timescale (Large et al. 2002; Madison and Merker 2004; Palmer et al. 2014; Thaut et al. 1998). What mechanisms allow for this precise level of temporal adaptation?

Researchers often use perturbation tasks to investigate the mechanisms underlying temporal adaptation of auditory-motor synchronization (cf. Large et al. 2002; Palmer et al. 2014; Repp 2002; Thaut et al. 1998). In this paradigm, individuals synchronize their responses (e.g., finger taps) with an auditory stimulus that unexpectedly changes its period, phase, or both. Dynamical systems theory proposes that the mechanisms supporting temporal adaptation in these tasks are internal oscillations or rhythms that entrain or synchronize with stimulus rhythms by adjusting their period and phase to match stimulus changes (Large and Jones 1999; Strogatz and Stewart 1993). As predicted by these mathematical models, individuals adapt more quickly to phase than to period changes and to slowing than to speeding changes in an auditory stimulus (Large et al. 2002; Loehr et al. 2011; Palmer et al. 2014). Furthermore, comparison of nonlinear oscillator models with linear timekeeper models indicates that nonlinear oscillator models better explain adaptation to changing auditory stimuli than linear timekeeper models. Specifically, only nonlinear oscillator models correctly predict faster adaptation to slowing than to speeding period perturbations of the same magnitude (Loehr et al. 2011). This asymmetry arises because slowing perturbations are handled more efficiently by the sinusoidal period adaptation function in the nonlinear model.

A fundamental principle of dynamical systems theory states that these internal oscillations have a natural frequency at which movement is optimized and toward which individuals should be drawn (Hoyt and Taylor 1981). Natural frequencies have been measured by individuals' Spontaneous Production Rates (SPRs), or the rates at which performers produce regular rhythmic auditory sequences in the absence of external cues (cf. Palmer et al. 2019; Scheurich et al. 2018; Zamm et al. 2016, 2018). Individuals produce auditory sequences with least temporal variability at their SPRs compared with other rates and tend to drift back toward their SPRs when producing sequences at a different rate (Zamm et al. 2018). Individuals also synchronize more accurately with a partner whose SPR is similar to their own (Zamm et al. 2016). Furthermore, individuals tend to anticipate a metronome more when synchronizing with slower rates and lag more when synchronizing with faster rates relative to their SPRs (Scheurich et al. 2018). These findings suggest that natural frequencies measured as SPRs may represent an optimal coordination mode. Previous studies examining temporal adaptation of auditory-motor synchronization, however, have not accounted for individual differences in SPRs.

Because synchronization in music performance occurs at such a precise timescale, musical training may enhance temporal adaptation. Musicians synchronize more accurately with a regular auditory stimulus than nonmusicians (for reviews on sensorimotor synchronization and the role of musical training, see Aschersleben 2002; Palmer and Zamm 2017; Repp 2005; Repp and Su 2013). Only a few studies have addressed the impact of musical training on synchronization with a changing auditory stimulus. Madison and Merker (2004) compared musicians and nonmusicians synchronizing with a metronome containing both perceptible and imperceptible deviations in its beat period. Both groups performed similarly when deviations were imperceptible, but musicians adapted more than nonmusicians when deviations became perceptible. In that study, each deviation in the period of the metronome lasted at most two beats, allowing only for investigation of phase adjustment but not period adjustment. One study of temporal adaptation to longer period changes did not find differences between musicians and nonmusicians (Large et al. 2002). However, with a sample size of only three participants per group, it was not possible to draw conclusions about the influence of musical training. Repp's (2010) study showed that musicians adapted faster to period changes in an auditory stimulus than nonmusicians. Again, the sample size of musicians was small, and one-third of musicians were regular participants in similar studies. Furthermore, perturbations always occurred in the same sequence location, making them predictable to participants. Adaptation at individuals' SPRs was not considered in any of these studies.

2. Current Research

The current study investigated effects of musical training on temporal adaptation to period perturbations while taking into account individuals' SPRs. We measured participants' SPRs with a previously validated musical tapping task developed for use with musicians and nonmusicians (Scheurich et al. 2018). Participants then synchronized their tapping with rates that were equal to, faster than, or slower than their SPRs, and continued synchronizing when the period unexpectedly changed. We focused only on period perturbations (not phase perturbations) to compare different predictions of nonlinear and linear models for slowing versus speeding perturbations (Loehr et al. 2011). Adaptation to period perturbations was measured by the phase of participants' taps relative to the metronome following period perturbations. Relative phase measures were then modeled with a damped harmonic oscillator model (Large et al. 2002;

Palmer et al. 2014) and an exponential decay model (Pfordresher and Kulpa 2011) to test different mechanisms that may account for temporal adaptation.

Consistent with previous research, we predicted that (1) musicians would adapt more quickly to period perturbations than nonmusicians; (2) participants would lag the metronome more following speeding period perturbations and anticipate the metronome more following slowing period perturbations; (3) participants would adapt more quickly to slowing than to speeding period perturbations; and (4) participants would adapt more quickly to period perturbations that moved toward the SPR than away from the SPR. We also predicted that the damped harmonic oscillator model would better account for temporal adaptation to period perturbations than the exponential decay model because the exponential decay model does not contain a periodic component. Additionally, its parameters would indicate faster adaptation and closer return to baseline synchronization for musicians compared with nonmusicians following period perturbations.

3. Methods

3.1 Participants

Sixteen musicians (mean age = 22 years; SD = 2; 10 females) and 16 nonmusicians (mean age = 22 years; SD = 4; 11 females) participated in the study. Musicians with at least 6 years of private music instruction (mean years = 11; SD = 3) on an instrument were recruited. Percussionists were excluded because of their superior synchronization ability (Krause et al. 2010). Nonmusicians with no private music instruction in the past 6 years and less than 2 years of instruction overall (mean years = 0.21; SD = 0.44; one nonmusician who recalled having less than 2 years of training but not the exact amount was excluded from this calculation) were recruited. Participants had normal hearing sensitivity (< 30 dB HL threshold) within the frequency range of stimuli used in this study (125–750 Hz) as determined by an audiometry screening with a Maico MA-40 audiometer through headphones, normal pitch and meter perception as measured by the Montreal Battery of Evaluation of Amusia (MBEA; Peretz et al. 2003), and were familiar with the musical stimuli. The two groups did not differ significantly in age, $t(30) = 0.39$, $p = 0.54$, or in years of education, $t(30) < 0.01$, $p > 0.99$. An additional 4 musicians and 16 nonmusicians failed the screening criteria and were excluded.

3.2 Stimulus Materials and Equipment

The scale and meter tests of the MBEA were used to evaluate participants' pitch and meter perception. The test contained 31 "Scale" trials (one catch trial, 30 regular trials) and 30 "Meter" trials. Participants had to correctly answer the scale subtest catch trial, and achieve at least 73% and 67% accuracy on "Scale" and "Meter" tests, respectively (Peretz et al. 2003).

Musical stimuli included isochronous versions of "Mary Had a Little Lamb" (presented in F Major) and "Twinkle, Twinkle Little Star" (presented in G Major), which were chosen for their familiarity among participants. Each half note in "Mary Had a Little Lamb" (3 per repetition) and in "Twinkle, Twinkle Little Star" (6 per repetition) were replaced with two quarter-note beats, and each whole note in "Mary Had a Little Lamb" (1 per repetition) was replaced with four quarter-note beats, yielding a total of 32 beats ("Mary Had a Little Lamb") and 48 beats ("Twinkle, Twinkle Little Star") per repetition. "Mary Had a Little Lamb" was used as the practice melody to teach participants how to perform the tapping task and "Twinkle, Twinkle Little Star" was used as the melody for experimental trials.

Perturbation stimuli used in the synchronization-perturbation task, based on Large et al. (2002), were constructed to present period perturbations at unpredictable trial locations. Each trial began with eight clicks of the metronome presented at one of three fixed "Base rates" (SPR, 18% Faster than SPR, 18% Slower than SPR). After the first eight clicks, participants began tapping the melody with the metronome for 20–25 beats to establish the Base rate. Within each experimental trial, eight total period perturbations (where 1 perturbation equals an Away from plus Return to Base rate) occurred in the metronome with different Perturbation Types (8% Slower or Faster than Base rate). There were four period perturbations of each Perturbation Type (i.e., four 8% Slower and four 8% Faster). Within each Perturbation Type, half were of each Perturbation Direction. Period perturbations were defined as a single uniform change in the inter-onset interval (IOI) that lasted 13–22 beats. To make period perturbations within each trial as unpredictable as possible, the duration and order of period perturbations were quasi-randomized such that Perturbation Types never perfectly alternated throughout a trial and no more than two successive period perturbations lasted for the same duration. Additionally, half of all period perturbations were positioned to start on a weak metrical beat of the melody and the other half on a strong metrical beat. Each trial also contained one baseline section during which the Base rate continued without period perturbations for 13–20 beats. Nine unique experimental trials were constructed (three per Base rate), consisting of 285–315 metronome beats (See Fig. 1 for a sample experimental trial).

Insert Figure 1 Here

Six practice trials (two per Base rate) were also constructed. Three trials introduced each Base rate for two repetitions of the melody without period perturbations. Three additional practice trials introduced period perturbations. These trials were designed in the same way as experimental trials, except that each trial contained four rather than eight total period perturbations. Practice trials containing period perturbations consisted of 161–190 metronome beats.

Participants tapped melodies on a Force-Sensitive Resistor (FSR) of an Arduino connected via a MIDI cable to a Dell computer running FTAP (Finney 2001; see Online Resource for timing resolution). Auditory feedback associated with a metronome and participants' taps was delivered in a woodblock timbre (timbre number 116) and piano timbre (timbre number 1), respectively, via an Edirol Studio-Canvas SD-80 tone generator at a comfortable listening level through AKG K271 Studio headphones.

3.3 Design

Participants completed three primary tasks: the spontaneous production rate task, the synchronization-perturbation task, and the maximal rate task, in this order. The between-subjects factor was Group (Musician and Nonmusician). The synchronization-perturbation task additionally contained four within-subjects factors: Base rate (SPR, 18% Slower than SPR, 18% Faster than SPR), Perturbation Direction (Away from and Return to Base rate), Perturbation Type (Slowing and Speeding), and Serial Position following each perturbation (1–12). The dependent variables were the SPRs (mean IOI) measured during the spontaneous production rate task and the relative phase between taps and metronome onsets following period perturbations in the synchronization-perturbation task. These variables were examined with parametric Analyses of Variance (ANOVAs). In addition, we examined parameter estimates from fits of the damped harmonic oscillator model to the relative phase data, and we compared fits of this model with the exponential decay model (see "Data analysis"). Model parameter estimates were examined with non-parametric Wilcoxon matched-pairs signed-ranks tests and Mann–Whitney tests. There were a total of 72 period perturbations across all experimental trials. Trials were blocked by Base rate.

Half of each group’s participants received Base rates ordered fastest to slowest, and the other half ordered slowest to fastest.

3.4 Procedure

After giving informed consent, participants were seated next to the Arduino which was placed on a table where participants could rest their tapping arm. Participants were introduced to the tapping task and were given a chance to practice before completing the experimental tasks. They were instructed to tap each beat of the practice melody (rather than the melody rhythm) with the index finger of their dominant hand, and that each time they tapped they would hear the next melody tone. Participants were instructed to practice until they felt comfortable with the tapping task.

Participants then completed the spontaneous production rate task with the experimental melody. They were instructed to tap each beat of the melody at a comfortable and steady rate. Participants completed one practice trial in which they tapped the melody four times without stopping. Participants were offered more practice, after which they completed three experimental trials; in each experimental trial, they tapped the melody four times without stopping.

Participants then completed a musical background questionnaire that assessed their age, education, musical engagement (i.e., training, ensemble playing, and listening), musical ability (i.e., absolute pitch, and synchronization and singing abilities), and history of neurological or speech disorders. This took approximately 10–15 min to complete, during which the experimenter computed participants’ SPRs (see “Data analysis”) for use in the synchronization-perturbation task.

During the synchronization-perturbation task, participants were instructed to synchronize their tapping of the experimental melody with a steady (regular) metronome set at the first Base rate. Participants were told they would hear a metronome cue for eight beats, and that they should begin synchronizing with the metronome on the ninth beat, continuing until they no longer heard auditory feedback, signaling the end of the trial. After completing one practice trial, participants were given the option to do more practice trials with the steady metronome. Then participants completed a practice trial in which they were told that the metronome would sometimes speed up or slow down, and they should continue synchronizing when the rate changed. Participants finally completed three experimental trials with period perturbations. This procedure was repeated for each Base rate.

Participants then completed the maximal rate task. They were instructed to tap the same experimental melody as before, and that this time there would be no metronome and they should tap the melody as fast as possible. Participants completed one practice trial and one experimental trial in which they tapped the melody once through.

In the final part of the experiment, participants completed the scale and meter subtests of the MBEA. The entire experiment lasted approximately 1 h and 30 min and participants received compensation for their participation. All procedures were approved by the McGill University Research Ethics Board.

3.5 Data Analysis

Participants’ SPRs were calculated from the spontaneous production rate task as the mean IOI for the middle two repetitions of the melody in each experimental trial to capture participants’ maximally stable behaviour (Loehr and Palmer 2011; Scheurich et al. 2018; Zamm et al. 2015). Outlier IOI values that were more than three standard deviations from the mean were excluded from analysis (musicians = 0.52% of total IOIs; nonmusicians = 0.69% of total

IOIs). Participants' maximal rates were calculated in the same way except that the analysis only included one repetition of the melody from the experimental trial.

Adaptation to period perturbations was assessed by examining relative phase between taps and metronome onsets following period perturbations. Taps in the synchronization-perturbation task were aligned with the metronome using a nearest neighbour approach (cf. Pecenka and Keller 2011; Scheurich et al. 2018). Relative phase was computed for the first twelve beats following each perturbation using Eq. 1 (Large et al. 2002; Palmer et al. 2014), where ϕ_n is the relative phase at tap *n*, T_n is the onset time of tap *n*, S_n is the stimulus (metronome) onset time closest to tap *n*, and S_{n+1} is the onset time of the next stimulus.

$$(1)\ \phi_n = \frac{T_n - S_n}{S_{n+1} - S_n}$$

As shown in Eq. 1, relative phase was computed as the tap onset T_n minus the stimulus onset S_n, leading to a signed asynchrony measure in the numerator where a negative value indicates that the tap preceded the stimulus; this signed asynchrony is represented as a proportion of the metronome IOI (the denominator). When there were one or more missed taps in the first 12 beats following a perturbation, the 12 serial positions were extended to include extra taps (as in Large et al. 2002 and Palmer et al. 2014). For cases in which those extra taps extended up to the final Serial Position of one stimulus period before the next stimulus period began, the calculation of the stimulus IOI was adjusted to reflect the period with which participants synchronized rather than the new stimulus period. For cases in which there were not enough extra taps to replace missing taps, any missing taps at the end of the perturbation were replaced with cell mean relative phase values for that serial position. Relative phase was then adjusted (ϕ_a in Eq. 2) by subtracting each participant's mean relative phase in the baseline sections that contained no perturbations (ϕ_b in Eq. 2) from the relative phase following each perturbation (ϕ_n

in Eq. 2; similar to Large et al. 2002 and Palmer et al. 2014) to compare synchronization following perturbations with each participant's baseline synchronization performance.

(2) $\phi_a = \phi_n - \phi_b$

A damped harmonic oscillator model was fitted to the adjusted relative phase time series in a similar way to previous studies (Large et al. 2002; Palmer et al. 2014). Equation 3 shows the model, where n is the serial position following a perturbation and $\phi_a(n)$ is the adjusted relative phase at serial position n. The model contains five free parameters: A, oscillator amplitude; b, damping coefficient (inversely related to adaptation time); f, oscillation frequency; θ, phase; and c, intercept (related to relative phase after adaptation).

(3) $\phi_a(n) = Ae^{-bn}\cos(2\pi fn + \theta) + c$

The model was fitted to the adjusted relative phase time series using the Levenberg–Marquardt nonlinear least squares algorithm in R (R Core Team 2012) using the package minpack.lm (Elzhov et al. 2016), weighting the first four taps following each perturbation more heavily than the remaining eight taps and setting initial parameter values of $A = 0.08$ (matching the stimulus perturbation magnitude), $b = 1$, $f = 0.15$, and $\theta = 0$. Initial values of c were systematically varied between -0.1 and 0.1 to account for individual differences observed across Musicians and Nonmusicians in return to baseline synchronization following perturbations. Finally, b was constrained to be greater than 0, and f to be between 0 and 0.5.

The primary parameters of interest were the damping coefficient (b parameter), final adaptation achieved following perturbations (c parameter), and oscillation frequency (f parameter). Outlier parameter values for b, c, and f were defined as values more than four standard deviations from the mean parameter estimate and the model's goodness of fit was evaluated using Variance Accounted For (VAF). Only model fits for which the model converged, VAF values reached significance, and there were no outlier parameter values for the parameters of interest were included in analyses of parameter values (Musicians = 90.63% of fits; Nonmusicians = 69.27% of fits).

Fits of the damped harmonic oscillator model were compared with fits of an exponential decay model shown in Eq. 4, originally formulated to model temporal adaptation following removal of delayed auditory feedback, which reflects similar dampening but contains no periodic component (Pfordresher and Kulpa 2011).

$$(4)\ \phi_a(n) = (\phi_{initial} - \alpha) \times 2\left[1 - \frac{1}{1+\exp\,(-\beta n)}\right] + \alpha$$

In Eq. 4, n is the serial position following a perturbation and $\phi_a(n)$ is the adjusted relative phase at serial position n. The model contains two free parameters: α, asymptote (related to relative phase after adaptation, comparable to c in the damped harmonic oscillator model); and β, slope (related to adaptation time, comparable to b in the damped harmonic oscillator model). The model also contains one fixed variable, $\phi_{initial}$, which is the initial relative phase value following a perturbation (comparable to A in the damped harmonic oscillator model). Fits of this model were carried out as for the damped harmonic oscillator model. Initial values of α, like c of the damped harmonic oscillator model, were systematically varied between − 0.1 and 0.1 to account for individual differences observed across Musicians and Nonmusicians in return to baseline synchronization following perturbations. The initial value of β was set equal to 1. The parameter α was unconstrained, and the parameter β was constrained to be greater than 0.

The damped harmonic oscillator and exponential decay models were compared using the Akaike Information Criterion (AIC; Akaike 1973) to account for the difference in number of free parameters between models. Smaller values of AIC are considered better fits. VAF was used for across-group comparison of the damped harmonic oscillator model. Only model fits for which models converged and there were no outlier parameter values for parameters of interest (*b*, *c*, and *f* parameters for the damped harmonic oscillator model; α and β parameters for the exponential decay model) were included in model comparisons and across-group comparisons within model (damped harmonic oscillator model: Musicians = 92.71% of fits and Nonmusicians = 80.21% of fits; exponential decay model: Musicians = 99.48% of fits and Nonmusicians = 98.96% of fits). If the damped harmonic oscillator model performs better than the exponential decay model, this would suggest that the periodic component of the model, which is not present in the exponential decay model, may be needed to describe participants' adaptation to period perturbations.

4. Results

4.1 Spontaneous Production Rates

We first investigated the stability of SPRs within and across individuals with different musical backgrounds by comparing SPRs across Trials and Groups. Figure 2 shows the distribution of SPRs across all participants. There were large individual differences in SPRs, which ranged from 254 to 616 ms across participants. A mixed ANOVA on mean IOIs by Trial (1, 2, and 3) and Group (Musician and Nonmusician) showed a significant main effect of Trial, $F(2, 60) = 14.40$, $p < 0.001$. Post hoc comparisons revealed that participants' SPRs became slightly faster from Trial 1 (mean = 432 ms) to Trials 2 (mean = 418 ms) and 3 (mean = 405 ms; Holm-adjusted p's < 0.001; Holm 1979), and from Trial 2 to Trial 3 (Holm-adjusted $p < 0.05$). The main effect of Group was non-significant, $p = 0.27$, as was the interaction between Group and Trial, $p = 0.68$.

Insert Figure 2 Here

4.2 Synchronization-perturbation Performance

4.2.1 Baseline Synchronization Accuracy

We next investigated whether baseline synchronization accuracy, measured during the stable (no perturbation) portion of each trial, differed across Groups and Base rates by examining the last 12 taps in the baseline section of each trial. A mixed ANOVA on mean unadjusted relative phase values by Group and Base rate (SPR, 18% Slower, and 18% Faster) showed a significant main effect of Group, $F(1, 30) = 48.20$, $p < 0.001$. Nonmusicians anticipated the metronome more (mean = − 0.12 or 12% early) than Musicians (mean = − 0.04 or 4% early) in the absence of perturbations. The main effect of Base rate was non-significant, $p = 0.74$, as was the interaction between Group and Base rate, $p = 0.85$.

4.2.2 Adaptation to Rate Perturbations

We next investigated adaptation to period perturbations. A mixed ANOVA on mean adjusted relative phase values by Group, Base rate, Perturbation Direction (Away from and Return to Base rate), Perturbation Type (Slowing and Speeding), and Serial Position (1–12) indicated multiple significant main effects and interactions. We focus on the main effects and interactions relevant to the primary questions of Group and Base rate effects on temporal adaptation; all significant main effects and interactions can be found in Table 1. A significant main effect of Group, $F(1, 30) = 8.81$, $p < 0.01$ showed closer return to baseline synchronization for Musicians (mean = − 0.0006 or less than 1% early) than Nonmusicians (mean = 0.0371 or more than 3% late). Results also showed a significant main effect of Base rate, $F(2, 60) = 3.96$, $p < 0.05$, with closer return to baseline synchronization for the 18% Slower Base rate (mean = 0.008 or less than 1% late) than the SPR (mean = 0.019 or less than 2% late) and 18% Faster

Base rates (mean = 0.028 or more than 2% late), and closer return to baseline synchronization for the SPR Base rate than the 18% Faster Base rate (Holm-adjusted *p*'s < 0.001).

Insert Table 1 Here

The significant interaction among Base rate, Perturbation Type, and Serial Position, *F*(22, 660) = 2.25, $p < 0.01$, is shown in Fig. 3. Adaptation tended to take longer and participants tended to lag the metronome cue more at faster than at slower Base rates. In addition, Fig. 3 shows that taps following a Speeding period perturbation tended to initially lag the cue more, and taps following a Slowing period perturbation tended to initially lead the cue more. There was also a significant interaction among Group, Perturbation Type, and Serial Position, *F*(11, 330) = 7.32, $p < 0.001$, and among Group, Perturbation Direction, Perturbation Type, and Serial Position, *F*(11, 330) = 2.53, $p < 0.01$.

Insert Figure 3 Here

Figure 4 shows the interaction among Group, Perturbation Direction, Perturbation Type, and Serial Position. Four additional repeated measures ANOVAs were conducted that separated the data by Group and Perturbation Type to focus on effects of Perturbation Direction and Serial Position on temporal adaptation. As shown in Fig. 4, both Musicians and Nonmusicians tended to lag the cue more initially following Speeding perturbations and lead the cue more initially following Slowing perturbations. Musicians showed a significant interaction between Perturbation Direction and Serial Position for Speeding, *F*(11, 165) = 5.39, Bonferroni-adjusted

$p < 0.001$, and Slowing period perturbations, $F(11, 165) = 7.41$, Bonferroni-adjusted $p < 0.001$. Musicians tended to adapt faster to period perturbations when they returned to the Base rate. For Nonmusicians, the interactions between Perturbation Direction and Serial Position for Speeding, Bonferroni-adjusted $p = 0.29$, and Slowing period perturbations, Bonferroni-adjusted $p > 0.99$, were non-significant. There was no advantage of returning to the Base rate for Nonmusicians.

Insert Figure 4 Here

4.2.3 Model Comparisons

We compared fits of the simpler exponential decay model (Pfordresher and Kulpa 2011) with fits of the damped harmonic oscillator model (Large et al. 2002; Palmer et al. 2014). A Wilcoxon matched-pairs signed-ranks test showed that the damped harmonic oscillator model provided a better fit to the data (median AIC = − 80.74) than the exponential decay model (median AIC = −63.84; $Z = 4.93$, $p < 0.001$, one-tailed); all 32 participants demonstrated smaller AIC values for the damped harmonic oscillator model than for the exponential decay model.

4.2.4 Damped Harmonic Oscillator Model Fits

Next, we addressed the modulating influences of musical training on temporal adaptation, reflected in the complex interactions, with the damped harmonic oscillator model fits. First, we examined the overall fits of the damped harmonic oscillator model to adjusted relative phase values following period perturbations across groups (Large et al. 2002; Palmer et al. 2014). A Mann–Whitney test on mean VAF values showed that the damped harmonic oscillator model provided a better fit to Musician data (median VAF = 0.83) than to Nonmusician data (median VAF = 0.75; Mann–Whitney $U = 186$, $p < 0.05$, one-tailed).

Next, we examined parameter values resulting from fitting the damped harmonic oscillator model to each experimental condition per participant. Example *b* parameter estimates are shown for one condition in Fig. 5 for a Musician (top) and Nonmusician (bottom). Musicians had significantly larger *b* parameter estimates (median = 0.54) than Nonmusicians (median = 0.32), indicating faster adaptation to period perturbations (Mann–Whitney $U = 207$, $p < 0.01$, one-tailed). Example *c* parameter estimates are shown for one condition in Fig. 6 for a Musician (top) and Nonmusician (bottom). Musicians had significantly smaller *c* parameter estimates (median = 0.00) than Nonmusicians (median = 0.02), indicating closer return to baseline synchronization following period perturbations (Mann–Whitney $U = 186$, $p < 0.05$, one-tailed). Finally, example *f* parameter estimates are shown for one condition in Fig. 7 for a Musician (top) and Nonmusician (bottom). Musicians had significantly larger *f* parameter estimates (median = 0.13) than Nonmusicians (median = 0.10), perhaps indicating greater responsiveness to period perturbations (Mann–Whitney $U = 182$, $p < 0.05$, one-tailed). To confirm that results were not driven by larger removal of non-significant model fits for Nonmusicians than Musicians, we ran the same analyses including both significant and non-significant fits. Results were similar for *b* and *c* parameters; the *f* parameter was no longer significantly different across groups (median for both groups = 0.13, $p = 0.43$, one-tailed).

Insert Figure 5 Here

Insert Figure 6 Here

Insert Figure 7 Here

Finally, we tested whether *b*, *c*, and *f* parameter estimates were correlated. None of the correlations between mean values of *b*, *c*, and *f* reached significance between or within groups (range of *p* values = 0.19–0.61). Thus, these parameters appear to account for different aspects of individual variability.

Additional correlations were run between *b*, *c*, and *f* parameter estimates and individual difference variables for the musician group to further examine the relationship between temporal adaptation and musical experience. These variables included: years of private music instruction, number of hours per week spent training on the primary instrument, number of ensembles currently involved with, and the frequency of ensemble performance. Frequency of ensemble performance was coded on a scale from 0 to 5 (0 = never; 1 = less than once a month; 2 = once a month; 3 = once a week; 4 = twice a week; and 5 = more than twice a week). One participant was excluded from correlations with frequency of ensemble performance as they did not specify an answer. Only the correlation of musicians' *c* parameter estimates with the number of ensembles they were currently involved with approached significance ($r = -0.48$, uncorrected $p = 0.06$) prior to correction for number of tests (see Supplementary Table 1 for a summary of these results).

4.2.5 Maximal Rates

To confirm that effects did not reflect participants' biomechanical limits reached during the synchronization-perturbation task, we compared participants' maximal rates with their prescribed (metronome) synchronization rate in the fastest condition (8% Faster than 18% Faster

Base rate). Thirty-one of 32 participants showed faster maximal rates than the fastest prescribed synchronization rate. For the one exception (Nonmusician), we compared this participant's maximal rate with their mean tapping rate across the final 6 serial positions following all 8% Faster than 18% Faster Base rate perturbations (i.e., the fastest observed synchronization rate after adaptation). This participant's fastest observed synchronization rate was faster than their maximal rate (fastest observed synchronization rate = 233 ms; maximal rate = 242 ms), confirming that the participant could indeed tap faster than their measured maximal rate.

5. Discussion

The current study investigated influences of musical training on temporal adaptation of auditory-motor synchronization, implementing a perturbation paradigm. In contrast to previous studies (for reviews see Repp 2005; Repp and Su 2013), individual differences were taken into account by measuring participants' Spontaneous Production Rates and by subsequently tailoring the rates in the perturbation task to each individual's SPR. We examined musicians' and nonmusicians' temporal adaptation following unexpected period changes in the metronome. Findings indicated more rapid and accurate temporal adaptation for musicians than nonmusicians. Musicians also showed greater sensitivity for whether perturbations moved away from or toward the metronome base rate. Temporal adaptation did not show an effect of SPRs, but instead showed an effect of rate: adaptation was more effective at slower than faster base rates.

Musically trained participants showed greater synchronization accuracy than nonmusicians, consistent with previous findings (cf. Aschersleben 2002; Scheurich et al. 2018). The current study extends those findings to musicians' superior synchronization during both perturbed and unperturbed stimulus rates. The two participant groups did not differ in SPRs, and there was no advantage for synchronization accuracy when stimulus rates were set to participants' SPRs. It is possible that spontaneous production rates may represent an individual's optimal temporal range, rather than a single optimal rate. Had a wider range of stimulus rates been used, an advantage for synchronization accuracy at participants' SPRs might have been observed (Scheurich et al. 2018).

How quickly and closely participants returned to baseline synchronization following period perturbations were modulated by the base rate; participants tended to adapt more quickly and closer to baseline synchronization for slower base rates. Within a perturbation paradigm, slower rates may allow participants more time to respond to period perturbations, leading to greater adaptation (Peters 1989). Additionally, musicians but not nonmusicians tended to be more perturbed when period perturbations moved away from than when they returned to the base rate. Interestingly, we did not show an advantage of being perturbed toward the SPR. As previously discussed, a wider range of rates may have yielded an SPR advantage. Importantly, these findings were not a function of participants' biomechanical limits, confirmed with a condition in which participants were pushed to their maximal rates.

A damped harmonic oscillator model provided a better fit to relative phase measures than an exponential decay model that did not contain a periodic component (Pfordresher and Kulpa 2011). The greater number of parameters in the damped harmonic oscillator model did not account for the model's advantage. Fits to relative phase measures yielded larger damping coefficients for musicians than nonmusicians, suggesting that musicians adapted faster to period perturbations than nonmusicians as reported by Repp (2010). Additionally, musicians had smaller intercepts than nonmusicians, suggesting that musicians returned closer to baseline synchronization following period perturbations than nonmusicians. Finally, musicians had larger oscillation frequencies than nonmusicians. The more oscillatory behaviour of musicians may reflect greater responsiveness or sensitivity to period perturbations, as has been shown perceptually (Repp 2010). Future research could further investigate this finding with a wider range of period perturbations.

One limitation of the current study is that only a single isochronous version of a familiar melody was used. Future research could examine more rhythmically complex stimuli while also providing simple to complex auditory feedback. Although the melody was familiar to all participants, the rhythmic structure was adjusted to be isochronous so as to create an easier task for musically untrained participants to perform. Future work could extend this paradigm to examine adaptation to unfamiliar melodies. Additionally, some participants did not tap at their fastest possible rate in the maximal rate task; that is, their performance in the synchronization-perturbation task was faster than their maximal rate performance. Future research could measure maximal rates with isochronous finger tapping in the absence of melody feedback. Participants could also be given more practice with the task to improve maximal rate measures.

In sum, musical training influenced temporal adaptation to period perturbations under conditions in which individual differences in SPRs were taken into account. Musicians synchronized more accurately and adapted more quickly to period perturbations than nonmusicians. Musicians also appeared to be more responsive or sensitive to period perturbations than nonmusicians. These findings were further supported by damped harmonic oscillator model fits, which better accounted for temporal adaptation than an exponential decay model through parameters reflecting adaptation time, achieved adaptation, and oscillation frequency. Together, these findings suggest that musical training enhances temporal flexibility and adaptability critical for achieving successful auditory-motor coordination.

6. Acknowledgements

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7. Conflict of Interest

The authors declare that they have no conflict of interest.

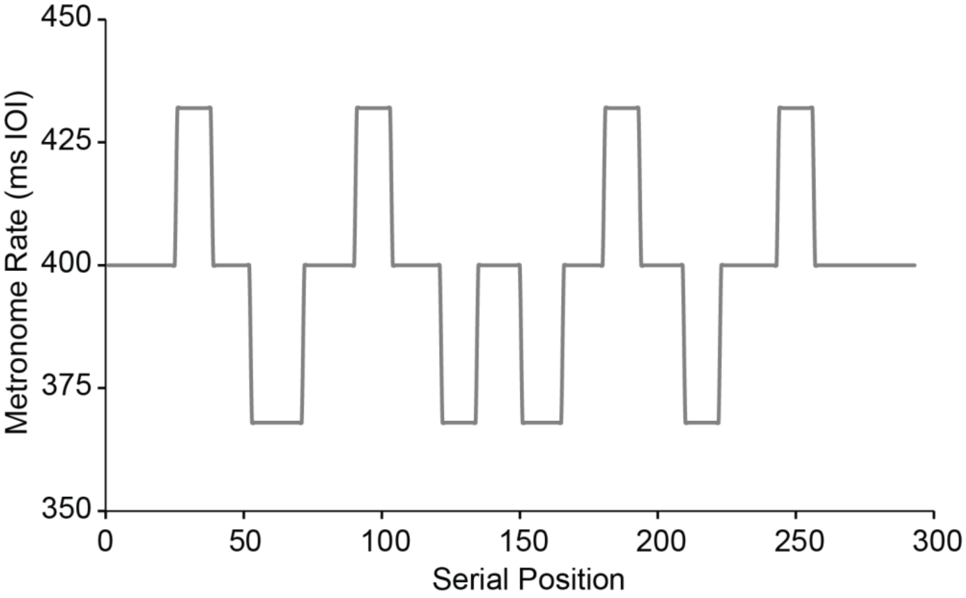


Figure 1. Sample experimental trial from the synchronization-perturbation task at a 400 ms IOI Base rate. The solid line shows changes in the metronome rate from the Base rate. In this sample trial, the baseline section occurs after the final return to Base rate for an additional 21 beats until the end of the trial.

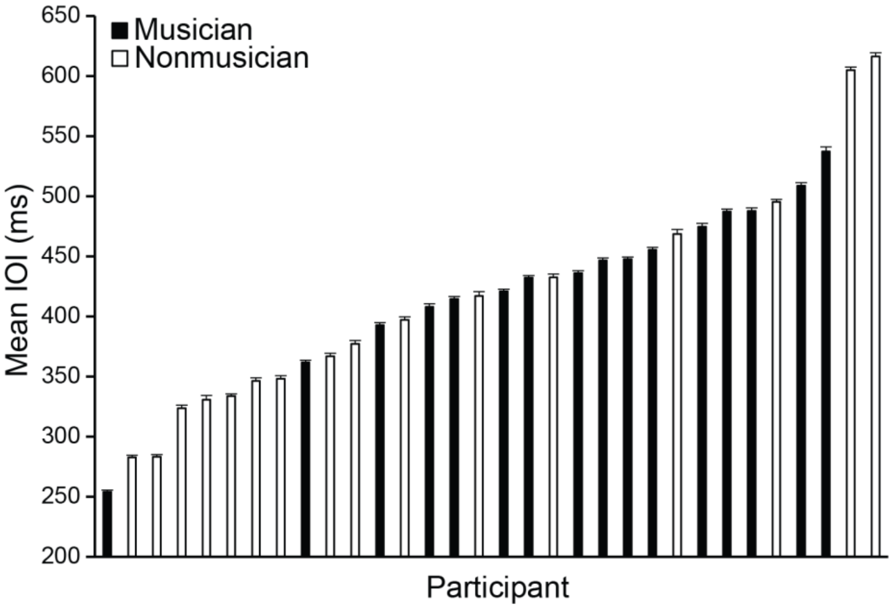


Figure 2. Distribution of mean IOIs from the Spontaneous Production Rate task across participants, ordered from fastest to slowest. Each bar represents a single participant; black bars represent Musicians and white bars represent Nonmusicians. Error bars represent standard error.

Table 1. Summary of significant main effects and interactions in the synchronization-perturbation task.

Main effect or interaction	***F* value**	***p* value**
Group	8.81	0.006
Base rate	3.96	0.024
Perturbation Type	45.79	< 0.001
Serial Position	3.95	< 0.001
Group X Serial Position	2.06	0.023
Base rate X Serial Position	1.97	0.005
Perturbation Type X Serial Position	81.27	< 0.001
Group X Perturbation Type X Serial Position	7.32	< 0.001
Base rate X Perturbation Type X Serial Position	2.25	0.001
Perturbation Direction X Perturbation Type X Serial Position	2.69	0.003
Group X Perturbation Direction X Perturbation Type X Serial Position	2.53	0.004

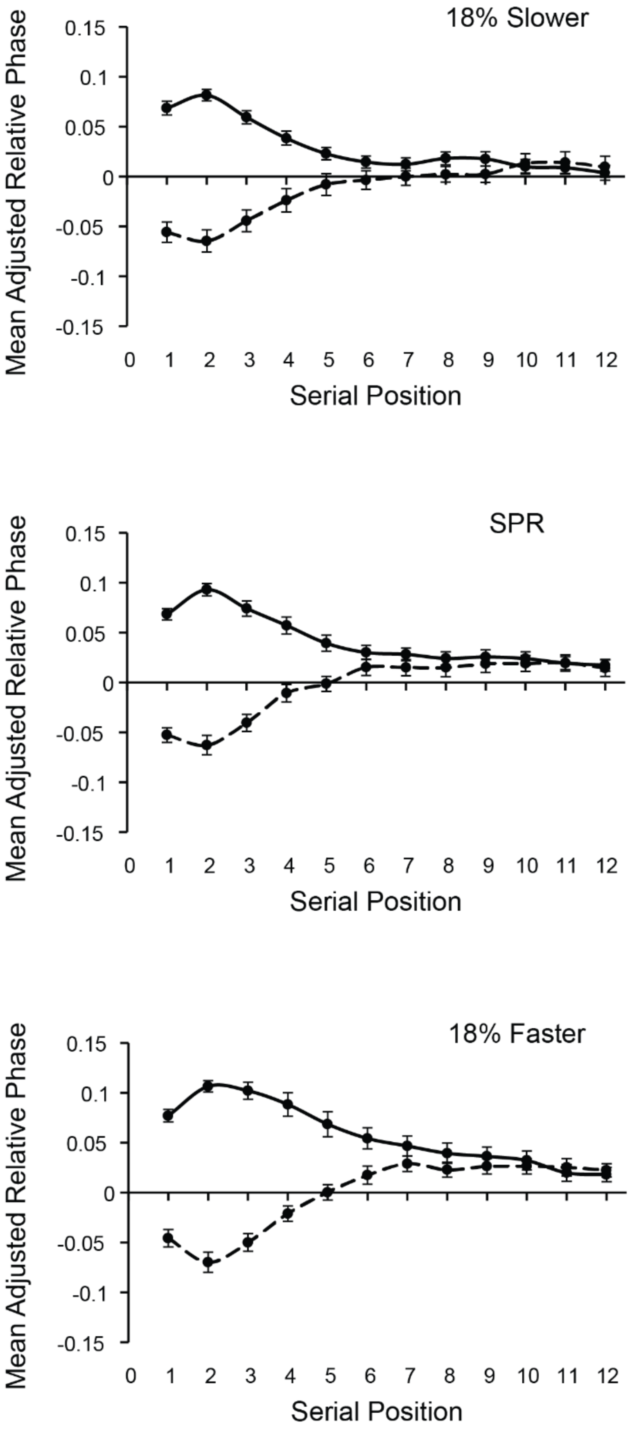


Figure 3. Mean relative phase by Base rate, Perturbation Type, and Serial Position following perturbations. Solid lines show responses to Speeding perturbations, and dashed lines show responses to Slowing perturbations. Error bars represent standard error.

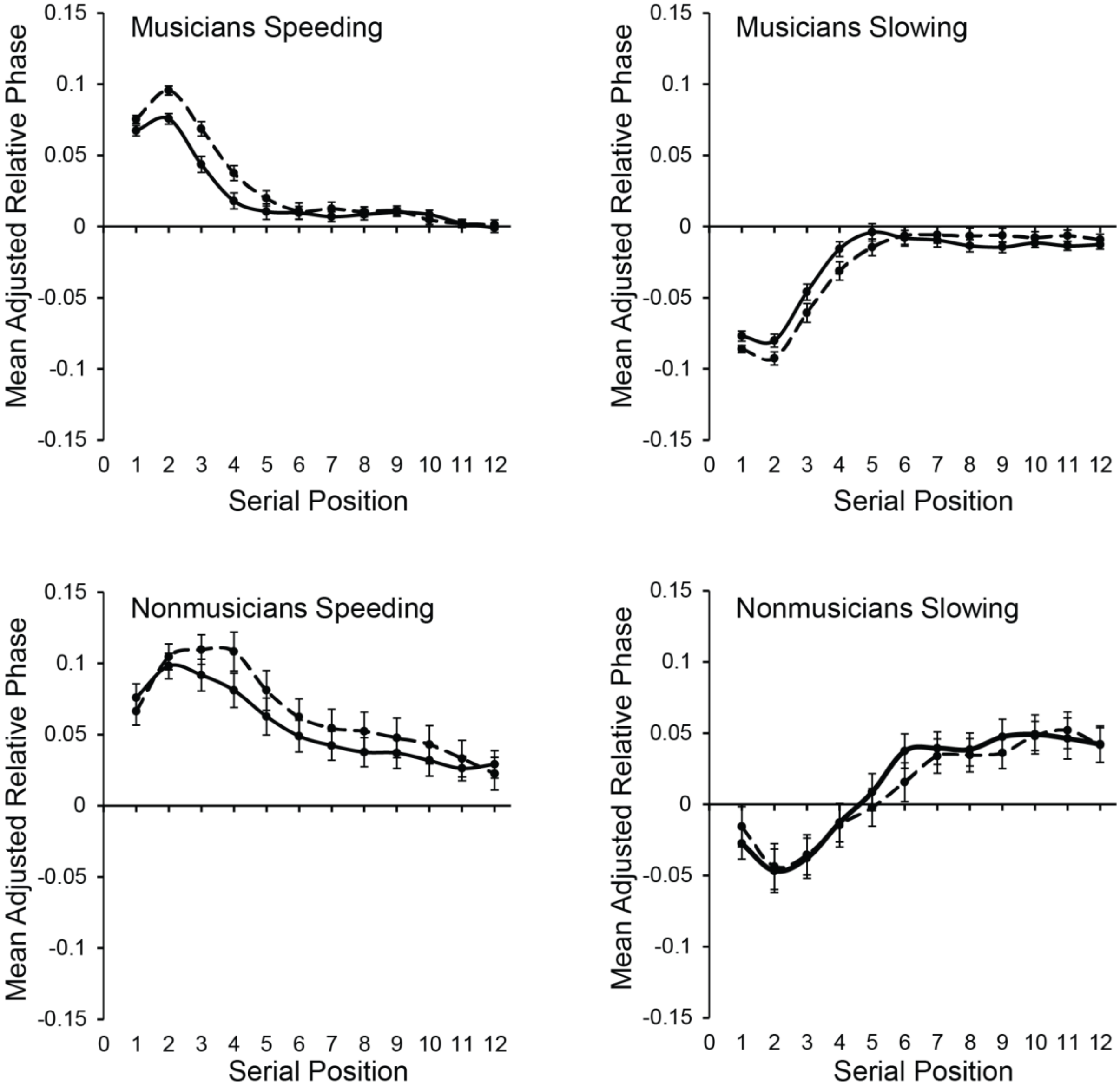


Figure 4. Mean adjusted relative phase following perturbations by Group and Perturbation Type. Solid lines show responses that return to the Base rate, and dashed lines show responses that move away from the Base rate. Error bars represent standard error.

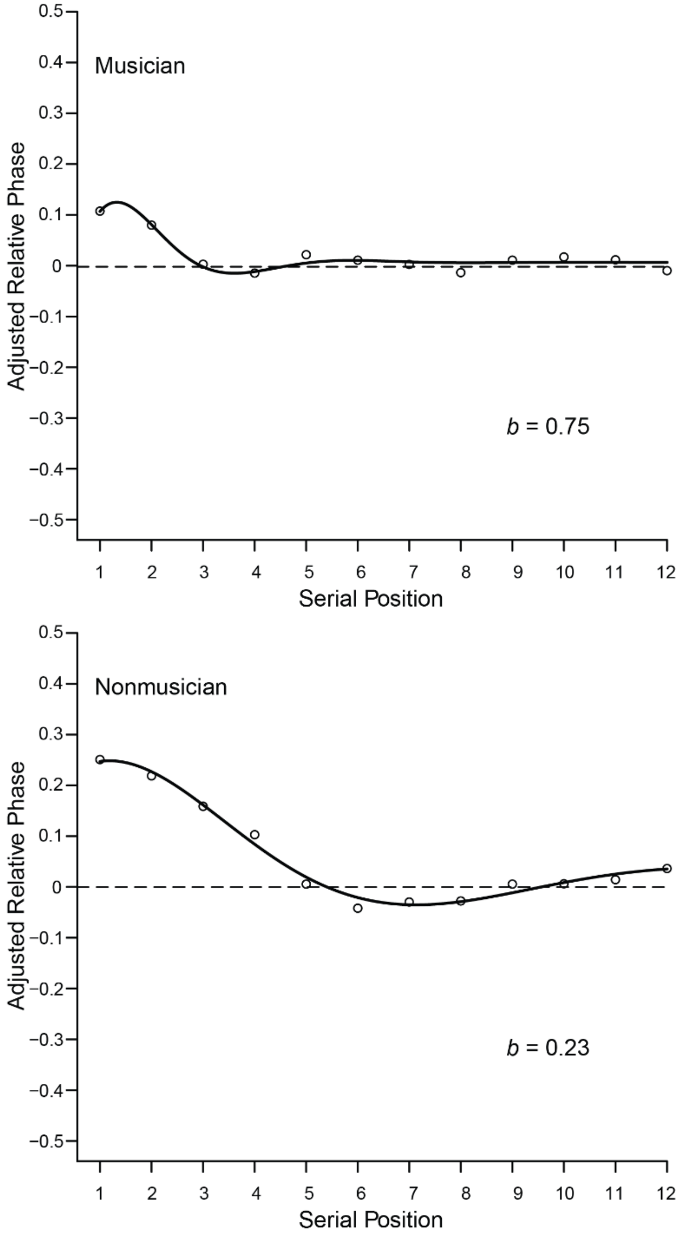


Figure 5. Example damped harmonic oscillator model fits to data demonstrating *b* parameter differences between Musicians and Nonmusicians. Black lines represent model fits and markers represent data. Top: Musician's performance in 18% Slower Base rate condition (Speeding, Return to Base rate), demonstrating high *b* (faster dampening; $c = 0.01$ and $f = 0.22$). Bottom: Nonmusician's performance in 18% Slower Base rate condition (Speeding, Return to Base rate) demonstrating low *b* (slower dampening; $c = 0.02$ and $f = 0.08$).

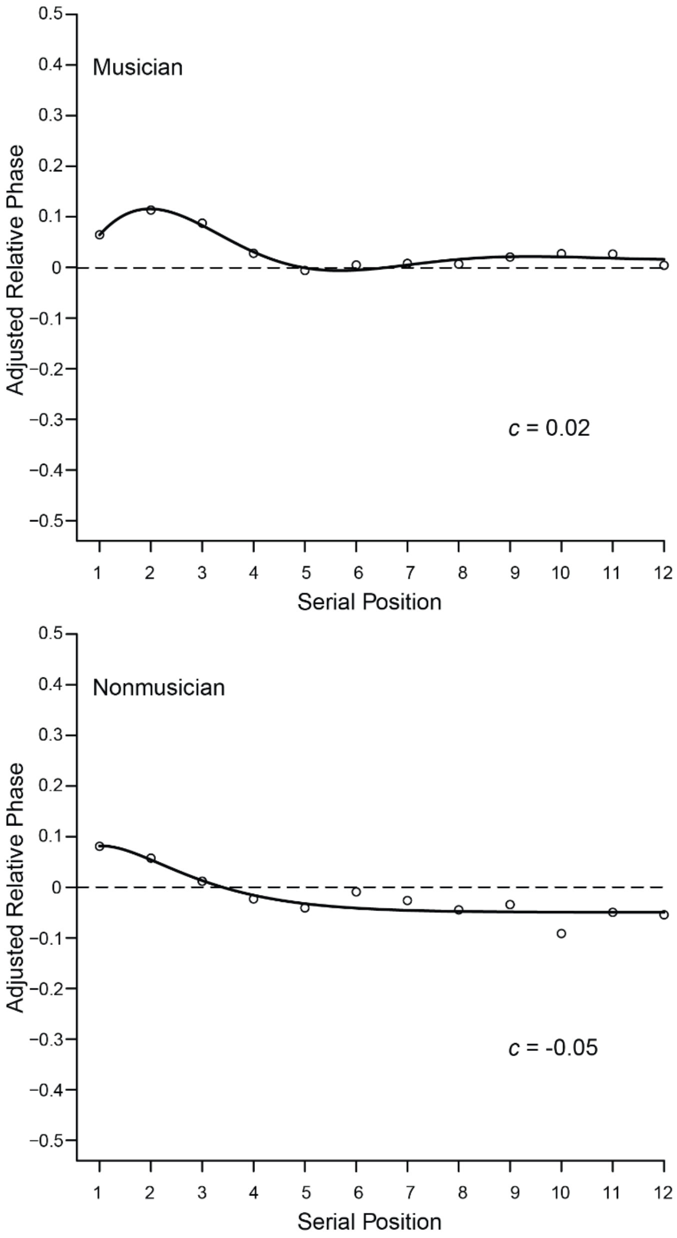


Figure 6. Example damped harmonic oscillator model fits to data demonstrating *c* parameter differences between Musicians and Nonmusicians. Black lines represent model fits and markers represent data. Top: Musician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate), demonstrating small *c* (intercept values near 0; *b* = 0.40 and *f* = 0.14). Bottom: Nonmusician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate) demonstrating large *c* (intercept values far from 0; *b* = 0.89 and *f* = 0.01).

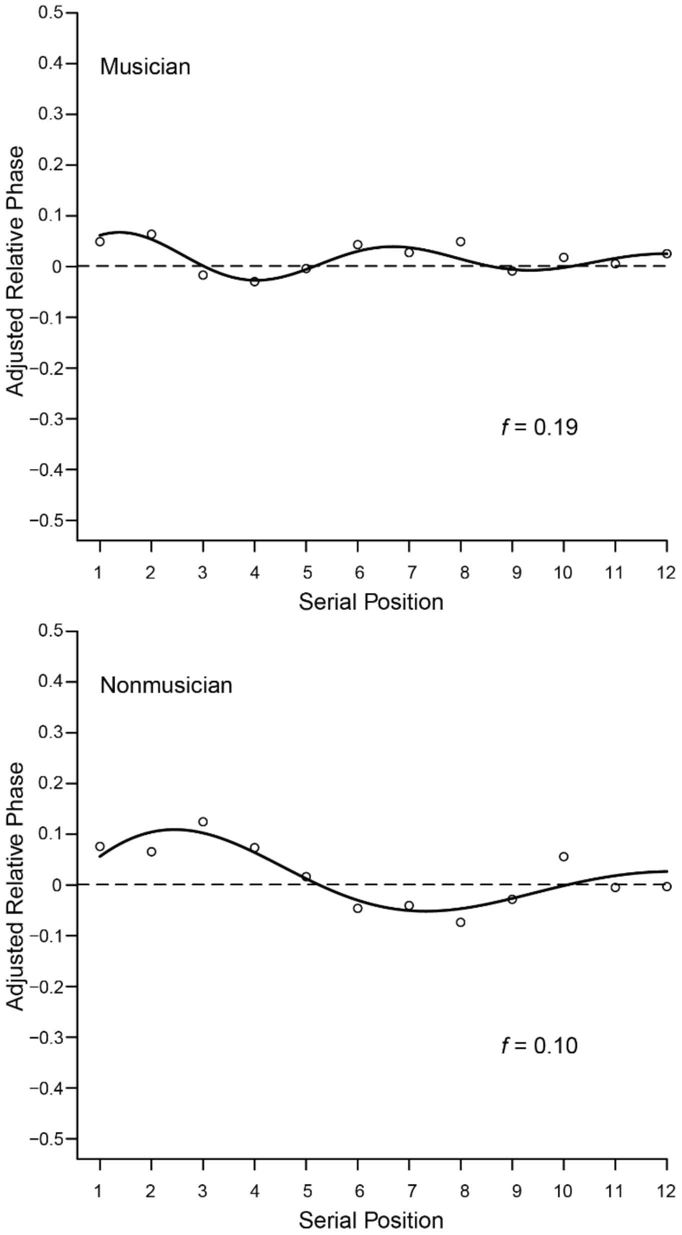


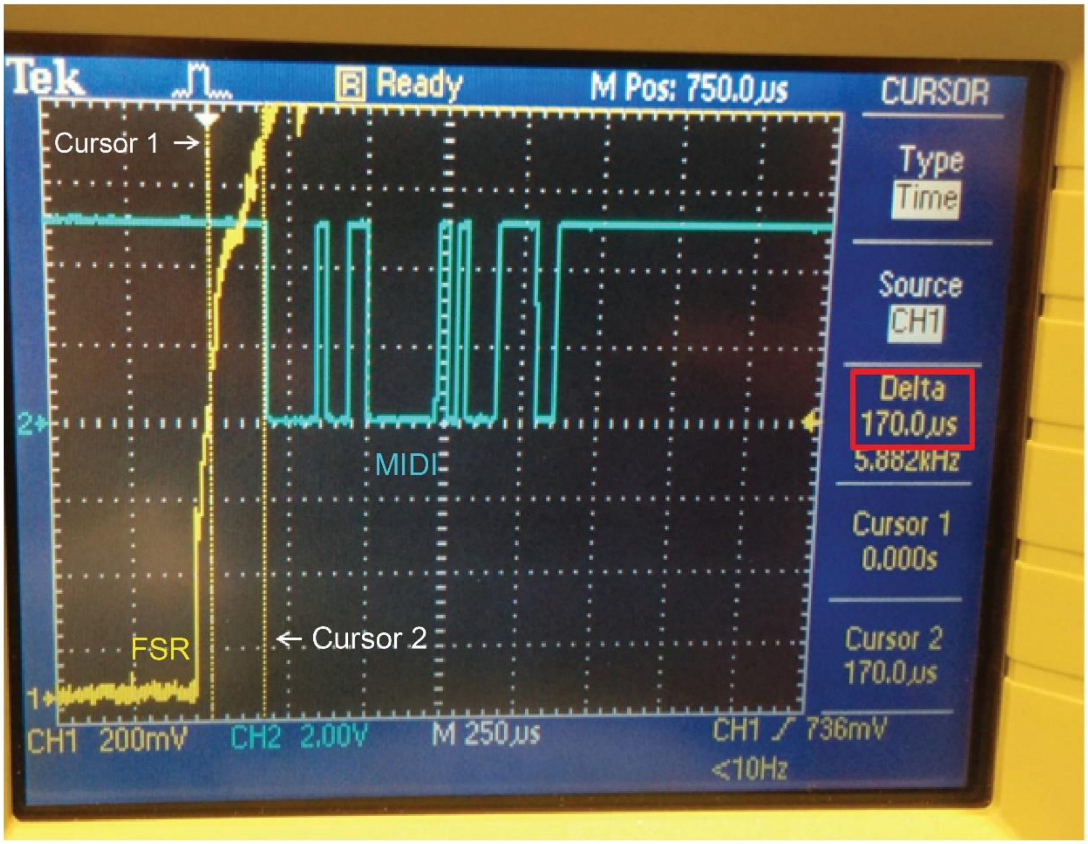
Figure 7. Example damped harmonic oscillator model fits to data demonstrating *f* parameter differences between Musicians and Nonmusicians. Black lines represent model fits and markers represent data. Top: Musician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate), demonstrating high *f* (faster oscillation frequency; *b* = 0.13 and *c* = 0.01). Bottom: Nonmusician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate), demonstrating low *f* (slower oscillation frequency; *b* = 0.15 and *c* = 0.001).

8. Supplementary Material

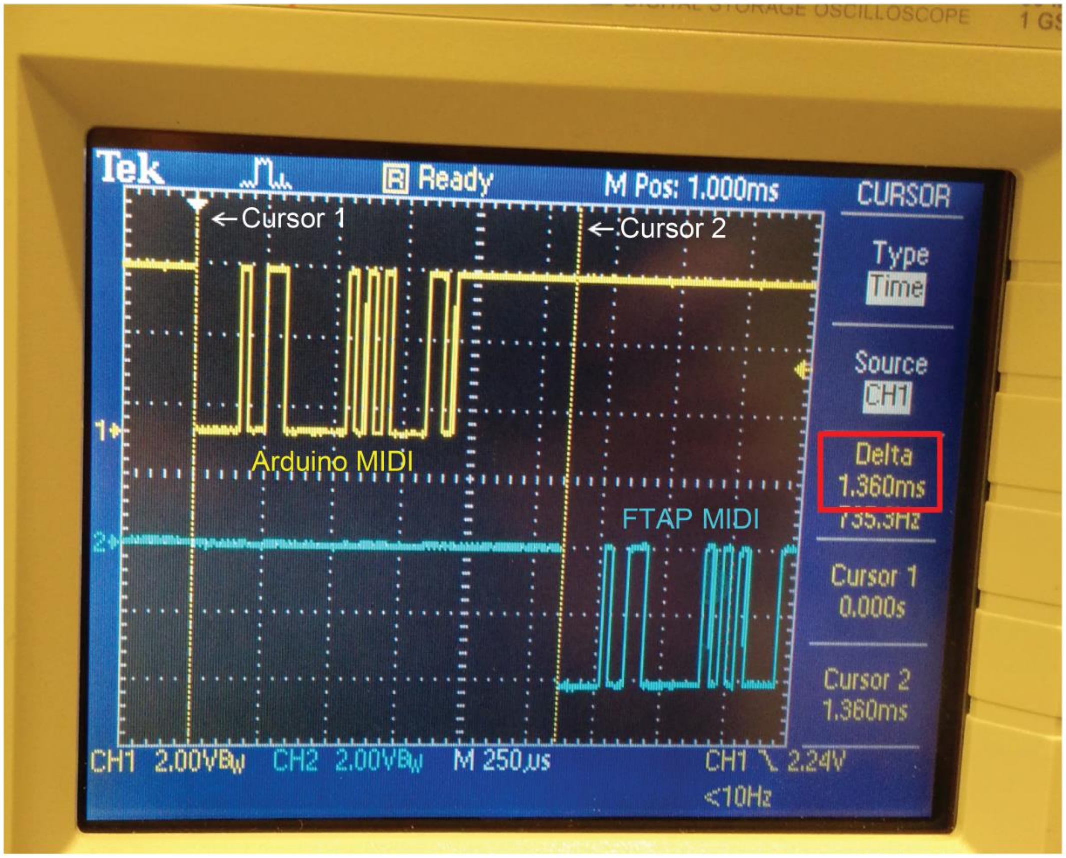
The time from when the tap reaches threshold (0.73 V) on the force sensitive resistor (FSR) to the start of the MIDI signal sent out from the Arduino was measured using a Tektronix TDS 2002 oscilloscope. Data from 100 taps confirmed that this duration was on average 174 microseconds (SD = 53 microseconds; see Supplementary Figure 1).

The time from the start of the MIDI signal sent out from the Arduino to the start of the MIDI signal sent out from FTAP via an M-Audio UNO MIDI-USB connector was also measured with a Tektronix TDS 2002 oscilloscope. Data from 100 taps confirmed that this duration was on average 1.40 milliseconds (SD = 0.15 milliseconds; see Supplementary Figure 2).

Supplementary Table 1 summarizes correlations of musical training measures (i.e., number of years of private music instruction, number of hours per week spent training on the primary instrument, number of ensembles currently performing with, and frequency of ensemble performance) with adaptation measures (i.e., damped harmonic oscillator model parameter estimates) for the musically trained participants. Frequency of ensemble performance was coded on a scale from 0 (do not perform in any ensembles) to 5 (perform in one or more ensembles more than twice per week). Shown in the table are the *r*-values for each correlation with the corresponding uncorrected *p*-values in parentheses.



Supplementary Figure 1. One sample trial measuring the time from when the tap reaches threshold on the FSR (yellow trace) to the start of the MIDI signal sent out from the Arduino (blue trace). Cursor 1 is aligned with the time at which the tap reaches threshold on the FSR, and cursor 2 is aligned with the time at which the MIDI signal begins. Delta (170 microseconds) calculates the difference between cursors 1 and 2.



Supplementary Figure 2. One sample trial measuring the time from the start of the MIDI signal sent out from the Arduino (yellow trace) to the start of the MIDI signal sent out from FTAP (blue trace). Cursor 1 is aligned with the time of the start of the MIDI signal sent out from the Arduino, and cursor 2 is aligned with the time of the start of the MIDI signal sent out from FTAP. Delta (1.36 milliseconds) calculates the difference between cursors 1 and 2.

Supplementary Table 1. Summary of Correlations Between Musical Training Measures and Damped Harmonic Oscillator Model Parameter Estimates for the SPR Baserate

	c Parameter Estimate	*b* Parameter Estimate	*f* Parameter Estimate
Years of Private Music Instruction	-0.25 (0.34)	-0.31 (0.24)	-0.34 (0.20)
Hours per Week Training on Primary Instrument	-0.31 (0.24)	-0.02 (0.93)	-0.05 (0.85)
Number of Ensembles Currently Involved With	-0.48 (0.06)	0.34 (0.20)	0.02 (0.95)
Frequency of Ensemble Performance	-0.23 (0.41)	0.40 (0.14)	0.16 (0.58)

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Chapter 4

Musical Training Enhances Rate Adaptation of Synchronization in Real Time

The study presented in Chapter 3 implemented a version of the tapping task validated in Chapter 2 to examine 1) whether musical training enhances adaptation to changing rates during synchronization and 2) the nonlinear mechanisms underlying enhancement of adaptation with musical training. Results showed that musicians adapted both more quickly and more efficiently to unexpected rate changes than nonmusicians, building on the findings from Chapter 2. Interestingly, results did not show that participants adapted less quickly or efficiently to rate changes that moved away from individuals' Spontaneous Production Rates, which would have suggested a constraint of SPRs on synchronization as in Chapter 2. Given the more limited range of rates in the study presented in Chapter 3, it is possible that participants were not pushed far enough away from their SPRs to see an effect. Results also showed that a nonlinear damped harmonic oscillator model better fit adaptation responses for both musicians and nonmusicians. Furthermore, musicians' enhanced adaptation was reflected by the *b* and *c* parameters of this model, showing faster adaptation time and closer return to baseline synchronization, respectively. These results give further evidence that musical training enhances the flexibility with which individuals coordinate their actions with sound.

With mounting behavioral evidence that musical training enhances rate flexibility of auditory-motor synchronization, the next study in this dissertation set out to validate a novel method for characterizing neural signatures of flexibility in musicians. The frequency-tagging approach commonly used to examine neural entrainment during auditory-motor tasks does not allow for the investigation of time-dependent characteristics of the neural signal which are critical to examining rate flexibility. Recurrence Quantification Analysis, on the other hand, allows for the investigation of these time-dependent characteristics and has been successfully used both in the second study presented in Chapter 2 and in previous research on postural sway (Schmit, Regis, & Riley, 2005; Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006) to examine behavioral flexibility. Therefore, the next study develops and validates a novel application of RQA for EEG data to characterize flexibility in the brain.

Capturing Intra- and Inter-Brain Dynamics with Recurrence Quantification Analysis

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Keywords: joint action, neural dynamics, electroencephalography, recurrence quantification analysis

Abstract

We investigated the application of non-linear analysis techniques for capturing stability of neural oscillatory activity within and across brains. Recurrence Quantification Analysis (RQA), a technique that has been applied to detect stability and flexibility of motor performance, was extended to observe and quantify changes in patterns of non-linear neural activity. Participants synchronized their finger-tapping with a confederate partner who tapped at two different rhythms while neural activity was recorded from both partners using electroencephalography (EEG). Auto-recurrence (intra-brain) and cross-recurrence (inter-brain) of EEG activity were able to distinguish differences across tapping rhythms in stability of neural oscillatory activity. We also demonstrated the efficacy of RQA to capture how both period and phase changes in neural dynamics evolve over time.

1. Introduction

Researchers have become increasingly interested in capturing complex oscillatory signals common to human behaviors, and which often show non-linearities that evolve over time. This can be seen in individual motor behaviors like postural sway and finger-tapping (Schmit, Regis & Riley, 2005; Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006; Scheurich, Zamm, & Palmer, 2018), and in joint motor behaviors like conversational speech and music performance (Dale & Spivey, 2006; Demos, Chaffin, & Kant, 2014). One way in which these complex signals can be represented is through Recurrence Plots (RPs), which display the points in time at which an individual returns to previous behavioral states (i.e., self-similarity), or the points in time at which two individuals visit the same behavioral state (i.e., similarity between individuals; Eckmann, Kamphorst, & Ruelle, 1987). RPs are useful tools for observing transitions between states in a system and can be further quantified using Recurrence Quantification Analysis (RQA). These quantifications give insights into the behavioral dynamics of one or more systems over time through measures such as recurrence rate: how often a system returns to previous states or two systems visit the same state; and mean diagonal line length: the time over which one or more systems are stable (Marwan, Romano, Thiel, & Kurths, 2007; Marwan & Webber, 2015). One advantage of RQA is that it can be applied both within individuals during solo tasks (i.e., auto-recurrence) and between individuals during joint tasks (i.e., cross-recurrence; Marwan, Romano, Thiel, & Kurths, 2007; Marwan & Webber, 2015). Thus, these tools have been useful for characterizing dynamics of motor behaviors over time both within and across individuals during a variety of solo and joint behaviors (e.g., Schmit, Regis, & Riley, 2005; Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006; Romero, Fitzpatrick, Schmidt, & Richardson, 2016; Demos & Chaffin, 2017; Scheurich, Zamm, & Palmer, 2018).

Complex oscillatory signals are not unique to behavior, but are also observed in human brain activity. This can be seen, for example, in the oscillatory neural activity that underlies rhythmic auditory-motor behaviors (e.g., Nozaradan, Zerouali, Peretz, & Mouraux, 2013; Nozaradan, 2014; Morillon & Baillet, 2017; Zamm, Debener, Bauer, Bleichner, Demos, & Palmer, 2018). However, common methods for examining oscillatory neural activity supporting these kinds of behaviors often do not measure dynamics over time, but instead assume stationarity of the signal. RQA has been applied to oscillatory neural activity, as measured through electroencephalography (EEG), in a limited scope. This has been primarily in clinical settings, in which outcomes such as recurrence rate and mean diagonal line length, which provide information about the stability of neural activity, have been used successfully to classify periods of epileptics' EEG activity as normal, pre-ictal, and ictal activity (Acharya, Sree, Chattopadhyay, Yu, & Ang, 2011). Furthermore, RQA outcomes have been applied for monitoring consciousness of patients undergoing anesthesia (Becker, Schneider, Eder, Ranft, Kochs, Zieglgänsberger, & Dodt, 2010). In addition to its clinical applications, researchers have proposed RQA as a method for studying event-related potentials (ERPs). Although traditional methods of studying ERPs require averaging over many trials to obtain a clear waveform, RQA allows for the use of single trials to identify changes in ERP components, as demonstrated in an auditory perception experiment using the auditory oddball paradigm (Marwan & Meinke, 2004). No research, to our knowledge, has yet applied RQA to capture oscillatory neural activity that distinguishes different rhythmic auditory-motor behaviors.

The current study applies RQA to capture the dynamics of oscillatory neural activity during a 2-person rhythmic tapping task. Participants tapped at two different rhythms with a confederate partner while EEG was recorded from each partner. In one rhythm condition, the confederate tapped at twice the frequency of the participant. In the second rhythm condition, the confederate tapped at half the frequency of the participant. The neural activity at the participant's (constant) tapping frequency was compared across rhythm conditions. Only activity at the constant frequency was examined to identify changes in oscillatory neural activity related to changes in tapping ratios between partners as opposed to changes in absolute frequency. Auto- (intra-brain) and cross-recurrence (inter-brain) analyses of EEG activity were expected to reveal greater stability of oscillatory neural activity when the participants' tapping frequency was the dominant frequency (i.e., more auditory feedback at that frequency).

2. Methods

2.1 Participants

Data from eight adult musicians aged 18-30 years old with at least 6 years of private music instruction on an instrument other than percussion were taken from a larger study. Their duet tapping trials met a performance cut-off of at least 75% error-free trials (i.e., no missed taps) for each condition in which partners performed live together. Other conditions included in the larger study in which participants performed with pre-recordings of their partner were not examined in the current paper. A single confederate experimenter (more than 6 years of piano instruction) tapped with each participant to maintain consistent timing properties of live and pre-recorded conditions as well as social presence across participants. All participants and the confederate were right-handed and had normal hearing (< 30 dB HL threshold, 125 – 750 Hz) as determined by an audiometry screening. Participants and the confederate reported no current psychiatric or neurological conditions and were not taking medication affecting the central nervous system at the time of testing.

2.2 Equipment and Materials

Participants' hearing was assessed with a Maico MA40 audiometer. Participants tapped on a Roland A500s MIDI keyboard and the confederate tapped on a Yamaha PSR 500m MIDI keyboard. Auditory feedback was delivered in a sine tone timbre generated by a Roland Sound Canvas, amplified to a comfortable listening level using a Behringer Headphone Amplifier, through EEG-compatible earphones (Etymotic ER-1, Etymotic Research Inc.). Participants' auditory feedback was presented at pitch G4 (392.00 Hz), and the confederate's auditory feedback at pitch E5 (659.25 Hz). MIDI data were collected using FTAP software (Finney, 2001). FTAP was modified to integrate Lab Streaming Layer (LSL; Kothe, 2014) similar to Zamm, Palmer, Bauer, Bleichner, Demos, & Debener, 2017. This modification allowed for keystroke, metronome, and time triggers from FTAP on a Dell computer running Linux to be sent over the local area network and received by a second Dell computer running Windows 7, where LSL synchronized the keystroke and EEG data collection from both partners (Zamm et al., 2017).

2.3 EEG Data Recording

EEG data were recorded from each partner at a 512 Hz sampling rate via two separate but synchronized 64-channel BioSemi Active-Two systems (BioSemi, Inc.). Electrodes were positioned according to the 10-20 system. Data were recorded using a common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode which formed the reference (http://www.biosemi.com/faq/cms&drl.htm). External electrodes were placed above and below the right eye to detect eyeblinks, on the outer corner of each eye to detect lateral eye movements, and on the mastoids to detect muscle artefacts.

2.4 Stimulus Materials and Design

Each stimulus was constructed of an approximately 40-second series of taps generated by the Participant and Confederate. Each pair (Participant and Confederate) completed the joint tapping tasks in a within-subjects design with 2 rhythm conditions: 1-2 (Confederate-Participant) and 4-2 (Confederate-Participant). In the 1-2 condition, the confederate tapped at half the rate (~0.95 Hz) of the Participant (~1.89 Hz). In the 4-2 condition, the Confederate tapped at twice the rate (~3.78 Hz) of the Participant (~1.89 Hz). Thus, the Participants' tapping frequency was constant across conditions. Each pair completed one practice trial and 12 experimental trials in each rhythm condition. Rhythm was blocked within pair, and blocks were counterbalanced across pairs. The dependent variables were auto- (intra-brain) and cross-recurrence (inter-brain) outcomes of Recurrence Rate, describing how much of the RP is occupied by recurrent points (how often a single system returns to previous states in auto-recurrence, or two systems visit similar states in cross-recurrence), and Meanline, describing the average diagonal line length (the mathematical stability of the system(s); see **RQA Application to EEG**).

2.5 Procedure

After giving informed consent upon arrival to the lab, participants completed an audiometry screening. Then both the participant and the confederate were outfitted with EEG caps and electrodes. The participant and confederate were taken to the testing room where the confederate was introduced to participants as an experimenter who served as the partner in each pair to maintain consistency of interactions across pairs. The participant and the confederate were seated at two separate keyboards across from one another with a barrier placed between the keyboards such that the partners could only see one another above the shoulder.

The participant and confederate then completed the two tapping tasks together at the two different rhythmic ratios. They were instructed to tap with the index finger of their right hands on a single key of the keyboard while minimizing eyeblinks and eye movements. The participant and confederate were first presented with separate recorded examples of each tapping part in isolation, and then they were presented with a recorded example of how the two parts sounded together. After listening to the examples, the participant and confederate were instructed that they would hear a four-beat metronome cue sounded at the participant's prescribed rate at the beginning of each trial, and they were presented with a recorded example of how their parts sounded together with the metronome cue. The participants were instructed that they should synchronize with the confederate's tapping while maintaining the rate cued by the metronome, and the confederate was instructed to maintain a steady pulse. After completing a practice trial, pairs completed 12 experimental trials. This procedure was repeated for each rhythm condition. After completion of the tasks, participants were debriefed and received a small compensation. The whole experiment lasted approximately three hours.

2.6 EEG Preprocessing

EEG data were preprocessed in EEGLAB (Delorme & Makeig, 2004). Data were first prepared for artefact correction with Independent Component Analysis (ICA), using a procedure adapted from Zamm et al. (2017). Data were concatenated across all trials in all experimental tapping tasks, and re-referenced to the common average across electrodes. Electrodes reflecting poor signal quality were identified by visually inspecting electrode distributions of deviations from mean activity for each subject. Electrodes with very large deviations from mean activity were identified as noisy, and electrodes with no deviation from mean activity were identified as flat. These electrodes were removed, and data were subsequently filtered between 1 Hz and 40 Hz using a Hanning windowed sinc FIR filter (high and low pass filter order = 1000). Filtered data were then segmented into 1-second epochs, pruned for non-stereotypical artefacts, and submitted to extended infomax ICA. ICA components representing eyeblinks and lateral eye movements were visually identified and removed from the unfiltered data. After removing bad components, previously rejected electrodes with poor signal quality were spherically interpolated.

2.7 RQA Application to EEG

Power Spectral Density (PSD) estimates of ICA-corrected EEG activity were then computed similar to Zamm et al. (2017). PSD gives the amount of power present in the EEG signal at component frequencies. Preprocessed EEG data were high then low pass filtered using a Hanning windowed sinc FIR filter (high pass filter order = 1000, cutoff = 0.1 Hz; low pass filter order = 1000, cutoff = 20 Hz) and segmented into 3 10.56-second epochs (to control for tapping frequency drift). PSD was estimated for each electrode and epoch, and then was log-transformed before averaging across epochs and then trials. The electrode with maximal power on average across conditions, tapping frequencies, and participants was identified as electrode C1 (central and left-lateralized). This electrode is commonly identified as showing maximal activity in auditory-motor behaviors (e.g., Nozaradan, Zerouali, Peretz, & Mouraux, 2013; Nozaradan, 2014). Data from this electrode were used as input to auto- and cross-recurrence analyses.

ICA-corrected data from electrode C1 for participants and the confederate were then prepared for auto- and cross-recurrence analyses. First, the data were filtered at the participants' observed tapping frequencies. The filter frequency cutoffs were tailored per participant and confederate pair and rhythm condition to account for any deviations in expected tapping frequency. The data were high then low pass filtered using a Hanning windowed sinc FIR filter (high and low pass filter orders = 1000) with cutoff frequencies ± 2 standard deviations around the observed participant tapping frequency. Data were then segmented into 3 10.56-second epochs (for computational tractability) and z-scored per epoch.

Auto- and cross-recurrence analyses were run using the Cross Recurrence Plot Toolbox (Marwan, Romano, Thiel, & Kurths, 2007). Optimal auto- and cross-recurrence parameters were determined per epoch; final selected parameters were determined by examining the distribution of parameters across epochs. The optimal delay parameter was determined by computing Average Mutual Information (AMI). AMI gives the amount of information a time series shares with itself at different time delays, with the delays at which it shares least information with itself being optimal for RQA. The first delay at which shared information of the C1 time series with itself reached a minima was selected (selected delay = 68 samples, corresponding to 1/4 cycle of the participant tapping frequency). The optimal number of embedding dimensions was determined by computing False Nearest Neighbors (FNN). FNN gives the amount of false neighbors in phase space as a function of the number of embedding dimensions (copies of the time series at the specified delay). The number of embedding dimensions at which number of false nearest neighbors was minimized and adding more dimensions no longer reduced number of false nearest neighbors was selected (selected embedding dimensions = 4). Finally, the maximum phase space diameter, corresponding to the standard deviation of the time series, was computed using the selected delay and embedding dimensions. The optimal threshold for which points in phase space are considered recurrent was determined by computing 10% of this value (selected threshold = 0.49; Schinkel, Dimigen, & Marwan, 2008). For auto-recurrence, the Thieler window, minimum diagonal line length, and minimum vertical line length were set to 34 samples (corresponding to 1/8 cycle of the participant tapping frequency). For cross-recurrence, the Thieler window was set to 0 samples and the minimum diagonal and vertical line lengths were set to 34 samples.

3. Results

3.1 Auto-recurrence Outcomes

We first investigated how auto-recurrence (intra-brain) outcomes changed with Rhythm, and whether these patterns held or changed across Partners within each pair. Separate two-way ANOVAs were run on Recurrence Rate and Meanline with Rhythm (1-2 and 4-2) and Partner (Participant and Confederate) as factors and pair as random variable. Results are summarized in Table 1 and sample RPs are shown in Figure 1. There was a significant main effect of Rhythm on Recurrence Rate: Recurrence Rate was higher for the 1-2 Rhythm (in which the participant tapped at twice the rate of the confederate) than for the 4-2 Rhythm. There was no significant main effect of Partner, $F(1, 7) = 0.012$, $p = 0.92$, or significant interaction between Rhythm and Partner, $F(1,7) = 0.415$, $p = 0.54$, on Recurrence Rate. There was also a significant main effect of Rhythm on Meanline: Meanline was higher for the 1-2 Rhythm than for the 4-2 Rhythm. Again, there was no significant main effect of Partner, $F(1,7) = 0.017$, $p = 0.90$, or significant interaction between Rhythm and Partner, $F(1, 7) = 0.582$, $p = 0.47$, on Meanline. These effects were replicated with mixed models in which random effects of Partner and Rhythm were allowed to vary as a function of the pair.

Insert Figure 1 Here

Insert Table 1 Here

To ensure that the main effect of Rhythm on Meanline was not a function of differences in Recurrence Rate across Rhythms, we also examined the outcome of Meanline when Recurrence Rate was fixed to 10% across Rhythms during the process of computing the RQA. A two-way ANOVA was run on Meanline with Rhythm and Partner as factors and pair as random variable. The main effect of Meanline held when Recurrence Rate was fixed across Rhythms, $F(1, 7) = 17.577$, $p = 0.004$. Meanline was higher for the 1-2 Rhythm than for the 4-2 Rhythm. There was no significant main effect of Partner, $F(1, 7) = 0.001$, $p = 0.97$, or significant interaction between Rhythm and Partner, $F(1, 7) = 0.579$, $p = 0.47$.

Figure 1 shows RPs for an example epoch from one participant for each Rhythm. As can be seen in these examples, there are more recurrent points and longer diagonal lines in the 1-2 RP (when the participant's tapping frequency is the dominant performance frequency) than the 4-2 RP. The white space between the diagonal lines on each plot corresponds approximately to the participant tapping frequency (1.89 Hz or approximately 271 samples).

3.2 Cross-recurrence Outcomes

Separate one-way ANOVAs were conducted on the same outcome measures (Recurrence Rate and Meanline) from cross-recurrence quantification analysis with Rhythm as factor and pair as random variable. Results are summarized in Table 2 and sample RPs are shown in Figure 2. There was a significant main effect of Rhythm on Recurrence Rate: Recurrence Rate was higher for the 1-2 Rhythm than for the 4-2 Rhythm. There was also a significant main effect of Rhythm on Meanline: Meanline was higher for the 1-2 Rhythm than for the 4-2 Rhythm. These effects were replicated with mixed models in which random effects of Rhythm were allowed to vary as a function of the pair.

Insert Figure 2 Here

Insert Table 2 Here

To again ensure that the main effect of Rhythm on Meanline was not a function of differences in Recurrence Rate across Rhythms, we also examined the outcome of Meanline when Recurrence Rate was fixed to 10% across Rhythms during the process of computing the RQA. A one-way ANOVA was run on Meanline with Rhythm as factor and pair as random variable. The main effect of Meanline held when Recurrence Rate was fixed across Rhythms, $F(1, 7) = 14.264$, $p = 0.007$. Again, Meanline was higher for the 1-2 Rhythm than for the 4-2 Rhythm.

Figure 2 shows example cross-recurrence plots (CRPs) for a single epoch from one pair for Rhythms 1-2 and 4-2 for the same trials shown in Figure 1. As can be seen in these examples, the 1-2 CRP is more densely occupied by recurrent points than the 4-2 CRP; these points also form longer diagonal lines than those in the 4-2 CRP. This indicates that the two signals overlap more often and for longer periods in phase space during the 1-2 Rhythm than the 4-2 Rhythm, indicating greater inter-brain stability. Furthermore, the white space between diagonal lines indicates the period at which the two neural signals recur with one another, and this period corresponds approximately to the participant tapping frequency (1.89 Hz or approximately 271 samples). Phase shifts between the two signals over time can also be observed by the degree of curvature in the diagonal lines in each CRP.

4. Discussion

The current experiment examined the application of RQA to neurophysiological data collected during a rhythmic tapping task between partners. Both auto- and cross-recurrence measures were sensitive to changes in stability of neural oscillations across tasks. Stability of neural oscillations at the participant tapping frequency was greater both within and across brains, as shown by larger recurrence rate and meanline outcomes from auto- and cross-recurrence, respectively, when there was more auditory feedback for both partners at the participants' tapping frequency.

We showed intra- and inter-brain recurrence that corresponded approximately to the participant tapping frequency. We also showed phase shifts in time as observed by the degree of curvature of the diagonal lines. Future work can further examine the time delay in recurrent points between two signals using quantifications such as the diagonal recurrence profile (e.g., Richardson & Dale, 2005; Dale, Kirkham, & Richardson, 2011), and subsequently relate this to behavioral performance. In contrast to other inter-brain metrics such as phase coherence, one advantage of cross-recurrence is the ability to show and subsequently quantify inter-brain dynamics when neural signals occupy the same phase space.

One limitation of the current experiment is that we only examined neural activity filtered at the participant tapping frequency. Future work can extend this technique to look at other stimulus frequencies to further examine the time evolution of neural dynamics in a joint motor task. We were also limited in our analyses by a small sample size. With more pairs, it could be possible to apply more sophisticated analysis methods to RQA outcomes such as an Actor-

Partner Interdependence Model to examine how partners influence one another (Kenny, Kashy, & Cook, 2006). We also used PSD estimates for selecting a single electrode whose data were used for auto- and cross-recurrence analyses. Future work can also extend this technique to identify regions of interest (i.e., multiple EEG electrodes) on which Multidimensional Recurrence Quantification Analysis (MdRQA) could potentially be applied (Wallot, Roepstorff, & Mønster, 2016).

In sum, recurrence quantification techniques were sensitive to changes in the dynamics of oscillatory neural activity that occurred during a joint rhythmic task. This is the first demonstration, to our knowledge, of RQA techniques to show consistent intra- and inter-brain differences in a joint auditory-motor task. These findings suggest that the sensitivity of RQA to stability of oscillatory neural activity might lend the technique to more fine-grained characterization of non-linearities in neural dynamics in a variety of behaviors and participant populations.

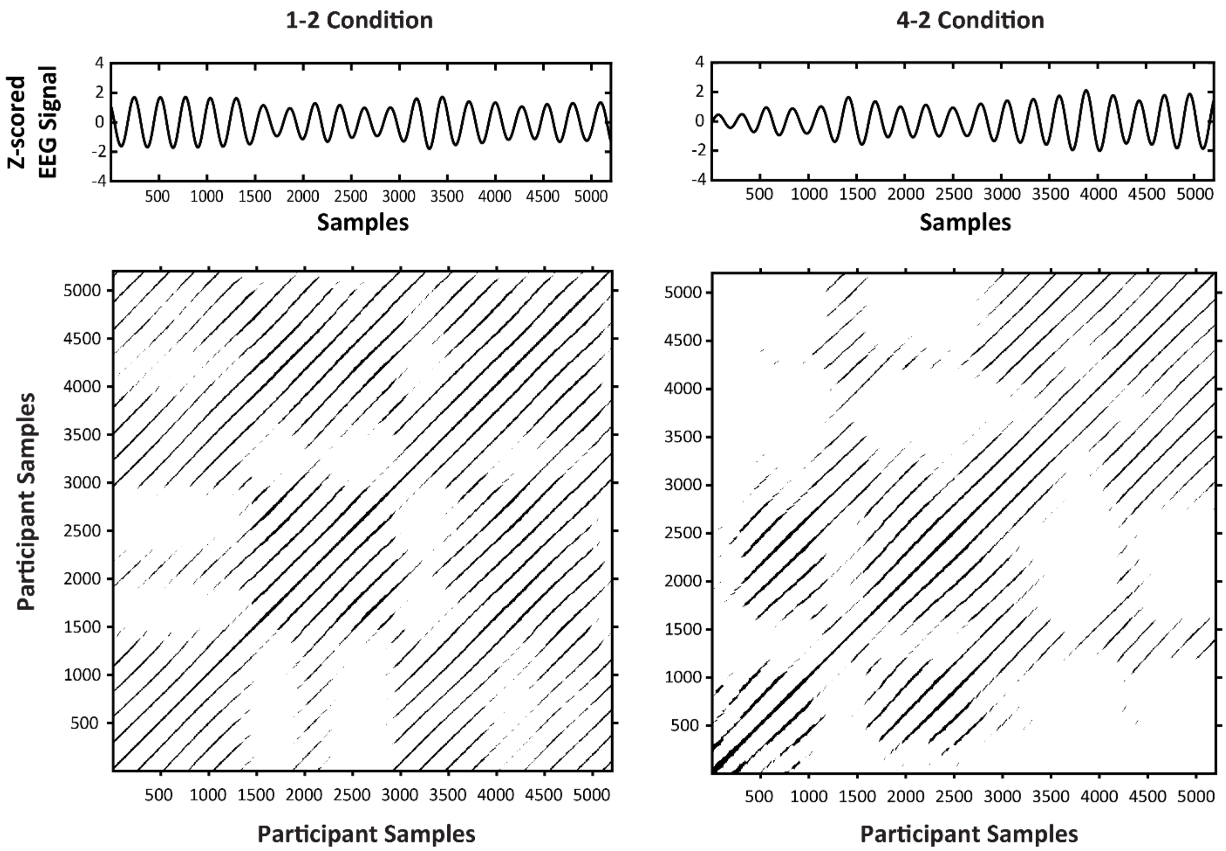

Figure 1. Time series and RPs with samples as a unit of time for one epoch from one participant for Rhythms 1-2 and 4-2. The time series shows the z-scored preprocessed signal from electrode C1.

Table 1. Auto-recurrence main effects of Rhythm.

Outcome	1-2	4-2	*F*	η^2	*p*
Recurrence Rate	3.06%	2.59%	23.03	0.79	0.002
Meanline	136.26	126.44	20.32	0.77	0.003

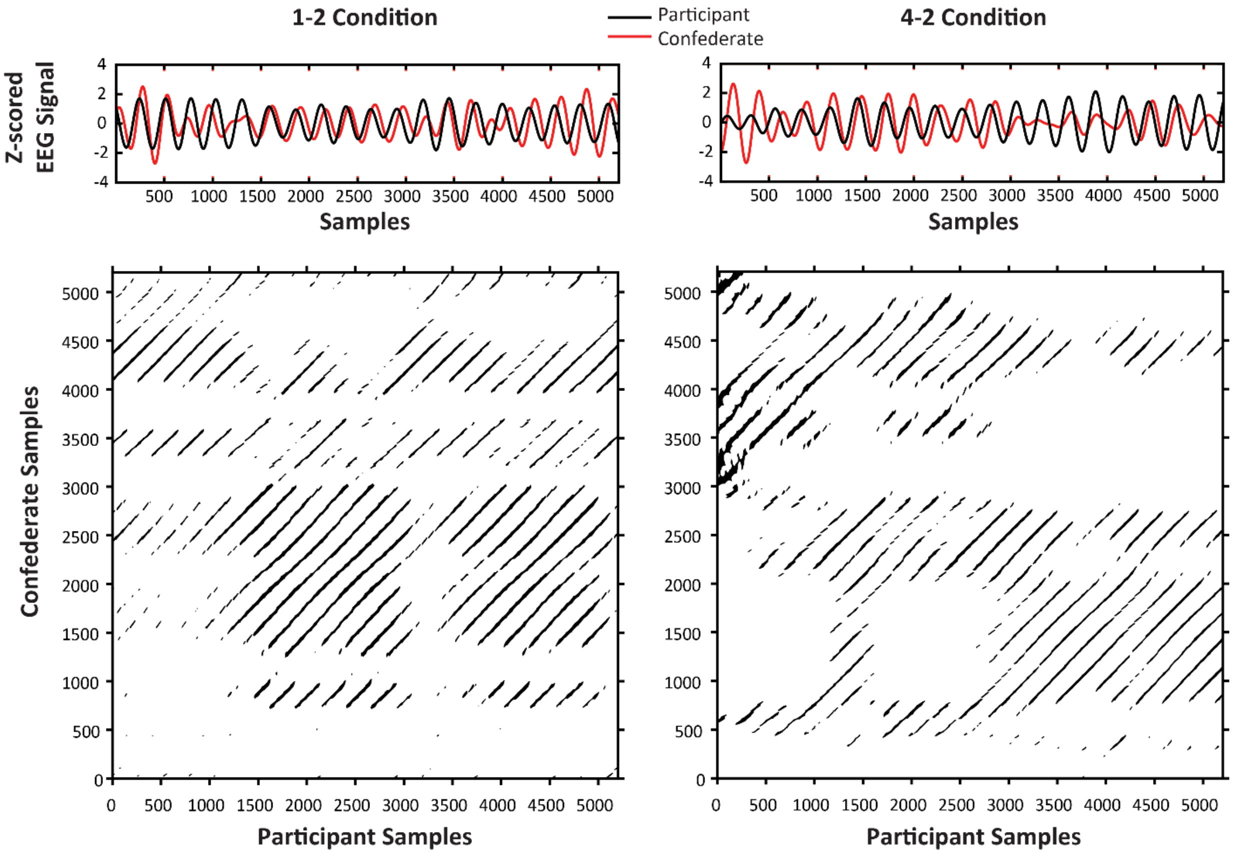

Figure 2. Time series and CRPs with samples as a unit of time for one epoch from one pair for Rhythms 1-2 and 4-2. Time series show the *z*-scored preprocessed signal from electrode C1 for the participant (in black) and the confederate (in red).

Table 2. Cross-recurrence main effects of Rhythm.

Outcome	1-2	4-2	*F*	η^2	*p*
Recurrence Rate	2.93%	2.53%	16.84	0.74	0.005
Meanline	131.22	122.78	16.81	0.74	0.005

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Chapter 5

RQA Captures Temporal Dynamics of Oscillatory Neural Activity Underlying Auditory-Motor Synchronization

The study presented in Chapter 4 developed a novel application of RQA for oscillatory neural activity as measured with EEG in a two-person auditory-motor synchronization task. Results indicated that RQA was sensitive to changes in the temporal dynamics of oscillatory neural activity that occurred with changes in task demands, showing greater neural stability at one partner's tapping rate when there was more auditory feedback at that rate. These results validate the novel application of RQA for oscillatory neural activity recorded as individuals synchronize their actions with an auditory stimulus.

Equipped with an appropriate method for examining the neural dynamics underlying auditory-motor synchronization, the final study in this dissertation has two primary aims. First, this study explores how musical training shapes the temporal dynamics of auditory-motor oscillatory neural activity. Second, this study examines how synchronization performance at participants' SPRs and slower rates specifically, where musicians previously showed a synchronization advantage, relates to the temporal dynamics of auditory-motor oscillatory neural activity. Musicians and nonmusicians tapped a familiar melody with a metronome at participants' SPRs and rates slower than their SPRs while EEG was recorded. Synchronization accuracy and consistency as well as neural predictability (determinism) and stability (meanline) of auditory-motor oscillatory neural activity were measured. Musicians were expected to synchronize more accurately and consistently than nonmusicians as the rate became slower, consistent with the results from Chapter 2. Additionally, musicians were expected to show greater predictability and stability of auditory-motor oscillatory neural activity. Greater synchronization consistency at slower rates, a behavioral measure of stability, was expected to relate to greater neural predictability and stability.

Stability of Neural Oscillations Supports Enhanced Auditory-Motor Synchronization with Musical Training

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Keywords: musical training, spontaneous production rates, rate flexibility, neural dynamics, electroencephalography, recurrence quantification analysis

Abstract

Previous research suggests that musical training leads to increased coactivation of auditory and motor regions, resulting in enhanced auditory-motor synchronization across rates. However, little is understood about the temporal dynamics of auditory-motor network interactions and how these temporal dynamics are shaped by musical training to support synchronization. The current study applied Recurrence Quantification Analysis (RQA), a nonlinear technique for characterizing the temporal dynamics of complex systems, to investigate changes in predictability and stability of auditory-motor network activity with musical training and how these changes relate to synchronization performance. Musicians and nonmusicians synchronized their tapping of a familiar melody with a metronome set at their Spontaneous Production Rate (SPR; comfortable movement rate) and rates slower than their SPR, where musicians have previously shown a synchronization advantage, while electroencephalography (EEG) was recorded. RQA outcomes of meanline (stability) and determinism (predictability) were computed from electrodes reflecting auditory-motor network activity. Musicians showed greater maintenance of synchronization accuracy across rates and synchronized more consistently overall than nonmusicians, consistent with previous research. Musicians also showed greater neural stability overall than nonmusicians. All participants showed greater neural predictability at slower rates. Importantly, neural predictability and stability correlated with synchronization consistency at slower rates such that as predictability and stability increased, so did consistency. This work suggests that musical training shapes the temporal dynamics of auditory-motor networks which support greater synchronization performance at slower rates.

1. Introduction

Musical behaviors across a wide range of contexts, from synchronizing body movements to a musical beat to adapting one's rate of performance to partners in a music ensemble, require coordination of the auditory and motor systems. Given the auditory-motor coupling necessary to successfully carry out these behaviors, there has been a lot of interest in the relationship between musical experience and auditory-motor synchronization abilities. More hours of weekly music practice have been linked to greater synchronization accuracy for highly demanding complex rhythms (Mathias, Zamm, Gianferrara, Ross, & Palmer, 2020). Years of musical training have been related to increased auditory-motor flexibility: Musicians synchronize more accurately and adapt more efficiently than nonmusicians across a range of rates (Scheurich, Pfordresher, & Palmer, 2019; Scheurich, Zamm, & Palmer, 2018). Specific aspects of musical experience may also play an important role in shaping auditory-motor synchronization abilities. Those with specialized percussion training show superior synchronization compared to their musically trained non-percussionist counterparts (e.g., Cameron & Grahn, 2014; Krause, Pollok, & Schnitzler, 2010). Even with a large body of literature that suggests a change in auditory-motor processes with musical training, the neural mechanisms underlying these changes are still not fully understood. The current study examines the neural dynamics underlying enhanced auditory-motor synchronization with musical training.

There has long been an interest in the structural and functional changes in the brain that accompany musical training. This research has pointed to specific changes in auditory and motor cortices, and their interactions. Structurally, musicians show increased volume of the auditory cortex, which is related to greater functional connectivity at rest between auditory and motor regions (Palomar-García, Zatorre, Ventura-Campos, Bueichekú, & Ávila, 2017). This finding suggests that structural changes result in functional changes in the interactions between auditory and motor regions. Supporting this idea, musicians who begin training earlier in life also show greater gray matter volume in the ventral premotor cortex (Bailey, Zatorre, & Penhune, 2014), a region that appears to play a critical role in auditory-motor integration (Zatorre, Chen, & Penhune, 2007; Chen, Penhune, & Zatorre, 2009). Indeed, this increased gray matter volume is correlated with synchronization accuracy (Bailey, Zatorre, & Penhune, 2014).

This research suggests that increased auditory-motor integration occurs with musical training and may support enhanced auditory-motor synchronization. Further work examining brain activity as individuals perform auditory-motor tasks also supports this hypothesis. Using fMRI, Lahav, Saltzman, and Schlaug (2007) examined changes in auditory-motor networks of nonmusicians after trained to play a melody on a keyboard by ear. Following training, listening to the melody alone invoked motor regions. Similar work with EEG has also shown that, following a period of musical training, nonmusicians had greater auditory-motor coactivation in response to separate auditory and motor tasks (Bangert & Altenmüller, 2003). This result is in line with EEG source localization findings with musicians: Pianists show greatest activity in motor cortex in response to previously played auditory sequences (Mathias, Palmer, Perrin, & Tillmann, 2015).

While there is substantial evidence to suggest that musical training increases integration of auditory-motor networks, there is very little research examining the temporal dynamics of these network interactions. There is increasing interest in using nonlinear techniques to further explore the temporal dynamics of neural activity. Specifically, Recurrence Quantification Analysis (RQA) provides a promising new approach to examine how musical training may shape auditory-motor network interactions thought to underlie enhanced synchronization performance.

RQA is a technique for characterizing the behavior of nonlinear, complex systems (e.g., Marwan & Webber, 2015). This technique allows for the characterization of interactions that comprise neural activity, making it the ideal candidate for beginning an exploration into the temporal dynamics of auditory-motor integration and how these dynamics are shaped by musical training. Previous work has already used RQA to characterize behavioral flexibility of auditory-motor synchronization in musicians and nonmusicians (Scheurich, Zamm, & Palmer, 2018). Importantly, this technique has also been used to examine the intra- and inter-brain dynamics supporting auditory-motor synchronization behaviors (Scheurich, Demos, Zamm, Mathias, & Palmer, 2019). RQA will be used in the current study to better characterize auditory-motor network interactions in musicians and nonmusicians, and how these interactions support auditory-motor synchronization.

It is also important to acknowledge that while musical training may increase integration of auditory and motor networks, it is not required for coactivation between these networks to occur (Keele, Pokorny, Corco, & Ivry, 1985; Chen, Penhune, & Zatorre, 2008). One alternative explanation for the enhanced auditory-motor synchronization observed in musicians proposes that musical training may result in enhanced executive functioning (Bugos, Perlstein, McCrae, Brophy, & Bedenbaugh, 2007) which may in turn lead to more precise synchronization. Indeed, some findings support the link between executive functioning, specifically inhibitory control, and auditory-motor synchronization performance (Puyjarinet, Bégel, Lopez, Dellacherie, & Dalla Bella, 2017; Slater, Ashley, Tierney, & Kraus, 2018). The current study will control for possible differences in inhibitory control between musicians and nonmusicians that may result in enhanced auditory-motor synchronization with musical training.

2. Current Research

The current study explores how the temporal dynamics of auditory-motor networks are shaped by musical training, and the relationship between these network dynamics and auditory-motor synchronization performance. Importantly, due to the ongoing COVID-19 public health crisis, data collection for the current study was interrupted. For this reason, we focus here on a small group of musicians and nonmusicians who participated in the study prior to Canada's lockdown. We present analyses on a subset of experimental tasks intended to provide an initial exploration of the research questions presented below, which can be investigated further once health experts deem it safe to return to the lab.

Due to its high temporal resolution suitable for the study of temporal dynamics, EEG was used to measure cortical activity as musicians and nonmusicians completed various motor, auditory, and auditory-motor tasks. To first measure and control for possible differences in inhibitory control between groups, we adapted a stop-signal and Stroop task to the auditory domain to measure inhibitory control in the current study. These tasks were adapted to the auditory domain given that the literature is less clear on the transfer of benefits from musical training to non-auditory executive functioning tasks (Gade & Schlemmer, 2021). To calibrate synchronization rates to each individual, participants tapped a familiar melody at a comfortable rate to measure their Spontaneous Production Rates (SPRs), following previous research (Scheurich, Pfordresher, & Palmer, 2019; Scheurich, Zamm, & Palmer, 2018). They then synchronized their tapping of the melody with a metronome at their SPRs and at slower rates. Slower (as opposed to faster) rates were chosen given previous findings suggesting that musical training provides a particular advantage to synchronization as the rate slows down (Repp & Doggett, 2007; Scheurich, Zamm, & Palmer, 2018). We predicted that synchronization accuracy would decrease for all participants as the rate became slower, but that musicians would show less of a decrease in synchronization accuracy than nonmusicians. We also predicted that synchronization consistency would be greater overall in musicians than in nonmusicians. We applied auto- and cross-recurrence quantification analysis to EEG activity at electrodes previously shown to have highest power during auditory-motor tasks, thought to reflect auditory-motor cortical activity (Scheurich, Demos, Zamm, Mathias, & Palmer, 2019; Nozaradan, Zerouali, Peretz, & Mouraux, 2015), to examine neural dynamics during auditory-motor synchronization. We predicted that musicians would show greater neural predictability (determinism) and stability (meanline) across synchronization rates than nonmusicians. Furthermore, we predicted that greater neural predictability and stability would be related to greater synchronization consistency, specifically, a behavioral measure of stability.

3. Methods

3.1 Participants

Three musicians (mean years old = 22, SD = 4; 2 females) and 3 nonmusicians (mean years old = 22, SD = 2; 2 females) participated in the experiment. Musicians had at least 6 years of private instrumental instruction (mean years = 10, SD = 5), excluding percussionists (e.g., Krause, Pollok, & Schnitzler, 2010). Nonmusicians had no private music instruction. All participants were right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971), had normal hearing in the frequency range of experimental stimuli as determined by an audiometry screening (< 30 dB HL threshold for 250-1000 Hz), reported no neurological disorders, and were not taking medication affecting the central nervous system at the time of participation. Groups did not differ in age, $t(4) = -0.12$, $p = 0.91$.

3.2 Stimulus Materials and Equipment

Participants' hearing thresholds were determined using a Maico MA 40 audiometer. Auditory feedback for the inhibitory control tasks (auditory stop-signal and auditory-Stroop tasks) was delivered to participants using AKG headphones, and their responses were collected using a HyperX Pulsefire gaming mouse (1000 Hz polling rate). For the tapping tasks, participants tapped on the force-sensitive resistor (FSR) of an Arduino that controlled and delivered auditory feedback from participants' taps when necessary in a piano timbre via an Edirol Studio-Canvas SD-80 tone generator through EEG-compatible earphones (Etymotic ER-1, Etymotic Research, Inc.). Auditory feedback from the metronome in the synchronization task was delivered in a woodblock timbre. Auditory feedback in the listening (auditory only) task was controlled with FTAP software (Finney, 2001) and delivered to participants at their measured SPRs (see **Data Analysis**) in a piano timbre. Two stimulus melodies (one familiar and one unfamiliar to participants) were used in this study. The familiar stimulus melody was "Twinkle, Twinkle Little Star," which was used for the tapping tasks with auditory feedback. The unfamiliar stimulus melody was "Lachend" (Zamm, Pfordresher, & Palmer, 2015), which was used for the auditory only task. MIDI data were collected using FTAP on a Dell computer running Linux. FTAP software was modified to integrate Lab Streaming Layer (LSL; Kothe, 2014) so that triggers from FTAP could be sent to a second Dell computer running LSL in Windows 10 over the local area network, as described and implemented previously (Scheurich, Demos, Zamm, Mathias, & Palmer, 2019; Zamm, Palmer, Bauer, Bleichner, Demos, & Debener, 2017).

The auditory stop-signal task consisted of a series of go- and stop-signal trials. At the beginning of each trial, a white fixation cross appeared on the screen 375-675 milliseconds prior to the presentation of the stimulus. A high- (255 Hz) or low-pitch (165 Hz) tone 100 milliseconds in duration was then presented. In go-signal trials, participants heard only a single tone and responded using the left mouse click to indicate a low tone and a right mouse click to indicate a high tone. In stop-signal trials, another tone of the same frequency and duration was presented following the first tone to indicate that participants should not respond in that trial. The duration between the two tones started at 250 milliseconds. With each correct response inhibition, this duration would increase 50 milliseconds and with each incorrect response made, this duration would decrease 50 milliseconds. Each trial ended after participants responded or 1000 milliseconds elapsed, and the cross was removed. A black screen was presented during the inter-trial interval of 533-883 ms. The trial timing structure was adapted from Enriquez-Geppert, Konrad, Pantev, & Huster (2010). The task had one practice block consisting only of go-signal trials (10 total; go-signal: 5 trials by 2 pitches), one practice block consisting of go-signal and stop-signal trials (20 total; 14 go-signal: 7 trials by 2 pitches; 6 stop-signal: 3 trials by 2 pitches), and one test block consisting of go-signal and stop-signal trials (100 total; 70 go-signal: 35 trials by 2 pitches; 30 stop-signal: 15 trials by 2 pitches). Trials within each block were pseudo-randomized such that at least one go-signal trial preceded each stop-signal trial as in Hughes, Johnston, Fulham, Budd, & Michie (2013).

The auditory Stroop task consisted of a series of Stroop (“high” and “low”) and non-Stroop (“cat” and “dog”) words recorded from a female speaker. Fundamental frequencies of the recorded words were adjusted to have a high (255 Hz) or low (165 Hz) tone of voice. Together, these created a series of congruent (e.g., “high” spoken in a high tone), incongruent (e.g., “high” spoken in a low tone), and neutral (e.g., “cat” spoken in a high tone) trials. The dimension of pitch was chosen for the auditory Stroop task because multiple studies have reported a Stroop effect for pitch similar to what is observed in the visual domain, the typical modality in which

Stroop tasks are administered (Leboe & Mondor, 2007; Morgan & Brandt, 1989; Walker & Smith, 1984). At the beginning of each trial, a white fixation cross appeared on the screen 375-675 ms prior to the presentation of the stimulus. Following the presentation of the stimulus, participants had 1500 ms to respond. Participants responded to the tone of voice, using a left mouse click to indicate a low tone and a right mouse click to indicate a high tone. The fixation cross disappeared following a response or lack thereof, indicating the end of the trial. A black screen was presented during the inter-trial interval of 533-883 ms. The trial timing structure was adapted from Enriquez-Geppert, Konrad, Pantev, & Huster (2010). The task had one practice block of 32 trials (16 Stroop: 4 trials by 2 words by 2 pitches; 16 non-Stroop: 4 trials by 2 words by 2 pitches) followed by one test block of 80 trials (40 Stroop: 10 trials by 2 words by 2 pitches; 40 non-Stroop: 10 trials by 2 words by 2 pitches). Trials within each block were pseudorandomized such that participants never received the same word or pitch more than twice in a row.

3.3 EEG Data Recording

EEG data were recorded at a 512 Hz sampling rate with a 64-channel BioSemi ActiveTwo system (BioSemi, Inc.). EEG was grounded using the common mode sense (CMS) and driven right leg (DRL) electrodes. Sixty-four scalp electrodes were placed according to the 10-20 system. Six external electrodes were place above and below the right eye, on the outer corner of each eye, and on the mastoids to monitor eyeblinks, lateral eye movements, and muscle artefacts, respectively.

3.4 Procedure

After providing written informed consent upon arrival to the lab, participants underwent an audiometry screening. Participants who passed the audiometry screening and then reported familiarity with the experimental melody moved on to the auditory stop-signal task. Participants were seated at a computer with headphones and were first instructed that they would hear a low- or high-pitch tone in each trial. Participants were instructed to indicate with the mouse whether they heard a low- (left mouse click) or high-pitch (right mouse click) tone. Participants were then presented with examples of the low- and high-pitch tones and completed the practice block with only go-signal trials. Following the first practice block, participants were instructed that in some trials they would hear a second tone following the first tone. Participants were instructed that they should not respond in trials when they heard two tones. They then completed the second practice block with both go-signal and stop-signal trials. Following the second practice block, participants completed the test block.

Following completion of the auditory stop-signal task, participants completed the auditory Stroop task. Participants were seated at a computer with headphones and were instructed that they would hear recordings of someone saying the words “high,” “low,” “cat,” or “dog” in a low or high tone of voice. Participants were instructed to listen to the tone of voice (ignoring the word) and indicate with the mouse whether they heard a low (left mouse click) or high (right mouse click) tone of voice. Participants were then presented with examples of each word spoken in a high and low tone of voice and subsequently completed a practice block to familiarize them with the task. Once familiarized, participants completed the test block.

Following completion of the auditory Stroop task, participants were outfitted with the EEG cap and electrodes and seated in front of a fixation cross. The Arduino was placed on a table next to participants where they could rest their arm while tapping. Following setup, participants completed the SMT task. They were instructed to tap at a comfortable and steady rate while focusing their gaze on the fixation cross in front of them. Participants first completed a practice trial to become comfortable with the task. They then completed three test trials.

Participants were then given earphones to complete the SPR task. Participants were instructed that they should tap the rhythm of “Twinkle, Twinkle Little Star” while focusing their gaze on the fixation cross in front of them. They were told that each time they tapped, a tone of the melody would sound and that they had control over when the next tone in the melody would sound. Participants completed one practice trial in which they tapped the melody once through to become comfortable with the task. They then completed a second practice trial in which they were instructed to tap the melody several times through until they no longer heard the sound of their taps, indicating the end of the trial. Once participants were comfortable with the task, they were instructed that they should tap the rhythm of the melody at a comfortable and steady rate. Participants then completed three test trials. Following the SPR task, participants completed several questionnaires while their SPRs were computed for use in the auditory only and synchronization tasks. These questionnaires assessed participants’ musical background and handedness.

Participants then completed the auditory only task. Participants were instructed to sit with their hands together while focusing their gaze on the fixation cross in front of them. They were instructed that they would hear a new melody and were then presented with one practice trial of the melody so they could become comfortable with how it sounded. Participants were instructed that they would hear the melody several times through and that the trial ended when they no longer heard the melody. After the practice trial, the experimenter confirmed that participants were not familiar with the melody. Participants were then instructed that in some trials there would be a small change in the timing of the melody, and that they should indicate at the end of each trial whether they heard a change or not. Participants completed three test trials in which they had to detect these changes.

Finally, participants completed the synchronization task. Participants were instructed that they would again be tapping the rhythm of “Twinkle, Twinkle Little Star” as they did before, but that this time they would hear a metronome and their goal was to synchronize their tapping with the metronome while focusing their gaze on the fixation cross in front of them. Participants first completed a practice trial in which they were instructed to begin synchronizing with the metronome after the first eight metronome clicks and to continue tapping the melody several times through until they no longer heard the sound of their taps, indicating the end of the trial. Participants then completed three test trials. This procedure was repeated for all rate conditions. Participants were debriefed following the synchronization task and given a small compensation for their time. The study lasted approximately 2.5 hours.

3.5 Design

The remaining sections focus only on the auditory Stroop, SPR, and synchronization tasks as a preliminary exploration of the research questions. The auditory Stroop task had a mixed design with the between-subjects independent variable Group (Musician and Nonmusician) and the within-subjects independent variable Trial Type (Congruent, Incongruent, Neutral). The SPR task was used to measure participants’ SPRs for the synchronization task (see **Data Analysis**). The synchronization task had a mixed design with the between-subjects independent variable Group (Musician and Nonmusician) and the within-subjects independent variable Rate (SPR, 15% slower than the SPR, and 30% slower than the SPR). All participants completed the rate conditions in the same order, starting with the SPR followed by the 15%

slower and then 30% slower rate conditions. This constant order was chosen to ease participants into the task, starting with their most comfortable rate.

3.6 Behavioral Data Analysis

Response accuracy in the auditory Stroop task was computed as the proportion of correct responses for each trial type, where trial types were defined as congruent (i.e., match between word and tone of voice), incongruent (i.e., mismatch between word and tone of voice), or neutral (i.e., neutral word presented in either tone of voice). Average reaction times (in ms) were computed for each trial type, excluding trials with incorrect and missing responses.

Participants' SPRs were calculated from the middle two repetitions of each trial from the SPR task, as in previous work (e.g., Loehr & Palmer, 2011; Scheurich, Zamm, & Palmer 2018; Scheurich, Pfordresher, & Palmer, 2019; Zamm, Pfordresher, & Palmer, 2015). SPRs were calculated as the mean Inter-Onset Interval (IOI) across repetitions and trials. Half notes were interpolated and outlier IOIs more than three standard deviations away from the mean were removed (Musicians = 1.16%; Nonmusicians = 2.55%). The resulting SPRs were then used to determine the metronome rates for the synchronization task.

To examine synchronization performance in the synchronization task, tap and metronome onsets were first aligned in each trial using a nearest neighbor approach (e.g., Pecenka & Keller, 2011; Scheurich, Zamm, & Palmer, 2018; Scheurich, Pfordresher, & Palmer, 2019). Signed asynchronies were then calculated as the tap minus metronome onset, with negative values indicating that a tap preceded the metronome and positive values indicating that a tap lagged the metronome. Signed asynchrony outliers more than three standard deviations from the mean signed asynchrony were removed (Musicians = 0.37%; Nonmusicians = 0.36%). Taps that did not align with a metronome onset were discarded. To assess whether participants were synchronized above chance in each trial, signed asynchronies were then converted to radians and the Rayleigh test for circular non-uniformity was run on the radian values per trial. A significant Rayleigh test indicates a significant mean direction (i.e., unimodal synchronization pattern), whereas a non-significant Rayleigh test indicates no significant mean direction (i.e., no synchronization or multimodal synchronization pattern; Fisher, 1993). Following previous work (Kirschner & Tomasello, 2009; Pecenka & Keller, 2011; Sowiński & Dalla Bella, 2013; Dalla Bella & Sowiński, 2015; Scheurich, Zamm, & Palmer, 2018), trials in which the Rayleigh test failed to reach significance were removed from all subsequent behavioral and EEG analyses (Musicians = 0% of total trials; Nonmusicians = 22% of total trials).

The mean signed asynchronies and standard deviations of the signed asynchronies were then computed for each synchronized trial. One might predict larger asynchronies for slower rates because there is more time to anticipate the metronome at these rates. Therefore, the mean of the relative phase values (signed asynchronies represented as a proportion of the metronome IOI) per trial were also computed to ensure that any effect of rate or group on synchronization performance was not simply due to the differing rates across participants or conditions.

3.7 EEG Preprocessing and Data Analysis

EEG data were preprocessed using EEGLAB (Delorme & Makeig, 2004). Data for all trials and tasks were first concatenated together and re-referenced to the common average across electrodes. Electrodes with poor signal quality were then detected by visually inspecting distributions of deviations from mean activity. Those with no deviation from mean activity or very large deviations from mean activity were identified as flat and noisy electrodes, respectively, and removed. The data were then filtered between 1 Hz and 40 Hz using a Hamming windowed sinc FIR filter (high and low pass filter order = 1000), segmented into 1-

second epochs, and pruned for non-stereotypical artefacts. Data were then submitted to extended infomax Independent Component Analysis (ICA). Resulting ICA components reflecting eyeblink and lateral eye movement artefacts were visually identified from component topomaps and removed from the unfiltered data. Finally, electrodes removed due to poor signal quality were spherically interpolated.

Following preprocessing, data were then prepared for auto- and cross-recurrence quantification analyses. Following previous research showing maximal power at C1 during an auditory-motor synchronization task (Scheurich, Demos, Zamm, Mathias, & Palmer 2019), C1 was selected to be used as input to auto-recurrence quantification analysis. This electrode was also one of several electrodes that showed maximal power at the beat frequency during the synchronization task in the current study. To further examine auditory-motor integration, separate electrodes capturing auditory and motor activity were selected to be used as input to cross-recurrence quantification analysis. FC1 was chosen as the auditory electrode based on auditory perception and right-handed tapping tasks showing maximal amplitude at this electrode at the beat frequency of an auditory stimulus (Nozaradan, Zerouali, Peretz, & Mouraux, 2015). C3 was chosen as the motor electrode based on a right-handed tapping task showing maximal amplitude at this electrode at the movement frequency (Nozaradan, Zerouali, Peretz, & Mouraux, 2015).

Data recorded from these channels during the synchronization task were prepared for RQA by filtering at the beat frequency of the metronome in the corresponding rate condition for each subject. Filter cutoffs were defined as two standard deviations above and below the tapping frequency in the corresponding rate condition for each participant to account for timing deviations from the metronome beat frequency. It should be noted that timing deviations in the mean tapping frequency from the metronome beat frequency were small and captured by the specified filter cutoffs (musician mean deviation = 0.33 ms; nonmusician mean deviation = 10.48 ms). A Hanning windowed sinc FIR filter was used (high and low pass filter order = 1000). A 9.9 second epoch, corresponding to the shortest melody repetition, was then extracted from the start of the second melody repetition for each significantly synchronized trial as this was the full repetition containing the fewest behavioral IOI outliers for most conditions (Musicians = 0.61%; Nonmusicians = 2.18%). One additional trial for a musician in the SPR condition was missing due to a technical error. Data were finally *z*-scored per epoch.

Auto- and cross-recurrence parameter selection and analyses were done using the Cross Recurrence Plot Toolbox (Marwan, Romano, Thiel, & Kurths, 2007). Parameters were optimized per rate condition per participant given the changing rates across conditions and participants. The optimal delay parameter was determined using Average Mutual Information (AMI). For auto-recurrence, the optimal delay was selected by identifying the first local minimum, or the first delay at which the least information is shared with the first point in the time series. For cross-recurrence, the optimal delay selected was the mean first local minimum across the two electrodes. The optimal number of embedding dimensions was determined using False Nearest Neighbours (FNN) by identifying the number of dimensions for which the number of false nearest neighbours in the phase space is minimized. The optimal number of embedding dimensions for both auto- and cross-recurrence was found to be the same across rate conditions and participants (selected embedding dimensions = 4), consistent with previous research implementing the same pipeline (Scheurich, Demos, Zamm, Mathias, & Palmer, 2019).

Manipulations of rate can create a potential confound in the interpretation of observed differences in auto- and cross-recurrence outcomes across groups and conditions. Given the same time window with a slower and faster rate, the faster rate may show greater recurrence simply because there are more cycles of that frequency in the analysis window compared to the slower rate. To control for this potential confound, recurrence rate was fixed to 10% as has been done previously (Scheurich, Demos, Zamm, Mathias, & Palmer, 2019). For auto-recurrence, the Thieler window and the minimum diagonal and vertical line lengths were set to 24 samples for all rate conditions and participants, corresponding to 1/2 of the smallest optimal delay across rate conditions and participants (i.e., approximately 1/8 of the cycle of the fastest rate). For cross-recurrence, the Thieler window was set to 0 samples and the minimum diagonal and vertical line lengths were set to 25 samples for all rate conditions and participants, corresponding to 1/2 of the smallest optimal delay across rate conditions and participants (i.e., approximately 1/8 of the cycle of the fastest rate).

The auto- and cross-recurrence outcomes of interest were determinism and meanline. A sample recurrence plot is shown in Figure 1 alongside the time series as a visual demonstration of these outcomes described below. Determinism describes the proportion of recurrent points that fall along diagonal lines and represents predictability for periodic systems like the one investigated here (Marwan & Webber, 2015). The computation of determinism is shown in Eq. 1 as was previously described in Marwan, Romano, Thiel, & Kurths (2007), where l refers to the diagonal line length, $P(l)$ refers to the histogram of the diagonal lines of length l, and l_{min} refers to the minimum diagonal line length.

$$(1)\ DET = \frac{\sum_{l=l_{min}}^{N} l\,P(l)}{\sum_{l=1}^{N} l\,P(l)}$$

Meanline describes the average diagonal line length and represents the average prediction time (Marwan & Webber, 2015). This metric has been used as an index of stability (e.g., Rosen, Epstein, & Van Orden, 2013). The computation of meanline is shown in Eq. 2 as was previously described in Marwan, Romano, Thiel, & Kurths (2007). The notable change from Eq. 1 to Eq. 2 is the denominator. Whereas the denominator in Eq. 1 represents the total number of individual recurrent points, the denominator in Eq. 2 represents the total number of diagonal lines.

$$(2)\ L = \frac{\sum_{l=l_{min}}^{N} l\,P(l)}{\sum_{l=l_{min}}^{N} P(l)}$$

Insert Figure 1 Here

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4. Results

4.1 Inhibitory Control

To assess Musicians' and Nonmusicians' inhibitory control, we first ran a two-way mixed ANOVA on accuracy in the Stroop task with Group (Musician and Nonmusician) and Trial Type (Congruent, Incongruent, and Neutral) as factors. Results showed no significant main effect of Group, $F(1, 4) = 1.31$, $p = 0.32$, no significant main effect of Trial Type, $F(2, 8) = 3.05$, $p = 0.10$, and no significant interaction between Group and Trial Type, $F(2, 8) = 0.86$, $p = 0.46$.

We next ran a two-way mixed ANOVA on reaction time for accurate trials in the Stroop task with Group and Trial Type as factors. Results showed a main effect of Group that approached significance, $F(1, 4) = 6.24$, $p = 0.07$. There was a trend for Musicians to respond faster overall (mean = 536 ms, SE = 31.40 ms) than Nonmusicians (mean = 613 ms, SE = 17.90 ms). There was no significant main effect of Trial Type, $F(2, 8) = 3.19$, $p = 0.10$, and no significant interaction between Group and Trial Type, $F(2, 8) = 0.18$, $p = 0.84$.

4.2 SPRs

As can be seen in Figure 2, there was a wide range in participants' SPRs (minimum = 302.95 ms; maximum = 549.63 ms). To examine whether SPRs varied across groups and trials, a two-way mixed ANOVA was run on the mean IOI with Group and Trial (1, 2, and 3) as factors. Results showed no significant main effect of Group, $F(1, 4) = 1.79$, $p = 0.25$, no significant main effect of Trial, $F(2, 8) = 2.85$, $p = 0.12$, and no significant interaction between Group and Trial, $F(2, 8) = 2.26$, $p = 0.17$.

Insert Figure 2 Here

4.3 Synchronization Accuracy

We next examined synchronization accuracy of the two groups across all rate conditions. Given the missing data in the synchronization task due to non-synchronized trials and technical difficulties, a linear mixed model was run with participant as the random factor, Group and Rate (SPR, 15% Slower, and 30% Slower) as the fixed factors, and the mean signed asynchrony as the predicted variable. Results showed a significant effect of Rate, $F(2, 35.87) = 9.13$, $p < 0.001$, and a significant interaction between Group and Rate, $F(2, 35.87) = 7.05$, $p = 0.003$. Post hoc comparisons showed that Nonmusicians' synchronization accuracy decreased (signed asynchronies became more negative) from the SPR to the 30% Slower Rate (Holm-adjusted $p < 0.001$; Holm, 1979) and from the 15% Slower Rate to the 30% Slower rate (Holm-adjusted $p = 0.003$), whereas Musicians' synchronization accuracy did not differ across rates, as shown in Figure 3. There was no significant effect of Group, $F(1, 3.83) = 1.88$, $p = 0.25$.

Insert Figure 3 Here

To ensure the observed pattern of signed asynchronies was not due to the changing rates across participants and conditions, we also examined relative phase in which the signed asynchronies are represented as a proportion of the metronome rate. A linear mixed model was run with participant as the random factor, Group and Rate as the fixed factors, and relative phase as the predicted variable. Results confirmed a significant effect of Rate, $F(2, 35.51) = 3.81$, $p = 0.03$, and a significant interaction between Group and Rate, $F(2, 35.51) = 5.18$, $p = 0.01$. There was no significant effect of Group, $F(1, 3.93) = 0.39$, $p = 0.57$. Replicating results for the signed asynchronies, post hoc comparisons showed that Nonmusicians' synchronization accuracy decreased (relative phase became more negative) from the SPR to the 30% Slower Rate (Holm-adjusted $p = 0.003$) and from the 15% Slower Rate to the 30% Slower Rate (Holm-adjusted $p = 0.04$), whereas Musicians' synchronization accuracy did not differ across rates (Figure 4). Therefore, differences in rates across participants and conditions could not account for the observed effects.

Insert Figure 4 Here

4.4 Synchronization Consistency

We next examined synchronization consistency, measured via the standard deviation of the signed asynchrony, of the two groups across rate conditions. A linear mixed model was run with participant as the random factor, Group and Rate as the fixed factors, and the standard deviation of the signed asynchrony as the predicted variable. Results showed a significant effect of Group, *F*(1, 3.93) = 101.54, $p < 0.001$. Musicians were more consistent (smaller standard deviations; mean = 24.50 ms, SE = 0.97 ms) than Nonmusicians (mean = 87.00 ms, SE = 4.78 ms) across all rates. There was no significant effect of Rate, *F*(2, 37.24) = 0.72, $p = 0.50$, and no significant interaction between Group and Rate, *F*(2, 37.24) = 1.28, $p = 0.29$.

4.5 Auto- and Cross-Recurrence Outcomes

We next assessed the predictability and stability of oscillatory neural activity during the synchronization task. We first ran auto-recurrence quantification analysis on electrode C1 (representing auditory-motor network activity) and examined the outcomes of determinism and meanline. Two separate linear mixed models were run with participant as the random factor, and Group and Rate as the fixed factors. In the first model, determinism was the predicted variable. Results showed a significant effect of Rate, *F*(2, 34.17) = 20.41, $p < 0.001$. Post hoc comparisons showed that determinism was higher at the 15% and 30% Slower Rates than at the SPR (Holm-adjusted *p*'s < 0.001), and at the 30% Slower Rate than at the 15% Slower Rate (Holm-adjusted $p = 0.02$), as shown in Figure 5. There was no significant effect of Group, *F*(1, 4) = 2.20, $p = 0.21$, and no significant interaction between Group and Rate, *F*(2, 34.17) = 0.13, $p = 0.88$. In the second model, meanline was the predicted variable. Results showed a significant effect of Group, *F*(1, 38) = 5.22, $p = 0.03$. Meanline was higher for Musicians (mean = 153.00 samples, SE = 3.34 samples) than for Nonmusicians (mean = 141.00 samples, SE = 3.92 samples). There was no significant effect of Rate, *F*(2, 38) = 0.17, $p = 0.85$, and no significant interaction between Group and Rate, *F*(2, 38) = 0.52, $p = 0.60$.

Insert Figure 5 Here

We next ran cross-recurrence quantification analysis on electrodes FC1 (representing auditory network activity) and C3 (representing motor network activity) and examined the outcomes of determinism and meanline. Two separate linear mixed models were run with participant as the random factor, and Group and Rate as the fixed factors. In the first model, determinism was the predicted variable. Results showed a significant effect of Rate, $F(2, 34.06) = 50.24$, $p < 0.001$. Post hoc comparisons showed that determinism was higher at the 15% and 30% Slower Rates than at the SPR (Holm-adjusted p's < 0.001), and at the 30% Slower Rate than at the 15% Slower Rate (Holm-adjusted $p = 0.02$), as shown in Figure 6. There was no significant effect of Group, $F(1, 4) = 1.30$, $p = 0.32$, and no significant interaction between Group and Rate, $F(2, 34.06) = 0.14$, $p = 0.87$. In the second model, meanline was the predicted variable. Results showed no significant effect of Group, $F(1, 3) = 5.54$, $p = 0.10$, no significant effect of Rate, $F(2, 36.33) = 1.31$, $p = 0.28$, and no significant interaction between Group and Rate, $F(2, 36.33) = 0.29$, $p = 0.75$.

Insert Figure 6 Here

4.6 Brain-Behavior Correlations

We next examined the relationship between behavioral consistency and neural predictability and stability at each rate. We predicted that as neural predictability and stability increased, so would behavioral consistency. Figure 7 shows the simple correlations between each participant's standard deviation of the signed asynchrony and EEG auto-recurrence outcome of determinism at each rate. Correlations were significant at the 15% Slower Rate, $r(4) = -0.84$, $p = 0.04$, and at the 30% Slower Rate, $r(3) = -0.94$, $p = 0.02$, but not at the SPR, $r(4) = -0.41$, $p = 0.42$. As can be seen in Figure 7, as determinism increased, the standard deviation of the signed asynchrony decreased. Figure 8 shows the simple correlations between each participant's standard deviation of the signed asynchrony and EEG auto-recurrence outcome of meanline at each rate. Correlations were large and negative at the slower rates, but only reached significance at the 15% Slower Rate, $r(4) = -0.99$, $p < 0.001$. Correlations were not significant at the SPR, $r(4) = -0.38$, $p = 0.46$, or at the 30% Slower Rate, $r(3) = -0.74$, $p = 0.15$. As can be seen in Figure 8, similar to determinism, as meanline increased, the standard deviation of the signed asynchrony decreased.

Insert Figure 7 Here

Insert Figure 8 Here

We next ran simple correlations between each participant's standard deviation of the signed asynchrony and the same outcomes from EEG cross-recurrence at each rate. Figure 9 shows the simple correlations with determinism at each rate. Correlations were large and negative at the slower rates, but only reached significance at the 30% Slower Rate, $r(3) = -0.92$, $p = 0.03$. Correlations were not significant at the SPR, $r(4) = -0.34$, $p = 0.51$, or at the 15% Slower Rate, $r(4) = -0.71$, $p = 0.12$. As can be seen in Figure 9, as determinism increased, the standard deviation of the signed asynchrony decreased. Simple correlations with meanline were also negative at all rates and large at the 30% Slower Rate, but did not reach significance at any rate (SPR: $r(4) = -0.25$, $p = 0.64$; 15% Slower: $r(4) = -0.33$, $p = 0.52$; 30% Slower: $r(3) = -0.77$, $p = 0.13$).

Insert Figure 9 Here

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5. Discussion

The current study explored changes in the temporal dynamics of auditory-motor network interactions with musical training, and the relationship between these temporal dynamics and auditory-motor synchronization performance. Behaviorally, nonmusicians showed a decrease in synchronization accuracy as the rate became slower. This finding persisted in analyses of relative phase that accounted for differences in rates across participants. Nonmusicians also showed greater synchronization variability than musicians. Neurally, both groups showed an increase in the determinism outcome for both auto- and cross-recurrence quantification analysis as the rate became slower. Furthermore, musicians showed a higher meanline outcome for auto-recurrence than nonmusicians. Brain-behavior comparisons showed significant correlations between the determinism outcome for auto- and cross-recurrence and the standard deviation of the signed asynchrony at slower rates, and between the meanline outcome for auto-recurrence and the standard deviation of the signed asynchrony at the 15% slower rate. Importantly, although there was a trend for musicians to respond more quickly than nonmusicians on accurate trials from the auditory Stroop task, there were no significant differences in inhibitory control measures between musicians and nonmusicians.

The findings that musicians were better able to maintain synchronization accuracy across rates and to synchronize more consistently overall than nonmusicians replicates previous work (e.g., Repp & Doggett, 2007; Scheurich, Zamm, & Palmer, 2018). Importantly, these group differences cannot be attributed to differences in inhibitory control in this small sample. Although musicians trended toward faster reaction times for accurate trials than nonmusicians in the auditory Stroop task, there were no significant differences between musicians and nonmusicians in inhibitory control. Instead, we suggest that musicians' greater stability of auditory-motor neural activity, as indicated by the higher auto-recurrence meanline outcome, may reflect stronger auditory-motor integration supporting synchronization. This is consistent with previous work suggesting that the strength of neural entrainment is correlated with synchronization performance (Bouvet, Bardy, Keller, Dalla Bella, Nozaradan, & Varlet, 2020; Nozaradan, Peretz, & Keller, 2016). Our work similarly shows a relationship between neural stability and synchronization consistency, specifically at the slower synchronization rates.

Interestingly, neural predictability increased for both groups as the rate became slower. Coordinating movements becomes more demanding at slower rates (Fujiyama, Hinder, Garry, & Summers, 2013; McPherson, Berger, Alagapan, & Fröhlich, 2018). Building upon this idea, the current study tailored the task demands to each individual by determining the synchronization rates relative to participants' SPRs rather than fixing the rates across individuals. Task demands should be lowest at the individual's SPR, representing their most comfortable rate, and increase as the rate becomes slower than their SPR. Extending previous work suggesting increased deterministic structure of movement with increasing task demands (Balasubramaniam, Riley, & Turvey, 2000; Mazaheri, Salavati, Negahban, Sanjari, Parnianpour, 2010), our findings show increased deterministic structure of auditory-motor neural activity as the rate becomes slower, reflecting increasing task demands. It is possible that this increased neural predictability may be critical to maintaining synchronization performance specifically when task demands are high. Further supporting this idea, the correlation between neural predictability and synchronization consistency at participants' SPRs, where task demands should be lowest, was not significant. These correlations only began to emerge at slower rates, where task demands should be highest. With more data, one could assess whether the strength of these relationships increase as the rate becomes slower (task demands become higher) to further investigate the importance of increased neural predictability at slower rates to behavioral outcomes.

It is important to acknowledge a few limitations in the interpretation of these findings. Unfortunately, due to the ongoing COVID-19 public health crisis, data collection was interrupted and therefore the sample consists only of three individuals in each group. To draw more precise conclusions, it would be necessary to collect data from a larger sample of participants in the future. Furthermore, electrodes were selected for RQA based on previous work suggesting that they reflect auditory-motor activity. However, because of the poor spatial resolution of EEG, the contributions of other networks to the activity measured from these electrodes cannot be ruled out. It is also likely that the two electrodes selected for cross-recurrence share some similar sources given the distribution of activity across the scalp and their close spatial proximity to one another. Future work could use source localization to extract source activity from auditory and motor networks on which RQA could then be applied. Additionally, researchers may consider using other techniques such as magnetoencephalography given that it has better spatial resolution while still preserving some temporal resolution. Future work could also apply multivariate techniques such as multidimensional recurrence quantification analysis to account for contributions from additional networks (Wallot, Roepstorff, & Mønster, 2016).

In sum, musicians maintained their synchronization accuracy as the rate became slower and synchronized more consistently than nonmusicians in the absence of group differences in inhibitory control. The increase in synchronization consistency with musical training was related to increased predictability and stability of auditory-motor neural activity. Additionally, predictability of auditory-motor neural activity increased as the rate became slower (i.e., as task demands increased), independent of musical training. These findings suggest that musical training may enhance auditory-motor synchronization abilities by increasing the stability of auditory-motor neural activity, which may reflect greater auditory-motor integration with musical training.

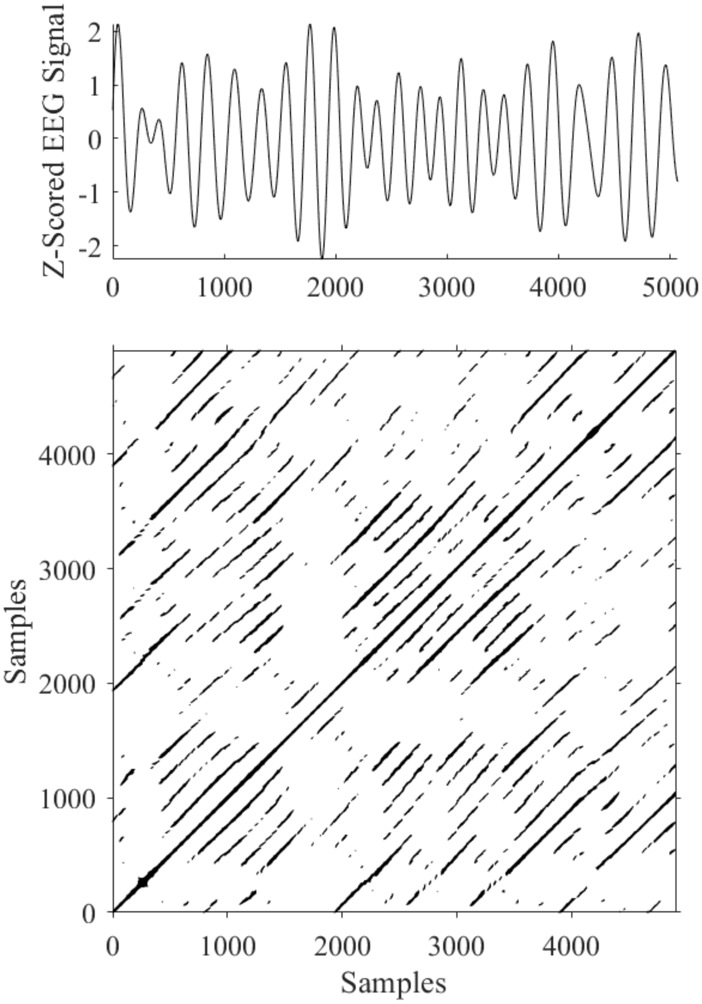

Figure 1. Sample auto-recurrence plot and corresponding time series from a musician for a single trial at the SPR synchronization rate. Determinism represents the proportion of recurrent points falling on diagonal lines and meanline represents the average length of the diagonal lines in the plot.

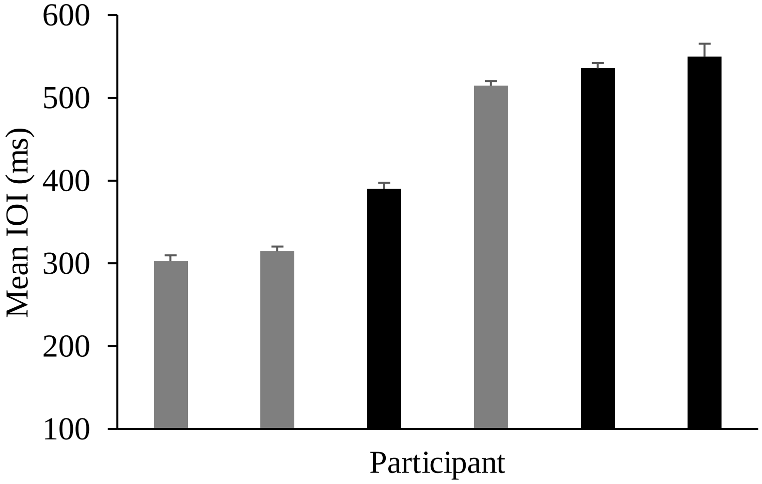

Figure 2. Distribution of participants' SPRs from fastest to slowest. Gray bars represent nonmusicians, and black bars represent musicians. Error bars show standard error.

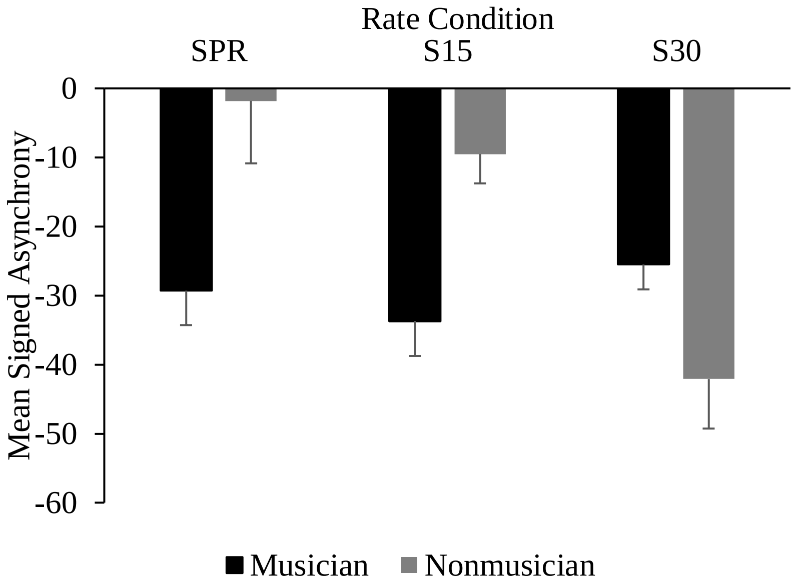

Figure 3. Mean signed asynchronies displayed by rate and group. Error bars show standard error.

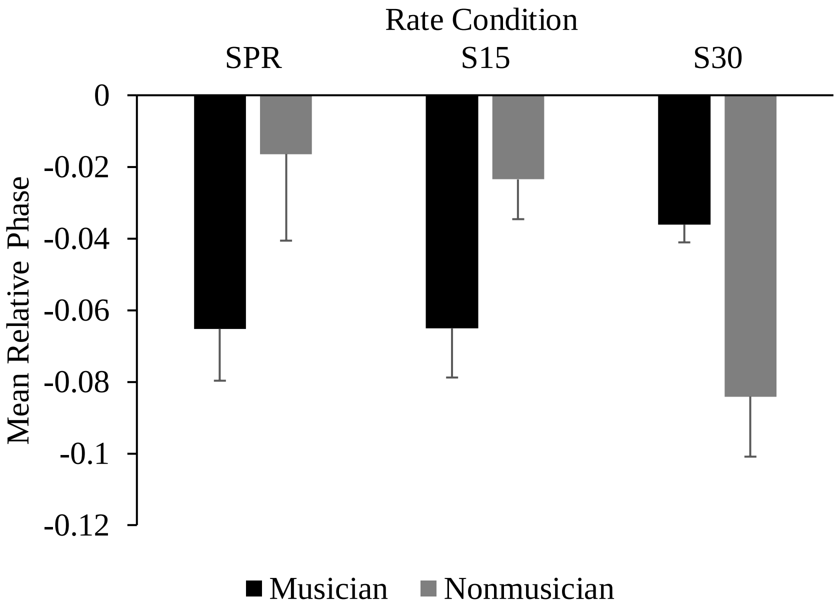

Figure 4. Mean relative phase displayed by rate and group. Error bars show standard error.

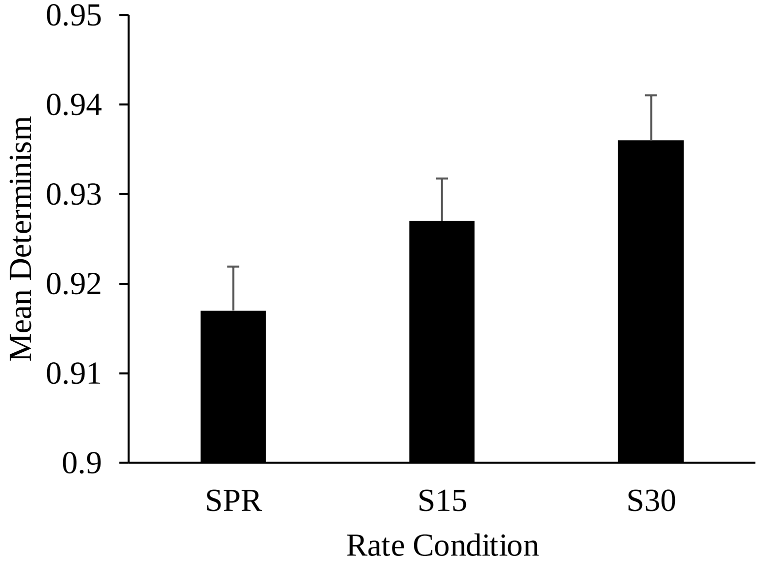

Figure 5. Mean determinism from auto-recurrence across groups displayed by rate. Error bars show standard error.

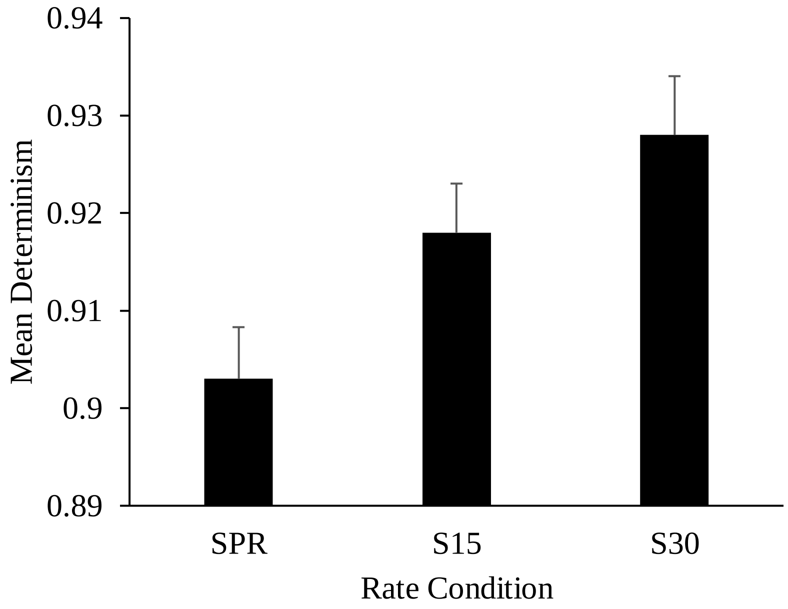

Figure 6. Mean determinism from cross-recurrence across groups displayed by rate. Error bars show standard error.

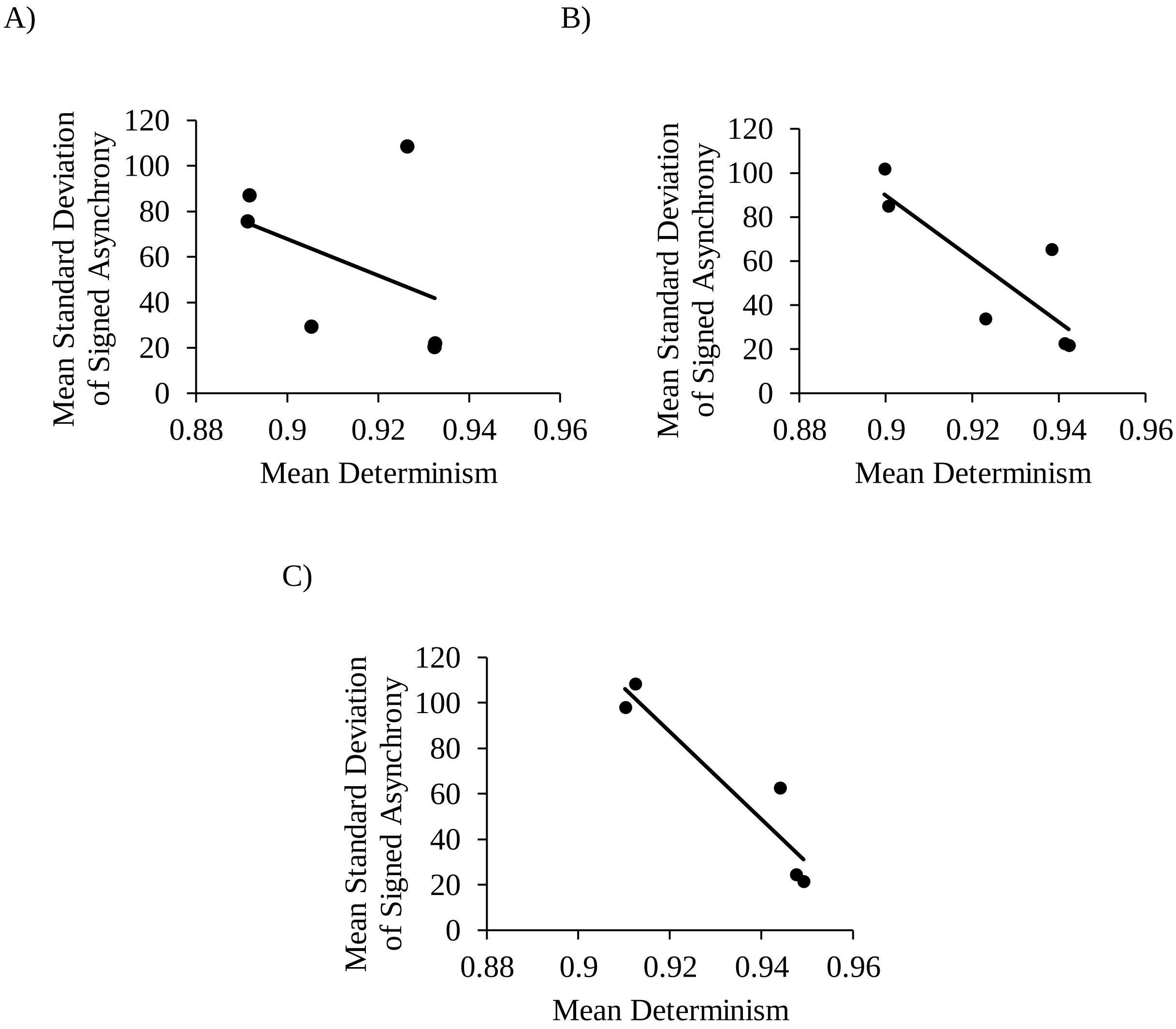

Figure 7. Correlations between mean determinism from auto-recurrence and the mean standard deviation of the signed asynchrony for the SPR (A), 15% (B), and 30% (C) Slower Rates.

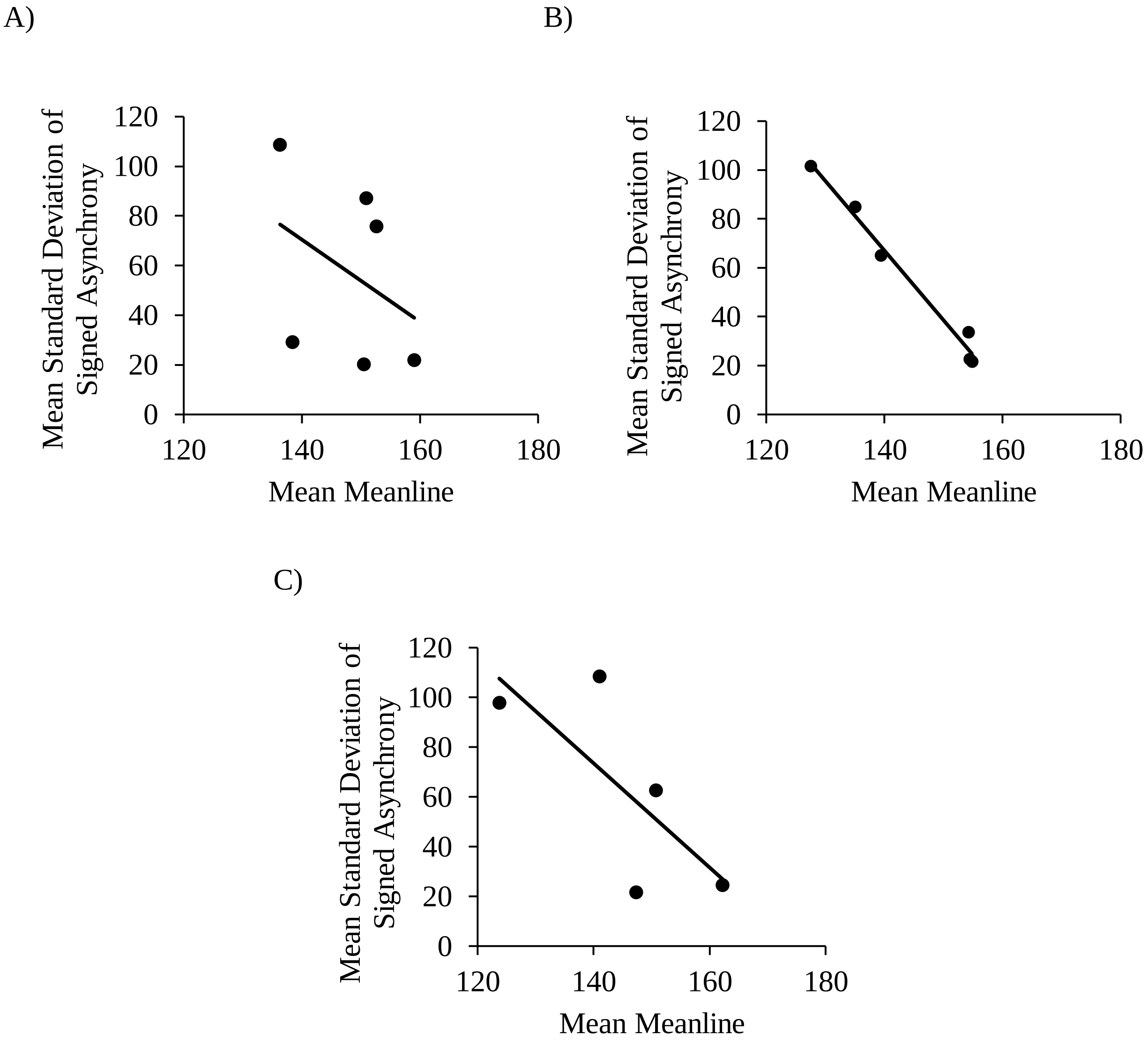

Figure 8. Correlation between mean meanline from auto-recurrence and the mean standard deviation of the signed asynchrony for the SPR (A), 15% Slower (B), and 30% (C) Slower Rates.

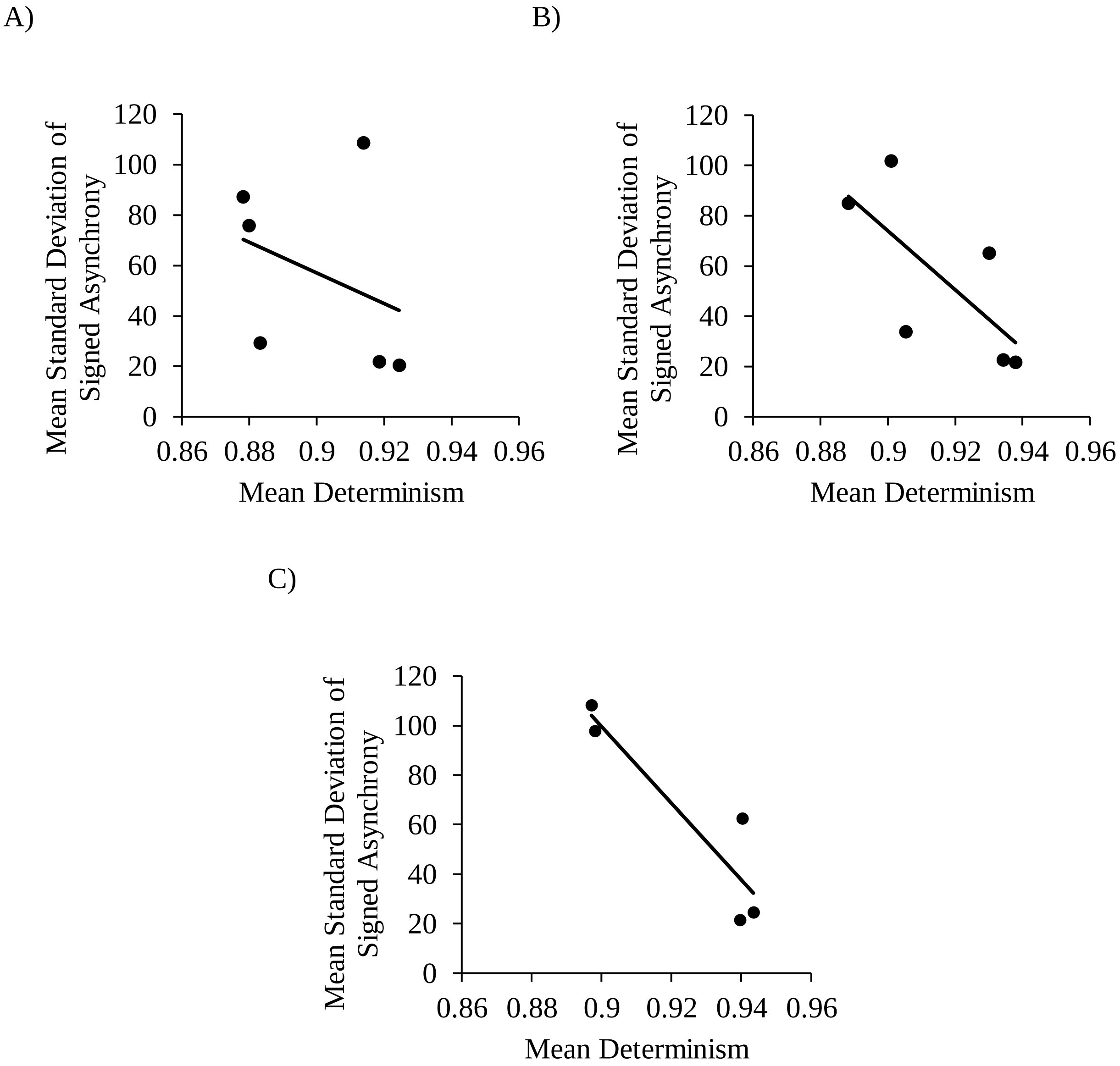

Figure 9. Correlation between mean determinism from cross-recurrence and the mean standard deviation of the signed asynchrony for the SPR (A), 15% Slower (B), and 30% (C) Slower Rates.

6. References

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Chapter 6

General Discussion

1. Overview of Aims and Hypotheses

The flexibility to coordinate actions with auditory sequences at different rates is critical to many individual and group activities. Previous work has suggested that both Spontaneous Production Rates (e.g., Zamm, Wang, & Palmer, 2018; Zamm, Wellman, & Palmer, 2016) and musical training (e.g., Aschersleben, 2002; Repp, 2010; Repp & Doggett, 2007) influence rate flexibility of auditory-motor synchronization. However, little is known about how these two factors interact, and the behavioral and neural mechanisms by which they influence rate flexibility. The goal of this dissertation was to investigate the interactive effects of SPRs and musical training on rate flexibility, and to identify behavioral and neural markers of rate flexibility.

Motivated by an abundance of literature suggesting that musical training enhances auditory-motor synchronization performance (e.g., Aschersleben, 2002; Repp, 2010; Repp & Doggett, 2007; Thompson, White-Schwoch, Tierney, & Kraus, 2015), this dissertation first hypothesized that the ability to synchronize and adapt to rates that do not match an individual's SPR is enhanced by musical training. Second, this dissertation hypothesized that enhanced rate flexibility with musical training is characterized by less repetitive, predictable, and mathematically stable behavior, as would be suggested from a dynamical systems perspective (Schmit, Regis, & Riley, 2005). These hypotheses were tested with musicians and nonmusicians in Chapters 2 and 3.

This dissertation also developed a novel application of Recurrence Quantification Analysis to investigate the hypothesis that greater behavioral flexibility is supported by more predictable and mathematically stable auditory-motor oscillatory neural activity at the performance rate. The use of RQA to characterize a neural signature of behavioral flexibility was motivated by encouraging findings suggesting that this technique is sensitive to changes in the dynamics of neural oscillations in both the temporal (Acharya, Sree, Chattopadhyay, Yu, & Ang, 2011; Becker, Schneider, Eder, Ranft, Kochs, Zieglgänsberger, & Dodt, 2010; Niknazar, Mousavi, Vahdat, & Sayyah, 2013) and frequency (Ladeira, Marwan, Destro-Filho, Ramos, & Lima, 2020) domains, which have been linked to beat perception (Tal, Large, Rabinovitch, Wei, Schroeder, Poeppel, & Golumbic, 2017) and synchronization performance (Bouvet, Bardy, Keller, Dalla Bella, Nozaradan, & Varlet, 2020; Nozaradan, Peretz, & Keller, 2016). Chapter 4 validated the novel application and Chapter 5 tested this hypothesis.

In the sections that follow, the contributions of each study, their importance within the context of the current knowledge, and the key research themes of the dissertation are discussed. The dissertation then concludes with a discussion of directions for future research.

2. Research Contributions

2.1 Musical Training Enhances Rate Flexibility of Synchronization

The first study presented in Chapter 2 introduced and validated a novel musical tapping task to measure SPRs and examine rate flexibility of auditory-motor synchronization in broader populations. Pianists performed and tapped familiar melodies at a comfortable rate (their SPRs). Findings showed that rates measured through music performance and the novel tapping task were highly correlated across melodies, across tasks, and did not differ across tasks. The validated novel tapping task was then implemented with musicians and nonmusicians. Participants tapped a familiar melody at a comfortable rate (their SPRs), and subsequently synchronized their tapping of the same familiar melody with a metronome at their SPRs, and at rates faster and slower than their SPRs. Findings first showed that musicians' SPRs were slower than nonmusicians' SPRs. Second, musicians synchronized more accurately at slower rates than nonmusicians. Third, musicians showed more error correction than nonmusicians and both groups showed more error correction at slower rates. Finally, musicians' enhanced rate flexibility was characterized by less recurrent, predictable, and stable synchronization behavior.

The findings presented in Chapter 2 provide a critical new framework for understanding rate flexibility of auditory-motor synchronization. Much of the previous work has focused on SPRs or musical training in isolation to examine their influences on synchronization. Studies looking at effects of SPRs have exclusively investigated their constraints on coordination in music performance (Loehr & Palmer, 2011; Zamm, Pfordresher, & Palmer, 2015; Zamm, Wang, & Palmer, 2018; Zamm, Wellman, & Palmer, 2016). On the other hand, studies looking at effects of musical training have not accounted for individual differences in SPRs even though evidence suggests that musical training may contribute to these individual differences (Drake, 1999; Drake, Jones, & Baruch, 2000; Drake, Penel, & Bigand, 2000). The second study presented in Chapter 2 importantly showed that SPRs and musical training have interactive effects on rate flexibility, and thus should not be studied in isolation. Importantly, the first study in Chapter 2 describes a novel task that gives researchers a feasible tool for continuing to investigate these interactive effects.

Chapter 2 also identified an asymmetry in the effect of musical training on rate flexibility at non-SPR rates. Previous research has suggested that musicians have an advantage in synchronization as the rate becomes slower (Repp & Doggett, 2007), and that musicians tend to tap more slowly than nonmusicians (Drake, Penel, & Bigand, 2000). Similarly, the second study presented in Chapter 2 showed both slower SPRs in musicians than nonmusicians and greater synchronization accuracy at slower rates in musicians than nonmusicians. In contrast, musicians and nonmusicians did not differ in their synchronization accuracy at faster rates. These findings suggest that musical training may enhance rate flexibility of synchronization via a mechanism specific to supporting successful coordination at slower rates. Furthermore, this finding provides evidence to suggest that there may be separate mechanisms underlying synchronization at slower versus faster rates. This is further supported by the finding that error correction was greater at slower rates than at faster rates, suggesting that as the interval between onsets increases (i.e., the rate becomes slower) cognitive control may play a larger role (Lewis & Miall, 2003).

Another important contribution from Chapter 2 is the use of RQA to characterize the temporal dynamics of musicians' and nonmusicians' synchronization behavior. While previous work has implemented RQA to relate more deterministic and mathematically stable behavior to less flexible systems, it focused primarily on postural control (Negahban, Salavati, Mazaheri, Sanjari, Hadian, & Parnianpour, 2010; Schmit, Regis, & Riley, 2005; Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006). The second study presented in Chapter 2 provides evidence that the inflexibility observed in nonmusicians can also be characterized by more recurrent, deterministic, and mathematically stable patterns of synchronization.

2.2 Musical Training Enhances Rate Adaptation to Perturbations

The study presented in Chapter 3 examined adaptation to rate perturbations toward and away from musicians' and nonmusicians' SPRs. Participants tapped an isochronous version of a familiar melody at their SPRs, and subsequently synchronized with a metronome initially set at their SPRs, and faster and slower rates. They continued to synchronize their tapping of the melody with the metronome as it unexpectedly sped up and slowed down. Findings showed that all participants adapted more quickly to slowing than to speeding perturbations, independent of whether the rate moved toward or away from the SPR, and musicians adapted more quickly than nonmusicians overall. Model comparisons showed that a nonlinear damped harmonic oscillator model provided a better fit to the data than a linear exponential decay model. Furthermore, damped harmonic oscillator model fits further supported musicians' more efficient adaptation, showing faster rate adaptation and closer return to baseline synchronization for musicians than nonmusicians.

The findings presented in Chapter 3 extend those in Chapter 2 by looking at the influences of musical training and SPRs on rate adaptation to perturbations. While previous work has also examined adaptation to phase and period perturbations in musicians and nonmusicians (Large, Fink, & Kelso, 2002; Repp, 2010), this research has not examined how adaptation in these groups may be influenced by whether the rate is moving toward or away from an individual's SPR. Interestingly, while Chapter 3 provided evidence that musical training enhances rate adaptation, there was no evidence to suggest a simultaneous influence of participants' SPRs. Findings from Chapter 3 rather showed a more general effect of rate such that adaptation was faster for slower rates for both musicians and nonmusicians. This extends prior work with musicians only, showing faster adaptation of music performance to slowing rate perturbations (Loehr, Large, & Palmer, 2011). The lack of a SPR effect in Chapter 3 suggests that the SPR may be best reconceptualized as an optimal range, rather than a singular rate, as has now been suggested by other researchers (Amrani & Golumbic, 2020). Under this view, when testing a larger range of rates, an effect of individual SPRs may emerge.

Another important contribution of Chapter 3 is the comparison of linear and nonlinear models of rate adaptation in musicians and nonmusicians. A longstanding debate within the literature is whether auditory-motor synchronization is supported by linear timekeeping mechanisms (Vorberg & Schulze, 2002; Wing & Kristofferson, 1973) or nonlinear dynamics of underlying oscillations (Large & Jones, 1999; Large & Palmer, 2002; Strogatz & Stewart, 1993). Findings from Chapter 3 add to a growing body of literature suggesting that nonlinear dynamics of underlying oscillations can better account for synchronization performance than linear timekeeping mechanisms (Loehr, Large, & Palmer, 2011; Roman, Roman, & Large, 2020). Furthermore, parameters of the nonlinear model reflecting adaptation time and return to baseline synchronization were able to differentiate musicians and nonmusicians. These findings suggest that parameters of the nonlinear model may also provide useful indicators of flexible or inflexible behavior. Used in combination with machine learning techniques, nonlinear modelling could then help to identify specific patterns of abnormal or inflexible behavior that may point to certain interventions targeted at improving flexibility.

2.3 RQA Captures the Temporal Dynamics of Neural Oscillations Underlying Synchronization

The study presented in Chapter 4 examined the use of a novel application of RQA to oscillatory neural activity to capture the temporal dynamics of neural oscillations underlying auditory-motor synchronization. Musicians synchronized their tapping with a confederate partner in two different rhythm conditions as EEG was recorded from both partners. In one condition, the confederate tapped twice as often as the participant; in the other condition, the confederate tapped half as often as the participant. Findings from auto-recurrence showed higher intra-brain recurrence and stability at the participant tapping frequency (the constant frequency) when that frequency contained more auditory feedback relative to the confederate tapping frequency. Findings from cross-recurrence similarly showed higher inter-brain recurrence and stability at the participant tapping frequency when that frequency contained more auditory feedback relative to the confederate tapping frequency.

The findings presented in Chapter 4 show the sensitivity of RQA to capture changes in the temporal dynamics of oscillatory neural activity related to changes in auditory-motor synchronization. More and more research is applying RQA to neural activity at rest, event-related neural responses to stimuli, and frequency domain characteristics of neural activity (Acharya, Sree, Chattopadhyay, Yu, & Ang, 2011; Becker, Schneider, Eder, Ranft, Kochs, Zieglgänsberger, & Dodt, 2010; Ladeira, Marwan, Destro-Filho, Ramos, & Lima, 2020; Marwan & Meinke, 2004). Crucially, Chapter 4 provides a method for quantifying task-based changes in the temporal dynamics of oscillatory neural activity at a behavioral frequency of interest. This method allows for the investigation of distinct patterns of oscillatory dynamics that give rise to distinct patterns of synchronization performance.

2.4 Musical Training Enhances Stability of Auditory-Motor Neural Activity and Synchronization

The final study presented in Chapter 5 implemented the method developed in Chapter 4 to explore the temporal dynamics of auditory-motor oscillatory neural activity supporting synchronization flexibility in musicians and nonmusicians. Participants tapped a familiar melody at their Spontaneous Production Rates, and subsequently synchronized their tapping with a metronome at their SPRs and rates slower than their SPRs while EEG was recorded. To control for possible differences in inhibitory control between groups, participants also completed an auditory Stroop task. Participants completed additional inhibitory control, auditory, and motor tasks, but due to the ongoing public health crisis, these tasks are beyond the scope of this dissertation. Findings showed that musicians were better able to maintain synchronization accuracy as the rate became slower and synchronized more consistently across rates than nonmusicians. Findings from auto- and cross-recurrence on electrodes reflecting auditory-motor activity during the synchronization task showed increasing neural predictability as the rate became slower and higher neural stability in musicians than nonmusicians. Finally, neural predictability and stability correlated with synchronization consistency at slower rates such that as neural predictability and stability increased, so did synchronization consistency.

The findings presented in Chapter 5 provide a new understanding of how the neural mechanisms supporting auditory-motor synchronization are shaped by musical training. Previous work has shown changes in auditory-motor networks resulting from musical training relate to synchronization performance. However, much of this research has either focused on changes in the structure of auditory and motor regions or level of co-activation between these regions (Bailey, Zatorre, & Penhune, 2014; Bangert & Altenmüller, 2003; Grahn & Rowe, 2009; Lahav, Saltzman, & Schlaug, 2007; Palomar-García, Zatorre, Ventura-Campos, Bueichekú, & Ávila, 2017). Chapter 5 extends these findings by showing changes in the temporal dynamics of auditory-motor activity with musical training that can be related to enhanced synchronization performance, specifically enhanced synchronization consistency.

Chapter 5 also importantly controlled for possible differences in inhibitory control between musicians and nonmusicians by measuring participants' performance on an auditory Stroop task. Unlike previous research that has suggested a link between enhanced inhibitory control in musicians and auditory-motor synchronization performance (Puyjarinet, Bégel, Lopez, Dellacherie, & Dalla Bella, 2017; Slater, Ashley, Tierney, & Kraus, 2018), the findings presented in Chapter 5 did not show differences in inhibitory control between musicians and nonmusicians. While it has been suggested that observing no differences in executive control more generally between these groups may be due to lack of far transfer to non-auditory tasks (Gade & Schlemmer, 2021), this cannot account for the lack of differences in Chapter 5 which used an auditory inhibitory control task. Thus, the findings presented in Chapter 5 suggest that the relationship between musical training and inhibitory control may be more complex than simply near versus far transfer of skills.

Most critically, the findings presented in Chapter 5 provide a new understanding of the neural mechanisms underlying enhanced synchronization consistency at slow rates specifically. Previous work has linked the strength of neural entrainment to the beat with synchronization accuracy (Bouvet, Bardy, Keller, Dalla Bella, Nozaradan, & Varlet, 2020; Nozaradan, Peretz, & Keller, 2016). Furthermore, previous work has shown that synchronization consistency increases as the consistency of the auditory brainstem response to an auditory stimulus, as measured using inter-trial phase locking, increases (Tierney & Kraus, 2013). The findings in Chapter 5 similarly show that as neural predictability and stability increase, so does synchronization consistency. However, this relationship only emerged as the synchronization rate became slower, and thus it appears to be specific to rates slower than an individual’s SPR. This important new finding suggests that neural predictability and stability becomes critical to maintaining synchronization consistency as the task demands increase.

3. Key Research Themes

3.1 Nonlinear Dynamics Framework of Rate Flexibility

One of the key research themes in this dissertation was the adoption of a nonlinear dynamics framework for studying rate flexibility of auditory-motor synchronization. This approach describes auditory-motor synchronization as arising from a system of nonlinear coupled oscillators (Haken, Kelso, & Bunz, 1985). When internal oscillations entrain with auditory rhythms, synchronization can occur (Large, Herrera, & Velasco, 2015; Large & Jones, 1999; Large & Palmer, 2002). As described in detail in the General Introduction, experimental evidence suggests that a wide range of observed behavior can be accounted for using nonlinear dynamical systems models (Loehr, Large, & Palmer, 2011).

The research presented in this dissertation provides further support for a few key components of the nonlinear dynamics framework. Perhaps the most critical distinction of nonlinear models from other models of auditory-motor synchronization is the nature of the coupling between the auditory sequence and the action. Nonlinear models contain a periodic component that results in nonlinear coupling (Loehr, Large, & Palmer, 2011). The importance of this periodic component was directly tested in this dissertation (Chapter 3), where it was shown to produce model fits that could better account for the observed behavior than those without a periodic component. This included more efficient adaptation for slowing rate perturbations, which is not predicted by an alternative linear timekeeper approach.

The nonlinear dynamics framework also makes critical predictions about the behavior of an underlying oscillator with respect to its natural frequency. When coupling with other frequencies, the oscillator will tend to be pulled toward the natural frequency (Winfree, 1987). This prediction was directly tested in this dissertation (Chapter 2) by measuring individuals' natural frequencies as their Spontaneous Production Rates (e.g., Zamm, Pfordresher, & Palmer, 2015; Zamm, Wang, & Palmer, 2018; Zamm, Wellman, & Palmer, 2016) and subsequently pushing individuals away from their SPRs. Supporting this prediction, findings showed that individuals tended to anticipate more at slower rates and lag more at faster rates relative to their SPRs. Importantly, the research presented here tested this prediction for the first time in nonmusicians, showing a stronger influence of SPRs at slower rates specifically. These findings suggest that the predictions of nonlinear dynamical systems models may have particularly important functional consequences when it comes to studying broader populations.

3.2 Musicians as Models of Flexible Systems

A second key research theme in this dissertation was the use of musical training as a model for flexible behavior. Increased practice with a particular skill confers greater flexibility in performing that skill (MacKay, 1982). This makes musical training a particularly good test case for studying flexibility of auditory-motor synchronization. Musicians accumulate years of practice performing music, often involving synchronization with a metronome in solo practice or with other individuals in ensemble performance. Indeed, a large body of research suggests that musical training enhances auditory-motor synchronization, with musicians showing greater synchronization accuracy and more efficient adaptation to rate changes than nonmusicians (Aschersleben, 2002; Repp, 2010).

The research presented in this dissertation extended this work by examining whether musical training can help individuals overcome constraints on rate flexibility, specifically looking at constraints placed by individuals' natural frequencies on auditory-motor synchronization. Musicians were better able to synchronize with rates slower than their Spontaneous Production Rates, whereas musicians and nonmusicians synchronized similarly with rates faster than their SPRs (Chapter 2). This finding is consistent with previous research indicating that musical training may provide a specific advantage at slower rates (Drake, Penel, & Bigand, 2000; Repp & Doggett, 2007), and was further observed in Chapter 5. The asymmetry observed between slower and faster rates may further suggest that musical training overcomes constraints of SPRs at slower rates by benefiting cognitive systems specifically (Lewis & Miall, 2003).

Chapter 3 also showed that musicians were better able to adapt to rate changes in real time than nonmusicians, independent of their SPRs. This finding is consistent with previous research suggesting more efficient adaptation of musicians to changes in the rate of an auditory sequence (Madison & Merker, 2004; Repp, 2010). The rates presented to participants in Chapter 3 did not span as wide a range as those in Chapter 2, where the largest differences observed between musicians and nonmusicians were at the slowest rate. Thus, both musically trained and untrained individuals may not be impacted by their SPRs until pushed toward more extreme rates, at which point musical training may help overcome constraints. Despite this, musicians displayed greater rate flexibility as demonstrated by their more efficient adaptation, suggesting that musical training improves flexibility even in the absence of additional constraints on behavior.

3.3 Auditory-Motor Integration as a Mechanism for Enhanced Rate Flexibility

A third key research theme in this dissertation was the underlying mechanism by which musical training enhances rate flexibility. The General Introduction described two prime candidates: 1) auditory-motor integration and 2) inhibitory control. Musical training strengthens co-activation of auditory and motor brain networks (Lahav, Saltzman, & Schlaug, 2007), and this increased auditory-motor integration has been related to enhanced synchronization performance (Bailey, Zatorre, & Penhune, 2014). Additionally, some research suggests that musical training enhances inhibitory control (Bugos, Perlstein, McCrae, Brophy, & Bedenbaugh, 2007), which has also been related to enhanced synchronization performance (Slater, Ashley, Tierney, & Kraus, 2018).

The research presented in this dissertation examined the contributions of both auditory-motor integration and inhibitory control mechanisms to rate flexibility of auditory-motor synchronization. The findings presented in Chapter 5 did not show differences in inhibitory control between musicians and nonmusicians, despite adapting the task to the auditory domain

(Morgan & Brandt, 1989) to avoid issues related to far transfer (Gade & Schlemmer, 2021). These findings stand in contrast to previous research suggesting an enhancement in inhibitory control with musical training. Thus, inhibitory control may only be enhanced under specific circumstances. For example, the type of musical training appears to be an important factor as percussionists have been shown to display enhanced inhibitory control over non-percussionists and nonmusicians (Slater, Ashley, Tierney, & Kraus, 2018; Slater, Azem, Nicol, Swedenborg, & Kraus, 2017).

The findings presented in Chapter 5 instead suggest that strengthened auditory-motor integration may be the underlying mechanism by which musical training enhances rate flexibility. RQA on electrodes previously shown to reflect auditory-motor activity (Scheurich, Demos, Zamm, Mathias, & Palmer 2019; Nozaradan, Zerouali, Peretz, & Mouraux, 2015) revealed more stable oscillatory neural activity in musicians than nonmusicians. Furthermore, predictability and stability of auditory-motor oscillatory neural activity was related to synchronization consistency at slower rates where musicians show a synchronization advantage. Thus, auditory-motor integration may be a critical mechanism by which musical training allows for more flexible synchronization at slow rates specifically.

3.4 Recurrence Quantification Analysis for Identifying Behavioral and Neural Signatures of Rate Flexibility

A final key research theme in this dissertation was the transition from traditional linear methods to nonlinear analytical techniques. Previous work has primarily implemented analytical techniques with assumptions that are often violated for data such as neural oscillations, including the assumption of signal stationarity. These methods also often treat sources of variability as nuisance variables, despite previous work suggesting that many sources of variability contain valuable information about the system of interest (e.g., Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006). This presents the need for adopting new techniques well-suited for investigating these nonlinearities.

The research presented in this dissertation used Recurrence Quantification Analysis, a nonlinear dynamical systems analytical technique, to examine both the behavioral and neural characteristics of rate flexibility. In the behavioral domain, researchers have demonstrated the importance of treating nonlinearities as more than nuisance variables. A study examining postural sway patterns in patients with Parkinson's disease compared traditional measures of postural sway variability with RQA outcomes computed from the same data. Results showed that although traditional measures showed greater variability of postural sway in Parkinson's patients, RQA metrics critically revealed a more deterministic, less random structure of the variability that represented a loss of flexibility (Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006). Similarly, RQA of synchronization data in Chapter 2 revealed more recurrent, deterministic, and mathematically stable behavior in nonmusicians than musicians, reflecting their greater inflexibility. These findings support the idea that analyzing sources of variability can provide important insights into the system of interest, and disregarding this variability can lead to an incomplete understanding of the mechanisms at play.

The research presented in this dissertation also described and implemented a novel application of RQA to oscillatory neural activity recorded with EEG (Chapter 4). Findings revealed that RQA is sensitive to subtle changes that occur in the temporal dynamics of oscillatory neural activity with changes in auditory-motor synchronization task demands. Chapter 5 then expanded this novel approach to examine neural signatures of rate flexibility with musical training. In contrast to the behavioral signatures of flexibility observed in Chapter 2, findings showed that more consistent synchronization performance at slower rates was associated with more deterministic and mathematically stable oscillatory neural activity. This is in line with previous work suggesting a relationship between consistency of neural activity and synchronization performance (Tierney & Kraus, 2013), and may reflect stronger and more stable entrainment supporting successful synchronization (Nozaradan, Peretz, & Keller, 2016).

That RQA was sensitive to differences across groups and changes across rates in the temporal dynamics of both synchronization behavior and oscillatory neural activity makes it a promising approach for future use. Furthermore, these findings demonstrate the importance of treating nonlinearities as variables of interest rather than nuisance. Nonlinearities are characteristic features of all biological systems, and are therefore critical for fully understanding the behavioral and neural mechanisms underlying rate flexibility of auditory-motor coordination.

4. Future Directions

4.1 Naturalistic Forms of Movement

This dissertation extended previous work that had measured Spontaneous Production Rates exclusively in musicians through music performance by developing a novel auditory-motor task that could easily be performed by nonmusicians. This was a necessary first step for investigating the interactive effects of SPRs and musical training on rate flexibility of auditory-motor synchronization. With these initial insights in mind, it is important to move beyond simple finger-tapping tasks and begin to examine more naturalistic forms of movement that both musicians and nonmusicians engage in while synchronizing.

Some studies have already begun to examine synchronization of naturalistic body movements to auditory stimuli such as bobbing the head or tapping the foot. Su and Pöppel (2012) compared the ability of musicians and nonmusicians to find the beat of an auditory stimulus who either moved along with that stimulus or did not. Regardless of musical training, moving one's body naturally along with the stimulus aided participants in finding the beat. Other research has also shown that individuals without professional musical training successfully synchronize full body movement with a metronome and music (Phillips-Silver, Toiviainen, Gosselin, Piché, Nozaradan, Palmer, & Peretz, 2011). Interestingly, even bouncing an infant along to the beat of an auditory stimulus appears to have an effect on the infant's perception of rhythm: infants prefer to listen to an auditory stimulus that matched the rhythm of their movement (Phillips-Silver & Trainor, 2005). These studies seem to suggest that individuals possess a natural inclination to match the beat of an auditory stimulus when using more naturalistic movements. Thus, SPRs and musical training may play different or lesser roles in the synchronization of more naturalistic behaviors.

Another important consideration when beginning to move toward studying synchronization of more naturalistic body movements is how the kinematics of different movements may influence an individual's performance. Previous work has suggested that movements executed in different ways can change performance (Manning, Harris, & Schutz, 2017). This was also suggested in the first study presented in Chapter 2, where changing whether the arm rested on a surface may have influenced the temporal dynamics of finger-tapping. Considering more naturalistic body movements, Tranchant, Vuvan, and Peretz (2016) compared synchronization of bouncing with synchronization of clapping to a metronome and music. Synchronization with the rate of the metronome and music was better for clapping than for bouncing. This may result from the additional auditory feedback produced by clapping the hands, or the additional gravitational pull placed on the body during bouncing (Tranchant, Vuvan, & Peretz, 2016). Given that auditory-motor synchronization performance seems to differ depending on the type of movement under investigation, the influences of SPRs and musical training may further interact with the movement being studied. This should be considered in future research looking at naturalistic forms of movement.

4.2 Expertise Beyond Musical Training

Musical training was considered in this dissertation as a possible factor allowing individuals greater flexibility around constraints of SPRs. There is considerable research suggesting that musical training enhances auditory-motor synchronization (e.g., Aschersleben, 2002; Repp, 2010; Repp & Doggett, 2007; Thompson, White-Schwoch, Tierney, & Kraus, 2015), making this an excellent starting point for an investigation into the factors that increase flexibility. With a better understanding of how musical training facilitates flexibility, it is important to begin considering other facilitatory factors, including other areas of expertise.

One factor that could be explored in future research is dance expertise. Like musicians, dancers must coordinate their actions precisely in time with music or with other dancers to create a coherent performance. Given the similar demands of music and dance performance, it may be that expert dancers also show enhanced flexibility of auditory-motor synchronization. Some recent research has begun to examine the influences of dance expertise on synchronization performance. Jin, Wang, Lv, Lu, Chen, & Zhou (2019) compared dancers' and non-dancers' synchronization of finger-tapping with auditory, visual, and audiovisual stimuli. Dancers synchronized more accurately and more consistently compared with non-dancers. Similarly, dancers have been shown to coordinate finger movements more stably with an auditory metronome (Miura, Fujii, Okano, Kudo, & Nakazawa, 2016). These findings suggest that dance expertise is a prime candidate for future research examining additional factors that facilitate flexibility of auditory-motor synchronization.

Another area that could be explored in future research is expertise in sports involving rhythmic movements, such as rowing. Although further removed from the musical contexts largely considered in this dissertation, rowing similarly requires high precision of motor coordination: Rowers must coordinate their strokes in time with one another to propel the boat forward (Vuoskoski & Reynolds, 2019). The possible facilitatory effects of expertise in these kinds of rhythmic sports has been largely unexplored to date. Future research in this area could importantly provide further insight into the common underlying mechanisms across a range of rhythmic activities that give rise to highly flexible coordination behavior.

4.3 Musical Interventions for Improving Flexibility

This dissertation showed that musical training can help overcome constraints of SPRs, allowing for more flexible coordination. The findings presented here further suggest that musical training enhances flexibility by increasing the predictability and stability of auditory-motor oscillatory neural activity at the frequency of the behavior. One of the critical implications for these findings is in using musical interventions in rehabilitation for neurological disorders where flexibility of coordination is impaired. With an understanding of how musical training can enhance flexibility in healthy populations, musical interventions can be optimally designed and their use in rehabilitative settings can be better understood.

One area of interest that has received increasing attention from researchers is the use of musical interventions for patients with Parkinson’s disease. One of the characteristic symptoms of Parkinson’s disease, which has been quantified using RQA, is increased rigidity of the motor system (Schmit, Riley, Dalvi, Sahay, Shear, Shockley, & Pun, 2006). Rhythmic auditory stimulation embedded within music has already been shown to improve walking patterns in patients with Parkinson’s disease (Thaut, McIntosh, Rice, Miller, Rathbun, & Brault, 1996).

Importantly, the use of this kind of musical intervention shows additional benefits for alleviating symptoms of depression in these patients (Hayashi, Nagaoka, & Mizuno, 2006), making this an ideal, non-invasive intervention. Similar to the findings presented here that musical training is related to increased neural stability at the frequency of the behavior, there is some initial evidence to suggest that improvements in walking patterns may be related to enhanced neural power at the frequency of walking (Calabrò, Naro, Filoni, Pullia, Billeri, Tomasello, Portaro, Di Lorenzo, Tomaino, & Bramanti, 2019). Future work can aim to better understand how musical interventions with Parkinson's patients affect the underlying neural mechanisms supporting walking behaviors, and how these interventions can be optimally designed to account for the wide range of individual differences observed in the disease.

Applications of musical interventions may not be limited to movement disorders. Other disorders such as autism spectrum disorder may also receive benefits from musical interventions (for a review, see Quintin, 2019). Individuals with autism spectrum disorder may present with motor difficulties, and there is some evidence to suggest that movement with music can improve motor proficiency in these individuals (Atigh, Akbarfahimi, & Zarei, 2017). Interestingly, individuals with speech disorders may also benefit from musical interventions. For example, some evidence suggests that children with dyslexia may show abnormal neural entrainment to auditory stimuli (Colling, Noble, & Goswami, 2017). The findings presented in this dissertation suggest that musical training could be a promising avenue of future investigation as an intervention for these disorders.

5. Concluding Remarks

In sum, the findings presented in this dissertation suggest that musical training can help overcome constraints of Spontaneous Production Rates, allowing for more flexible auditory-motor synchronization. Importantly, this enhanced flexibility can be characterized by more predictable and stable dynamics of auditory-motor oscillatory neural activity. This dissertation provides important building blocks for improving our understanding of the factors that give rise to flexible coordination behavior as well as the neural mechanisms supporting flexibility.

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