Cardiac Dynamics in Auditory Rhythm Perception and Production

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August, 2023

A thesis submitted to McGill University in partial fulfilment of the requirements of the degree of

Doctor of Philosophy in Experimental Psychology

Table of Contents

Abstract

This dissertation investigates how auditory rhythm perception and production affect cardiac dynamics. The first hypothesis is that individual differences in biological rhythms modulate musicians’ performance rates and cardiac responses during performance. Chapter 1 describes a study that measures pianists’ cardiac activity while performing simple melodies across four times of day (09h, 13h, 17h, 21h), using a novel application of a nonlinear analysis technique to cardiac data. Results showed that performance rates were slowest in the morning (first session), particularly for pianists with less musical training, while consistent within individual across the 12h day. Cardiac activity was most predictable and stable in the morning, and melody familiarity also affected cardiac predictability. These findings point to time of day and practice effects of auditory rhythms on cardiac activity. The second hypothesis is that auditory rhythm production results in more recurrent, more predictable cardiac dynamics than auditory rhythm perception. The third hypothesis is that cardiac activity will become more recurrent and more predictable for simple rhythms than complex rhythms. Chapter 2 describes a study that measures musicians’ behaviour and cardiac rhythms during perception of and synchronisation with simple and complex auditory rhythms. Findings indicated that synchronisation with complex rhythms was worse than synchronisation with simple rhythms. Cardiac recurrence and predictability were greater during rhythm perception than during synchronisation, indicating greater potential entrainment of cardiac activity during perception. Cardiac dynamics were more recurrent during simple rhythm synchronisation than complex rhythm synchronisation, but the opposite was true for perception, suggesting possible roles of task difficulty and auditory/motor timing in cardiac dynamics. The final hypothesis is that learning, in the form of short-term training, will reduce cardiac recurrence and predictability during auditory rhythm production. Chapter 3 describes a study that tested short-term learning effects on complex rhythm synchronisation in individuals with a variety of musical experience. Consistent with Chapter 2, synchronisation was better for the simpler of the two rhythms, and cardiac dynamics were most recurrent for the simpler rhythm. Individuals' cardiac recurrence and predictability were consistent across training and different rhythms, indicating stable individual differences in cardiac dynamics during auditory-motor synchronisation. Overall, the findings in this dissertation demonstrate 1) the applicability of nonlinear analysis techniques to cardiac data during auditory-motor synchronisation tasks, 2) stable individual differences in auditory-motor synchronisation behaviour and cardiac dynamics, and 3) task difficulty and rhythm complexity interact to influence cardiac dynamics. These findings contribute to understanding the physiological underpinnings of auditory rhythm perception and production.

Résumé

Le but de cette thèse est d’étudier les effets de la perception et la production de rythmes auditifs sur le système cardiaque. La première hypothèse stipule que les différences individuelles en rythmes biologiques contribuent au tempo de la performance et de la réponse cardiaque des musiciens. Le chapitre 1 décrit une étude où l'activité cardiaque des pianistes a été mesurée lors de quatre sessions au cours d’une même journée (09h, 13h, 17h, 21h), durant lesquelles ils jouaient des mélodies simples. Une nouvelle application d'une technique d'analyse non linéaire a été employée pour l'analyse des rythmes cardiaques. Les résultats ont montré que le tempo des performances était plus lent le matin (première session), notamment pour les pianistes avec moins d'années de formation, mais le tempo des performances de chaque individu était stable au cours des 12 heures de la journée. Les rythmes cardiaques étaient plus prédictibles et stables le matin, et la prédictibilité des rythmes cardiaques était également influencée par la familiarité des mélodies. Dans l’ensemble, ces résultats indiquent qu'il y a un effet de l'heure de la journée et de l'entraînement avec les rythmes auditifs sur les rythmes cardiaques. La deuxième hypothèse stipule que la production de rythmes auditifs, comparée à la perception des mêmes rythmes, entraîne des rythmes cardiaques plus répétitifs et plus prédictibles. Pour la troisième hypothèse, il est attendu que les rythmes cardiaques deviendront plus répétitifs et prédictibles pour les rythmes simples que pour les rythmes complexes. Le chapitre 2 décrit une étude où le comportement et les rythmes cardiaques ont été mesurés chez les musiciens dans une tâche d’écoute passive et une tâche de synchronisation avec des rythmes auditifs simples et complexes. Les résultats ont montré que la synchronisation était moins bonne avec les rythmes complexes qu’avec les rythmes simples. La récurrence et la prédictibilité des dynamiques cardiaques étaient plus importantes pendant la perception que pendant la synchronisation, ce qui indique que l’entraînement des rythmes cardiaques est plus important lors de tâches perceptives. Une plus grande récurrence dans les rythmes cardiaques était observée quand les musiciens se synchronisaient avec les rythmes simples qu’avec les rythmes complexe, mais l'inverse a été observée pendant la perception, suggérant que la difficulté d'une tâche et le timing auditif-moteur peuvent contribuer aux dynamiques cardiaques. La dernière hypothèse stipule que l'apprentissage à court-terme réduit la récurrence et la prédictibilité cardiaque pendant la production de rythmes auditifs. Le chapitre 3 décrit une étude dans laquelle les effets de l'apprentissage à court-terme sur la synchronisation avec les rythmes complexes ont été testés chez des individus avec différents niveaux d'expérience musicale. Comme dans le chapitre 3, une meilleure synchronisation et une plus grande récurrence dans les dynamiques cardiaques ont été observées pour le rythme le plus simple. Les individus ont montré, pour tous les niveaux d’apprentissage et les deux types de rythme, de la stabilité dans la récurrence et la prédictibilité des rythmes cardiaques, ce qui indique que les différences individuelles dans les dynamiques cardiaques sont stables pendant les tâches de synchronisation auditives-motrices. Dans leur ensemble, les résultats de cette thèse démontrent 1) la possibilité d'appliquer les techniques d'analyses non linéaires aux données cardiaques pendant des tâches synchronisation auditive-motrice, 2) une stabilité dans les différences individuelles en synchronisation auditive-motrice et dans la dynamique de l’activité cardiaque, et 3) l’effet d’interaction entre la difficulté d'une tâche et la complexité rythmique sur les dynamiques cardiaques. Ces résultats contribuent à notre compréhension des bases physiologiques de la perception et de la production des rythmes auditifs.

Acknowledgements

Thank you to Dr Caroline Palmer for your dedication to my success in the PhD programme and beyond. You have taught me a lot about what it is to be a scientist, and you have undoubtedly helped me to become a stronger researcher over the last 5 years. You kept my progress going during a global pandemic, finding creative ways to continue data collection. Although you skillfully helped me navigate that time, I truly hope that you will never have to go through that again. The SPL is a textbook demonstration of supportive scientific collaboration and camaraderie amongst undergraduates, graduate students, and post-doctoral researchers; thank you for setting this standard in our research environment.

Many individuals have contributed to the research presented in this dissertation. Thank you to the members of my advisory committee, Dr Blaine Ditto and Dr Mathieu Roy, for providing invaluable feedback on my research. Thank you to Chantale Bousquet, Dr Barbel Knauper, and Nina Pinzarrone for your guidance. A massive thank you to Sebastian Andric, Selva Asgharizadeh, Amy Friedman, Yuki Landry, Leen Mshasha, Nour Saba, Sasha Sorger-Brock, and Negar Tahmazian for assisting with data collection, organisation, and analysis at various points over the last 5 years. Thank you to my labmates in the SPL, past and present, for creating a stimulating research environment: Polina Plitchenko, Eléonore Scholler, Ella Sahlas, Fran Spidle, Ajin Tom, Emma Tomiuk, Shelby Trapid, Pauline Tranchant, Bavo Van Kerrebroeck, Harish Venkatesan, Wenbo Yi, and Luke Zhang. A particular thank you to past labmates and friends Drs Valentin Bégel, Rebecca Scheurich, and Jessica Slater. Your insight and support bolstered me at countless points over the years. Finally, many thanks to Louis Deng and Sandra Kuliver for their technical assistance; you made tedious tasks more fun.

At times, I felt a little lost during my PhD. The COVID-19 pandemic threw a wrench in conducting research and brought me face to face with big questions about what I was doing and where I would go next. Dr Kristine Onishi played a major role in showing me what I love about being a part of the scientific community. Thank you for renewing my passion for psychology and introducing me to the joys and challenges of teaching. You went above and beyond as a mentor when you didn't have to, and I am incredibly grateful for that.

A number of individuals have been integral over the years to my development as a scientist. Thank you to Dr Mario Liotti who supported me in my first research project on music and emotion and to Dr Marc Thompson for being a kind and diligent supervisor. Thank you to the best philosophy professor I had, Dr David Anderson, whose deep thinking inspired me to be curious and ask questions. An additional thank you to all those who have pushed me intellectually and met my queries with an open mind over the years.

It is probably impossible to give enough thanks to my parents for their multi-faceted support, so I'll just say: Thank you for instilling in me the value of learning for the sake of learning, for your uncompromising acceptance of who I am, and for the many dinners ordered "on you" in the past 5 years when I complained about being tired. To my older brothers, Eric and Ian, and my sister-in-law Ruby: Thank you for serving as models of how to be successful academically and for encouraging me throughout my PhD. Thank you to my friends who have shared in the ups and downs of this journey, particularly Carolyn Deady, Clara Freeman, and Eilish Rodden. Finally, to Joshua Starr. Thank you for weathering all kinds of storms with me; you are kind, supportive, and a fantastic math and coding teacher.

Oh, and thank you to my cat, Nova, and the cricket symphony outside my window that reminds me why I study what I study.

Contribution to Original Knowledge

A large body of literature has investigated a number of behavioural and physiological factors that affect auditory-motor synchronisation in humans. Within this body of literature, how cardiac rhythms are related to perception and production of auditory rhythms has received relatively little attention. The work presented in this dissertation contributes to this body of literature by examining cardiac activity during auditory rhythm perception and production tasks.

The first manuscript of this dissertation (Chapter 1) investigates how biological rhythms are related to spontaneous performance tempo. Specifically, the study probes whether performance tempo changes according to time of day, and whether circadian-related effects of cardiac activity are related to performance tempo. Important findings from this study include 1) slower spontaneous performance rates earlier in the day, a novel finding that is consistent with time of day effects on performance rates, 2) stable individual differences in performance tempo across a 12h day, which extends previous work examining individual differences in performance rates, and 3) time of day and melody effects of music performance on nonlinear cardiac dynamics. Notably, this study contains a novel application of a nonlinear analysis technique to cardiac data during music performance.

The second manuscript in this dissertation (Chapter 2) examines how listening to versus synchronising with a simple or a complex auditory rhythm affects cardiac activity. Results from this study show that cardiac rhythms are affected differently during auditory rhythm perception and synchronisation, and that simple and complex rhythms affect cardiac activity in different ways during perception and production. These findings are important in establishing a link between cardiac activity, task difficulty, and rhythm complexity.

The final manuscript in this dissertation (Chapter 3) builds on previous research into musical training effects (long-term training) on auditory-motor synchronisation by investigating how short-term training on complex auditory rhythms influences performance and cardiac activity. The behavioural findings from this study support recent theoretical models of coupled oscillators (Kim & Large, 2019); additionally, cardiac-behaviour correspondences are shown to occur even with short-term training, and stable individual differences in nonlinear cardiac dynamics are shown to exist for the first time in an auditory-motor synchronisation context.

Contribution of Authors

General Introduction and Literature Review

I, Shannon Wright, am the sole author of the contents of this section. Caroline Palmer provided comments on this section.

Chapter 1: Physiological and Behavioural Factors in Musicians' Performance Tempo

Authors: Shannon Wright (first author), Caroline Palmer

Both authors contributed to design and implementation of the experiment. I, Shannon Wright, conducted data collection, performed analyses, and wrote the manuscript. Caroline Palmer contributed to data analysis, writing, and revision of the manuscript.

Chapter 2: Auditory rhythm complexity affects cardiac dynamics in perception and synchronisation

Authors: Shannon Wright (first author), Caroline Palmer

Both authors contributed to design and implementation of the experiment. I, Shannon Wright, conducted data collection, performed data analyses, and wrote the manuscript. Caroline Palmer contributed to data analysis, writing, and revision of the manuscript.

Chapter 3: Short-term training and rhythm complexity affect auditory-motor synchronization

Authors: Shannon Wright (first author), Caroline Palmer

Both authors contributed to design and implementation of the experiment. I, Shannon Wright, conducted data collection, performed data analyses, and wrote the manuscript. Caroline Palmer contributed to data analysis, writing, and revision of the manuscript.

General Discussion

I, Shannon Wright, am the sole author of the contents of this section. Caroline Palmer provided comments on this section.

List of Figures

General Introduction and Literature Review

Chapter 1

Chapter 2

Chapter 3

General Introduction and Literature Review

Auditory and motor rhythms are pervasive in human and non-human animal behaviour. Vocalisations in non-human animals display predictable, rhythm-like qualities (De Gregorio et al., 2021; James & Sakata, 2017; Roeske et al., 2020). Humans demonstrate precise temporal coupling between the auditory and motor systems, known as auditory-motor synchronisation, in rhythmic behaviours such as speech, dance, and music performance. Many studies have investigated neural mechanisms of successful temporal coordination between the auditory and motor systems in humans during passive auditory rhythm perception (Fujioka et al., 2009; Fujioka et al., 2012; Nozaradan et al., 2011) and auditory-motor synchronisation with rhythms (Gilmore & Russo, 2021; Mathias et al., 2020; Nozaradan et al., 2015; Scheurich et al., 2020) . The role of cardiac activity in rhythm perception, rhythm production, and auditory-motor synchronisation has received comparatively less attention. The central and peripheral nervous systems have extensive bidirectional projections (Benarroch, 2012; Porges, 2007), and higher-level neural activity can be modulated by cardiac activity (Sandman, 1984); bidirectional modulation also occurs between cardiac activity and cognition (Barber et al., 2020; Fairclough et al., 2005) and perception (Al et al., 2020; Tanaka et al., 2021). An open question is how cardiac activity is influenced during auditory rhythm perception and production. This dissertation addresses the relationship between auditory rhythms and cardiac activity during perception and action.

Rhythm Complexity in Perception and Production

What is a Rhythm?

At the most basic level, a rhythm refers to sequences of events that are temporally predictable based on the timing of past events in the sequence (Fraisse, 1982). The perception of a rhythm in acoustic signals is multi-faceted and can arise from different acoustic factors. For example, systematic changes in pitch, intensity, and/or temporal intervals between tone onsets in a sequence of acoustic tones can give rise to a percept of a repeating pattern (Drake, 1993; Drake et al., 1991; Huron & Royal, 1996). Tempo and metre are two key components in auditory rhythm perception and production (Honing, 2013). Tempo refers to the rate of the elements in a sequence and is a key factor in rhythm perception because it can influence whether elements in a sequence will be identified as distinct (when the tempo is too fast) or identified as unrelated (when the tempo is too slow) (Repp, 2005). Metre refers to the multiple timescales at which rhythms are perceived in the same auditory sequence, meaning that a single acoustic stimulus can be perceived as rhythmic on several temporal levels (McAuley, 2010). The beat frequency level is typically known as the pulse frequency (Large et al., 2015) and is usually the most perceptually salient frequency in a rhythm. Hierarchy in temporal structure can be perceived at frequencies slower than the beat frequency (they evenly subdivide the beat) and frequencies that are faster than the beat frequency (they are integer multiples of the beat frequency) (Large et al., 2015). Much research in auditory cognitive neuroscience focuses on auditory rhythms that arise from predictable temporal relationships between tones or elements in a sequence. These types of auditory rhythms will be the focus in this dissertation.

Theoretical Perspectives on Rhythm Complexity

Interval theories of rhythm perception and production posit the existence of an internal clock that tracks the duration of events (McAuley, 2010). Single-clock models maintain there is one internal timekeeper (Wing & Kristofferson, 1973). In a single clock model, the simplest rhythms will be those whose elements form integer multiple ratios with one another (such as 1:1 or 1:2) because the internal timekeeper does not need to adjust its period to track interval durations. Another approach to defining rhythm complexity has been referred to as a "rule-based approach" (McAuley, 2010). In this approach, a hierarchical internal clock (in contrast to a single internal clock) is assumed to operate in an individual (Povel & Essens, 1985). This internal clock can be modulated by an auditory rhythm. Whether the temporal structure of a rhythm is such that events in the rhythm are integer multiples of one another, or can be divided into equal time units, known as metrical coding, is key in determining whether it is a simple or a complex rhythm (Chen et al., 2008b; Essens & Povel, 1985). In particular, rhythms that are weakly metrical will only weakly modulate the internal clock while rhythms that are strongly metrical will strongly modulate the internal clock; weakly metrical rhythms are thus considered complex, and strongly metrical rhythms are thus considered simple (McAuley, 2010; Povel & Essens, 1985). Indeed, behavioural studies in which individuals spontaneously produce or reproduce sequences of tones suggest that humans show a production bias towards sequences whose elements are related in simple integer multiple ratios typical of meter in Western music (Chen et al., 2008b; Essens, 1986; Essens & Povel, 1985).

Another approach to modelling rhythm complexity comes from nonlinear dynamical systems theory. Nonlinear dynamics is the study of change in complex systems, systems whose outputs are not necessarily proportional to their inputs (Guastello & Liebovitch, 2009), and of which biological organisms are an excellent example (Freeman, 1991). The nonlinear dynamical framework defines rhythm complexity by appealing to principles of coupled oscillators. Buzsaki (2006) provides an intuitive definition of an oscillator: The motion of a car circling a racetrack is repetitive and slightly varied, but ultimately bounded by the limits of the track. An oscillator thus shows periodicity (repetition or regularity) in its behaviour. When oscillators are coupled, it means they interact to influence one another’s periodic behaviour (Strogatz, 2003). Coupling between two oscillators occurs when the phase or period of those oscillators entrain to create a stable phase or period relationship (Guasetello & Liebovitch 2009).

Whether two oscillators become stably coupled is largely a function of how similar their natural frequencies are, and the extent to which one oscillator can drive the other to match its phase or period (known as coupling strength; Dotov & Trainor, 2021; Large et al., 2015). From these two parameters, the stability of the phase- or period-coupling of the oscillators is determined, and a region of stable coupling or synchronisation is established (Treffner & Turvey, 1993). For oscillators whose natural frequencies form near-simple integer multiple ratios (such as 2:1), synchronisation is likely even at relatively low coupling strengths; conversely, oscillators whose natural frequencies deviate away from simple integer multiple ratios (such as 3:2) require greater coupling strength to achieve stable coupling (Hessler & Amazeen, 2014; Large et al., 2015; Treffner & Turvey, 1993).

Neural resonance theory, proposed by Large & Snyder (2009), makes predictions about rhythm perception and production that come from nonlinear dynamical systems theory of coupled oscillators. Large and Snyder propose there is resonance, or entrainment, between endogenous neural oscillations and exogenous auditory rhythms: Neural oscillations can become period and/or phase coupled to auditory rhythms. This coupling is posited to underlie rhythm and beat perception (Large & Snyder, 2009; Large et al., 2015). A number of neurophysiological studies show that auditory rhythms modulate and entrain neural oscillations (Fujioka et al., 2009; Fujioka et al., 2012; Gilmore & Russo, 2021; Nozaradan et al., 2011). According to neural resonance theory, neural oscillations will be preferentially entrained by acoustic rhythms when tone onsets occur within a certain time window of the neural oscillation (Bauer et al., 2015; Large & Palmer, 2002). As the ratio between natural frequencies of oscillators in part governs the stability of coupled oscillators, it follows that auditory rhythms forming a simple integer ratio with neural rhythms will be those that are most easily perceived and produced. This leads to the definition of simple rhythms as ones that have a large synchronisation region (ex. 1:1, 1:2) and complex rhythms as ones that have a small synchronisation region (ex. 3:2, 2:3).

Behavioural Evidence of Rhythm Complexity

Behavioural studies in which participants synchronise their fingers taps with stimulus tones support a human bias toward auditory rhythms with simple-integer ratios. Synchronisation of finger taps with an auditory rhythm has been shown to be more accurate for simple integer ratio rhythms (ex. 2:1) than for non-integer ratio complex rhythms (ex. 3:2) (Deutsch, 1983). Participants have shown success in synchronising their finger taps with various 3:2 rhythms at fast tempi about 60% of the time, producing mean tapping ratio values of 1.76 (a mean tapping ratio of 1.5 would represent perfect synchrony) (Repp et al., 2005). Similarly, Snyder et al. (2006) had participants tap to drum patterns with 3:2 interval ratios (long-short-short and short-short-long patterns) as well as continue tapping the rhythmic pattern in silence. Participants showed some tapping synchrony with the 3:2 rhythm pattern as their mean tapping ratio was 1.679. Participants also showed some ability to continue tapping the 3:2 pattern without the auditory cue (mean tapping ratio of 1.732) but tended towards the simpler 2:1 ratio pattern when unconstrained by the auditory cue (Snyder et al., 2006). Bimanual tapping accuracy and perceptual detection accuracy have been shown to decrease as auditory rhythms deviate further from simple integer ratios (Dotov & Trainor, 2021). This study also showed that when participants continued tapping auditory rhythms in the absence of a stimulus cue, they were more likely to produce simple integer ratios than complex integer ratios (ex. 1:2 more likely than 3:7).

Experience is one important factor that influences humans' perception and production of complex rhythms. Cross-cultural work on the production of complex rhythms has yielded some evidence for rhythm complexity consistent with the nonlinear dynamics view (Ravignani et al. 2016) while also emphasising that long-term cultural experience with complex rhythms affects synchronisation with complex rhythms (Jacoby & McDermott, 2017). Individuals from cultures whose music frequently contains complex 3:2 rhythm structures tend to synchronise finger taps more stably with 3:2 auditory rhythms (Polak et al., 2018), switch between tapping 1:2 rhythms and 3:2 rhythms more efficiently (Ullal-Gupta et al., 2014), and better detect temporal disruptions in 3:2 rhythms (Hannon et al., 2012) compared to individuals whose musical culture contains few complex rhythmic structures. Notably, this perceptual advantage does not extend to highly complex rhythms (7:4 ratios) that do not correspond to culturally-familiar music (Hannon et al., 2012). Short-term experience with complex rhythms can also improve tapping accuracy. Individuals show more accurate complex rhythm production after listening to complex rhythms compared to listening to simple rhythms or no rhythms (Tillmann et al., 2011), and non-musicians show improved synchronisation performance with complex polyrhythms (rhythms with two tone streams) after 10 training trials (Tajima & Choshi, 2000).

Together, these behavioural studies constitute support for the nonlinear dynamical systems definition of rhythm complexity. Simple, small integer ratio rhythms tend to yield better production and synchronisation than larger, non-integer ratio rhythms. Long-term (cultural) and short-term experience (training) can modulate complex rhythm perception and production, suggesting there is a component of familiarity and experience in rhythm complexity.

Connecting Auditory Rhythms and Cardiac Activity

Neural resonance theory specifically addresses how auditory rhythms influence neural oscillations. How auditory rhythms influence other biological oscillations can be investigated through a similar nonlinear dynamical systems framework. Of particular interest is how cardiac activity is related to perception and production of auditory rhythms. Cardiac activity is intrinsically oscillatory: Cardiac cells are autonomous oscillators, meaning they fire in a periodic fashion independent of central nervous system input (Shaffer et al., 2014). A number of physiological inputs modulate cardiac period and contribute to heart rate variability (HRV), intrinsic variability from heartbeat to heartbeat that exists across a wide range of species (Heathers, 2014; Paton & Pickering, 2012; Porges, 2007). The sympathetic nervous system (SNS) input typically acts to decrease heartbeat periods (increase heart rate) and decrease heart rate variability (Shaffer et al., 2014). In contrast, the parasympathetic nervous system (PNS) via the vagal nerve typically acts to increase heartbeat periods (slow down heart rate) (Shaffer et al., 2014).

Cardiac activity is often measured using linear methods in both a time and a frequency domain. Common linear measures of cardiac activity in the time domain include heartbeat intervals measured in milliseconds (often called R-R interval which denotes the peak-to-peak interval in an electrocardiogram, ECG) and the standard deviation of normal-to-normal heart beats (SDNN) or the root mean square of successive differences (RMSSD), which capture HRV (Berntson et al., 1997; Camm et al., 1996; Heathers, 2014; Shaffer et al., 2014). The PNS and SNS exert influence on the heart at different timescales, with the PNS exerting influence at a much faster timescale than the SNS, resulting in cardiac oscillations at different frequencies (Berntson et al., 1993). In the frequency domain, heartbeat oscillations linked to the SNS are typically reflected in a low-frequency band between .04 and .15 Hz, although this frequency band does not exclusively reflect SNS influence (Berntson et al., 1997; Heathers, 2014). Heartbeat oscillations linked to the PNS are typically reflected in a high frequency band between .15 Hz and .4 Hz (Laborde et al., 2017; Shaffer et al., 2014).

Effects of Auditory Rhythms on Cardiac Activity

Loudness. The sound level (loudness) of auditory and musical rhythms influences cardiac activity. Listeners' heart rates increase when they hear louder passages (greater sound intensity) in a complex piece of classical music (Mikutta et al., 2013). do Amaral and de Abreau (2015) measured cardiac activity as participants heard a Baroque and a heavy metal piece of music at a range of loudness levels (60-70 dB, 70-80 dB, and 80-90 dB); compared to silent baseline, listeners had decreased HRV in the loud (80-90 dB) heavy metal condition. Finally, cardiac activity is sensitive to changes in loudness in isochronous tone sequences (Chuen et al., 2016). Baseline tones (65 dB) were suddenly increased in loudness (70 dB, 75 dB, and 80 dB) in the middle of the isochronous sequence. Overall, heart rate increased following the sudden increase in loudness (Chuen et al., 2016). Together, these studies show that loud musical rhythms and increases in loudness levels tend to raise heart rate and decrease heart rate variability. These findings are perhaps unsurprising as loud sounds produce an acoustic startle reflex, which puts an animal in an alert/defensive mode (Samuels et al., 2007) and results in increased physiological arousal (Turpin et al., 1999).

Tempo. Tempo effects on cardiac activity demonstrate with some consistency that fast tempo auditory rhythms lead to increased heart rate and decreased HRV, and slow tempo auditory rhythms lead to decreased heart rate and increased HRV during perception; however, this effect has not been systematically observed (Koelsch & Jäncke, 2015). Comparing cardiac activity during perception of an excitative song (fast tempo) and a sedative song (slow tempo) showed that a fast piece of classical music elicited faster heart rates and a slow piece of classical music elicited slower heart rates in listeners (Iwanaga et al., 1996; Iwanaga & Moroki, 1999). A similar finding has been reported for fast jazz music compared to slow jazz music (Nomura et al., 2013). Gomez and Danuser (2007) measured cardiac activity during perception of short noise excerpts and short instrumental Western classical music excerpts, finding tempo of auditory sequences correlated positively with listeners' heart rates. A series of studies showed how tempo (60 BPM vs 80 BPM) of an isochronous tone sequence influences cardiac activity (Watanabe et al., 2015). Notably, listeners in these studies also breathed at slow or fast tempi while listening to the auditory rhythms. Heart rate was generally faster and high-frequency HRV lower during the fast tempo tone sequences, particularly when listeners also breathed at a fast rate (Watanabe et al., 2015). Other studies have shown similar effects, with fast tempo during certain musical genres leading to decreased HRV compared to slow tempo music of a different genre (da Silva et al., 2014).

Other studies indicate more mixed effects of tempo on heart rate. Ooishi et al. (2017) presented listeners with slow classical music (56 BPM) and extremely fast classical music (233 BPM) and compared cardiac activity to a silent baseline condition. Only the slow tempo condition led to a decrease in heart rate and an increase in HRV; listeners' cardiac activity was not affected by the fast tempo condition. Bretherton et al. (2019) played participants a familiar musical tune ("Baa Baa Black Sheep") in increasing tempo order (60 BPM to 180 BPM in steps of 10), decreasing tempo order (180 BPM to 60 BPM in steps of 10), or a tempo-constant condition (120 BPM). Compared to a silent baseline, participants showed faster heart rates at the slowest tempo in the tempo decrease condition and greater HRV at the slowest and fastest tempi in the tempo decrease and tempo increase conditions, respectively.

There are large individual differences in cardiac activity (Picard et al., 2009), making individual differences an important consideration in how auditory sequences affect cardiac activity. One approach (Van Dyck et al., 2017) has been to titrate auditory rhythms to individual listener's resting heart rates, so that listeners heard music at the tempo of their resting heart rate, then at +- 15%, +- 30%, and +-45% of resting heart rate. Tempi that were 30% and 45% slower than a listeners' baseline heart rate tended to decrease the listener's heart rate from baseline, but no effects of faster tempi on cardiac activity were observed suggesting asymmetric effects of tempo on cardiac activity. Heartbeat entrainment to isochronous beats was tested by presenting listeners with simple drumbeat sequences that were 25%, 40%, and 55% faster than their real-time heart rate (Mütze et al., 2018). Synchronisation between heartbeats and drumbeat onsets was measured by comparing heartbeat onsets to inter-tone onsets in the auditory rhythm. There was no evidence at the group-level that heartbeats entrained in period or in phase to isochronous musical rhythms at varying tempi; instead, there large individual differences in mean heart rate and the period and phase relationships between heartbeats and acoustic tones (Mütze et al., 2018). Finally, Watanabe et al. (2017) showed that fast auditory rhythms tended to accelerate heart rates only in listeners’ with slow resting heart rates.

The findings discussed above indicate that auditory rhythms can affect cardiac activity while also demonstrating that tempo is not sufficient to explain auditory rhythm effects on cardiac activity during perception. Notably, many studies investigating relationships between auditory rhythms and cardiac activity have been purely perceptual. Individual differences in baseline cardiac activity as well responses to auditory rhythm tempo indicate that auditory rhythm perception has a nuanced effect on cardiac activity.

Rhythm. To date, there is little evidence as to how auditory-motor synchronisation influences cardiac activity during auditory rhythm production or synchronisation. A number of studies have investigated how music performance influences cardiac activity (Chanwimalueang et al., 2017; Harmat et al., 2011; Iñesta et al., 2008; Nakahara et al., 2011; Sebastiani et al., 2022; Williamon et al., 2013). These studies use highly trained musicians, full musical excerpts, and simulated performance conditions. Although informative as to how music performance influences cardiac activity, few studies have focused on specific auditory features such as rhythmic structure or complexity. Vickhoff et al. (2013) compared singers' respiratory and cardiac activity when they read a short text, hummed with self-selected breathing points, sang a hymn with musical structure in a group, and sang a group mantra with phrases lasting 10 seconds. They found the largest peak in spectral density (low-frequency band around .1 Hz) for the highly structured mantra condition, suggesting that musical structure and respiratory rhythms influenced cardiac activity. However, given that extensive coupling exists between the cardiac and respiratory systems (Paton & Pickering, 2012), it is difficult to generalise these findings to a non-singing, rhythmic auditory-motor task. Nonetheless, it suggests that there may be important coupling that occurs between auditory rhythm structure and cardiac activity.

Neurophysiological studies show that rhythm complexity modulates neural activity and neural oscillations during auditory rhythm perception and production. The neural correlates of rhythm perception and reproduction via finger tapping have been investigated using fMRI (Sakai et al., 1999). Auditory rhythms formed simple small integer ratios (1:2:4 and 1:2:3) or complex integer ratios (1:2.5:3.5). During rhythm reproduction, participants produced the small integer ratio rhythms more accurately than the complex integer ratio rhythm, with the intervals in the complex ratio rhythms tending towards simple integer ratios when participants reproduced them with finger taps (Sakai et al., 1999). Neural correlates of the simple and complex integer rhythms were different during both perception and reproduction tasks: simple integer ratio perception and reproduction were correlated with left motor and parietal regions while complex integer ratio perception was additionally correlated with right motor, parietal, and prefrontal areas. As Sakai et al. (1999) used a rhythm reproduction task, it is possible that memory for rhythms played a role in their findings.

An electroencephalography (EEG) experiment from Mathias et al. (2020) directly compared perception and finger tapping performance for a two-part rhythm with a simple inter-tone interval ratio (1:1), a moderate inter-tone interval ratio (1:2), and a complex inter-tone interval ratio (3:2). Musically trained participants were asked to detect omitted tones in a perceptual condition and to perform one part of each rhythm in a production condition (the second part of the ratio). Participants showed lower accuracy detection of omitted tones in the complex 3:2 rhythm compared to the simple 1:1 rhythm condition. Neurophysiological findings showed the largest peak in spectral power for perception of the simple 1:1 rhythm. For the production task, Mathias et al. (2020) found larger tapping asynchronies for the 3:2 rhythm than for the simple 1:1 and moderate 1:2 rhythms. During the simplest rhythm (1:1), the largest peak in spectral power at the frequency of the tap and stimulus was observed, suggesting that neural oscillations are modulated by rhythm complexity. Finally, the spectral power peak was larger during the production task than the perception task, indicating stronger neural responses during the production versus perception task. The auditory rhythms as well as the design of the tasks (perception, production) in Mathias et al. (2020) are of particular relevance to the work presented in Chapter 2 and Chapter 3 of this dissertation.

The relationships between cardiac, neural, and auditory rhythms has been investigated in one recent study from Zhao and Kuhl (2020). During magnetoencephalography, participants listened to isochronous tone sequences differing in the position of strong and weak tones such that one sequence had every second tone amplified by 10 dB and the other had every third tone amplified by 10 db. This created auditory rhythms with a duple metre (frequency peak at 1.67 Hz), and auditory rhythms with a triple metre (frequency peak at 1.1 Hz). Entrainment of neural activity to the beat and metre of the auditory rhythms was measured by the ratio of the power present in neural oscillations at the beat level to the power present at the metre level. Zhao and Kuhl (2020) saw that neural activity tended to entrain to the beat rather than the metrical level of the auditory rhythms and that participants' HRV was lower (more stable heart period) during perception of both rhythms compared to silent baseline. Furthermore, participants' task-specific HRV correlated negatively with the beat:metre frequency power ratio while their baseline HRV correlated negatively with the beat:metre frequency power ratio only in the duple condition (Zhao & Kuhl, 2020). The temporal relationships of tones in the auditory rhythms were not manipulated in this study, meaning rhythm complexity was not different across auditory conditions. Yet, this study indicates that auditory rhythms may regularise cardiac activity and that cardiac and neural activity may interact during auditory rhythm processing.

Overall, there is some conflicting evidence as to how auditory rhythms influence cardiac activity. This may be due, in part, to methodological differences between studies that use a single tempo manipulation for all participants, studies that titrate auditory rhythm tempo to a listeners' baseline heart rate, or studies that control breathing rates while measuring cardiac rhythms.

Tempo remains the most widely investigated parameter of auditory rhythms affecting cardiac activity, but it is only one dimension of auditory rhythms, and it has primarily been studied in perceptual contexts. In contrast to research investigating how rhythm complexity affects neural activity, the effect of rhythm complexity on cardiac activity has received little attention. How auditory rhythms, and specifically rhythm complexity, affect cardiac activity is thus open for further investigation.

Individual Difference Factors in Behaviour and Physiology

Individual differences in movement tempo are a relevant consideration in how cardiac activity is affected during auditory rhythm production and synchronisation. Spontaneous motor tempo (SMT) refers to a movement rate that an individual produces without external cues guiding their movement rate (McAuley et al., 2006). The SMT is thought to represent a state of maximal energy efficiency, and individuals have demonstrated SMTs in walking (Hoyt & Taylor, 1981), cycling (Moussay et al., 2002), and finger tapping (McAuley et al., 2006). Person-specific factors observed to affect SMT include age (McAuley et al., 2006), attention (Amrani & Golumbic, 2020), and memory (Rabinowitz & Lavner, 2014).

Spontaneous production rates (SPR) refer to the natural rate at which an individual produces a motor sequence, such as an auditory rhythm, corresponding to the rate at which an individual shows the least temporal variability in their movement (Zamm et al., 2018). Individual differences in SPR are well-documented (Palmer et al., 2019; Scheurich et al., 2018; Zamm et al., 2016), and individuals show consistency in their SPR across melodies, limb, and testing session (Zamm et al., 2015). There is evidence that SPRs constrain individual rhythm production rates (Scheurich et al., 2018) as well as interpersonal coordination (Zamm et al., 2015; Zamm et al., 2016; Tranchant et al., 2022), which suggests that SPRs have a critical role in how we successfully coordinate our own actions as well as actions with others. As auditory rhythm tempo affects cardiac activity during perception, it is a natural extension to investigate how individual differences in movement tempo are related to cardiac activity during auditory rhythm production and synchronisation.

Circadian rhythms are another individual difference factor in cardiac activity and behaviour. Circadian rhythms are approximately 24-hour endogenous rhythms in biological activity (Roenneberg et al., 2003a). Circadian effects on heart rate show that heart rate increases in the morning, plateaus, and decreases in the evening; the inverse is true for HRV (Vandewalle et al., 2007). The exact temporal pattern of heart rate and HRV across a 24-hour period is modulated by an individual's chronotype (Bonnemeier et al., 2003; Vandewalle et al., 2007), which refers to the phase at which an individual's circadian clock is entrained to the light-dark cycle, affecting their sleep-wake timing (Roenneberg et al., 2003b).

Both gross and fine motor performance vary across the day (Dosseville et al., 2002; Edwards et al., 2007; Monk, 2005; Moussay et al., 2002; Reilly et al., 2007) and circadian effects on cognition have been identified (Dijk et al., 1992; Lehmann et al., 2013). SMT tends to be slower earlier in the morning (Hammerschmidt et al., 2021) and, most recently, later chronotypes have shown slower SMT in the morning compared to the evening (Hammerschmidt & Wöllner, 2023). Musicians tend to practice music at times of day that align with their chronotype, independent of the previous night’s sleep timing (Wright & Palmer, 2022). Pianists with a later chronotype (go to bed and wake up late; night owls) play piano scales more stably in the evening while pianists with an earlier chronotype (go to bed early and wake up early; early birds) play piano scales more stably in the morning (Van Vugt et al., 2013). Circadian rhythms and time of day thus constitute another potential source of individual differences in cardiac activity and behaviour during rhythm perception and production.

Analysis Techniques for Cardiac Activity during Behavioural Tasks

Cardiac activity is commonly measured via electrocardiogram (ECG) whereby multiple electrodes are placed in different positions on the chest and abdomen. More recently, cardiac data collected with consumer-grade heart rate monitors that attach around the chest have been validated against traditional ECG (Gilgen-Ammann et al., 2019) and used during behavioural tasks (Konvalinka et al., 2011; Luque-Casado et al., 2016; Moussay et al., 2002; Tozman et al., 2015). R-R interval time series (heartbeat-to-heartbeat intervals) are generated from the heart rate monitor and can be analysed using linear and nonlinear methods.

Linear time-domain statistics such as mean heart rate/R-R intervals and SDNN/RMSSD (heart rate variability) and linear frequency spectrum decompositions (Berntson et al., 1997; Heathers, 2014; Shaffer et al., 2014) are commonly applied to cardiac data. Linear statistics assume at least some degree of stationarity (stable mean and covariance) in a signal (Berntson et al., 1997); however, physiological time series' such as cardiac activity are typically non-stationary, particularly when they are long or task-demands occur (Berntson et al., 1997). Non-stationarity has been shown to bias linear analyses of cardiac and respiratory data (Weber et al., 1992). Moreover, heartbeats are affected by a set of inputs (Paton & Pickering, 2012; Porges, 2007), and the cardiac system is a complex system (Marwan et al., 2002). Linear statistics capture only a single snapshot (ex. a mean) of a time-evolving variable, which results in the loss of important information about the real-time dynamics of that time-evolving variable.

Recurrence Quantification Analysis

Nonlinear analysis methods are able to capture nonlinear change and patterns in cardiac activity over time. Recurrence, the presence of repeated patterns in a dynamic signal, is particularly relevant to the dynamics of physiological systems (Marwan et al., 2007; Webber & Zbilut, 2005). Recurring patterns in a system are foundational to recurrence quantification analysis (RQA): RQA is a nonlinear analysis technique that captures and quantifies repeating patterns in a signal, describing the dynamics of a system (Marwan et al., 2007; Webber & Zbilut, 2005). Repeating patterns in a signal reflect states that a system often revisits, otherwise known as attractor states to which the system is drawn and requires a "kick" to leave (Guastello et al., 2009). Auto-RQA can be used to detect and quantify the structure of repeating patterns in a single cardiac time series signal.

The first step in RQA is to recover the higher dimensionality of a time series signal. An R-R interval time series is a 1-dimensional representation of heartbeat period over time; it does not contain the full dynamics of the system because the cardiac signal has been projected from higher into lower-dimensional space (Webber & Zbilut, 2005). To recover the dynamics of cardiac activity, a multi-dimensional phase space must be reconstructed (Nayak et al., 2018). A phase space is an abstract space in which a dynamical system exists: It contains all the possible states in which a system could be (Kelso, 1995; Nayak et al. 2018). Within the phase space, dynamical systems form trajectories of movement, which are created by vectors denoting the current state and the direction of the system's movement; a system's dynamics are thus displayed in the phase space trajectory (Webber & Marwan, 2015). The time delay method proposed by Takens (1981) can be used to recover the phase space (the lost dimensionality) of a measured system and regain information about the original system (Webber & Zbilut, 2005). Takens' theorem holds that for a complex system in which only a single variable has been measured, creating time-delayed copies of the 1-dimensional signal allows for reconstruction of the higher-dimensional system in its phase space (Marwan et al., 2007; Takens, 1981; Webber & Marwan, 2015; Webber & Zbilut 2005). Conceptually, this reconstruction can be thought of as unfolding the system from its 1-dimensional representation to its multi-dimensional representation in the phase space.

Two critical parameters must be set in order to achieve the reconstruction of phase space via the time-delay method. The embedding dimension parameter (*m*) refers to the dimensionality in which the system is thought to exist. Selection of *m* is key for the correct unfolding of the system in higher dimensional space. One common way to choose *m* is to use the False Nearest Neighbours (FNN) method. False nearest neighbours refer to points in a phase space that appear to be close to each other, but when the embedding dimension is increased (the system is further unfolded), the points do not remain close to each other; the embedding dimension *m* is thus considered optimal when the lowest value of *m* results in a stable number of false neighbours at *m* and *m*+1 (Nayak et al., 2018; Webber & Zbilut, 2015). The time delay parameter (tau, τ) determines the point in the signal at which a time-delayed copy will be created (Nayak et al., 2018). Tau corresponds to points in the signal where there is low dependency between observations, meaning there is little information shared between x_i and $x_{i+\tau}$ (Webber & Marwan, 2015). This method indicates orthogonal points in the signal and the dimensions that will show up in the phase space (Marwan et al., 2007; Webber & Zbilut, 2005).

Once the system's trajectory in phase space has been reconstructed, recurrent points in the system can be identified and recurrence plots can be constructed. As Webber & Zbilut (2015) note, recurrent points in a system are often not identical; rather, recurrent points are those deemed *sufficiently similar* according to a pre-determined radius (ε) that functions as a threshold distance. Two points are considered recurrent if the distance between them is smaller than the threshold set by ε (Webber & Zbilut, 2015). Recurrence plots are 2-dimensional graphical representations of the recurrent states in a multi-dimensional system of interest (Eckmann et al., 1987; Webber & Zbilut, 2015). When two points x_i and x_j meet the criterion for being recurrent with one another, then a dot is placed in the 2-dimensional recurrence plot (Eckmann et al., 1987). This process is repeated for all points in the signal, eventually leading to a complete recurrence plot. In the case of an auto-recurrence plot, both the x and y axes of the recurrence plot contain the same measured time series, so the plot is symmetrical around the line of identity.

The structures in a recurrence plot reflect important information about the temporal relationships between points in a time series signal. Figure 1 demonstrates how recurrence plots capture the features of a time series signal. The recurrence plot of a highly periodic signal, such as a pure sine wave, contains diagonal line structures in which the temporal interval between diagonal lines reflects the period of the signal (Figure 1a). The same sine wave with noise added, as shown in Figure 1b, results in recurrence plots containing diagonal line structures with breaks (reflecting the noise) as well as off-diagonal recurrent points. When the temporal relationships between values in the same time series of Figure 1b are shuffled, as in Figure 1c, the diagonal line structures in the recurrence plot disappear and recurrent and non-recurrent points become distributed throughout the recurrence plot. Recurrence plots are thus sensitive indicators of the temporal structure of time series signals.

The recurrence plot is a useful tool for visualising recurrent states in a system. It is, however, merely descriptive. The next step in RQA is to use specific metrics to quantify the structures that occur in the recurrence plot. Metrics of particular relevance for RQA applied to cardiac activity are recurrence rate, determinism, and laminarity. Recurrence rate is the proportion of recurrent points to all possible points (recurrent and non-recurrent) in the recurrence plot. Determinism captures the proportion of total recurrent points in the recurrence plot that form diagonal lines and is a measure of the sequential predictability of a system (Marwan et al., 2007). Greater determinism values mean a more predictable system. Laminarity captures the proportion of total recurrent points in the recurrence plot that form horizontal or vertical lines (Marwan et al., 2007) and is a measure of the system's tendency to become stuck in a particular state. Greater laminarity values mean a system is changing states more slowly or less often.

Applications of Recurrence Quantification Analysis

Recurrence plots and RQA have been applied to biological times series data such as neural oscillations (Scheurich et al., 2019), repetitive movement and postural sway (Schmit et al., 2005) and cardiac dynamics. RQA has been applied to cardiac activity in various clinical populations (Javorka et al., 2008; Marwan et al., 2007; Schlenker et al. 2016) as well as during behavioural tasks. Cardiac dynamics were assessed with RQA during a 30-minute firewalking ritual, comparing cardiac activity during a firewalk with a baseline period (Konvalinka et al., 2011). Firewalkers had greater determinism and laminarity in their cardiac dynamics during the firewalk compared to the baseline. Javorka et al. (2009) used RQA to assess cardiac dynamics in healthy young adults during an orthostatic challenge (a change from a supine position to a standing position). Participants stayed in a supine position for 20 minutes, then transitioned over a 5 second period to a standing position which was maintained for 15 minutes. Determinism and laminarity were both greater in the standing position compared to the supine position (Javorka et al., 2009). Mental arithmetic led to increased cardiac recurrence, determinism, and laminarity compared to a rest condition (Dimitriev et al., 2016).

Recurrence quantification analysis techniques have been applied to neurophysiological activity recorded from EEG during auditory rhythm production. EEG was used to measure neural activity of a confederate tapper and a participant who performed a joint rhythmic-tapping task (Scheurich et al., 2019). In one condition, the participant tapped twice for every tap the confederate made (1:2 condition) and in the other condition, the participant tapped twice for every four taps the confederate made (4:2 condition). Participants' neural oscillations were more recurrent in the 1:2 condition compared to the 4:2 condition, showing that neural oscillations are sensitive to differences in auditory rhythms during auditory-motor synchronisation.

In sum, nonlinear analysis methods for cardiac activity overcome issues of non-stationary time series data. Cardiac activity is known to show nonlinear, patterned behaviour. Recurrence quantification analysis is thus an appropriate technique for understanding cardiac activity during a complex behavioural task and has been applied in behavioural paradigms. The studies in this dissertation draw upon and extend previous work to apply RQA to cardiac dynamics during auditory-motor synchronisation.

Overview of Research

The research in this dissertation complements previous behavioural investigations by addressing previously-unexamined factors involved in auditory-motor synchronisation. This dissertation also investigates nonlinear cardiac rhythms during auditory perception and production tasks, a novel approach to understanding how physiological activity relates to auditory-motor synchronisation. **Chapter 1** investigates individual differences in performance rates and asks how biological rhythms are related to performance rates across a 12h day in trained pianists. It applies a nonlinear analysis technique to cardiac data in a novel context, demonstrating the usefulness of nonlinear analysis approaches to physiological time series data. **Chapter 2** examines nonlinear cardiac dynamics during perception and production of simple and complex auditory rhythms in trained musicians. This study extends Chapter 1 by directly comparing rhythm perception and production, and it draws on nonlinear dynamical systems theory to make predictions about how rhythm complexity affects cardiac dynamics. **Chapter 3** extends both Chapter 1 and Chapter 2, investigating short-term training effects on complex rhythm synchronisation and nonlinear cardiac dynamics in individuals with a range of musical experience. This study examines short-term practice effects, in contrast to long-term musical training, on auditory-motor synchronisation; it also compares behavioural and nonlinear cardiac measures during synchronisation with two complex rhythms, and probes individual differences in nonlinear cardiac activity during an auditory-motor synchronisation task.

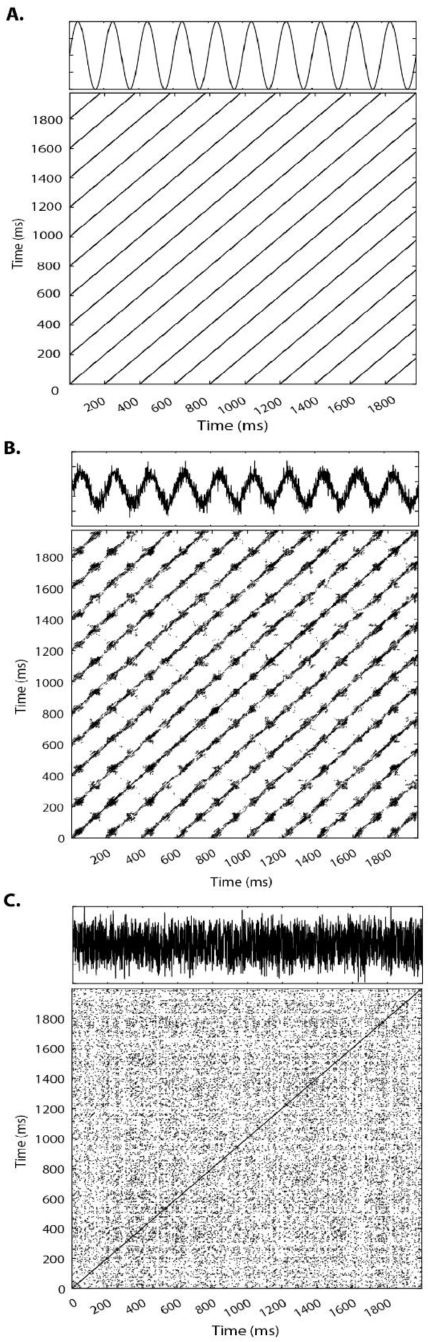

Figure 1. Time series and corresponding auto-recurrence plots for signals with varying degrees of noise. A) Pure 5 Hz sine wave. B) 5 Hz sine wave plus Gaussian white noise. C) Randomly-shuffled 5 Hz sine wave plus Gaussian white noise.

Chapter 1: Physiological and Behavioural Factors in Musicians’ Performance Tempo

Wright, S. E., & Palmer, C. (2020). Physiological and behavioral factors in musicians’ performance tempo. *Frontiers in Human Neuroscience, 14*. https://doi.org/10.3389/fnhum.2020.00311

Abstract

Musicians display individual differences in their spontaneous performance rates (tempo) for simple melodies, but the factors responsible are unknown. Previous research suggests that musical tempo modulates listeners' cardiovascular activity. We report an investigation of musicians' melody performances measured over a 12-hour day and subsequent changes in the musicians' physiological activity. Skilled pianists completed four testing sessions in a single day as cardiac activity was recorded during an initial five minutes of baseline rest and during performances of familiar and unfamiliar melodies. Results indicated slower tempi for familiar and unfamiliar melodies at early testing times. Performance rates at 09h were predicted by differences in participants' alertness and musical training; these differences were not explained by sleep patterns, chronotype, or cardiac activity. Individual differences in pianists' performance tempo were consistent across testing sessions: participants with a faster tempo at 09h maintained a faster tempo at later testing sessions. Cardiac measures at early testing times indicated increased heart rates and more predictable cardiac dynamics during music performance than baseline rest, and during performances of unfamiliar melodies than familiar melodies. These findings provide the first evidence of cardiac dynamics that are unique to music performance contexts.

Keywords: circadian rhythms; music performance; cardiac dynamics; alertness; recurrence quantification analysis; chronotype

Introduction

The ways in which musical behaviours interact with human cognition and action have been of great interest to psychologists. For example, models of musical rhythm perception have posited networks of electrophysiological activity, based on populations of neuronal oscillators that fire in synchrony with musical rhythms (Large, Herrera & Velasco, 2015); these proposals suggest a tight link between musical behaviors and physiological activity. Several studies have focused on the effects of music perception on physiological measures such as heart rate and heart rate variability (see Koelsch & Jäncke, 2015 for a review). Less is known about influences of music performance on physiological processes that underlie cognition and action. We report an investigation of musicians' melody performances measured over a 12-hour day and subsequent changes in the performers' physiological activity.

Circadian Effects on Cognitive and Motor Performance

Several studies have documented time of day (circadian) effects on motor and cognitive performance. Circadian rhythms refer to approximately 24h biological oscillations entrained to the light-dark cycle. For example, body temperature is known to fluctuate predictably over a 24h cycle (Czeisler & Klerman, 1999), serving as a robust marker of circadian phase, and peaks and troughs in alertness tend to follow the body temperature curve (Dijk, Duffy, & Czeisler, 1992). Heart rate and heart rate variability (HRV) also fluctuate predictably over a 24h period: Heart rate tends to rise in the early morning and decrease in the evening, whereas HRV is typically highest at night and lowest during the day (Bonnemeier et al., 2003; Vandewalle et al., 2007). Edwards et al. (2007) reported that participants' improved accuracy on a simple task of flicking a counter into a target coincided with their late-afternoon peak in body temperature and alertness. A similar finding was reported by Reilly et al. (2007) for soccer-specific motor skills. Rhythmic motor tasks such as pedaling a bike (Atkinson et al., 2005; Moussay et al., 2002) and tapping a steady rhythm with one’s finger (Dosseville et al., 2002) have also been shown to have time of day effects, with peak rates of movement occurring in the late afternoon. Furthermore, Dosseville et al. (2002) found that un-cued rhythmic finger tapping rates increase as heart rate increases. Overall, these studies suggest that rhythmic motor performance is influenced by time of day effects and cardiac activity, which shows circadian rhythmicity. We address whether music performance is influenced by circadian fluctuations in physiology similar to other sequential motor activities.

Motor performance is also influenced by circadian-linked individual differences in chronotype, sleep habits, and alertness (Tamm et al., 2009; Waterhouse et al., 2007; Vitale et al., 2015). Chronotype, which depends on the phase of entrainment of one's circadian rhythms to the light-dark cycle (Roenneberg, Daan, & Merrow, 2003), refers to the timing of one's sleep and wake in a 24h period. The commonly-known phenomenon of being an "early bird" or a "night owl" (Roenneberg et al., 2003b) refers to differences in the timing of the peaks and troughs of one’s circadian rhythms (Baehr et al., 2000): Early birds wake up and go to sleep earlier than night owls, and early birds are more alert in the morning and night owls more alert in the evening. Van Vugt et al. (2013) found that night owl pianists performed scales with greater temporal stability in the evening relative to the morning, while early bird pianists performed scales with more stability in the morning relative to the evening. Differences in chronotype, sleep habits, and alertness may influence performing musicians, who often work in the evening (Gjermunds et al., 2019).

Individual Variability in Music Performance

Large individual differences in music performances of the same musical works have been documented (Palmer 1996; Repp 2005). One common difference across performing musicians is the tempo at which they perform a given piece. Tempo is a factor that differentiates individuals as they speak, walk, tap, and perform other rhythmic movements. These natural movement rates reflect the rate at which individuals comfortably execute a performance in the absence of external stimulus cues. Individual differences in natural movement rates have been observed not only in music performance (Loehr et al., 2011; Palmer et al., 2019; Scheurich et al., 2018; Zamm et al., 2015, 2016) but also in a wide range of rhythmic movements such as walking (Hoyt & Taylor, 1981; Nessler & Gilliland, 2009), speaking (Ding et al., 2017; Jungers et al., 2003), biking (Moussay et al., 2002), and finger tapping (Dosseville et al., 2002; Fraisse, 1982). Individual differences in musicians' spontaneous rates for simple melodies tend to be consistent within individuals but differ widely across individuals (Loehr & Palmer, 2011; Palmer et al., 2019; Scheurich et al., 2018; Zamm et al., 2015). Performers tend to drift toward their spontaneous rate in solo performances when they are initially cued at different rates (Zamm et al., 2018). Moreover, these individual differences in spontaneous rates play an important role in coordinating performances with others: pianists with similar spontaneous rates showed more synchronous performance in duets than pianists with dissimilar rates, in a variety of novel musical works (Zamm et al., 2016). Mechanisms that account for individual differences in musicians' performance rates for the same musical works remain largely unknown; we test whether circadian-related variations in physiology can explain some of these individual differences.

Cardiac Activity During Music Behaviours

Both the rhythms of cardiac activity and of musical behaviours form long time series of interrelated events; a few studies have addressed how heart rate modulations and musical tempo change together over time. For example, passive listening to music has shown decreased heart rate in response to slower-tempo music (Van Dyck et al., 2017) and increased heart rate during fast-tempo music (Gomez & Danuser, 2007). Heart rate variability during music listening changes less predictably; da Silva et al. (2014) found no difference in HRV between rest (baseline) and music listening, whereas Bretherton et al. (2019) reported that only some tempo manipulations elicited HRV changes relative to a rest condition. Fewer studies have examined changes in musicians' cardiac activity as they perform. De Manzano et al. (2010) found increased heart rate as pianists played familiar music for which they reported large amounts of "flow". Studies of performance anxiety have shown that musicians' heart rate increased when they performed in front of an audience as compared to alone (Brotons, 1994; LeBlanc et al., 1997; Vellers et al., 2015). These studies did not, however, compare resting baseline conditions to music performance. Moreover, the impact of music performance on cardiac activity may be affected by time of day, as cardiac activity shows a circadian rhythm (Bonnemeier et al., 2003; Vandewalle et al., 2007). We investigate how cardiac activity is modulated by music performance, within and across times of day.

Despite the unfolding nature of time series for both cardiac activity and musical behaviours, most studies of heart rate and musical tempo tend to rely on linear measures that fail to capture the nonlinear dynamics of the cardiovascular system and of human musical behaviours. The time series formed by music performances and cardiac activity are plausibly more complex than can be captured with a single mean value for beat-to-beat intervals or a standard deviation of those intervals. Recent studies have used nonlinear methods of recurrence quantification analysis (RQA) to capture aberrant cardiac activity over time in cardiovascular patient populations (for examples, see Arcentales et al., 2011; Javorka et al., 2008; Javorka et al., 2009). Other studies of cardiac dynamics in healthy control populations during sit-to-stand transition tasks show greater cardiac predictability during the more physically demanding standing task (Schlenker et al., 2016). Konvalinka et al. (2011) used RQA techniques to measure cardiac dynamics during a thirty-minute firewalking ritual during which music was heard. The cardiac dynamics became more predictable (recurrent) during the ritual than during a 30-minute pre-ritual baseline measure. Goshvarpour and Goshvarpour (2012) similarly found greater predictability in cardiac dynamics during meditation than during a resting baseline state. Based on these findings, we expect that the predictability of cardiac dynamics may increase during music performance, relative to rest.

The current study had three aims. First, we investigated time of day effects on music performance rates by measuring musicians' performances of simple melodies across a 12h day while measuring their cardiac activity. To disentangle musical familiarity effects from time of day effects, performances of both familiar (previously learned) as well as unfamiliar (novel) melodies were measured. Second, we examined influences of circadian rhythms on individual differences in performance tempo. Based on previous findings, we hypothesised that performers with slower spontaneous rates may show slower heart rates and lower alertness than individuals with faster spontaneous rates (within the same time of day). Based on Van Vugt et al.'s (2013) study, early chronotypes were predicted to show less variable performance rates in the morning, whereas late chronotypes should show less variable performance in the evening, respectively. Third, we investigated how the time series formed by music performance and the accompanying cardiac dynamics changed, by comparing cardiac activity during music performance with cardiac activity during a rest period. We predicted that linear measures of heart rate would be faster and HRV would be lower during music performance relative to rest. Nonlinear measures of performers' cardiac dynamics were expected to show more predictability during music performance than during rest. We also examined whether performances of unfamiliar music generated more predictable dynamics than performances of familiar music, based on previous findings of increased cardiac patterning during more demanding tasks (Javorka et al., 2008; Konvalinka et al., 2011) and increased temporal patterning in novices' (nonmusician) productions of musical rhythms than in musicians' productions (Scheurich et al., 2018).

Methods

Participants

Thirty-two trained pianists with at least 6 years of private piano instruction from the Montreal community participated in the study (mean years of private instruction = 10.6; range = 6-16). Sample size was based on studies of musicians' spontaneous performance tempo that reported moderate effect sizes for comparable samples (Palmer et al., 2019, *n* = 32 musicians; Zamm et al., 2016, *n* = 40 musicians). Participants' mean age was 19.5 years (range = 18-27, male = 7). 28 participants were right handed. Exclusion criteria included diagnosed hearing problems or sleep disorders, doing overnight shift work, habitually drinking more than 3 cups of coffee per day, or having taken a transcontinental flight within the 3 week period prior to participating in the study. Additionally, participants had normal hearing for the range of frequencies used in the music stimuli (<30 dB HL threshold for 125-750 Hz frequencies), as determined by audiometry screening, and had to memorise and perform short melodies without errors. Six additional participants were excluded from the study due to an inability to perform the melodies correctly from memory (3), equipment issues in collecting cardiac data (2), and having fewer than six years of private piano instruction (1). Participants received a small honorarium for their participation, and the study was reviewed by the Institutional Review Board of McGill University.

Stimulus Materials and Equipment

Two musical melodies, primarily isochronous, were included in the study: Frère Jacques ("Twinkle, Twinkle", C Major) and a Canon by Thomas Tallis (D Major). The Frère Jacques theme, composed in the 18th century, was chosen for its familiarity, whereas the Tallis canon, composed in the 16th century, was chosen for its unfamiliarity. Both musical pieces contained 8 measures composed in binary (4/4) metre with the majority of quarter-note beat durations. Frère Jacques contains a few eighth notes and half notes in addition. Pianists performed each melody with their right hand, and they were provided with suggested fingerings.

Participants performed melodies on a Roland RD-700 keyboard. Participants' auditory feedback from the keyboard was received directly through AKG K271 Studio headphones. Tones were sounded with a classical piano timbre, and the volume was set by participants to a comfortable listening level. MIDI keystroke information from the performances was recorded with FTAP (Finney, 2001) on a Dell T3600 PC running Linux (Fedora 16).

Cardiac activity was recorded with a Polar H10 heart rate monitor connected via Bluetooth to the application Elite HRV (Personal Pro) run on an iPad Mini. Sublingual temperature was measured with a digital oral thermometer (Personelle Digital Thermometer), following suggestions that sublingual temperature is a reasonable and pragmatic proxy to core body temperature under specific guidelines (Taylor, Tipton & Kenny, 2014). The temperature measures followed guidelines of a minimum measuring period of 5 minutes as well as ensuring the mouth is closed for the whole duration of the measurement (Pušnik & Miklavec, 2009; Taylor et al., 2014).

Alertness measures included the Psychomotor Vigilance Task (PVT) and a Visual Analogue Scale (VAS). The PVT is a computer-based reaction time task in which participants are asked to click the mouse button as soon as a visual stimulus appears on the computer screen (Dinges & Powell, 1985). The 3-minute version of the PVT was used, which has been previously validated (Basner, Mollicone, & Dinges, 2011), and presents visual stimuli at randomly varying interstimulus intervals ranging from 1 to 4 seconds. The PVT measures were collected on a Dell T5810 computer with a HyperX Pulsefire gaming mouse (1000 Hz polling rate) that recorded reaction times. The VAS task (Folstein & Luria, 1973; Monk, 1987) consisted of participants indicating their current level of alertness by making a vertical tick mark on a 10 cm line.

Participants completed a series of questionnaires about their sleep habits, including the Epworth Sleepiness Scale (ESS; Johns, 1991), the Pittsburgh Sleep Quality Index (PSQI; Buysse et al., 1989), and a sleep diary from Carney et al. (2012). Chronotype was measured with the Munich Chronotype Questionnaire (MCTQ; Roenneberg et al., 2003b). All participants completed the Edinburgh Handedness Inventory and a musical background questionnaire. Participants also completed a short questionnaire about their activities in the hour preceding each laboratory session that might affect alertness, body temperature, or cardiac measures.

Design

Participants came to the lab for four testing sessions (09h, 13h, 17h, and 21h) in a single day. The order of testing sessions remained constant across participants (each pianist’s first session began at 9h). Baseline physiological recordings and melody performance tasks were completed at each testing session by all participants, making this a within-subjects 4 (Testing

Time) by 2 (Task: 5-minute Rest/Music performance) repeated-measures design. The task order was always rest first, followed by music performance. Within the music performance task, the ordering of the familiar and unfamiliar melody performances was alternated between participants and testing sessions: Half of the participants performed the Familiar melody first at the 09h testing session, and the other half began with the Unfamiliar melody. At subsequent testing sessions, participants alternated which melody they performed first. Each participant performed a total of 32 melody performance trials (4 times of day X 2 melodies X 3 trials) over the course of the experiment.

The main behavioural dependent variables from the melody performances were spontaneous production rate (SPR, mean interonset interval, IOI in ms) and variability of interonset intervals (measured by the coefficient of variation, SD/mean IOI). Primary physiological dependent variables included sublingual temperature (°C), heart rate (mean inter-heartbeat interval, RR), heart rate variability (measured by the standard deviation of normal-to-normal intervals, SDNN), alertness (PVT reaction times and VAS subjective scores), chronotype, and sleep deprivation measures computed from the sleep diary (described below).

Procedure

Participants were first screened for eligibility via e-mail; if eligible, electronic copies of the musical notation (without melody titles) for the melodies used in the study were sent to participants, and participants were asked to memorise the melodies before their participation in the study. Participants also received a sleep diary which they were asked to complete for the week preceding the laboratory session.

Upon arrival at the lab, participants read and signed a consent form before completing an audiometry screening in which pure tones were presented over closed headphones (Maico

MA40), to ensure they could hear the range of frequencies involved in the music performance task at a threshold of < 30 db. Participants who passed the audiometry screening were invited to continue to a melody memorisation task. First, participants were presented with a melody in notation. After practicing the first melody (Familiar or Unfamiliar) both with and without musical notation, participants were given up to three practice trials to perform the melody from memory without pitch errors. Then the participants repeated the task with the second melody. All participants performed the melodies without pitch errors in the memorisation phase.

Next, participants attached the heart rate monitor around their chest. A 5-minute baseline sublingual temperature and heart rate recording was taken during the Rest task while participants were seated and completing questionnaires. To ensure correct temperature readings, participants were instructed to insert the thermometer under their tongue and breathe normally through their nose; they were instructed to keep movement to a minimum and to avoid crossing their legs so as not to influence heart rate measures. During this time, participants marked their current alertness level in the VAS task. At the end of the 5-minute rest period, participants removed the thermometer but kept the heart rate monitor on for the rest of the testing session.

Participants then completed the Psychomotor Vigilance Task. They were instructed that red numbers would appear on a black screen, and they were to click the mouse as soon as, but not before, they saw the red numbers appear. If participants clicked the mouse before the red numbers appeared, the letters "fs" appeared on the screen to inform the participant they had made a false start. A new trial was then begun. Each trial continued until participants clicked the mouse.

Participants then sat at the piano keyboard and were presented with the first melody in music notation. They were instructed to perform a practice trial consisting of four repetitions at a steady, comfortable rate without pauses. The experimenter removed the music notation and participants repeated a practice trial of the same length from memory. Once participants were comfortable with the task, they moved on to the experimental trials. Each experimental trial consisted of 4 repetitions of the melody performed from memory (in the absence of music notation) without pauses at a comfortable, steady rate. After completing all trials of the first melody, participants filled out a brief questionnaire about their activities prior to the testing session; then the same practice and experimental trials were repeated for the second melody. At the end of the melody performance task, participants removed the heart rate monitor and received a small honorarium. The same procedure was repeated at each testing session with the addition of a debriefing period at the end of the final session. The duration of the first testing session (which included the audiometric screening and memorisation practice) was approximately 45 minutes; subsequent testing sessions took approximately 25 minutes.

Data Analysis

Pitch errors in melody performances were identified by comparing the recorded MIDI data with the contents of the musical score, using the MIDI Matcher Toolbox in Matlab (Large, 1993). Repetitions containing a pitch error were excluded from analysis as timing errors are likely to co-occur with pitch errors (Drake & Palmer, 2000); 0.03% of all repetitions were excluded from analysis. The half-note durations in Frère Jacques were interpolated at the quarter-note level, and eighth notes that did not align with the quarter-note beat were excluded from the analyses. Interonset intervals (IOI), coinciding with quarter-note beats in both melodies, were computed. IOI’s greater or less than 3 standard deviations away from the mean IOI for that trial were excluded from behavioural analyses (0.13% of all IOIs).

Each participant's Spontaneous Production Rate (SPR) was computed on the IOIs from the middle two of four melody repetitions in each trial, similar to previous studies (Zamm et al 2016; Palmer et al 2019), as the middle of each trial tends to show more stable tempo due to musicians' tendencies to slow down at phrase boundaries at beginnings and endings of trials (Palmer, 1989; Repp 1990). Participants' SPR for each melody was then calculated from the mean IOI of the middle 2 repetitions of each trial and averaged across trials within melody. Similarly, the mean Coefficients of Variation (CV) were calculated from the same IOIs in the middle two repetitions and a mean CV was computed across trials.

Linear analyses of cardiac data were completed using Kubios (HRV Standard, 3.1.0). Mean RR intervals and the SDNN were computed for each five-minute baseline recording as well as during the total duration of melody performances, including practice and experimental trials, in order to have the longest consecutive measurement period possible. Recurrence quantification analysis (RQA) was also conducted on cardiac data using the CRP Toolbox 5.22 (Marwan, 2019, run with MATLAB 2018a (v9.4.0)). RQA is a nonlinear analysis technique, often used on behavioural and cardiac data (Demos, Frank, & Chaffin, 2011; Javorka et al., 2008; Marwan et al., 2013), that identifies recurrent states in a dynamical system using Takens' (1981) method of higher-dimensional reconstruction (Webber & Zbilut, 2005; Nayak et al., 2018). Time-delayed copies of the cardiac signals are generated and projected into multidimensional phase space (Konvalinka et al., 2011) with the parameter tau denoting the time delay. For each resting period (baseline) and music performance, tau was chosen based on the first local minimum of the average mutual information function. Tau therefore varied across participants and within participants by testing session and task (Javorka et al., 2009), and the resulting range was 2-12. The False Nearest Neighbour (FNN) method was used to select an embedding dimension; FNN values close to zero indicate that the signal is projected into a sufficient number of dimensions (Nayak et al., 2018; Webber & Zbilut, 2005). Embedding dimensions were chosen on an individual basis and ranged from 4-8. A Theiler window fixed to the time delay (Javorka et al., 2009) was applied to the data, as cardiac signals tend to show high autocorrelation (Martin-Gonzalez et al., 2018). Recurrence rate, the percentage of recurrent points in the system, was fixed to 5% as per previous RQA studies of cardiac signals (Javorka et al., 2008; Javorka et al., 2009).

Recurrence plots, 2-dimensional representations of the recurrent points in a system, were generated to visualise the cardiac dynamics. Each point in the plot represents a system state that is recurrent with a previous state (Webber & Zbilut, 2005). The time series signal is plotted against itself such that the recurrence plot is symmetric across the diagonal. Two parameters were used to quantify the observed recurrence. First, determinism (DET) measured the percentage of points in the recurrence plot forming diagonal lines (excluding the line of identity), where the minimum number of points required to be considered a line was set to 2 (Eq. 1). Determinism is a measure of the predictability of a system over time (Webber & Zbilut, 1994). Second, laminarity (LAM) captures the percentage of points forming vertical (or horizontal) lines in the recurrence plot (Eq. 2) and is an indicator of the extent to which a system "gets stuck" in a specific state (Nayak et al., 2018).

$$\%DET = 100 * \frac{\sum_{l=lmin}^{N} lP(l)}{\sum_{l=1}^{N} lP(l)} \tag{1}$$

$$\%LAM = 100 * \frac{\sum_{v=vmin}^{N} vP(v)}{\sum_{v=1}^{N} vP(v)} \tag{2}$$

Chronotype was determined from the MCTQ which estimates an individual's mid-sleep point based on self-reported times of sleep onset and wake for both work and free days (Roenneberg et al., 2003b). As imposed social schedules may mask an individual's natural mid-sleep point and lead to sleep debt (Wittman, Dinich, Merrow, & Roenneberg, 2006), an adjusted value of mid-sleep on work-free (weekend) days (MSF) that accounts for possible sleep debt was used to estimate one's chronotype (Roenneberg et al., 2004). The adjusted value (MSF_{sc}) is derived according to the following equation:

$$MSF_{sc} = MSF - .5[TS_F - (5(TS_w) + 2(TS_F)/7)], \qquad (3)$$

where TS_w is the average total sleep duration (in minutes) on work days and TS_F is the average total sleep duration (in minutes) on free days. This equation yields a time (ex. 04:00h) corresponding to the midpoint of the individual's sleep cycle. Midpoints earlier than 05:00h typically denote an earlier chronotype and later midpoints denote a later chronotype (Roenneberg et al., 2003b).

Alertness scores were derived for each testing session. Mean reaction times on the PVT were calculated per participant for correct response trials. A score from 1-10 on the VAS at each testing session per participant was analysed, with higher scores indicating greater alertness.

Results

Time of Day Effects in Music Performance. To test for differences in mean SPR values across the day, a two-way ANOVA on mean SPR by Time of Day (09h, 13h, 17h, 21h) and Melody (Familiar, Unfamiliar) was performed. This analysis indicated significant main effects of Time of Day ($F(3,93) = 17.42$, $p < .01$, partial eta-squared = .36), and of Melody ($F(1,31) = 41.73$, $p < .01$, partial eta-squared = .57), and no significant interaction. Shown in Figure 1 (top), mean SPR was significantly slower at 09h than at all other testing sessions, and was slower at 13h than at 21h (Tukey's *HSD* = 13.72, $p < .05$). SPR was faster for the Unfamiliar melody performances (mean = 362.61 ms) than the Familiar performances (mean = 397.84 ms); this finding is not surprising as the Familiar melody's rhythm contained half and quarter notes which constrained the fastest rate possible, whereas the Unfamiliar melody contained only quarter notes.

To test whether the stability of music performance changed over the day, the same ANOVA was conducted on mean CV. There were significant main effects of Time of Day ($F(3,93) = 3.827$, $p = .012$, partial eta-squared = .11) and of Melody ($F(1,31) = 9.200$, $p = .005$, partial eta-squared = .23), and no significant interaction. Figure 1 (bottom) shows the CV values; the CV at 09h was significantly larger than at 17h and 21h, and the CV at 13h was significantly larger than at 21h (Tukey *HSD* = .002, $p < .05$). Paralleling the findings of mean SPR becoming faster across the day, pianists became more stable in their performances across the day. The mean CV for Familiar melody performances (mean = .05) was greater than for Unfamiliar melody performances (mean = .045), consistent with the varying rhythmic structure of the Familiar melody compared with the isochronous rhythm of the Unfamiliar melody. Overall, these findings suggest a 09h effect on SPR and CV that diminished over the day.

To examine whether performers' alertness levels varied over the testing sessions, we tested participants' reaction times on correct trials in the Psychomotor Vigilance Task in a one-way ANOVA by Time of Day (09h, 13h, 17h, 21h). Mean reaction times varied significantly across the day ($F(3,93) = 3.70$, $p < .01$, partial eta-squared = .11). Mean reaction times at 09h were significantly slower (mean = 233.57 ms) than mean reaction times at 21h (mean = 224.50 ms) (*HSD* = 7.29, $p < .05$). No other time of day comparisons were significant. In line with the primarily late chronotype sample, these findings suggest that participants were less alert at 09h than at 21h. Mean subjective alertness scores (Visual Analogue Scale, VAS) did not show significant effects of time of day.

The sublingual body temperatures were assessed with a one-way ANOVA by Time of Day (09h, 13h 17h, 21h). There was a significant main effect (*F*(3,93) = 6.28, *p* = .001, partial eta-squared = .17); post-hoc analyses indicated that body temperature at 09h was significantly higher (mean = 36.73 °Celsius) than body temperature at 13h and 17h (*HSD* = .237, *p* < .05), with no other comparisons differing significantly. Consistent with previous work (Christie & McBrearty, 1979; Monk, 2005) participants' sublingual temperature decreased slightly in the middle portion of the day and rose again through the evening.

Individual Differences in Performance Tempo. Next, we examined individual differences in spontaneous production rate (SPR). Figure 2 shows the mean spontaneous rates of individuals' Familiar melody performances at each testing session, ordered in each graph from fastest to slowest individual at 09h. The similarity of the faster-to-slower patterns across the four graphs suggests that the individual differences in performance tempo were consistent. To test whether the SPR values were stable across times of day, Spearman’s rank order correlations were applied to test whether the ordering of individuals at the 09h session matched the ordering at the 13h, 17h, and 21h sessions. The rank-ordered SPR values held from the 09h session to each testing session (13h *rho* = .87, *p* < .01; 17h *rho* = .85, *p* < .01; 21h *rho* = .82, *p* < .01). Figure 3 shows the same pattern of individuals’ SPR values across testing sessions for the Unfamiliar melody performances, where each graph is again ordered by fastest to slowest individual at 09h. Similar to the Familiar melodies, the individual differences at 09h were significantly retained across all testing sessions (13h *rho* = .84, *p* < .01; 17h *rho* = .88, *p* < .01; 21h *rho* = .81, *p* < .01). These findings suggest that large individual differences in spontaneous rates existed for both familiar and unfamiliar melodies, and the individual differences were consistent across times of day.

To address whether individual differences in SPR were related to chronotype, we computed participants' chronotype from the Munich Chronotype Questionnaire (MCTQ), following Eq. 3. The mean and median midsleep point on free days (MSF_{sc}) were 05h14 and 05h08, respectively (range = 03h13 to 09h21). Individuals with MSF_{sc} values later than about 05h are typically considered a late chronotype or night owl (Roenneberg et al., 2003b). The present sample MSF_{sc} was positively skewed, with 3 of 32 participants in the < 04h range, 23 of 32 participants in the 04h-05h range, and 6 of 32 participants in the ≥06h range. Although chronotype appears nearly normally distributed in the general population, the overrepresentation of night owls in the present sample is consistent with previous findings for this age group (Roenneberg et al., 2003b) as well as for musicians (Gjermunds et al., 2019). Due to the lack of variability in chronotype and the overrepresentation of night owls, the relationship between chronotype and SPR could not be assessed; the 3 earliest chronotypes and the 6 latest chronotypes did not show SPR patterns that differed from the remaining cohort.

We next examined the individual differences in spontaneous rates (mean SPR) in terms of amount of musical training and alertness (reaction times on correct trials from the PVT) using a multiple regression model that predicted mean SPR from years of musical training and reaction time (RT). The multiple regression fits for the Familiar melody performances, predicting mean SPR from RT and Musical Training, were significant at 09h ($R = .523$, $p < .01$) and at 13h ($R = .51$, $p < .05$). Semi-partial correlations indicated significant contributions to the SPR of both RT (standardised coefficient = .35, $p = .035$) and Musical Training (standardised coefficient = -.378, $p = .02$) at 09h. The semi-partial correlations at 13h indicated similar contributions of RT (standardized coefficient = .35, *p* = .04) and Musical Training (standardized coefficient = -.3305, *p* = .04). At both 09h and 13h, individuals' slower tempi were associated with longer RT values in the PVT (lower alertness) and with less musical training. The same multiple regression model did not predict individuals' SPR values at 17h or at 21h. The same multiple regression model fit to mean SPR values for the Unfamiliar melody performances showed similar influences of alertness (RT) but not of musical training. The multiple regression fit reached significance at 09h (*R* = .45, *p* = .04) but not at any other testing session. The semi-partial correlations indicated significant contributions of RT at 09h (standardised coefficient = .3958, *p* = .024). Consistent with performances of the Familiar piece, participants with lower alertness scores (higher RT values) performed the Unfamiliar melody at a slower tempo at the first session of the day.

There was no significant relationship between acute sleep deprivation (average duration of sleep in 1 week - duration of single night sleep preceding laboratory session) and individual SPR values at any testing session, for Familiar or Unfamiliar melody performances, suggesting that individual differences in SPRs were not accounted for by differences in acute sleep deprivation.

Cardiac Dynamics during Music Performance. Linear cardiac measures (RR interval and SDNN) were examined to identify whether cardiac activity varied across the day and across music and rest. A two-way within-subjects ANOVA on mean RR interval by Time of Day (09h, 13h, 17h, 21h) and Task (Baseline rest, Music Performance) showed a significant main effect of Task (*F*(1,31) = 13.51, *p* = .001, partial eta-squared = .30), and no main effect of Time of Day or interactions. RR interval was shorter during music performance (mean = 712.57 ms) than during baseline rest (mean = 734.12 ms), indicating that pianists' heart rate increased from baseline to music performance. To examine the two melodies performed at each testing session, a follow-up two-way ANOVA on mean RR interval by Time of Day (09h, 13h, 17h, 21h) and Melody (Familiar, Unfamiliar) was performed. There was a significant main effect of Melody (*F*(1,31) = 6.27, *p* = .02, partial eta-squared = .17) and a significant Time of Day x Melody interaction (*F*(3,93) = 3.20, *p* = .03, partial eta-squared = .09). As seen in Figure 4, participants' RR intervals were shorter during Unfamiliar melody performances than during Familiar melody performances at 09h, 13h, and 17h, but not at 21h (*HSD* = 4.36, *p* < .05). Participants' heart rate increased during the Unfamiliar melody performance relative to the Familiar melody performance earlier in the day but not later in the evening. Similar analyses on mean SDNN values showed no significant effects of time of day or type of melody, and no interaction.

Nonlinear RQA measures of cardiac activity evaluated the predictability of performers' heart rate measures (R-R intervals, in ms). A two-way ANOVA on mean determinism (%DET, measuring predictability) by Time of Day (09h, 13h, 17h, 21h) and Task (Baseline rest, Music Performance) showed no main effect of Time of Day, a significant main effect of Task (*F*(1,31) = 4.15, *p* = .05, partial eta-squared = .12) and a significant Time of Day x Task interaction (*F*(3,93) = 6.48, *p* < .001, partial eta-squared = .17). There was greater determinism (predictability) during music performance (mean %DET = 45.699) than during baseline rest (mean %DET = 42.959). Figure 5 (top) demonstrates that the cardiac activity showed significantly greater determinism during music performance at 09h and 13h (*HSD* = .053, *p* < .05) but not at 17h and 21h. Recurrence plots for a single participant at 09h in Figure 6 demonstrate the greater amount of determinism or predictability during music performance than during baseline rest.

A follow-up two-way ANOVA on mean %DET by Time of Day (09h, 13h, 17h, and 21h) and Melody (Familiar, Unfamiliar) showed a significant main effect of Melody (*F*(1,31) = 6.348, *p* = .017, partial eta-squared = .17), and no main effects or interactions with Time of Day. Specifically, %DET values were larger during the Unfamiliar melody performances (mean = 46.99) than the Familiar melody performances (mean = 44.41). Figure 7 shows a pair of recurrence plots illustrating this difference for a single subject, where a greater proportion of recurrent points form diagonal lines in the plot on the right (Unfamiliar performance). Thus, greater determinism (predictability) in cardiac activity was seen during music performances compared to rest, and for Unfamiliar melody performances compared to Familiar melody performances.

The same analyses were performed to identify whether laminarity in the cardiac system (how much the system got stuck in a recurrent state) changed with Time of day and Task (Baseline rest and Music Performance). The mean laminarity (LAM) values indicated a significant main effect of Task (*F*(1,31) = 5.415, *p* = .027, partial eta-squared = .15), no main effect of Time of Day, and a significant Time of Day x Task interaction (*F*(3,93) = 3.678, *p* = .015, partial eta-squared = .11). Recurrence plots for a single participant in Figure 8 show that a greater proportion of points form vertical/horizontal lines during the melody performances (mean %LAM = 53.74) than during baseline rest (mean %LAM = 50.25). Post-hoc comparisons of the interaction showed that mean laminarity values were significantly greater during music performance than baseline only at 09h (*HSD* = .055, *p* < .05), also shown in Figure 5 (bottom). A follow-up ANOVA on mean LAM value by Time of Day and Melody (Familiar, Unfamiliar) showed a significant main effect of Time of Day (*F*(3,93) = 4.107, *p* = .009, partial eta-squared = .17) and no effects or interactions with Melody. Overall, there was greater laminarity and determinism (predictability) in cardiac rhythms during music performance than during baseline rest; that difference was larger at earlier testing sessions. In addition, there was greater determinism during Unfamiliar melody performances than during Familiar melody performances, controlling for time of day.

Discussion

This study examined time of day effects on musicians’ performance tempo for simple melodies, and whether circadian effects on physiology could account for individual differences in performance tempo. Trained pianists' performance rates for familiar and unfamiliar melodies were recorded at four testing sessions in a single day (09h, 13h, 17h, 21h) while cardiac activity was recorded. Resting measures of performers’ cardiac activity, alertness, and body temperature were recorded at each testing session. Additionally, this study utilised a nonlinear analysis technique (RQA) to investigate cardiac dynamics during music performance both within and across times of day.

Overall, musicians’ spontaneous performance rates were slower and more variable at 09h and became slightly faster and less variable at later testing sessions. The largest difference in SPR and variability of performances was between 09h and 21h, similar to previous findings on spontaneous motor rates of tapping (Dosseville et al., 2002) and cycling (Moussay et al., 2002), which have shown slowest rates in the morning and fastest rates in the evening. These results suggest that melody performances increased in tempo and in temporal regularity from the morning to the evening, a finding that is somewhat consistent with a sample of largely night-owl chronotypes (Van Vugt et al., 2013). Participants completed all testing sessions in the same order in this study (to control for sleep differences between testing sessions); therefore, it is possible that some changes in melody performance rate and temporal variability were attributable to practice effects over the session trials. In the context of motor sequencing, performing repeated trials of specific finger sequences in a blocked (rather than randomised) fashion typically results in faster learning rates (Caramiaux et al., 2018; Fogel et al., 2017). The observed changes in participants' melody performances across times of day were similar for unfamiliar and familiar melodies, which is consistent with practice effects over trials (as opposed to familiarity with the musical melodies).

Musicians showed large individual differences in spontaneous performance rates (SPR), replicating previous studies on natural movement rates in music performance (Palmer et al., 2019; Zamm et al., 2015) and tapping tasks (Scheurich et al., 2018). Importantly, the individual differences in pianists' performance tempo were consistent across the day for both familiar and unfamiliar melodies: Pianists who performed quickly in the morning also performed quickly in the evening, and the same was true for pianists with slower rates. These findings are consistent with dynamical systems theory predictions that an individual's natural movement rate, a property of a periodic oscillatory system (Kelso, 1997), may serve as an attractor state at which movement efficiency is maximised (Hoyt & Taylor, 1981; Zamm et al., 2018). Indeed, neuromuscular fatigue has been shown to be minimised at cyclists' spontaneous (uncued) pedaling rates for a given load resistance (Moussay et al., 2002; Takaishi et al., 1996), and reduced kinetic energy expenditure in pianists' finger movements is associated with increased temporal accuracy of performance (Goebl & Palmer, 2014). Our finding of consistency across testing sessions in individuals' performance tempo suggests that one's spontaneous production rate may be an energy-efficient state for melody performance that transcends time of day effects or familiarity with the melody.

Alertness measures also showed time of day effects and explained some of the individual variability in performance rates; participants who performed melodies at a slower rate at 09h and 13h had slower reaction times on the PVT task at these times. Lower alertness in the morning is not surprising for the later chronotype sample of musicians tested here (Roenneberg et al., 2003a). At early testing times, musicians' spontaneous performance rates were influenced by both physiological (alertness) and behavioural (musical training) variables. Participants with faster reaction times in the PVT task and more years of formal piano training tended to show faster performance rates at 09h and 13h. Interestingly, neither physiological nor behavioural variables predicted performance rates later in the day. Alertness and musical training may have greater effects on melody performance when musicians are less comfortable with a musical task (for example at the first 09h testing session), an interpretation consistent with the general increased temporal stability reported for musicians with increased training (Scheurich et al., 2018). This hypothesis could be addressed by randomising participants' first testing session to begin at different times of day in future studies.

Finally, the complexity of musicians' cardiac activity was compared between 5-minute rest periods and music performances, as well as between performances of familiar and unfamiliar melodies. Both linear and nonlinear measures of heart rate (R-R intervals) indicated significant differences from rest to music performance, with faster and more patterned (deterministic) heart rates during music performance than during rest, across times of day. The largest differences between music performance and rest were seen at 09h and at 13h. In addition, heart rates were faster during performances of unfamiliar melodies than familiar melodies, and laminarity (recurring patterns) of cardiac activity was greater for unfamiliar melodies than for familiar melodies. Increased predictability of cardiac signals has been observed during increases in task difficulty for both physical (Javorka et al., 2009; Konvalinka et al., 2011; Schlenker et al., 2016) as well as cognitive behaviours (Goshvarpour & Goshvarpour, 2012). Overall, the differences in cardiac dynamics between rest and music performance, and between performance of familiar and unfamiliar melodies, suggest that increased predictability and stability of cardiac signals may be a physiological marker of increased behavioral difficulty.

The current findings were limited by the simple musical materials used, and the chronotype sample of musicians obtained. Two simple melodies were included to reduce the memorisation demands on participants; those melodies had simple but not identical rhythmic structures. Future research may examine the roles of musical performance styles and rhythmic complexity in performance rates and cardiac rhythms. Furthermore, the chronotype of the obtained musician sample was biased toward night owls, in line with previous research (Gjermunds et al., 2019). It is possible that decreases in SPR and increases in performance stability over the day were specific to the night owl chronotype, as late chronotypes perform better on strength tasks (Tamm et al., 2009) and music performance tasks (Van Vugt et al., 2013) in the evening relative to the morning. Future research may extend these findings to a more diverse sampling of chronotypes.

In sum, pianists' rates of melody performances increased and variability decreased across the 12h day, similar to circadian influences on other motor skills. Time of day may be an important relationship for musicians to consider; there may be ideal times of day to practice or perform. Individual differences in performance rates early in the day were predicted by both alertness and musical training. In addition, large individual differences in the musicians' performance rates remained consistent across the 12-hour time period. Finally, pianists' cardiac dynamics became more predictable and recurred more during music performance than during a baseline rest interval, as well as during performances of an unfamiliar melody than a familiar melody. To our knowledge, these findings provide the first evidence that performing music affects nonlinearities of cardiac dynamics in specific and replicable ways within individuals.

Overall, these discoveries of performers' cardiac dynamics suggest possible applications to music therapy; the time of day at which music is performed, as well as the familiarity of the music, may influence music's ability to modulate physiological systems.

Acknowledgements

This research was funded in part by an NSERC-CREATE scholarship to Shannon E. Wright, and by NSERC Grant 298173 and a Canada Research Chair to Caroline Palmer. We gratefully acknowledge the assistance of Sebastian Andric, Jocelyne Chan, Amy Friedman, Nour Saba, Jessica Slater, and Frances Spidle. Correspondence can be addressed to Shannon E. Wright and Caroline Palmer, Department of Psychology, McGill University, 1205 Dr Penfield Ave, Montreal QC H3A 1B1 Canada.

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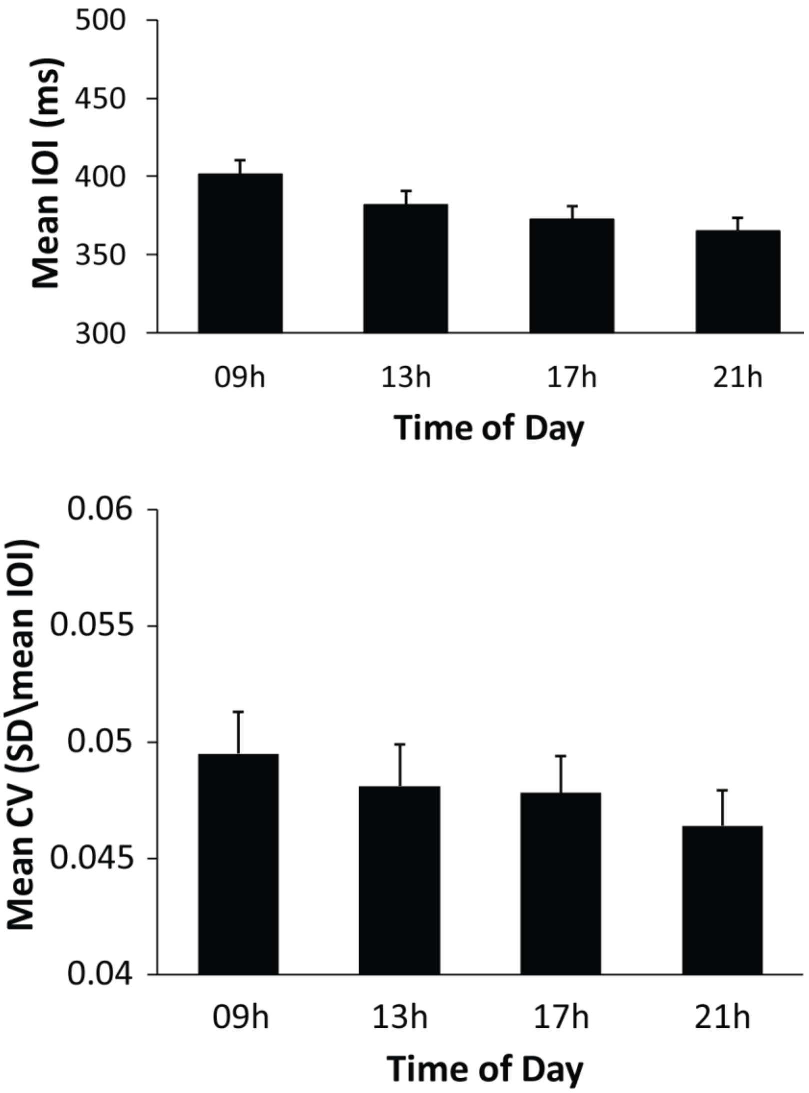

Figure 1. Performers' mean Spontaneous production rates (ms) by Time of Day (top) and mean CV by Time of Day (bottom) for all melody performances.

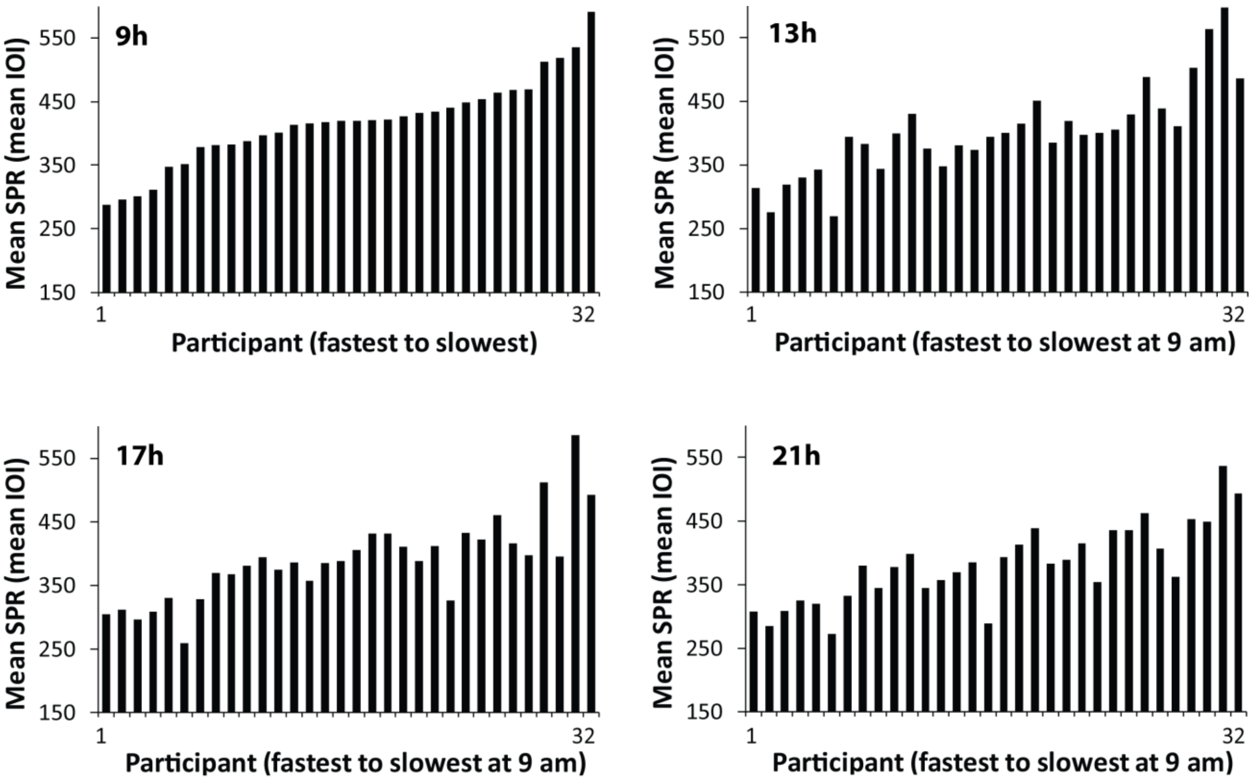

Figure 2. Distributions of performers' mean SPR values (mean IOI in ms) for the Familiar melody, ordered at each testing session from fastest to slowest performer according to 09h. Each bar = one performer.

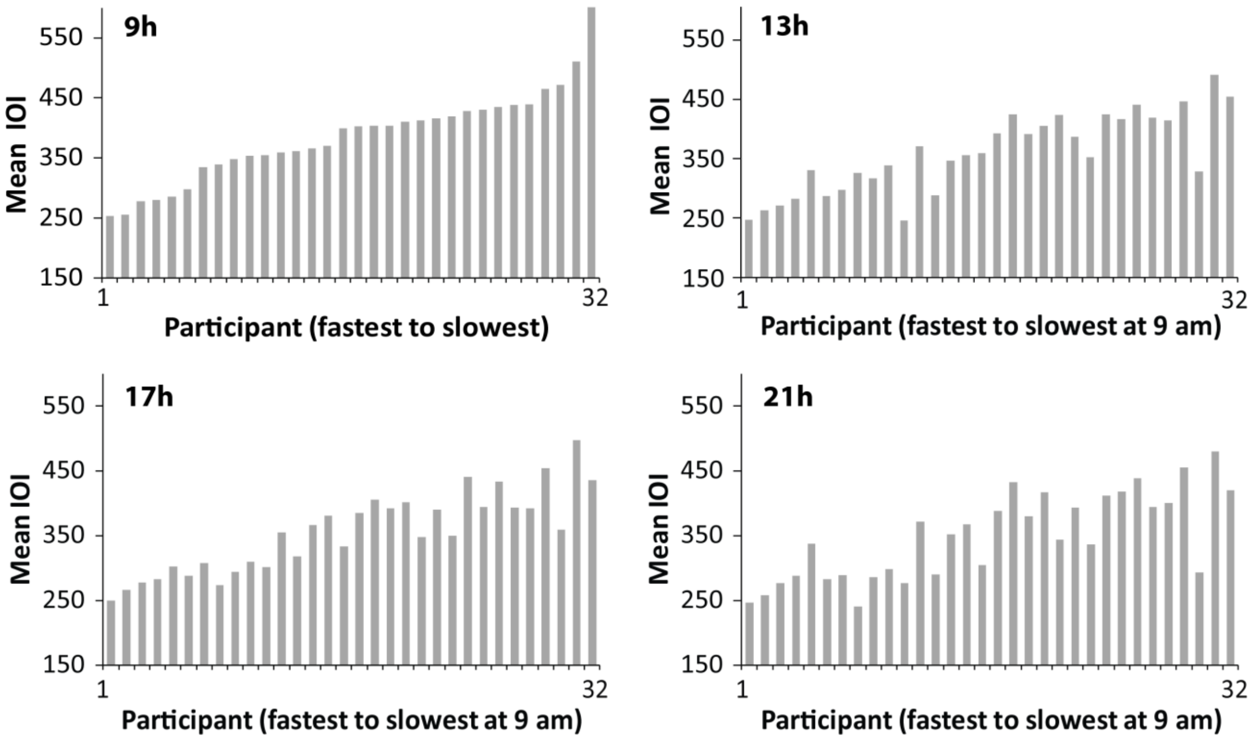

Figure 3. Distributions of performers' mean SPR values (mean IOI in ms) for the Unfamiliar melody, ordered at each testing session from fastest to slowest performer according to 09h. Each bar = one performer.

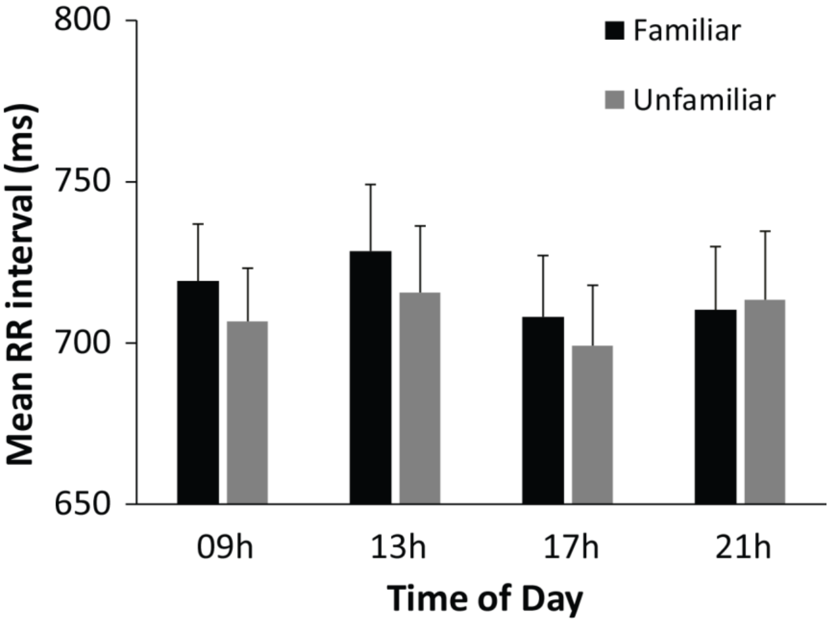

Figure 4. Performer's mean heartbeat interval (RR interval, in ms) by Time of Day and Melody.

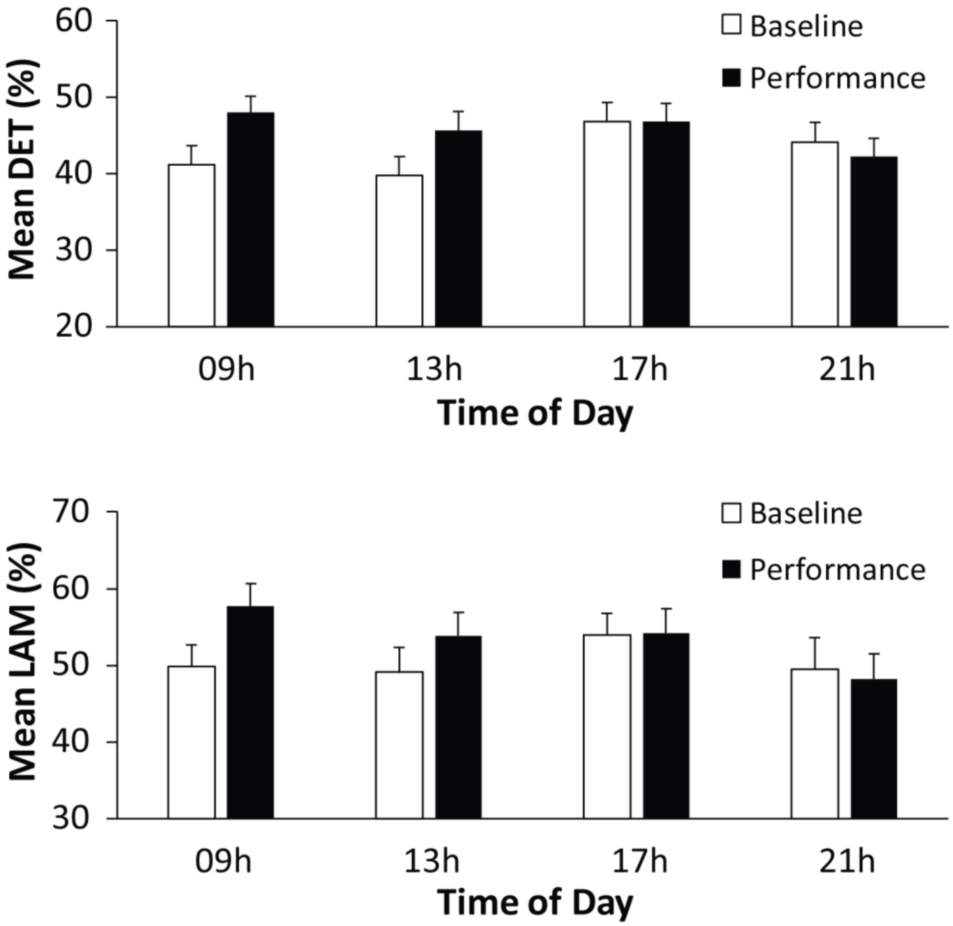

Figure 5. Performers' mean % Determinism (top) and mean % Laminarity (bottom), by Time of Day and Task (Baseline rest / Music performance).

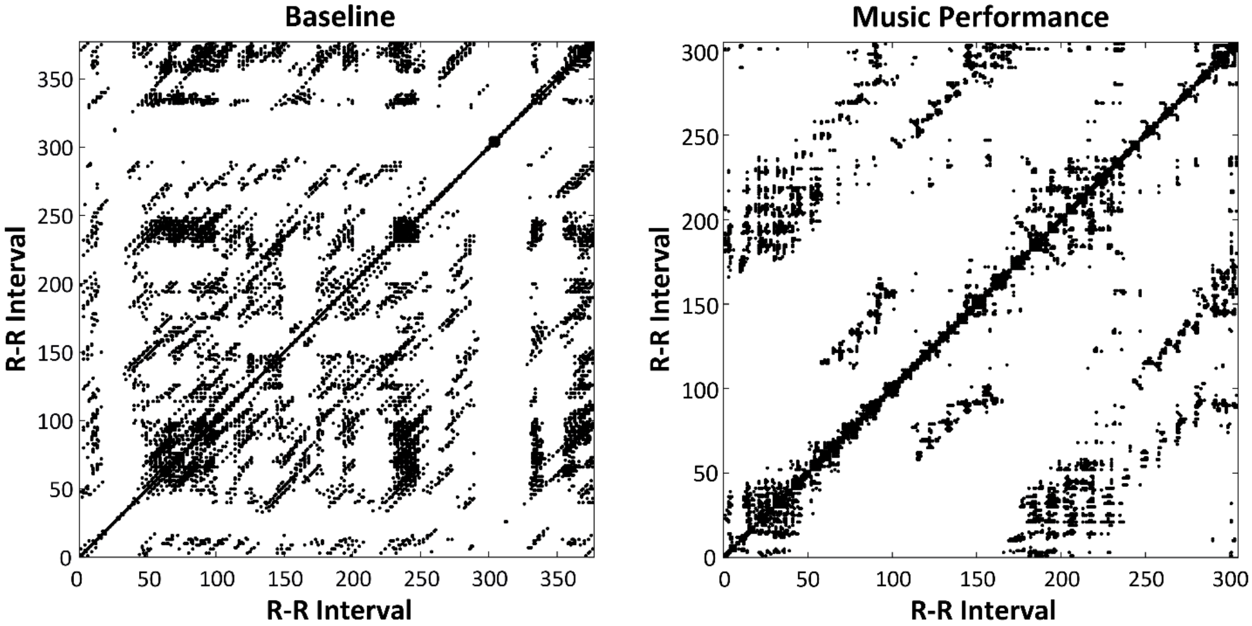

Figure 6. Recurrence plots for a single participant's heartbeat series (RR intervals, in ms, plotted on x- and y-axes) at 09h. Plots include 5-minute Baseline rest period (left) and Unfamiliar melody performance (right). The melody performance showed greater determinism (%DET = 58.88) than did the Baseline Rest (%DET = 39.62).

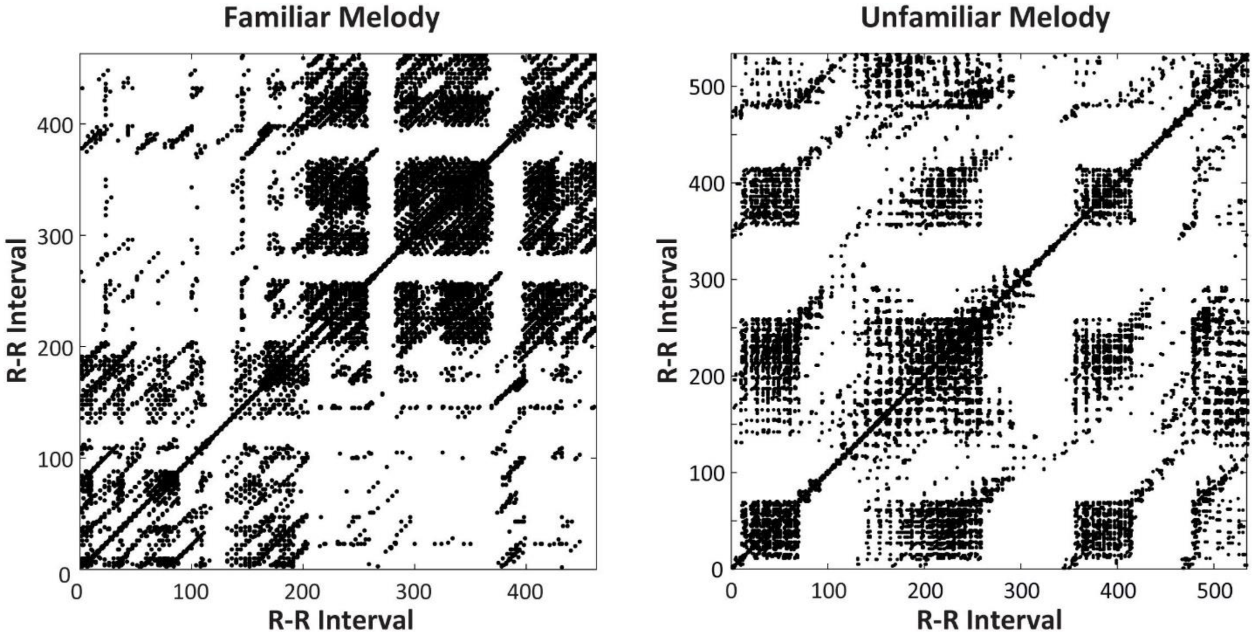

Figure 7. Recurrence plots for a single participant's heartbeat series (RR intervals, in ms, plotted on x- and y-axes) at 13h. Plots include Familiar melody performance (left) and Unfamiliar melody performance (right). The Unfamiliar melody performance showed greater Determinism (= 53.31%) than did the Familiar melody performance (= 44.04%).

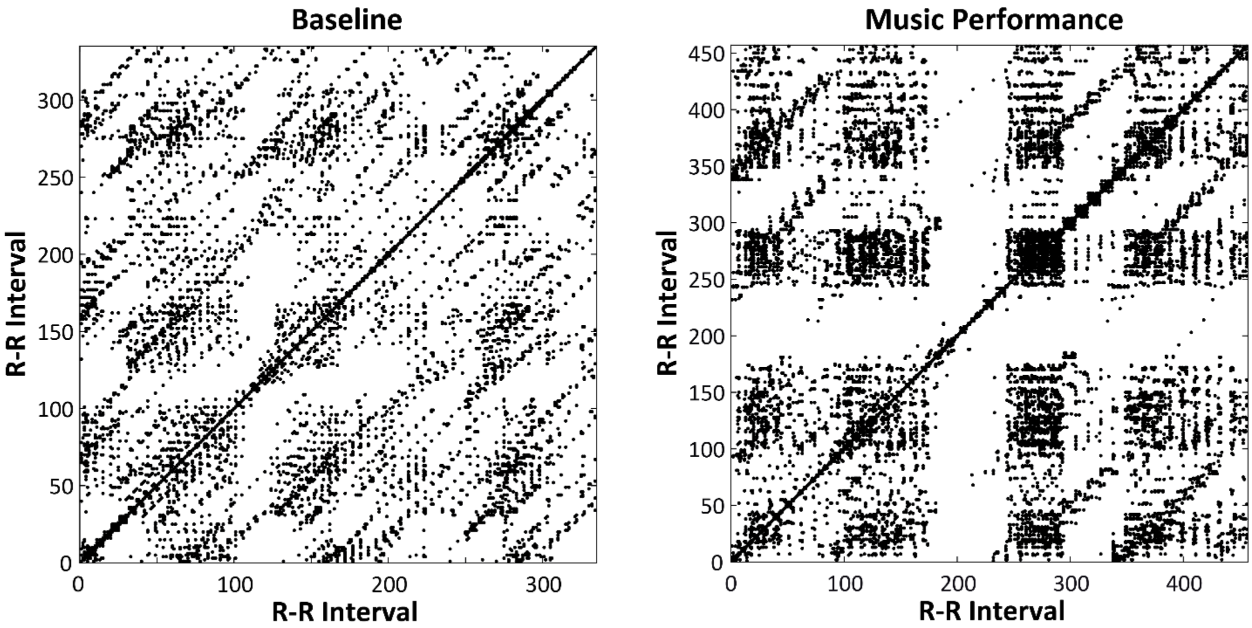

Figure 8. Recurrence plots for a single participant's heartbeat series (RR intervals, in ms, plotted on x- and y-axes) at 09h. Plots include Baseline rest (left) and Unfamiliar melody performance (right). The Melody performance showed greater Laminarity (= 51.6%) than did the Baseline Rest (= 27.0%).

Bridge between Chapter 1 and Chapter 2

Chapter 1 tested circadian and time of day effects on spontaneous production rates and concurrent cardiac activity in trained pianists. Results showed that spontaneous production rates were slower and more variable in the morning compared to the afternoon and evening. Slower production rates were also predicted by less musical training and lower alertness in the morning only. Large individual differences in spontaneous production rates were replicated and, notably, individuals were consistent in their spontaneous production rates across four times of day for both a familiar and an unfamiliar melody. Linear cardiac measures showed that heart rate was faster during music performance than during a silent baseline, particularly at the morning session. This study also applied a nonlinear analysis technique, recurrence quantification analysis, to the cardiac data, which is a novel application in a music performance context. Nonlinear measures showed time of day and performance effects, with greater cardiac predictability and stability during music performance in the morning compared to the afternoon and evening. Additionally, cardiac dynamic were more predictable during unfamiliar music performances compared to familiar music performances.

The study in Chapter 2 builds on Chapter 1 by testing how task difficulty affects cardiac dynamics. In Chapter 1, familiar and unfamiliar melodies elicited different cardiac dynamics in a manner consistent with task difficulty effects (Fuentes-García et al., 2019; Konvalinka et al., 2011; Schlenker et al., 2010). It was also difficult to disentangle time of day effects from task difficulty as the order of conditions was held constant across individuals, meaning evening performances may have been easier as the task was more familiar than in the first morning session. Chapter 2 compares behavioural and cardiac effects of rhythm complexity. This tests not only task difficulty but it also isolates a single acoustic feature, namely rhythm, whereas Chapter

1 involved melody and rhythm. This allows for greater control over which aspects of auditory rhythms and performance influence cardiac activity. Finally, Chapter 2 addresses the question: Is there something special about music *performance* that affects cardiac dynamics? It does this by directly comparing cardiac activity during rhythm perception and production, building on the design of silent baseline vs music performance in Chapter 1.

Chapter 2: Auditory rhythm complexity affects cardiac dynamics in perception and synchronisation

Wright, S. E., & Palmer, C. (2023). Auditory rhythm complexity affects cardiac dynamics during perception and production. [Manuscript submitted for publication].

Abstract

Accurate perception and production of auditory rhythms are key for human behaviors such as speech and music. Auditory rhythms in music range in their complexity: complex rhythms (based on non-integer ratios between successive tone durations) are more difficult to perceive and produce than simple rhythms (based on integer ratios). The physiological activity supporting this behavioral difference is not well understood. In a within-subjects design, we addressed how rhythm complexity affects cardiac dynamics during auditory perception and production. Musically trained adults listened to and synchronized with simple and complex auditory rhythms while their cardiac activity was recorded. Participants identified missing tones in the rhythms during the Perception condition and tapped on a keyboard to synchronize with the rhythms in the Synchronisation condition. Participants were equally accurate at identifying missing tones in simple and complex rhythms during the Perception condition. Tapping synchronisation was less accurate and less precise with complex rhythms than with simple rhythms. Linear cardiac analyses showed a slower mean heart rate and greater heart rate variability during perception than synchronisation for both simple and complex rhythms; only nonlinear recurrence quantification analyses reflected cardiac differences between simple and complex auditory rhythms. Nonlinear cardiac dynamics were also more deterministic (predictable) during rhythm perception than synchronisation. Individual differences during tapping showed that greater heart rate variability was correlated with poorer synchronisation. Overall, these findings suggest that linear measures of musicians’ cardiac activity reflect global task variability while nonlinear measures additionally reflect stimulus rhythm complexity.

Introduction

Listeners are adept at hearing and reproducing a wide range of auditory rhythms, such as those contained in dance steps or in musical melodies. Auditory rhythms are composed of sequences of regularly spaced events over time [1]. Some rhythms – those defined by complex ratios between the sequential tone durations - are less common and more difficult to perceive and produce [2, 3, 4, 5]. Behavioral differences between simple and complex rhythms and the physiological activities that support them are not well-understood. Auditory rhythms such as musical rhythms are known to influence cardiac activity; previous research has largely focused on how acoustic features of musical rhythms, such as tempo or pitch, affect cardiac activity during perception [6]. A few studies have shown changes in the periodicities present in cardiac rhythms during perception [7] and production [8] of different auditory rhythms. Yet little research has addressed the specific relationship between auditory rhythm complexity and physiological activity. The current study investigates how auditory rhythm complexity affects behavior and cardiac dynamics during perception and production, using a synchronisation paradigm.

Changes in heart rate mean and variability during cognitive-motor tasks are often attributed to changes in physiological arousal and task difficulty [9, 10, 11]. Slower heart rate and greater heart rate variability tend to correspond to lower arousal states [12]. Both musical acoustic features and musical task difficulty influence cardiac rhythms. Some studies show that fast-tempo musical rhythms tend to increase listeners' mean heart rate and decrease their heart rate variability, indicative of an arousal effect [6, 13, 14, 15, 16, cf. 17]. Other studies show that faster-tempo auditory rhythms tend to elicit faster heart rates without changes in heart rate variability [16, 18, 19, 20]. Slow-tempo music has been shown to slow down listeners' heart rates and increase heart rate variability [21, 22]. Task factors in music performance also influence physiological arousal: Performing music in front of an audience compared to performing alone increased musicians' heart rates and decreased heart rate variability [23]. Musical task familiarity also influences cardiac rhythms: Musicians’ heart rates increased during production of unfamiliar musical melodies compared with familiar melodies and a silent baseline condition [8]. Together, these studies suggest that auditory rhythms modulate listeners’ arousal levels, with task difficulty potentially contributing to this effect. Thus, we expected that changes in task difficulty based on auditory rhythm complexity might impact listeners’ heart rate and heart rate variability, such that simple rhythms result in slower heart rate and greater heart rate variability than complex rhythms.

Nonlinear dynamical systems theory provides an explanation for the difficulty of tracking complex rhythms in music. Oscillators (signals with recurring cyclic patterns with a natural or default frequency) are central in this theory: Rhythm complexity depends on the amount of coupling or interaction between two oscillators which is determined in part by the ratio of one oscillator frequency to the other oscillator frequency. Oscillators whose natural (default) frequencies form small integer ratio relationships, such as 1:2, show stronger coupling, compared to oscillators whose natural frequencies form non-integer ratios, such as 3:2 [24, 25, 26]. In this study, we compare simple rhythms whose tone durations form small integer ratios (1:2) with complex rhythms whose tone durations form non-integer ratios (3:2). Neural resonance theory extends this nonlinear dynamical systems perspective specifically to auditory rhythm perception, holding that rhythm perception is underpinned by internal neural oscillations that couple with external auditory rhythms; when neural oscillations and auditory rhythms form simple integer ratios, coupling is most likely to occur [24, 25]. The duration ratio distinction of simple and complex rhythms converges with auditory rhythm structures that are most frequently observed across musical cultures [27], and recent evidence suggests that small integer ratios primarily characterize the structure of certain non-human animal vocalizations [28, 29].

Production of auditory rhythms by humans supports the dynamical systems distinction between simple and complex rhythms. Individuals reproduced auditory rhythm sequences better when the successive tone intervals formed integer ratios such as 2:4 compared with 2:3 [2]. When asked to tap one hand in synchrony with non-integer ratio auditory rhythms, individuals tended to distort their taps toward simple integer ratios [4, 5, 30]. A similar effect has been found when individuals tap both hands with simple and complex polyrhythms (rhythms that are composed of more than one tone sequence) [31]. In an iterated learning paradigm in which individuals initially heard and reproduced random sequences of tones, individuals produced sequences that converged toward small integer ratio relationships between tones [32]. There is also some cross-cultural evidence for a bias toward producing simple auditory rhythms [33], although cultural familiarity with different musical rhythms may modulate these biases in both rhythm production [34] and rhythm perception [35].

A few studies directly assess simple and complex auditory rhythms in perception and production tasks. Repp et al. [36] measured participants as they listened to and tapped in synchrony with simple and complex rhythms that contained temporal perturbations. They found evidence of better perception and production for small-integer ratio rhythms (such as 1:1, 1:2 ratios) than for complex rhythms (such as 4:5, 7:11, 5:13), suggesting similar constraints on rhythm perception and production. However, there was no clear advantage across perception and production for all of the small integer ratios used in the experiment [36]. As most studies address perception or production tasks but not both, it is unknown whether the tendency toward simple over complex rhythms is stronger in perception or production.

Neurophysiological studies have investigated how rhythm complexity affects oscillatory neural activity. Stupacher et al. [37] presented participants with a simple isochronous rhythm (4:4) followed by a complex polyrhythm (4:3). After a short period of silence, a tone sounded and participants judged whether that tone was early, on time, or late for the polyrhythm. The simple and complex rhythm structures were observed in listeners' patterns of neural oscillations based on steady-state analyses of electroencephalograpy (EEG). Additionally, musicians' neural oscillations better tracked the complex polyrhythm during the silent period compared to nonmusicians' neural oscillations, confirming the musicians' advantage for complex rhythm processing [37]. Mathias et al. [38] directly compared neural oscillations with EEG while musicians perceived and produced auditory stimuli containing simple (1:1), moderate (1:2), and complex (3:2) rhythms. During perceptual trials, participants detected omitted tones in the auditory rhythms; during production trials, participants tapped the second part of the ratio of each auditory rhythm to produce the full rhythm. Detection of missing tones was most accurate for the 1:1 rhythm with no difference observed between the 1:2 and 3:2 rhythms. Tapping was more accurate and precise for the 1:1 and 1:2 rhythms compared to the 3:2 rhythms. Power spectral density measures (EEG) were greatest at frequencies that corresponded to the tapping frequency in the simple (1:1) rhythm compared to the moderate (1:2) and complex (3:2) rhythms [38]. These findings suggest that neurophysiological entrainment is stronger for simple rhythms than complex rhythms, particularly during production tasks compared to perceptual tasks.

One of the goals of the current study is to compare cardiac rhythms during auditory rhythm perception and production tasks. Previous studies of cardiac activity during rhythm perception and production tend to employ linear measures of cardiac activity, such as mean heart rate or RR interval and heart rate variability. For example, one study reported no difference in linear measures of listeners' heart rate variability during music perception of duple metre rhythms (a march) compared to triple metre rhythms (a waltz) [7]. Linear measures such as heart rate variability assume that the cardiac signal is stationary, meaning the mean and variance of the time series are relatively stable over time [39]. In reality, stationarity in cardiac activity is often not the case [40]; behavioral tasks are likely to have different effects on cardiac activity over time. Thus, it is possible that nonlinear cardiac measures, which address relationships within a single time series, may be more sensitive to rhythmic changes that take place within musical stimuli.

Recurrence quantification analysis (RQA) is a nonlinear analysis alternative that does not make assumptions about stationarity of the signal [41]. In RQA, a time-delayed copy of the cardiac time series is produced to reconstruct the signal in a multi-dimensional phase space [42, 43]. Points in the phase space are then assessed for their closeness; points that are sufficiently close to one another in the phase space are deemed to be recurrent [44]. These recurrent points are plotted in a 2-dimensional recurrence plot and quantified according to different metrics to describe the behavior of the system. RQA has been applied to identify disrupted cardiac dynamics in clinical populations such as syncope (fainting) [45, 46], sleep apnea [47], and ventricular tachyarrhythmia [48] as well as changes in cardiac rhythms that occur during behavioral tasks. Konvalinka et al. [49] reported increased predictability and stability in cardiac dynamics of firewalkers during a ritual fire walk compared to spectators' cardiac dynamics. Wright and Palmer [8] reported increased predictability in pianists' cardiac dynamics when they performed simple melodies compared to a silent baseline; furthermore, pianists' cardiac dynamics were most predictable when they performed novel (unfamiliar) melodies. It is unknown, however, how much cardiac rhythms change during perception or production of auditory rhythms and whether auditory rhythm complexity affects cardiac dynamics.

The current study investigated how auditory rhythm complexity affects cardiac dynamics during auditory perception and synchronisation tasks. The first aim was to determine whether rhythmic complexity, measured by the ratio of tone durations in two simultaneously presented rhythms, influences cardiac dynamics. The second aim was to compare how listening to auditory rhythms versus actively synchronizing one voice or part with those rhythms affects cardiac dynamics. Trained musicians, who have had experience synchronizing their movements to rhythmic sound, listened to and tapped in synchrony with simple and complex auditory rhythms. Based on previous studies, we expected worse tapping performance for complex rhythms (3:2 duration ratios) than for simple rhythms (1:2 duration ratios) [4, 5, 30, 38]. In line with Wright and Palmer's [8] findings, we expected greater recurrence and predictability of cardiac dynamics during the more difficult synchronisation task compared to perception, and greater predictability during the more complex rhythms compared to simple rhythms.

Methods

Participants

Twenty-five musically trained adults participated in the study (mean age = 22.24 years, sd = 3.78, N_{female} = 20). Participants had an average of 13.5 years of private musical instruction (range = 6-18 years; sd = 3.88 years). Participants were screened by email for eligibility; eligible participants had to be between 18 and 35 years of age and have at least 6 years of private musical instruction. Exclusion criteria included a history of cardiovascular, respiratory, neurological, or psychiatric disorders, a diagnosed hearing impairment, or having taken a transcontinental flight within 3 weeks of participating in the study. Participants were screened for normal hearing for the range of tone frequencies used in the auditory stimuli (< 30 dB HL threshold for 125-750 Hz frequencies), as determined by an audiometry screening at the beginning of the experiment. Participants were recruited via social media and flyer postings between May and October 2022 ; 10 participants were recruited for course credit in the Psychology Department at McGill University and 15 participants were recruited from the general adult population in Montreal. Individual participant identifiers available at the time of testing were removed following their participation. The study took place at McGill University and the protocol was reviewed by the Research Ethics Board (Ethics protocol #197-1018).

Stimulus Materials and Equipment

The auditory rhythms in all conditions were composed of two isochronous sequences of tones that differed in pitch and duration and formed specific temporal ratios with one another (Fig 1), similar to Mathias et al. [38]. The high-pitched tones were presented as 660 Hz sine tones and the low-pitched tones were presented as 392 Hz woodblock tones produced by a Roland Sound Canvas (SC-55) tone generator (timbre = 116). The high-pitched and low-pitched tones in the simple rhythm formed a 1:2 ratio such that the high-pitched tone (intertone interval = 1090 ms) occurred once for every two low-pitched tones (intertone interval = 545 ms). The high-pitched and low-pitched tones in the complex rhythm formed a 3:2 ratio such that the high-pitched tone (intertone interval = 363.33 ms) occurred three times for every two low-pitched tones (intertone interval = 545 ms). Thus, the low-pitched tone interonset interval (545 ms) was constant across both the simple and the complex rhythms; only the high-pitched tone interval changed across the rhythms. Each auditory rhythm was sounded for 1 minute and began with four woodblock tones (intertone interval = 545 ms). Each 1-minute auditory rhythm was repeated five times with a silent pause of 10 seconds between each repetition.

Fig 1. Simple and complex auditory rhythms used in the Perception and Synchronisation tasks. Black and grey tones were sounded in the Perception condition. Black indicates sounded tones and grey indicates participants' instructed taps that produced tones in the Synchronisation task. Circles indicate stimulus beats on which asynchronies between sounded tones and produced taps were computed.

Auditory stimuli in the Perception condition contained one omitted tone in either the high-pitched or low-pitched tone stream on two of the five trials for each rhythm (simple and complex) that participants were asked to detect. Tone omissions were placed at either the middle or the end of the rhythm sequence; trials with tone omissions were randomized across rhythm conditions and participants. Auditory stimuli in the Synchronisation condition contained only the high-pitched tone; each auditory rhythm began with four woodblock tones (presented with the same timbre as in the Perception condition) that served as the participants' tempo cue for tapping the low-pitched tone part (set to 545 ms). Thus, the participants' tapping rate in the Synchronisation task was constant across all trials of the simple and complex rhythms.

Sound was delivered through AKG K271 Studio headphones and participants tapped their finger on a Roland RD-700 electronic piano keyboard. Auditory stimuli and participants' auditory feedback were generated on the Roland Sound Canvas (SC-55) tone generator using MIDI (musical instrument digital interface) with 1-ms temporal resolution. Participant key taps were recorded in FTAP v.2.1.07b [50] on a Dell T3600 PC running Linux (Fedora 16). Cardiac activity was recorded with a Polar H10 chest strap heart rate monitor with 1-ms temporal resolution connected via Bluetooth to the application EliteHRV running on an iPad Mini. Questionnaires included a musical background questionnaire and a short questionnaire about participants' physical activity in the hour prior to the experimental session.

Design

Behavioral performance and cardiac activity were measured for all participants in all auditory rhythm conditions, making this a within-subjects Task (Perception and Synchronisation) by Rhythm (Simple vs Complex) design. In addition, each participant had a 5-minute silent baseline measure of cardiac activity collected. The order of conditions in the experiment was kept constant across participants, such that all participants first completed the physiological baseline measurement followed by auditory rhythm perception, then synchronisation. The synchronisation task followed the perceptual task to avoid unintentional motor imagery or motor planning during the perceptual task. The simple rhythm condition always preceded the complex rhythm condition so that participants began with the easier task.

Dependent variables for the Perception task were hit rate (% correct detection) and false alarm rate (% incorrect detection) for the omitted tones. The dependent variables for the Synchronisation task were the mean intertap interval (ITI) and the coefficient of variation (CV, standard deviation/mean ITI) as well as the tapping accuracy (participant tap onset time – stimulus tone onset time) for participant taps that coincided with stimulus tones, indicated with circles in Fig 1. Tapping precision was measured by the standard deviation of the mean signed asynchronies. Dependent variables for the cardiac signals included mean R-R intervals (normal heart beat-to-heart beat intervals, ms) and the root mean square of successive R-R interval differences (RMSSD, ms), a measure of heart rate variability (Schaffer et al., 2014). Nonlinear cardiac measures included Recurrence Rate (% Rec) and Determinism (% Det), described below (Data Analysis).

Procedure

Participants were invited to the lab to complete the 1-hour in-person testing session between 09h and 17h. Upon arrival at the lab, participants provided written informed consent by reading and signing a consent form and then completed an audiometric screening in which pure tones were presented over sound-attenuating headphones (Maico MA40). Only participants who reported hearing the range of tones used in the experiment (125 Hz – 750 Hz) at an average threshold of < 30 dB continued in the experiment.

Next, a 5-minute baseline cardiac recording was conducted. Participants attached the heart rate monitor around their chest and sat in a comfortable chair with their legs uncrossed. During the baseline recording, participants completed written questionnaires with minimal body movement. Participants then completed the Perception task. They were told that each rhythm they heard would have a high-pitched part and a low-pitched part and were asked to identify whether a trial had a missing tone by circling “yes” or “no” on a sheet of paper at the end of each trial. Participants listened to an example of a rhythm with and without a missing tone in initial practice trials for each rhythm. Participants completed five 1-minute Perception trials of the simple (1:2) rhythm followed by five 1-minute perception trials of the complex (3:2) rhythm.

Participants then completed the Synchronisation task. They were asked to tap the low-pitched part of the rhythm on a single key of the piano keyboard using their dominant hand, so that their taps synchronized with the high-pitched part of the rhythm to form the intended rhythm ratio in each condition. Participants heard the high-pitched part of the rhythm as well as their own taps (low-pitch part of the rhythm) during the Synchronisation condition. Participants received up to three practice trials tapping the rhythm before completing five 1-minute Synchronisation trials for each rhythm condition. At the end of the Synchronisation task, participants removed the heart rate monitor and were debriefed. The experimental session took approximately 1 hour to complete.

Data Analysis

Behavioral Data

Each participant's tapping data formed a time series of intertap intervals. Tap ITIs were examined for double taps (< 75 ms between two successive taps) and, when present (approximately 1.4% of all taps), the second tap was removed. The first 4 taps (indicating initial synchronisation) and the last 4 taps were then removed from each trial, similar to Mathias et al. [38]. Intertap intervals greater than 3 standard deviations from the mean ITI were removed (Simple rhythm = 0.67 % of all intervals; Complex rhythm = 0.65 % of all intervals) and the mean ITI and CV were then calculated for each trial using Matlab (version 9.8.0, 2020). The mean absolute asynchrony, mean signed asynchrony, and standard deviation of mean signed asynchrony were calculated in each trial for each tap that aligned with a stimulus event, as shown by the circles in Fig 1. Smaller absolute asynchrony values indicate more accurate tapping; negative mean signed asynchrony values indicate participants' taps anticipated the stimulus tone. A smaller standard deviation of the mean signed asynchronies indicates more precise tapping.

Cardiac Data

Cardiac data were processed in Kubios HRV Premium (version 3.5.0). R-R interval series were generated for each trial, and mean R-R interval and RMSSD, were calculated in Kubios. The RMSSD is primarily a measure of vagally-mediated beat-to-beat heart rate variability [51]. It was deemed an appropriate measure of heart rate variability as respiration does not have a large influence on RMSSD [52] and length of the time series being analyzed was short (1 minute).

The R-R values were then converted into beats per minute (BPM) that resulted in values every 300 ms (ie. measures faster than the maximal heart rate of all participants), following Wallot et al. [53]. Each R-R value in the time series (indicating onset times) was replaced with a string of BPM values. The BPM values were then averaged using a non-overlapping moving window of 300 ms, and the resultant time series served as input to the recurrence quantification analysis (RQA). The result of this transformation is an upsampling of the time series that creates a consistent length time series across trials and participants [53].

Auto recurrence quantification analysis (RQA) was used as the nonlinear analysis method of cardiac activity and was performed in Matlab with the CRP Toolbox 5.22 [54]. In contrast to the linear cardiac measures, RQA captures recurring patterns in cardiac activity over time. Symmetrical, binary (recurrent, non-recurrent) recurrence plots were generated, which capture the recurring patterns in the cardiac signal (see Fig S2). Recurrence plots were generated on normalized values of the cardiac timeseries. Two metrics were used to quantify the recurrence patterns observed in the recurrence plots. The first was Recurrence Rate, a measure of the total proportion of recurrent to non-recurrent points. The second was Determinism: The proportion of sequential recurrent points, corresponding to predictability of the cardiac signal. For a detailed description of RQA methodology and chosen parameters, see S1 Appendix.

Statistical tests for the behavioral and physiological measures were conducted in R Studio (version 4.2.0). Repeated-measures analyses of variance (using the function *ezANOVA* from the *ez* package in R) were used to investigate differences between more than two conditions, with a p-value below .05 determining statistical significance. Planned contrasts with the Holm-

Bonferroni correction were used to follow-up significant analyses of variance. Trial-level participant data was the input for all statistical tests. The number of participants was chosen based on previous findings and expected medium to large effect sizes for the within-subjects design [8, 38].

Results

Perception of missing beats

The effect of Rhythm (Simple, Complex) on missing tone identification in the Perception condition was tested with paired t-tests. There were no significant differences between Rhythm conditions for the hit rate ($t(24) = .681$, $p = .251$, *Cohen's* $d = .138$). Participants were equally good at detecting missing tones in the Simple rhythm (90.4%) and the Complex rhythm (88.0%). Similarly, there were no significant differences between rhythm conditions for the false alarm rate ($t\ (24) = 0.0$, $p = .50$, *Cohen's* $d = 0.0$). Participants did not make more false detections in the complex rhythm (7.2%) than the simple rhythm (7.2%).

Synchronisation of taps

We tested for differences in tapping variability across Rhythms (Simple, Complex) in the Synchronisation condition. Tapping CV was significantly larger for the Complex rhythm ($F\ (1,24) = 4.43$, $p = .046$, *generalized* $\eta^2 = .083$) indicating participants were less precise in their tapping during the Complex rhythm (mean CV = .059) compared to the Simple rhythm (mean CV = .048). As expected for the fixed tapping rates across stimuli in the rhythm conditions, participants' mean ITIs did not differ significantly between the Simple and Complex rhythms ($F\ (1,24) = .522$, $p = .477$, *generalized* $\eta^2 = .009$). Thus, the increased variability for the Complex rhythm was not a result of changes in tapping rate.

Next, we assessed participants' tapping synchronisation accuracy in the Synchronisation conditions. As shown in Fig 2a, mean absolute asynchrony values were significantly larger for the Complex rhythm than the Simple rhythm (F (1,24) = 21.1, p < .001, *generalized* η^2 = .278. As shown in Fig 2b, the Complex rhythm yielded significantly larger positive signed asynchrony values whereas the Simple rhythm yielded smaller negative values (F (1,24) = 25.46, p < .001, *generalized* η^2 = .330).

Fig 2. Behavioral synchrony measures by Rhythm condition in the Synchronisation task. A): Mean absolute asynchrony by Rhythm condition (in ms). B): Mean signed asynchrony by Rhythm condition (in ms). C): Mean standard deviation of signed asynchrony by Rhythm condition (in ms). Circles = individual participants' values.

Finally, analyses of the synchronisation tapping variability were conducted in the Synchronisation condition. The standard deviation of the signed asynchronies was significantly larger for the Complex rhythm than the Simple rhythm (F (1,24) = 18.5, p < .001, *generalized* η^2 = .255), as shown in Fig 2c. Overall, these results indicate that participants synchronized their taps less accurately and less precisely with the Complex rhythm, and they showed greater anticipation (ie, their taps preceded the stimulus more) with the Simple rhythm.

Linear measures of cardiac rhythms

We first compared the Baseline cardiac activity (at rest) with the cardiac activity during the auditory rhythm tasks. A one-way ANOVA on mean R-R intervals by Task (Baseline, Perception, Synchronisation) revealed a significant effect of Task (F(2,48) = 5.280, p =.008, *generalized* η^2 = .012). The R-R intervals were larger (heart rate was slower) during the

Perception condition (mean = 768.335 ms) compared to Baseline (mean = 744.161 ms) (Holm-Bonferroni corrected *t*(24) = 3.389, *p* = .002, *Cohen's d* = .26) and during Perception compared to Synchronisation (mean = 745.052 ms) (*t*(24) = 3.332, *p* = .003, *Cohen's d* = .24). There was no significant difference between the Baseline and Synchronisation conditions (*t*(1,24) = -.084, *p* = .934, *Cohen's d* = .01). A one-way ANOVA on RMSSD by Task (Baseline, Perception, Synchronisation) yielded no significant differences (*F*(2,48) = 1.360, *p* = .267, *generalized* η^2 = .005).

To test for auditory rhythm effects, we conducted two-way ANOVAs on the linear cardiac measures by Task (Perception, Synchronisation) and Rhythm (Simple, Complex). The ANOVA on mean R-R intervals showed a significant main effect of Task (*F* (1,24) = 11.103, *p* = .003, *generalized* η^2 = .014), confirming that heart rates were slower during Perception than during Synchronisation for both Simple and Complex Rhythms. There were no significant effects of Rhythm or Task x Rhythm interaction. The two-way ANOVA on RMSSD indicated a significant main effect of Task (*F*(1,24) = 5.609, *p* =.026, *generalized* η^2 = .075). There was greater heart rate variability during Perception than during Synchronisation for both Simple (Perception = 34.78 ms, Synchronisation = 32.17 ms) and Complex rhythms (Perception = 34.49, Synchronisation = 31.37). There were no other significant main effects or interactions. Overall, the linear cardiac findings indicate that heart rate was faster and less variable during the Synchronisation condition compared to the Perception condition.

Nonlinear measures of cardiac rhythms

We compared the nonlinear cardiac metrics for the Baseline condition (at rest) with the cardiac activity during the auditory rhythm tasks. For Recurrence Rate, there was a significant effect of Task (*F*(1,24) = 10.40, *p* < .001, *generalized* η^2 = .119), with greater cardiac recurrence during Perception (mean = 3.062%) than Baseline (mean = 1.803%) (pairwise comparisons, Holm-Bonferroni corrected $t(24) = 4.156$, $p < .001$, *Cohen's d* = .96) and during Synchronisation (mean = 3.283%) than Baseline ($t(24) = 4.286$, $p < .001$, *Cohen's d* = .93). Perception and Synchronisation conditions did not differ significantly (t(24) = -.546, $p = .590$, *Cohen's d* = .08). Determinism values, based on fixed recurrence rates (5%), showed similar main effects of Task ($F(1,24) = 4.395$, $p = .018$, *generalized* $\eta^2 = .027$). Follow-up pairwise comparisons (Holm-Bonferroni corrected) indicated greater Determinism during Perception (mean = 65.71%) than Baseline (mean = 62.51%) ($t(24) = 2.862$, $p = .009$, *Cohen's d* = .37) and during Perception than Synchronisation (mean = 62.85%) ($t(24) = 2.486$, $p = .02$, *Cohen's d* = .36). There was no significant difference between the baseline and Synchronisation conditions ($t(24) = -.267$, $p = .792$, *Cohen's d* = .04).

To test for auditory rhythm effects on the nonlinear cardiac measures, a 2-way ANOVA on Recurrence Rate was conducted by Task (Perception, Synchronisation) and Rhythm (Simple, Complex). This yielded a significant Task x Rhythm interaction ($F(1,24) = 11.542$, $p = .002$, *generalized* $\eta^2 = .022$), and no main effects. There was significantly more recurrence during perception of the Complex rhythm than during perception of the Simple rhythm, and significantly more recurrence during synchronisation with the Simple rhythm compared to synchronisation with the Complex rhythm (*HSD* = .039, $p < .05$; Fig 3). Fig 4 shows example recurrence plots for the same individual's trials of Simple and Complex rhythms from the Perception and Synchronisation tasks. The recurrence plot for Complex Rhythm-Perception contains more recurrent points (black dots, greater Recurrence Rate) than does the plot for Simple Rhythm-Perception by the same individual. The Synchronisation condition plots show the opposite pattern: Synchronisation with the Simple rhythm leads to more recurrent points than does Synchronisation with the Complex rhythm.

Fig 3. Mean recurrence rate (%) in the cardiac time series (beats per minute) by Task (Perception, Synchronisation) and Rhythm (Simple, Complex). Circles = individual data points.

Fig 4. Sample cardiac time series (in beats per minute) and recurrence plots (in number of samples) from one participant for each Auditory Condition and Rhythm condition. A) Perception task: Simple rhythm (left) and Complex rhythm (right). B) Synchronisation task: Simple rhythm (left) and Complex rhythm (right). Black dots in recurrence plots indicate points of recurring heartbeat intervals.

The same two-way ANOVA on Determinism showed a significant main effect of Task ($F(1,24) = 6.107$, $p = .021$, *generalized* $\eta^2 = .029$) with greater cardiac determinism (more predictability) during rhythm Perception than during Synchronisation for both Simple (Perception = 65.4%, Synchronisation = 63.3 %) and Complex (Perception = 66.0 %, Synchronisation = 62.4%) auditory rhythms. There was no significant effect of Rhythm or Task x Rhythm interaction. Fig 5 shows example recurrence plots for a single participant during individual trials of the Simple rhythm in Perception and Synchronisation conditions. There is greater determinism, or proportion of black dots forming diagonal lines (indicating sequential runs of recurrence in the time series), in the cardiac patterns during Perception compared to Synchronisation.

Fig 5. A) Mean % Determinism in the cardiac time series (beats per minute) by Task. Circles = individual data points. B) Sample cardiac time series (in beats per minute) and recurrence plots (in number of samples) from one participant for each Auditory Condition with the Simple rhythm. Left) Perception task. Right) Synchronisation task. Diagonal lines of black dots indicate determinism (predictability), sequential recurring heartbeat intervals in the cardiac time series.

Behavior-cardiac correlations

Simple correlations were used to assess behavior-cardiac relationships in the Synchronisation condition at the participant level (collapsed across trials). We compared each participant's mean heart rate variability with mean tapping variability (CV) and two measures of asynchrony. Significant moderate-sized correlations were observed between measures of tapping synchronisation and RMSSD for the Complex rhythm (Fig 6). In the Complex rhythm condition, participants with larger mean absolute asynchrony values (less accurate synchronisation) exhibited greater RMSSD values, indicating greater cardiac variability ($r = .41$, $p = .042$). Also in the Complex rhythm condition, participants with larger standard deviations of signed asynchronies (more variable synchronisation) showed larger RMSSD values ($r = .40$, $p = .0499$). The same correlations for the Simple rhythm were small and did not reach significance (mean absolute asynchrony: $r = .05$, $p = .821$; standard deviation of signed asynchronies: $r = .001$, $p = .998$). In sum, these synchronisation-cardiac correspondences indicate that worsened tapping accuracy and variability were correlated with greater heart rate variability during the Complex rhythms. There were no significant correlations between heart rate variability and tapping CV.

Fig 6. Simple correlations. A) Mean Absolute Asynchrony and RMSSD, in ms, and B) Mean Standard Deviation of Signed Asynchrony and RMSSD, in ms.

Discussion

This study demonstrated effects of rhythm complexity on cardiac dynamics during perception and production (synchronisation) of auditory rhythms. Musically trained adults listened to and tapped with simple rhythms (that formed a 1:2 duration ratio between the two rhythms) and with complex rhythms (that formed a 3:2 duration ratio between the two rhythms) while their cardiac activity was measured. Linear and nonlinear analysis methods were applied to the participants' cardiac dynamics measured during rhythm perception and production. Listeners identified omitted tones accurately in both simple and complex rhythms, indicating successful perception. Complex auditory rhythms were more difficult to synchronize with than were simple rhythms. Individual differences analyses indicated that more inaccurate and more variable synchronisation corresponded to greater heart rate variability. Finally, nonlinear analyses of recurring patterns in cardiac dynamics were differentially modulated by both the task (perception or synchronisation) as well as by stimulus rhythm complexity. Thus, nonlinear cardiac measures of recurrence rate and determinism were more sensitive to rhythm complexity than were linear measures.

Predictions from dynamical systems theory [24, 25, 26] as well as behavioral evidence [2, 4, 5, 30 38] indicate that synchronizing with complex rhythm ratios (such as the 3:2 rhythms used here) is more difficult than with simple ratios (such as the 1:2 rhythms used here). Our behavioral findings are consistent with these predictions: Tappers showed larger intertap interval variability (CV) and less accurate and less precise synchronisation of taps with the complex rhythm than the simple rhythm. Importantly, tapping rates were held constant between the simple and complex rhythm conditions. Thus, motor system demands were equated across the rhythms and cannot account alone for the poorer performance on the Complex rhythm task. There was also less anticipatory synchrony for the complex rhythm than the simple rhythm, reflected by taps that lagged the stimulus tones for the complex rhythm. Notably, there were no rhythm complexity effects for the missing tone detection task in the perceptual condition, suggesting that the observed production effect is not simply due to differences in perceptual processing of the simple and complex rhythms. Repp et al. [36] similarly found no clear advantage of simple over complex rhythms in a perceptual task that required detection of a temporal perturbation in an auditory rhythm. It may be that rhythm complexity affects production more than perception because auditory-motor coupling is required, yielding greater task difficulty.

Perception/production differences in cardiac rhythms indicated that cardiac activity was modulated by auditory perception and synchronisation tasks, above and beyond the complexity of the rhythm. Rhythm synchronisation resulted in faster heart rates (smaller R-R intervals) and decreased heart rate variability compared to rhythm perception. These findings are consistent with findings showing faster heart rates and decreased heart rate variability when pianists performed a complex musical piece compared to when they listened to the same piece [55]. The Synchronisation task may have been more difficult and resulted in greater physiological arousal, as it required individuals to simultaneously perceive one rhythm while producing another auditory rhythm. More difficult cognitive and motor tasks have been reported to result in increased autonomic arousal [9], including in the auditory domain [11]. A related interpretation is that greater physiological arousal in the Synchronisation condition reflected performance anxiety, leading to the observed changes in heart rate and heart rate variability [23]. However, the linear cardiac metrics were similar between the Baseline (no auditory stimulus) and Synchronisation conditions suggesting that performance anxiety cannot account for the observed differences.

Nonlinear measures of cardiac rhythms, including recurrence rates and determinism (predictability), showed that cardiac dynamics were more predictable during rhythm perception than synchronisation. These findings contrast with previous reports of increased cardiac predictability accompanying increased task difficulty [45, 49, 56]. Notably, Wright and Palmer [8] reported increased cardiac predictability when musicians performed unfamiliar (novel) musical rhythms compared to familiar musical rhythms; that study did not compare perception and performance conditions. The design of the current study allowed us to dissociate cardiac effects of simply perceiving auditory rhythms from perceiving while simultaneously producing the same rhythms. In the Perception condition, the timing of the stimulus rhythms was computer-generated with no variability; in the Synchronisation condition, the timing of the auditory rhythms was variable as participants produced one part of the rhythm. These findings suggest nonlinear properties of cardiac dynamics may be modulated by stimulus timing and rhythmic motor timing.

Effects of rhythmic timing on cardiac dynamics were also evidenced in the striking Task (perception/synchronisation) by Rhythm (simple/complex) interaction observed for cardiac recurrence rate (indicating repeating patterns). There was greater cardiac recurrence during perception of the Complex rhythm (which presented different temporal intervals between the two parts), and greater cardiac recurrence during synchronisation for the Simple rhythm. The order of the conditions (Perception, then Synchronisation) and rhythms (Simple, then Complex) was constant across participants, suggesting that the Task by Rhythm interaction cannot be explained simply by order effects. It also cannot be explained by participants' tapping rates between conditions, as no tapping rate differences were observed. It is possible that cardiac activity was less recurrent during synchronisation with the complex rhythm due to increased motor noise in participants' more variable asynchronies in this condition. The interpretation that cardiac rhythms (de)couple from the participant's tapped rhythms in the presence of motor noise. Finally, cardiac recurrence may not reflect the same underlying causes in perception and synchronisation/production of auditory rhythms, as motor timing and stimulus timing do not individually explain the observed interaction. Future research may disentangle this explanation by investigating how tapping rhythms in the absence of auditory feedback affects cardiac dynamics.

Correlations between individuals' synchronisation performance and linear cardiac measures support the interpretation that cardiac dynamics are sensitive to auditory and motor timing. Participants' lower accuracy and more variable synchronisation was correlated with increased heart rate variability in the complex rhythm condition only. This is interesting because poorer performance indicates that synchronizing with the complex rhythm was more difficult, yet heart rate variability increased, the opposite of task difficulty effects [57, 58]. Notably, those tasks did not manipulate the sequential stimulus timing, a factor unique to the current design. Thus, individual differences in synchronisation and heart rate variability are consistent with the interpretation that cardiac activity may reflect increased noise in auditory and motor timing.

Only nonlinear cardiac analyses were sensitive to rhythm complexity, as expected for time series analyses that derive recurrences from successive items in a time series (such as the sequential ratios between successive intertap intervals that defined the simple and complex rhythms). It is therefore not surprising that the recurrence measures were more sensitive than the linear measures to cardiac differences between the simple and complex auditory rhythms. Analysis of musicians' joint cardiac dynamics also show increased cardiac recurrence and predictability during ensemble music performance [59]. Nonlinear analysis methods may be strongly suited for detecting changes in cardiac rhythms during temporally patterned tasks such as auditory rhythm production.

There are a few important limitations in the findings to consider. First, musical training may influence physiological measures such as cardiac dynamics in response to auditory rhythms. Nonmusicians tend to exhibit greater variability in rhythmic tapping performance than musicians [60, 61]; comparison of musically trained with untrained individuals may reveal different relationships. Second, natural music produced in richer contexts introduces many more acoustic features such as pitch, timbre and tempo; cardiac dynamics are likely to be affected by additional features of complex musical pieces. Future research may compare simple and complex musical rhythms in natural musical settings to complement the constrained basic rhythm complexity findings reported here.

Overall, this study demonstrated that auditory rhythm perception and production influence cardiac activity in musically trained individuals. Complex auditory rhythms (those that formed non-integer duration ratios) were more difficult to tap than simple auditory rhythms (those that formed integer duration ratios). Synchronisation with auditory rhythms resulted in faster heart rate, decreased heart rate variability, and more predictable cardiac dynamics than perception of the same rhythms. Nonlinear cardiac dynamics showed more recurrence when participants synchronized with simple compared to complex auditory rhythms; participants who were worse at producing complex rhythms showed decreased heart rate variability. To our knowledge, this is the first study to demonstrate altered cardiac dynamics while individuals perceived and synchronized with auditory rhythms. These findings suggest that auditory-motor coupling during rhythm production may be an important modulator of cardiac dynamics that extends beyond perceptual influences.

Acknowledgements

We gratefully acknowledge the technical assistance of Selva Asgharizadeh, Louis Deng, and Sandra Kuliver. Correspondence should be addressed to Shannon Wright (shannon.eilyce.wright@mail.mcgill.ca) and Caroline Palmer (caroline.palmer@mcgill.ca).

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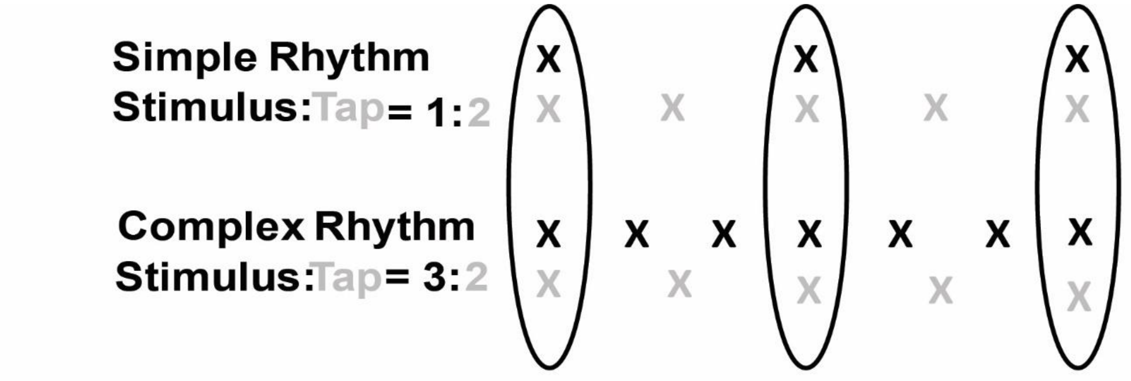
Simple Rhythm
Stimulus:Tap= 1:2
Complex Rhythm
Stimulus:Tap= 3:2
X
X
X

Figure 1

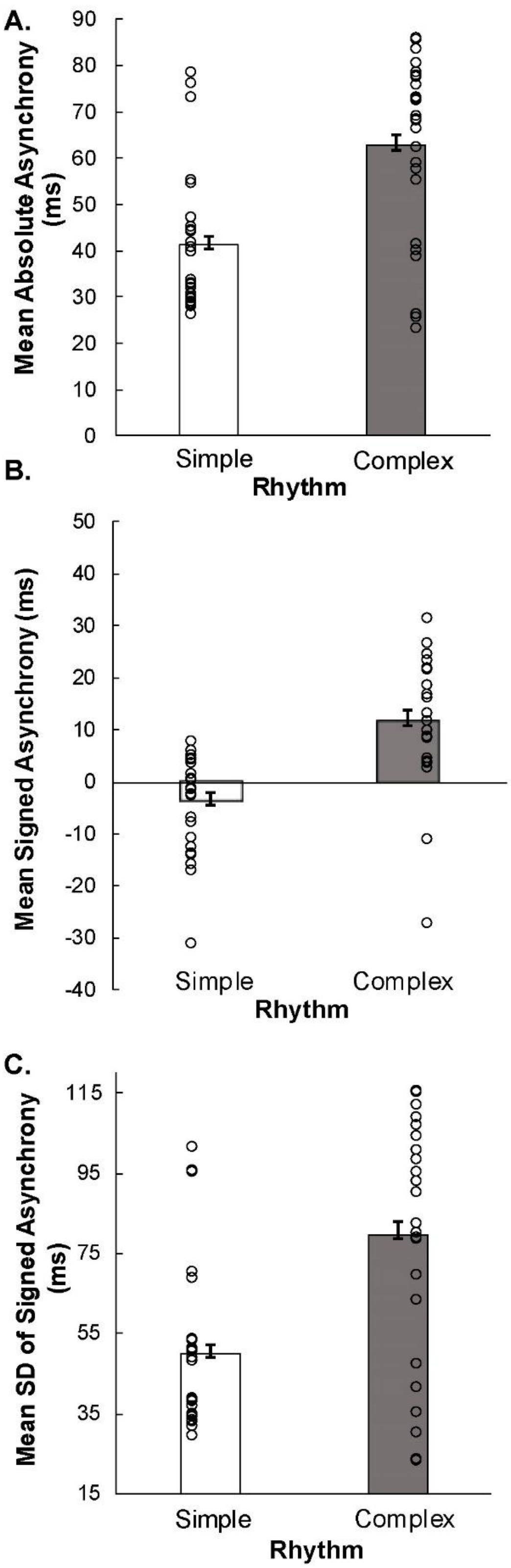
A.
Mean Absolute Asynchrony (ms)
0
10
20
30
40
50
60
70
80
90
Simple
Complex
Rhythm
B.
Mean Signed Asynchrony (ms)
-40
-30
-20
-10
0
10
20
30
40
50
Simple
Complex
Rhythm
C.
Mean SD of Signed Asynchrony (ms)
15
35
55
75
95
115
Simple
Complex
Rhythm

Figure 2

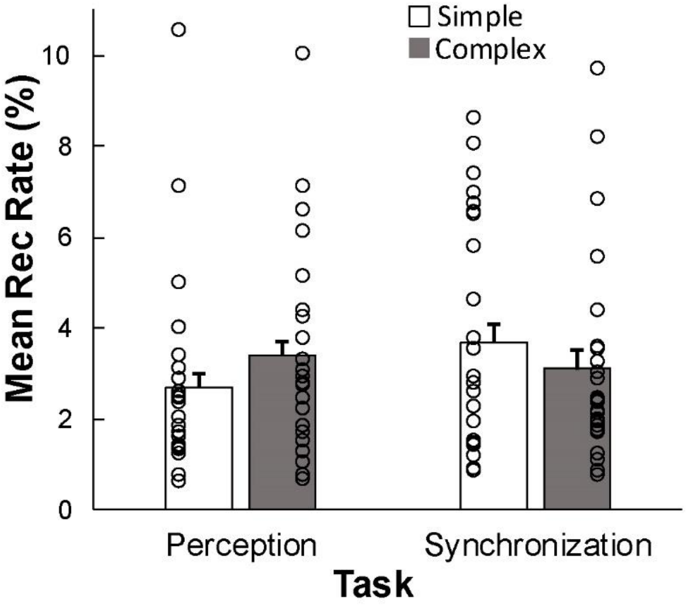
☐ Simple
■ Complex
Mean Rec Rate (%)
0
2
4
6
8
10
Perception
Synchronization
Task

Figure 3

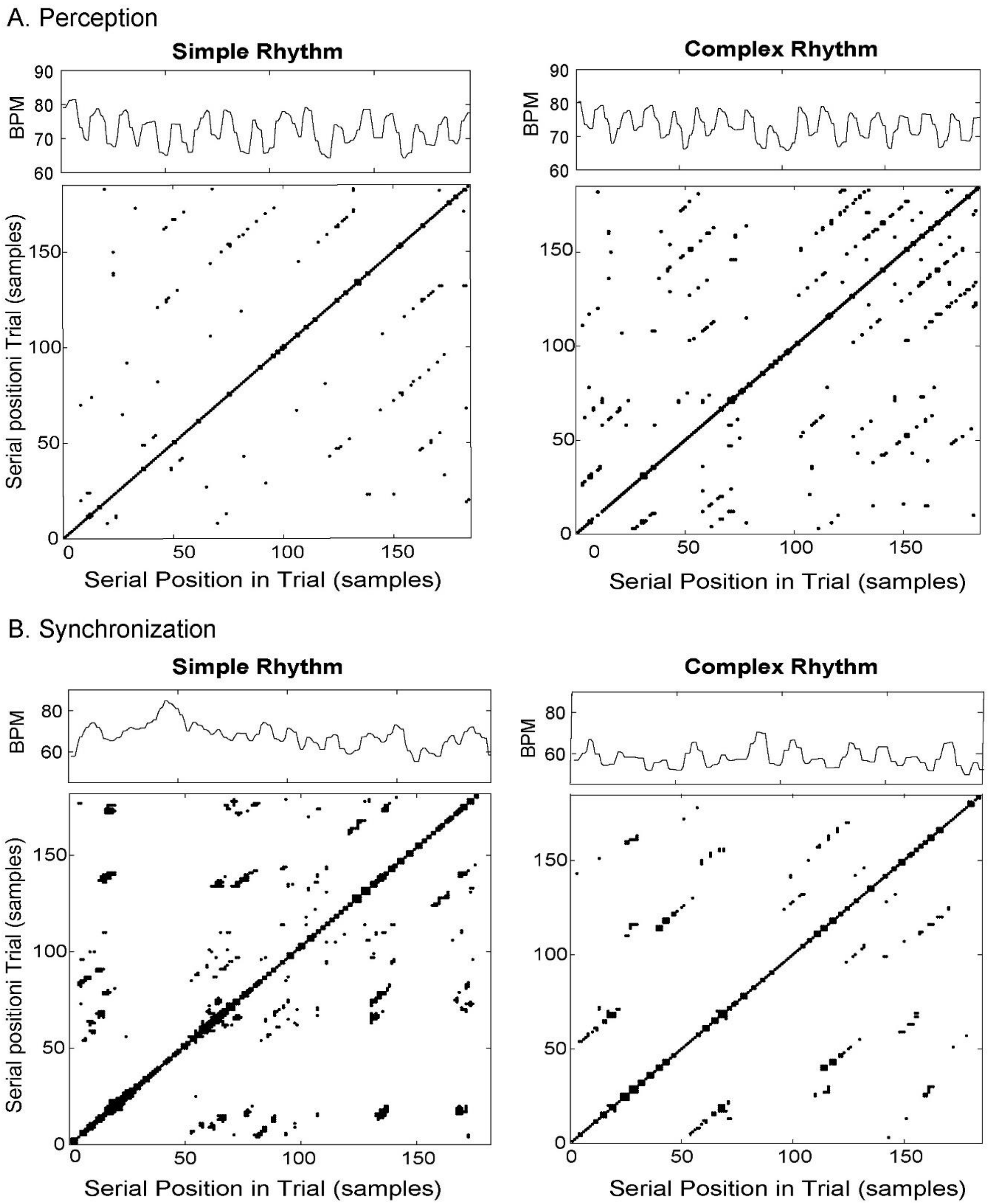
A. Perception
Simple Rhythm
Complex Rhythm
BPM
90
80
70
60
Serial positioni Trial (samples)
0
50
100
150
Serial Position in Trial (samples)
B. Synchronization
Simple Rhythm
Complex Rhythm
BPM
80
60
Serial positioni Trial (samples)
0
50
100
150
Serial Position in Trial (samples)

Figure 4

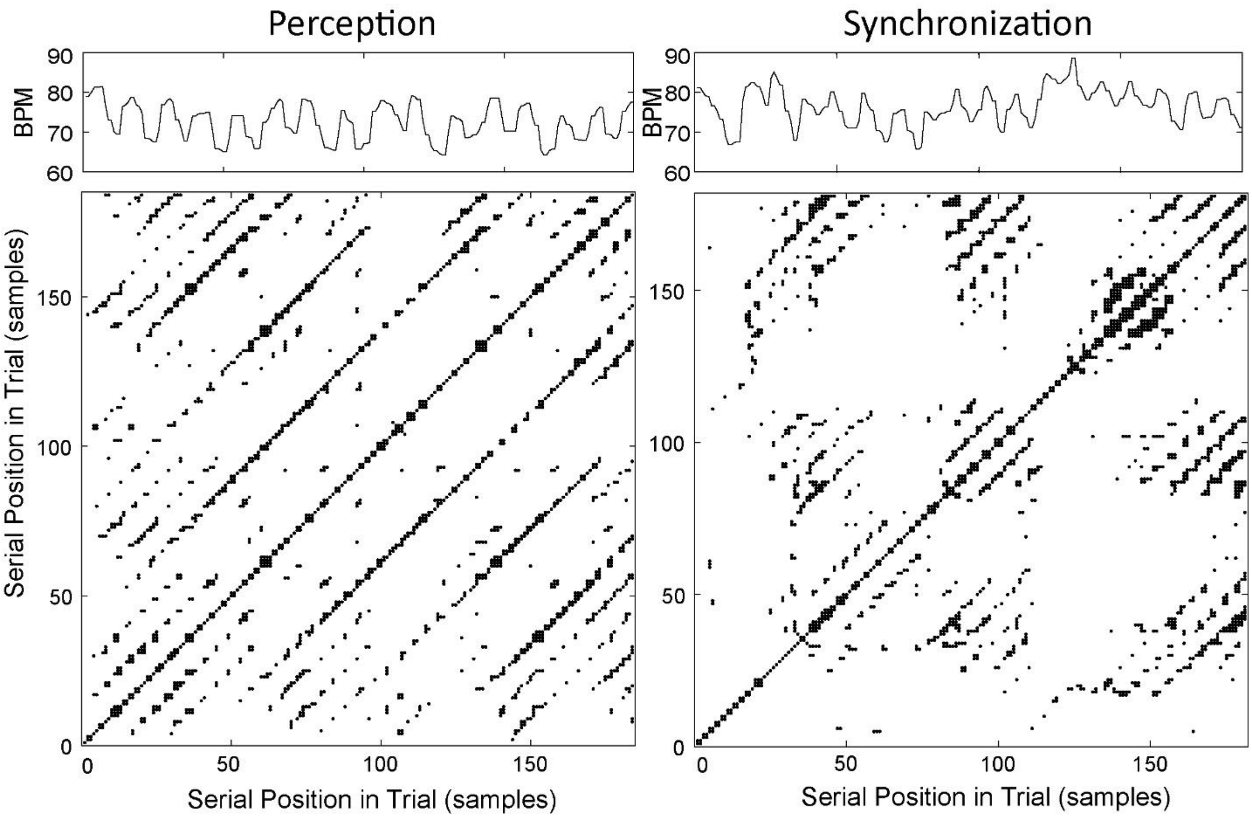
Perception
Synchronization
BPM
90
80
70
60
Serial Position in Trial (samples)
0
50
100
150
Serial Position in Trial (samples)

Figure 5

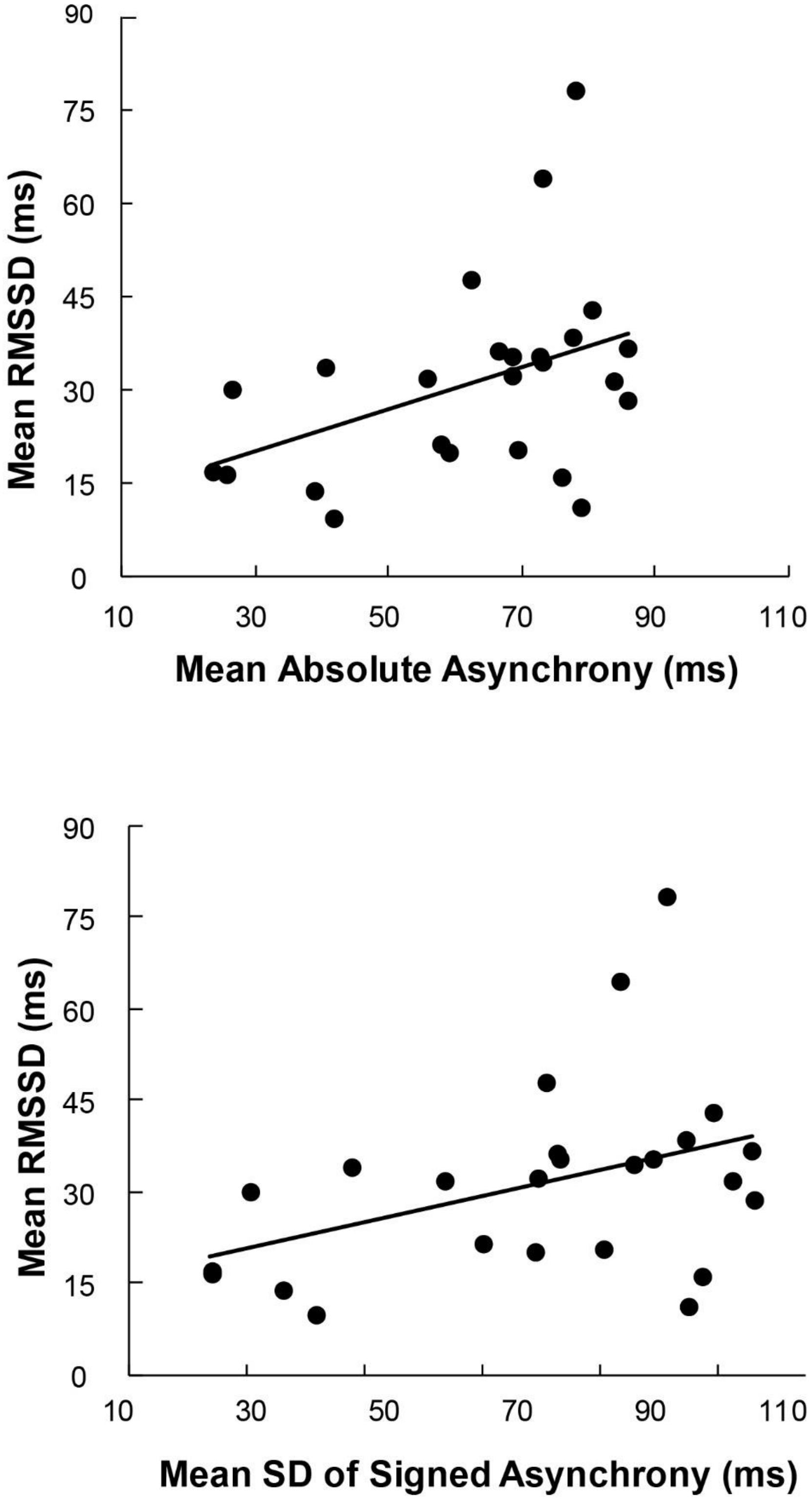
90
75
60
45
30
15
0
Mean RMSSD (ms)
10
30
50
70
90
110
Mean Absolute Asynchrony (ms)
90
75
60
45
30
15
0
Mean RMSSD (ms)
10
30
50
70
90
110
Mean SD of Signed Asynchrony (ms)

Figure 6

Supporting Information

S1 Appendix

Recurrence quantification analysis (RQA) was used as the nonlinear analysis method of cardiac activity. In contrast to the linear cardiac measures, auto-RQA captures cardiac dynamics - or changes in the heart's activity over time. A time-delayed copy of the normalized cardiac time series is produced to reconstruct the signal in a multi-dimensional phase space [1, 2]. A time delay parameter and an embedding dimension parameter are used to yield the reconstructed phase space. In the current study, the time delay was set to the first local minimum of the average mutual information function [3]. The time delay values at the trial level ranged from 4-29. The embedding dimension parameter, which determines the dimensionality of the phase space, was chosen using the False Nearest Neighbours method [3] in which the first local minimum was selected as the embedding dimension for each trial. Embedding dimensions ranged from 4-17. The time delay and embedding dimension values across trials and participants were fixed to the median of the observed values (time delay = 4, embedding dimension = 4). This prevents individual- and condition-level differences in the dependent variables from being artefacts of the parameters varying across individuals and/or conditions [3]. Figure S1 (top) shows an example of a phase space trajectory of a cardiac signal with a time delay = 4 and embedding dimension = 3.

Points in the phase space are then assessed for their closeness using a radius threshold parameter; points that are sufficiently close to one another in the phase space are deemed to be recurrent [3]. Recurrent points are then plotted in a 2-dimensional, binary (black=recurrent, white=not recurrent) auto-recurrence plot (Figure S1 bottom). We set the radius to 10% of the diameter of the phase space for the recurrence rate analysis [3], which allowed recurrence plots to vary in the proportion of recurrent points. For analyses on cardiac determinism, we held the recurrence rate constant at 5% to distinguish determinism effects beyond simple recurrence [4, 5].

Finally, points in the recurrence plot can be quantified according to different metrics to describe the behavior of the cardiac system. Those metrics in the current study included Recurrence Rate and Determinism. Recurrence rate is the proportion of recurrent points in a time series and represents how often the system returns to a previous state [2]. Determinism measures the proportion of recurrent points that occur sequentially in the time series (forming diagonal lines in the recurrence plot) and represents the predictability of the system [3, 6, 7].

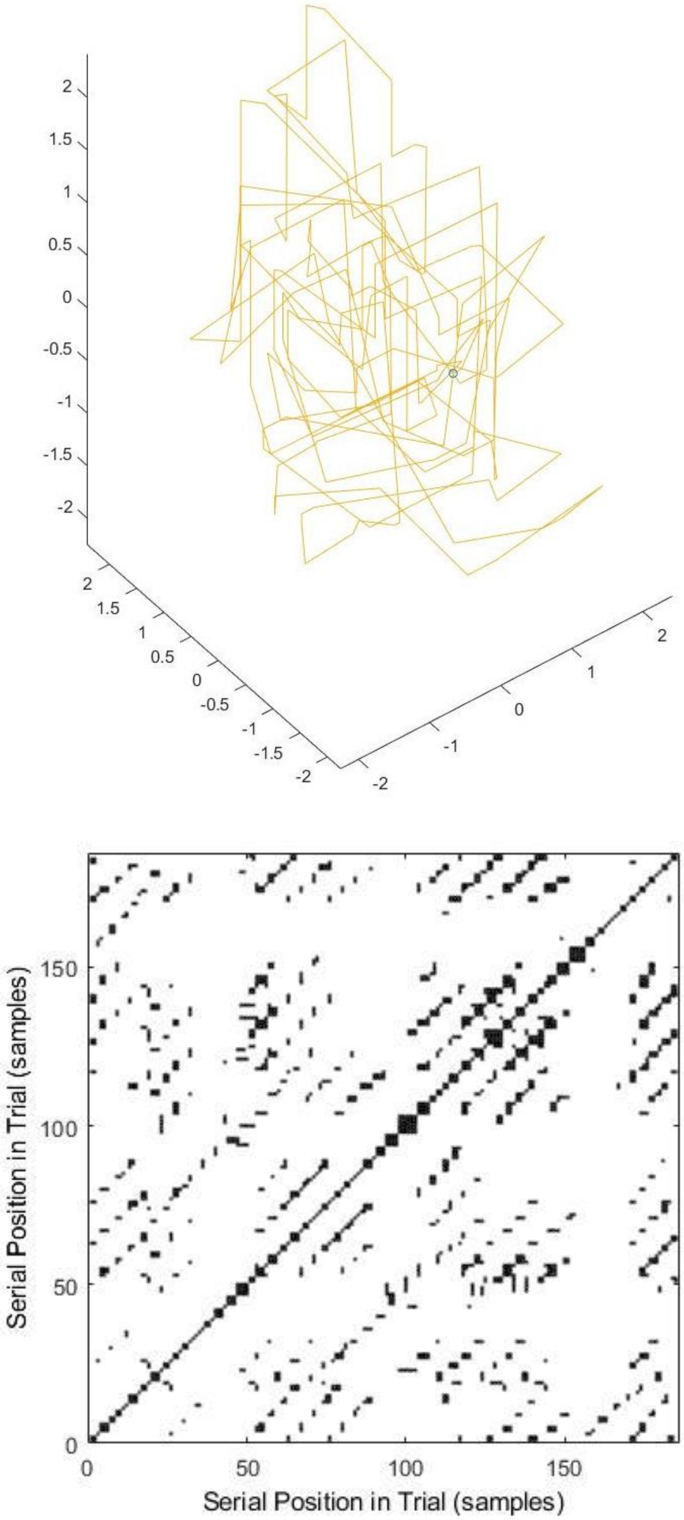

Figure S1. Top: Example of a single participant's phase space trajectory of cardiac activity for a 1-minute tapping trial with embedding dimension = 3 and time delay = 4. Bottom: The recurrence plot derived from the phase space. The cardiac time series is plotted on the x- and y-axes. Each black dot represents a point that was recurrent with another point in the phase space. White space represents non-recurrent points. The total proportion of black points in the recurrence plot is the Recurrence Rate. Diagonal structures represent sequential points of recurrence, signalling cardiac predictability. The proportion of black points that form diagonal lines is Determinism (%).

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Bridge between Chapter 2 and Chapter 3

Chapter 2 tested the effects of perception and production as well as rhythm complexity on behaviour and cardiac dynamics. Behavioural results indicated that synchronisation with a complex rhythm (3:2) was less accurate and more variable than synchronisation with a simple rhythm (1:2) whereas simple and complex rhythms were perceived equally well, highlighting a distinction between perception and production of complex rhythms. Some linear cardiac findings were in keeping with a task difficulty effect: Heart rate increased and heart rate variability decreased during synchronisation compared to perception. However, heart rate variability was greater when synchronisation performance was worse on the complex rhythm. Nonlinear cardiac analyses (RQA) indicated greater cardiac predictability during rhythm perception than synchronisation; cardiac dynamics were more recurrent for complex rhythm perception compared to simple rhythm perception, and for simple rhythm synchronisation compared to complex rhythm synchronisation. These findings suggest that task difficulty does not fully explain how auditory rhythm performance affects cardiac dynamics, and that *producing* auditory rhythms affects cardiac dynamics in a particular way.

Chapter 3 tests short-term training effects on complex rhythm synchronisation, thus building on the previous chapters in two ways. First, Chapters 1 and 2 of this dissertation exclusively recruited trained musicians as the tasks involved music performance and synchronisation with complex auditory rhythms. This is a reasonable approach as these are both difficult auditory-motor synchronisation tasks, and research has demonstrated musicians' advantage in auditory-motor synchronisation tasks such as synchronising finger taps with an auditory rhythm (Krause et al., 2010; Repp & Doggett, 2007; Scheurich et al., 2020; Tranchant et al., 2022). Chapter 3 expands the sample to investigate behavioural and cardiac responses of a wider range of participants, with and without musical training, in an auditory-motor synchronisation task. Second, Chapter 1 findings suggested a possible short-term practice effect on music performance and cardiac dynamics; Chapter 3 explicitly tests whether short-term training on complex auditory rhythms affects behaviour and cardiac dynamics.

Chapter 3: Short-term training and rhythm complexity affect auditory-motor synchronization

Wright, S. E., & Palmer, C. (2023). Short-term training and rhythm complexity affect auditory-motor synchronization. [Manuscript submitted for publication].

Short-term training and rhythm complexity affect auditory-motor synchronization

Abstract

Introduction: Previous findings suggest that long-term musical training and rhythm complexity affect performers' auditory-motor synchrony and their cardiac rhythms. We investigated effects of short-term training and rhythm complexity on auditory-motor synchronization and cardiac activity as individuals synchronized with auditory rhythms.

Methods: 42 adult participants synchronized their taps with sounded rhythms to form a 2:3 duration ratio (stimulus duration:tap duration) or a 3:2 duration ratio (tap rate held constant across rhythms). Participants received short training with one rhythm and received longer training with the other rhythm. Then participants completed five experimental trials in which they synchronized their sounded taps with the stimulus rhythm. Cardiac activity was recorded during synchronization.

Results: Tapping synchronization was more accurate and less variable for the 2:3 rhythm than the 3:2 rhythm. Nonlinear measures of cardiac activity showed the greatest cardiac recurrence for the 2:3 rhythm. Behavioral-cardiac correspondences emerged with training: Poorer synchronization was associated with more variable cardiac activity after long training, but not after short training. Finally, there were consistent individual differences in cardiac recurrence and predictability across training conditions.

Discussion: These findings demonstrate both short-term learning effects and rhythm complexity effects on behavior and cardiac dynamics during auditory-motor synchronization.

Keywords: learning; synchronization; auditory rhythm; cardiac dynamics; recurrence quantification analysis

Introduction

Humans display an impressive ability to synchronize their actions with sound, known as auditory-motor synchronization. Successful temporal coordination of action with sound, as seen in music performance or dance, requires some amount of practice and/or training. For example, long-term musical training increases temporal accuracy and reduces variability in auditory-motor synchronization tasks (Krause et al., 2010; Repp & Doggett, 2007; Scheurich et al., 2020). Musical training particularly improves synchronization with complex auditory rhythms (Chen et al., 2008; Mathias et al, 2020), and musicians’ cardiac activity is differentially affected during synchronization with simple and complex auditory rhythms (Wright & Palmer, 2023). Although several studies have focused on effects of long-term training (for a review see Koesch & Jancke, 2015), few address short-term training effects on auditory-motor synchronization and cardiac activity. The current study investigates how short-term training affects synchronization accuracy and cardiac activity during the production of complex rhythms. In the next sections, we review relevant findings on rhythm complexity and short-term training effects on auditory-motor synchronization and on simultaneous cardiac activity.

Auditory Rhythm Complexity

Simple auditory rhythms are composed of sequences of tone durations that form integer multiples such as 2-to-1 (Fraisse, 1982) and can be learned and produced with temporal accuracy in relatively short periods of training (Chen et al., 2012; Pfordresher & Chow, 2019; Madison et al., 2013). Complex auditory rhythms, composed of tone durations that form non-integer multiples such as 2:3 or 3:2, require more practice to be produced accurately (Mathias et al., 2016; Tajima & Choshi, 2000).

These behavioral distinctions between simple and complex auditory rhythms are consistent with nonlinear dynamical systems predictions for how people synchronize behaviors with sound. According to the dynamical systems perspective, an oscillator (a periodic, recurring time series with an associated amplitude and frequency; Pikovsky, 2001) will couple more easily with signals such as auditory stimuli when their frequencies (inverse of rate) form small integer ratios (such as 2:1) than non-integer ratios (such as 2:3 or 3:2) (Large & Snyder, 2009; Large et al., 2015; Treffner & Turvey, 1993). The stability of two coupled oscillators can be described as a ratio of their frequencies in what is known as Arnold Tongues (Kelso, 1995). The size and shape of the synchronization regions is governed by certain parameters: The winding number (the ratio of two oscillator natural frequencies), the coupling strength parameter (k), and the symmetry of the frequencies between ratios (for example, 2:3 = 3:2). For certain frequency ratios, such as 1:2 (winding number = .5), the stability region is large even for small values of k. This means that two oscillators will tend to show stable synchronization (Kelso, 1995; Large et al., 2015) for these simple rhythms. Conversely, for other frequency ratios, such as 2:3 (winding number = .67) or 3:2 (winding number = 1.5), the stability region is small, even at larger values of k, for these complex rhythms. This means that there is a narrower set of conditions under which two oscillators will couple when their natural frequencies are at 2:3 or 3:2 (the rhythms used in the current study). Notably, the symmetry of the frequencies contained in 2:3 and 3:2 rhythms suggests that they should have comparable regions of stability (Treffner & Turvey, 1993).

The dynamical systems prediction that auditory-motor synchronization will be easier when the stimulus and response durations form small integer ratios (Large & Snyder, 2009; Large et al. 2015) is supported by behavioral studies. Humans show greater temporal accuracy when synchronizing with small integer ratio rhythms compared to larger, non-integer ratio rhythms (Deutsch, 1983; Essens & Povel, 1985; Mathias et al., 2020; Sakai et al., 1999; Snyder et al., 2006; Dotov & Trainor, 2021). In an iterative learning paradigm (participants' output from one trial serves as the stimulus input to the next trial), individuals were asked to synchronize with auditory tone sequences; over iterations, participants taps tended towards small integer ratio rhythms such as 1:1 or 2:1, even when auditory rhythm cues did not always contain small integer ratios (Jacoby & McDermott, 2017). Small integer ratios in auditory rhythms tend to dominate cross-culturally (Savage et al., 2015), although cultural experience with complex rhythms improves synchronization accuracy and precision (Polak et al., 2018). Non-human animal vocalisations also tend to show small integer ratios over non-integer ratios (De Gregorio et al., 2021; Roeske et al., 2020).

Differences between simple and complex auditory rhythms are also evidenced in neurophysiological measures of perception and production. Mathias et al. (2020) showed that musically-trained participants tapped auditory rhythms based on simple (1:1), moderate (1:2), and complex (3:2) rhythmic structures. Tapping was more accurate and precise for the 1:1 and 1:2 rhythms compared to the 3:2 rhythms. Power spectral density measures (EEG) were greatest at frequencies that corresponded to the tapping frequency in the simple (1:1) rhythm compared to the moderate (1:2) and complex (3:2) rhythms (Mathias et al., 2020). These findings suggest that neurophysiological entrainment, the period-matching of neural oscillations with auditory rhythms, was stronger for simple rhythms than for complex rhythms. How short-term training influences synchronization with simple and complex auditory rhythms is addressed in the next section.

Short-term Training Improves Rhythm Production

Short-term training effects on auditory rhythm production have been demonstrated in a few studies. Musicians with a wide range of experience who practiced a novel piece 10 times show significant improvement in rhythmic accuracy from the first to the last performance; musicians with less experience tended to show the greatest improvement (Drake & Palmer, 2000). In another study, non-musicians synchronized their taps with an auditory rhythm cue, then continued tapping the rhythm in the absence of the cue; tapping variability decreased during the first 60 minutes of training, and then remained stable (Madison et al., 2013). Another study found decreased temporal variability in tapping period as non-musicians were trained to tap with isochronous auditory sequences (Nagasaki, 1990). Overall, these findings demonstrate that short-term training can improve auditory rhythm production for both musicians and non-musicians.

A few studies have demonstrated short-term learning of complex auditory rhythms in production tasks. Tillmann et al. (2011) used an implicit learning paradigm to test whether previous perceptual exposure to simple (1:2) and complex (2:3) rhythms improved tapping variability during subsequent synchronization. Participants who were previously exposed to 3:2 ratio rhythms showed less tapping variability with the 3:2 rhythm, compared with those who were exposed to a simple rhythm or to no rhythm. Short-term training improved non-musicians' complex (5:3 duration ratios) polyrhythm performance (two simultaneous tone streams forming complex duration ratios), although their temporal accuracy was tempo-dependent (Tajima & Choshi, 2000). Together, these studies demonstrate that short-term learning of complex auditory rhythms is possible, even in individuals who do not have experience with complex rhythms.

Cardiac Activity during Auditory Rhythm Production

Production of auditory rhythms can influence cardiac activity. Several studies document changes in cardiac activity with musical tempo; as tempo increases, mean heart rate tends to increase

(Bernardi et al., 2006; Egermann et al., 2015; Gomez & Danuser, 2007; Nomura et al., 2013; Watanabe et al., 2015; Watanabe et al., 2015; cf Mütze et al. 2018) and as tempo decreases, mean heart rate tends to decrease (Iwanaga et al., 1996; Van Dyck et al., 2017; Ooishi et al., 2017). Participants' heart rates increased and their heart rate variability decreased during synchronization with a simple isochronous tone sequence compared to a silent condition (Krabs et al., 2015). Finally, pianists exhibited faster heart rates when they performed a musical piece compared to when they listened to the same piece (Nakahara et al., 2011).

Several measures, both linear and nonlinear, address changes in cardiac rhythms during auditory perception and production (see Wright et al. 2022 for a review). Linear cardiac measures include mean heart rate (or R-R interval, ms) and heart rate variability metrics such as the root mean square of successive differences (RMSSD). Linear cardiac measures assume that the cardiac signal is stationary, meaning the mean and variance of the cardiac time series are relatively stable over time (Manuca & Savit, 1996). In reality, cardiac activity is often not stationary (Berntson et al., 1997), and dynamic behavioral tasks are likely to exert different effects on cardiac activity over time. Thus, nonlinear cardiac measures are well-suited to measure cardiac activity during auditory-motor synchronization tasks, and a number of nonlinear analysis techniques have been applied to cardiac rhythms during auditory rhythm production (Chanwimalueang et al., 2017; Sebastiani et al., 2022; Williamon et al., 2013; Wright & Palmer, 2020).

Recurrence quantification analysis (RQA) is a popular nonlinear method of cardiac analysis that identifies recurring patterns over time. The goal of the analysis is to recover higher-level dynamics of a multidimensional, nonlinear system from a single measured variable (Carello & Morena, 2005). Takens's (1981) theorem shows that time-delayed copies of a signal can be used to reconstruct a nonlinear system in multi-dimensional phase space where the trajectory (dynamics) of the system is recovered (Webber & Zbilut, 2005). Points in the phase space that are sufficiently close together are considered recurrent points (Webber & Marwan, 2015) and are plotted in a 2-dimensional recurrence plot, from which the recurrence dynamics of the system can be quantified. Auto-recurrence quantification (auto-RQA) identifies recurrence structures within a single time series (such as a cardiac rhythm). We apply auto-RQA to the participants' cardiac rhythms as they perform the synchronization task.

Auto-RQA has been applied to cardiac measures to distinguish healthy populations from clinical populations (Javorka et al., 2008; Javorka et al., 2009; Marwan et al., 2002; Naschitz et al., 2003; Schlenker et al., 2016; Zbilut et al., 1990), to examine exercise effects (Zimatore et al., 2020), and to characterize complex behavioral tasks. Auto-RQA analyses showed individuals' greater cardiac predictability during a firewalk ritual compared to a baseline (Konvalinka et al., 2011). Pianists' cardiac auto-RQA dynamics became more predictable during music performance compared to a silent baseline (Wright & Palmer, 2020). Trained musicians' cardiac auto-RQA dynamics also became more recurrent when they synchronized with simple auditory rhythms (1:2) compared to complex auditory rhythms (3:2) (Wright & Palmer, 2023). We extend these auto-RQA applications to investigate short-term training and rhythm complexity effects on cardiac measures during auditory-motor synchronization.

The current study investigates effects of short-term training on temporal accuracy and cardiac activity during an auditory-motor synchronization task with complex rhythms (2:3, 3:2 stimulus:tap durations). The first aim was to identify behavioral effects of short-term training on synchronization performance. In line with previous research (Drake & Palmer, 2000; Madison et al., 2013; Tillmann et al., 2011), we expected that greater short-term training would result in more accurate, less variable synchronization. The second aim was to characterize cardiac activity during the auditory synchronization task. In line with previous research (Wright & Palmer, 2020), we expected slower heart rate, greater heart rate variability, and less patterned cardiac activity after longer training amounts. Finally, we examined individual differences in synchronization behavior and cardiac dynamics, as suggested by previous research (Chen et al., 2008; Krause et al., 2010; Repp & Doggett, 2007; Scheurich et al., 2020; Wright & Palmer, 2020).

Methods

Participants

Forty-two participants (mean age = 21.05 years, SD = 2.74 years, female = 39, non-binary = 1) with a range of musical experience were recruited for the study. Participants' mean years of private instruction on a musical instrument was 8.57 years (SD = 4.32 years; min = 0, max = 17). To be included in the study, participants had to report no history of cardiovascular disease, respiratory disorders, or hearing impairments, and had to be between 18 and 35 years of age. An audiometry screening was used to confirm normal hearing for the range of tone frequencies in the auditory stimuli (< 30 dB HL threshold for 125-750 Hz frequencies). Participants were recruited from online postings to social media pages between October and December 2022. 32 participants were recruited from McGill University's Psychology participant pool; 8 participants were recruited from the general Montreal community. The study took place at McGill University, and the protocol was reviewed by the Research Ethics Board (Ethics protocol #197-1018).

Stimulus Materials and Equipment

Auditory stimulus rhythms were composed of two isochronous sequences of tones that differed in pitch and duration and formed specific temporal ratios with one another, as shown in Figure 1. The high-pitched tone was a 660 Hz sine tone, and the low-pitched tone was a 392 Hz woodblock tone. Tones were produced by a Roland Sound Canvas (SC-55) tone generator (timbre = 116). Each stimulus rhythm was a repeated high tone, and the participants' taps generated a low tone repeatedly. In the 2:3 (stimulus tones: response taps) rhythm, the high-pitched tone (intertone interval = 817 ms) was intended to occur twice for every three low-pitched tone taps (intertone interval = 545 ms). For the 3:2 rhythm, the high-pitched tone (intertone interval = 363 ms) was intended to occur three times for every two low-pitched tone taps (intertone interval = 545 ms). Thus, the low-pitched tone interonset interval (545 ms) was constant across both rhythms; only the high-pitched tone interval changed across the rhythms, meaning participants' tapping rate in the synchronization task was constant across all trials of the rhythms.

[Figure 1 here]

Auditory stimuli and participants' auditory feedback were generated on the Roland Sound Canvas (SC-55) tone generator using MIDI (musical instrument digital interface) with 1-ms temporal resolution. Sound was delivered through AKG K271 Studio headphones, and participants tapped their finger on a Roland RD-700 electronic piano keyboard. Participant key taps were recorded in FTAP (v.2.1.07b; Finney, 2001) on a Dell T3600 PC running Linux (Fedora 16). Cardiac activity was recorded with a Polar H10 chest strap heart rate monitor with 1-ms temporal resolution connected via Bluetooth to the application EliteHRV running on an iPad Mini. Questionnaires included a musical background questionnaire and a short questionnaire about participants' physical activity in the hour prior to the experimental session.

Design

Tapping performance and cardiac activity were measured from all participants in all synchronization conditions. The independent variables were Rhythm (2:3, 3:2) and Training (Short, Long). Participants received one level of training on each of the rhythms, making this a mixed design with Rhythm and Training as within-subjects variables and the Rhythm-to-Training assignment as a between-subjects variable (Short vs Long; coded as "Training"). The order of the Rhythm and Training variables were counterbalanced across participants. In addition, each participant completed a 5-minute silent baseline measure of cardiac activity before the start of the synchronization task.

The dependent variables for the synchronization task were the mean inter-tap interval (ITI) and the coefficient of variation (CV, standard deviation/mean ITI) as well as the mean absolute asynchrony (|participant tap onset time – stimulus tone onset time|) and mean signed asynchrony (participant tap onset time – stimulus tone onset time) for participant taps that coincided with stimulus tones, indicated with circles in Fig 1. Synchronization precision was measured by the standard deviation of the signed asynchronies. Dependent variables for the cardiac signals included mean R-R intervals (normal heartbeat-to-heartbeat intervals, ms) and the root mean square of successive normal R-R interval differences (RMSSD, ms), a measure of short-term heart rate variability (Schaffer et al., 2014). Nonlinear cardiac measures for auto-RQA included Recurrence Rate and Determinism, described below (Data Analysis).

Procedure

Participants completed the one-hour in-person testing session between 09h and 17h. Upon arrival at the lab, participants provided written informed consent and then completed the audiometric screening. Next, a 5-minute baseline (silent) cardiac recording was conducted. Participants attached the heart rate monitor around their chest, sat in a comfortable chair with their legs uncrossed, and completed written questionnaires with minimal body movement. Then, participants completed the synchronization task. Synchronization trials began with four woodblock tones (inter-tone interval = 545 ms) that served as the participants’ tempo cue for tapping the low-pitched tones of the rhythm. Then, the high-pitch tones sounded for one minute while the participants produced the low-pitch tones of the rhythm with their taps. Each 1-minute auditory rhythm was repeated five times with a silent pause of 10 seconds between each repetition, in order to give participants a brief rest between productions of the demanding complex rhythms.

Participants were instructed to tap the low-pitched part of the rhythm using their dominant hand on a single key of the piano keyboard, so that their taps synchronized with the high-pitched part of the rhythm to form the intended rhythm ratio. Participants were first familiarized with each rhythm ratio by listening to the intended rhythm ratio in which both parts were presented (high tone and low tone) twice at a slow tempo (inter-tap interval = 1090 ms). Then participants completed two familiarization synchronization trials at the slower tempo (inter-tap interval = 1090 ms). Next, participants listened to the intended rhythm ratio twice at the experimental tempo (inter-tap interval = 545 ms) and they completed two 30-second practice synchronization trials at that tempo.

Following the familiarization, participants completed the two rhythm conditions, each paired with Short or Long training. In the Short training condition, participants received no additional training trials and went on to complete five 1-minute experimental synchronization trials of the assigned rhythm. In the Long training condition, participants received two additional 1-minute practice trials before they completed the five 1-minute experimental synchronization trials. After completing the first rhythm condition, participants had a short break to answer a questionnaire about their handedness. Then the procedure was repeated for the second rhythm-training condition. Participants heard the high-pitched part of the rhythm as well as their own taps (low-pitch part of the rhythm) during all synchronization trials. At the end of the task, participants removed the heart rate monitor, and they were debriefed.

Data Analysis

Behavioral Data

One-minute sequences of the inter-tap intervals (ITIs) and asynchrony measures were generated for each trial. Double taps (< 75 ms between two successive taps) were corrected by removing the second tap (approximately 3% of all taps). The first four and the last four taps in each trial were removed from the ITI time series, as they tend to reflect slower tempi and are least accurate (Mathias et al, 2020). The mean and standard deviation of the ITIs and asynchrony values for the remaining taps in each trial were then computed. Individual ITIs greater than three standard deviations from the mean were removed (.68 % of all ITIs), and then the mean ITI and CV were re-computed. Behavioral measures were computed in Matlab (version 9.8.0, 2020).

Cardiac Data

R-R interval time series were processed in Kubios HRV Premium (version 3.5.0). Artifacts were manually corrected in each participant’s time series using Kubios’s threshold-based artefact correction method whereby R-R interval values that are greater or smaller than a local R-R interval average by a defined threshold value are corrected via cubic spline interpolation (Tarvainen et al., 2017). The data were then segmented by task (5-minute baseline, 1-minute synchronization trials). Linear measures of mean R-R interval, RMSSD, and HF power were calculated for each trial. RMSSD was selected as the time domain measure of heart rate variability as it tends to be minimally influenced by respiration and appropriate for short time series (Shaffer & Ginsberg, 2017; Camm et al., 1996).

Recurrence quantification analyses (RQA) were performed on the cardiac time series in MATLAB using the CRP Toolbox 5.22 (Marwan, 2022). Time series were converted into beats per minute (BPM), based on Wallot et al. (2013). For the cardiac data, each R-R value in the time series (indicating onset times) was replaced with a string of BPM values, then the BPM values were averaged using a non-overlapping moving window of 300 ms. The resultant time series served as input to the RQA. The result of this transformation is an upsampling of the time series that creates a consistent length time series across trials and participants (Wallot et al., 2013). Time series with two or more sequential missing taps represent pauses in tapping which may artificially affect the nonlinear analyses. Therefore, recurrence quantification analyses were performed only on trials that had no sequential missing taps (40 participants met this criterion).

Auto-RQA was then applied to participants’ transformed and normalized cardiac time series to quantify repeating patterns. Three parameters are used in RQA to reconstruct the dynamics of the time series and generate the recurrence plots which are 2-dimensional symmetrical plots of binary (recurrent, non-recurrent) values. First, a time delay parameter was chosen at the trial level using the first local minimum of the average mutual information function (Webber & Marwan, 2015). The time delay values in the current study ranged from 1-12. Second, the embedding dimension was chosen at the trial level and was set as the first local minimum of False Nearest Neighbors (Webber & Marwan, 2015). Embedding dimensions ranged from 2-10. The median time delay and embedding dimension across all trials were then used for the analysis (time delay = 4, embedding dimension = 4) to prevent individual- and condition-level differences in the dependent variables from being artefacts of the parameters varying across individuals and/or conditions (Webber & Marwan, 2015). Third, a radius value was chosen; the radius functions as a threshold value for determining whether two points in the phase space are recurrent. Radius values were set to 10% of the maximum diameter of the phase space (Webber & Marwan, 2015).

The metrics used to quantify cardiac auto-recurrence were recurrence rate and determinism. Recurrence rate is the proportion of recurrent points relative to all (recurrent and non-recurrent) points in the recurrence plot. In auto-RQA, recurrence rate is a measure of how often the system returns to a previous state (Webber & Zbilut, 2005). Determinism is the proportion of recurrent points that form diagonal lines in the recurrence plot (excluding the line of identity in auto-recurrence) and is a measure of sequential predictability within a signal (Marwan et al., 2007; Nayak et al., 2018; Webber & Marwan, 2015). In the determinism analyses, the recurrence rate was fixed at 6% to distinguish determinism effects above and beyond recurrence rate. For both recurrence rate and determinism analyses, a Theiler window was fixed to the time delay (4) as cardiac data tends to show strong autocorrelation (Javorka et al., 2008) which can inflate RQA metrics (Webber & Marwan, 2015).

Analyses of variance (ANOVA) on the behavioral and cardiac data were conducted in R Studio (version 4.2.0) with the ‘aov_car’ function from the ‘afex’ package. This function performs an analysis of variance using type 3 sums of squares. The Huynh-Feldt corrected p-values are reported when sphericity assumptions were violated. Simple linear correlations tested behavior-cardiac correspondences, and Spearman's Rho correlations were used to investigate individual differences in cardiac dynamics; correlations were performed with the 'cor.test' function in R Studio.

Results

Behavioral Synchronization

Two-way ANOVAs (Rhythm X Training) were conducted on the mean absolute asynchronies and mean signed asynchronies (accuracy), and the standard deviation of the signed asynchronies (variability). There was a significant main effect of Rhythm on mean absolute asynchrony ($F(1,40) = 5.422$, $p = .025$, $\eta^2 G = .042$). Mean absolute asynchronies were larger for the 3:2 rhythm (mean = 74.446 ms) than the 2:3 rhythm (mean = 68.201 ms). There was also a significant main effect of Rhythm on mean signed asynchronies ($F(1,40) = 4.88$, $p = .033$, $\eta^2 G = .051$). As shown in Figure 2, participants had larger, more positive (lagging) signed asynchronies for the 3:2 rhythm than the 2:3 rhythm. Similarly, there was a significant main effect of Rhythm on the standard deviation of signed asynchronies ($F(1,40) = 4.106$, $p = .049$, $\eta^2 G = .031$). Also shown in Figure 2, the standard deviation of signed asynchronies was larger for the 3:2 rhythm than for the 2:3 rhythm. There were no other significant main effects or interactions for mean absolute asynchrony, mean signed asynchrony, or the standard deviation of signed asynchronies. In sum, participants showed more accurate, more precise tap synchronization for the 2:3 rhythm than for the 3:2 rhythm.

[Figure 2 here]

Similar two-way ANOVAs assessed the mean and variability of participants' tapping rates (inter-tap intervals). There were no significant main effects or interactions of Rhythm and Training on mean inter-tap interval (ITI) (all *p's* > .287), indicating participants tapped near the prescribed tapping rate for each Rhythm and Training condition. There were also no significant main effects or interactions of Rhythm and Training on tap CV (all *p's* > .719). Years of musical training was generally not related to behavioral measures. A significant negative correlation was observed, however, between years of musical training and tap CV for the 2:3 rhythm after Short Training (r = -.68, p < .001). The same correlations were not significant for the 2:3 rhythm after Long Training (r = -.34, p = .329) or for the 3:2 rhythm after either Short (r = -.13, p =. 604) or Long Training (r = .06, p = .801).

Linear Cardiac Findings

Participants' cardiac measures were first compared during the Baseline (silent) condition (no tapping) and the synchronization tasks. A one-way ANOVA on RMSSD by Task (Baseline, 2:3 rhythm, 3:2 rhythm) showed a significant main effect of Task (F(2,82) = 16.854, p <.001 Huyhn-Feldt corrected, η^2 G=.037). As expected, RMSSD values were significantly larger during the Baseline condition (mean = 40.849 ms) compared to the 2:3 condition (mean = 33.478 ms; t(41) = -4.032, p < .001, *Cohen's d* = -.384) and the 3:2 condition (mean = 32.933 ms; t(41) = -4.621, p < .001, *Cohen's d* = -.412), indicating greater heart rate variability during Baseline compared to the synchronization tasks. There was no significant difference between the 2:3 and 3:2 rhythm conditions (t(41) = .66, p = .513, *Cohen's d* = .031). There were no significant effects of Task on mean R-R interval (F(2,82) = 1.19, p = .309, η^2 G=.002).

Next, we tested for learning effects on the linear cardiac measures (mean R-R interval, RMSSD, HF power) during synchronization using 2 (Rhythm) x 2 (Training) ANOVAs. There were no significant main effects or interactions of Rhythm and Training on mean R-R interval or RMSSD (all *p's* > .052). For HF power, there was a significant main effect of Rhythm (F(1,40) = 5.473, p = .024, η^2 G=.006). As shown in Figure 2, there was more HF power when participants synchronized with the 2.3 rhythm compared to the 3:2 rhythm. There were no other significant main effects or interactions on HF power.

Cardiac-Behavior Correlations

Simple correlations were conducted to determine correspondences between participants' linear synchronization variability (SD of signed asynchronies) and their linear cardiac variability (RMSSD). As shown in Figure 3, Long Training on the 3:2 rhythm resulted in a significant positive correlation between participants' RMSSD and standard deviation of signed tap asynchronies (r = .43, p = .043): Participants who showed more variable cardiac activity showed less precise tap synchronization. Long Training on the 2:3 rhythm yielded the same correspondences between participants' standard deviation of signed asynchronies and their RMSSD (r = .47, p = .042). The same correlations applied to the rhythms in the Short Training conditions were not significant (all *p's* > .279).

[Figure 3 here]

In sum, there were moderate positive correlations between participants' cardiac variability and the precision and accuracy of their tapping for the rhythm on which they received Long Training; correlations were small and non-significant when participants received only Short Training.

Recurrence Quantification Analysis

Recurrence rates were first examined by Task (Baseline, 2:3 rhythm, 3:2 rhythm). There was a significant main effect of Task ($F(2,78) = 3.387$, $p = .039$, $\eta^2\ G = .05$). Figure 4 shows cardiac auto-recurrence plots from a single participant on a single trial. Cardiac recurrence was greater in the 2:3 rhythm condition (mean = 2.519 %) than in Baseline (1.52 %; $t(39) = 2.244$, $p = .031$, *Cohen's d* = .53), but did not differ between the 3:2 rhythm and Baseline (2.254%; $t(39) = -1.622$, $p = .113$, *Cohen's d* = -.36) or between the 2:3 and 3:2 rhythm condition ($t(39) = .991$, $p = .328$, *Cohen's d* = .14). A similar 1-way ANOVA on cardiac determinism by Task (recurrence rate fixed to 6%) did not indicate a significant effect of Task ($F(2,78) = .706$, $p = .497$, η^2

G=.002). Finally, we tested for rhythm and training effects using a 2 (Rhythm) x 2 (Training) ANOVA on cardiac recurrence rate. There were no significant main effects or interactions (all *p's* > .321). The same 2 x 2 ANOVA on cardiac determinism indicated no significant main effects or interactions (all *p's* > .11).

[Figure 4 here]

To examine individual differences in cardiac dynamics, we first rank-ordered the recurrence and determinism values (smallest to largest) according to each participant's performance in the Long Training condition (hypothesizing that individual differences should be strongest after training). As shown in the top of Figures 5 (recurrence rate) and 6 (determinism), large individual differences existed across the participants. We then used the same ordering (by Long Training) to plot the recurrence and determinism for each individual's Short Training condition. If participants were consistent in their individual differences, then the ordering in the Short Training condition should increase from left to right, similar to the Long Training condition. Participants were indeed consistent in their amount of cardiac recurrence between the Short Training and Long Training conditions (Spearman's *rho* = .43, *p* = .006). As shown in Figure 5, participants with low cardiac recurrence after Long Training had low cardiac recurrence after Short Training. Similarly, participants were consistent in their amount of cardiac determinism between the Short Training and Long Training conditions (Spearman's *rho* = .85, *p* < .001): As shown in Figure 6, participants with low cardiac determinism after Long Training had low cardiac recurrence after Short Training. Further analyses on recurrence rate and determinism documented that the different rhythm conditions (2:3, 3:2) showed the same pattern of results as the aggregate data in Figures 5 and 6.

[Figure 5 here]

[Figure 6 here]

Discussion

Both rhythm complexity and short-term training influenced behavioral synchrony and cardiac activity during auditory-motor synchronization. Individuals with varying levels of musical experience synchronized with complex auditory rhythms (2:3 stimulus-to-tap duration ratio, 3:2 stimulus-to-tap duration ratio) after a short or long training period while their cardiac activity was recorded. Behavioral analyses showed that synchronization was more accurate and precise for the 2:3 rhythm than the 3:2 rhythm. Training effects were seen in increased correspondence between synchronization variability (SD of signed asynchronies) and cardiac variability (RMSSD, a linear measure) after Long Training but not Short Training. Finally, nonlinear analyses of cardiac dynamics demonstrated the most recurrence during the 2:3 rhythm condition, and cardiac dynamics showed large consistencies in individual differences across training conditions. We review these effects below.

Rhythm Effects

Several behavioral findings indicated participants' greater difficulty synchronizing with 3:2 (stimulus:tap) rhythms than with 2:3 rhythms. The 2:3 and 3:2 rhythms were chosen in an effort to match complexity across rhythms (Hessler & Amazeen, 2014; Treffner & Turvey, 1993) and to keep motor demands similar by keeping the inter-tap interval constant across the rhythm conditions. The behavioral findings of more accurate, less variable synchronization with the 2:3 rhythm than the 3:2 rhythm are consistent with nonlinear dynamical models of coupled oscillators in a driver-to-driven relationship (for example, the sounded auditory stimulus as the driver rhythm and the participant's taps as driven by the auditory stimulus). Recent findings indicate that greater regions of stable coupling exist between oscillators when the driver's oscillator period is equal to 2 beats (as in the 2:3 stimulus:tap rhythm) compared to when the driver's oscillator period is equal to 3 beats (as in the 3:2 rhythm) (Kim & Large, 2019). Thus, our findings constitute behavioral evidence from an auditory-motor synchronization task for the boosted importance of the driver rhythm in the stability of oscillator coupling (Kim & Large, 2019).

Cardiac activity was also affected by rhythm complexity. Linear high-frequency heart rate variability was greater for the 2:3 rhythm, suggesting it was a less difficult task than the 3:2 rhythm, based on findings that high-frequency HRV tends to be higher during easier cognitive tasks (Fairclough et al., 2005; Slade et al., 2021) and is interpreted as an indicator of parasympathetic activity (Shaffer et al., 2014). Nonlinear measures of cardiac recurrence were greatest when participants synchronized with the 2:3 rhythm compared to the silent baseline condition. This finding is consistent with previous research showing greater cardiac recurrence during synchronization with simple and complex rhythms compared to silent baseline (Wright & Palmer, 2023). These findings suggest that both linear and nonlinear measures of cardiac activity are sensitive to rhythmic changes during an auditory-motor synchronization task.

Training Effects

Short-term training effects were observed at the individual participant level and modulated both cardiac activity and tapping behavior. Heart rate variability (RMSSD) was greater when participants' synchronization performance was more variable but only after long training. The emergence of cardiac-behavior correspondences may require a longer timescale of training, especially for the complex rhythms used in this study, in order to detect individual differences. In other words, longer training periods than the 3-minute intervals used in the current study may demonstrate larger training effects.

Individual Differences

Nonlinear analyses of cardiac activity during synchronization revealed consistency in individuals' cardiac dynamics across training conditions. Individuals who showed higher cardiac recurrence after long training also showed higher cardiac recurrence after short training. Similarly, individuals who showed higher cardiac determinism after long training also showed higher cardiac recurrence after short training. These individual differences indicate that cardiac activity is affected by auditory-motor synchronization in predictable ways across different amounts of training and across rhythms. Thus, these findings extend the individual differences in cardiac activity reported in other contexts (Picard et al., 2009; Watanabe et al., 2017). The nonlinear recurrence quantification analyses may be particularly well-suited to capture individual differences in cardiac activity during auditory-motor synchronization tasks.

Most studies address long-term training by comparing musicians and non-musicians in auditory-motor synchronization tasks. The current study addresses short-term training in participants with a broad range of musical experiences. We observed an impact of amount of musical training only in its correlation with tapping variability (CV) and only in one Training condition (Short) with one rhythm (2:3); there were no other significant correlations between tapping behavior and musical training. One possibility is that short-term training effectively reduced the disparity between musicians and non-musicians in tapping variability for the easier (2:3) rhythm. We also observed large individual differences in consistency of cardiac rhythms in the same conditions. An open question is how long-term musical training and individual differences in cardiac activity may interact to influence auditory-motor synchronization.

Future Directions

Effects of short-term training in auditory-motor synchrony tasks have been investigated with different experimental designs. The majority of studies that found group-level short-term training effects on musical auditory-motor tasks (Drake & Palmer, 2000; Madison et al., 2013; Tajima & Choshi, 2000; Tillmann et al., 2011) used a larger number of training trials than the current study, which may have provided participants with more time for training. Although participants in the current study only received two minutes of training in the Long training condition, this was comparable in amount to the extra trials in the studies cited above (220 extra practice taps than in the Short training condition). It may be that the individual differences observed here in cardiac activity, as well as individual differences in synchronization ability and/or rate of learning, overshadowed group differences in short-term training. Identifying individual factors that contribute to these differences is an important direction for future research to understand how behavior and physiology change with expertise and training.

Conclusion

Overall, rhythm complexity and short-term training influenced synchronization behavior and cardiac activity in individuals with a range of musical experience. Participants showed better synchronization with the 2:3 than the 3:2 stimulus-to-tap ratio rhythm; additionally, cardiac activity became more patterned during synchronization of the 2:3 rhythm compared to a silent baseline. Short-term training effects were largely observed in individual differences: More training resulted in correspondences between cardiac activity and behavior that were absent with less training. Finally, individuals showed consistent patterns of recurrent and predictable cardiac dynamics across training conditions. To our knowledge, this is the first study to demonstrate short-term training effects on both behavior and cardiac activity during a rhythmic auditory-motor synchronization task. Future studies should determine how much of short- and long-term training effects are impacted by the individual differences observed in cardiac rhythms.

Acknowledgements

We gratefully acknowledge the technical assistance of Louis Deng, Sandra Kuliver, and Leen Mshasha for assistance. Correspondence should be addressed to Shannon Wright (shannon.eilyce.wright@mail.mcgill.ca) or to Caroline Palmer (caroline.palmer@mcgill.ca).

Funding Details

This research was supported by NSERC Grant 289173 and a Canada Research Chair to C Palmer.

Disclosure Statement

The authors report there are no competing interests to declare.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author, [S. E. W.], upon reasonable request.

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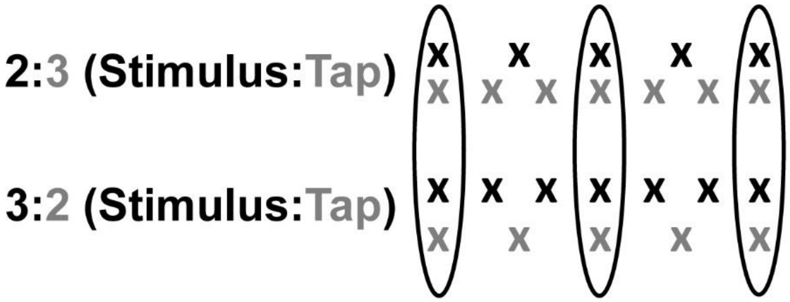

Figure 1. Participants produced the low tones (gray x's) to form the intended rhythm ratios in the synchronization task. Ovals denote tones that were analyzed in synchronization analyses.

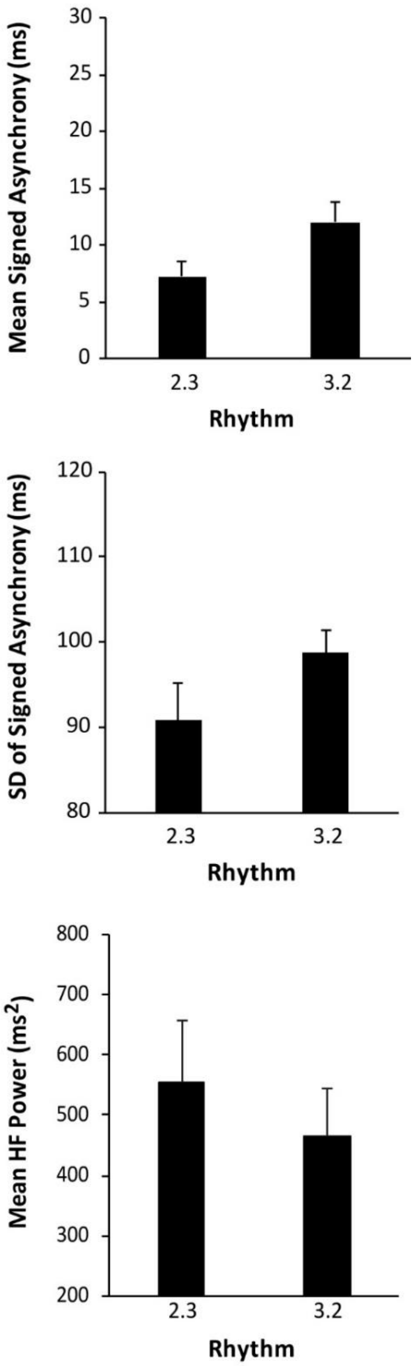

Figure 2. Rhythm condition effects on behavioral synchrony and cardiac rhythms. Top = Mean signed asynchrony values by Rhythm condition; Middle = Standard deviation of signed asynchronies by Rhythm condition; Bottom = Mean high-frequency HRV power by Rhythm condition.

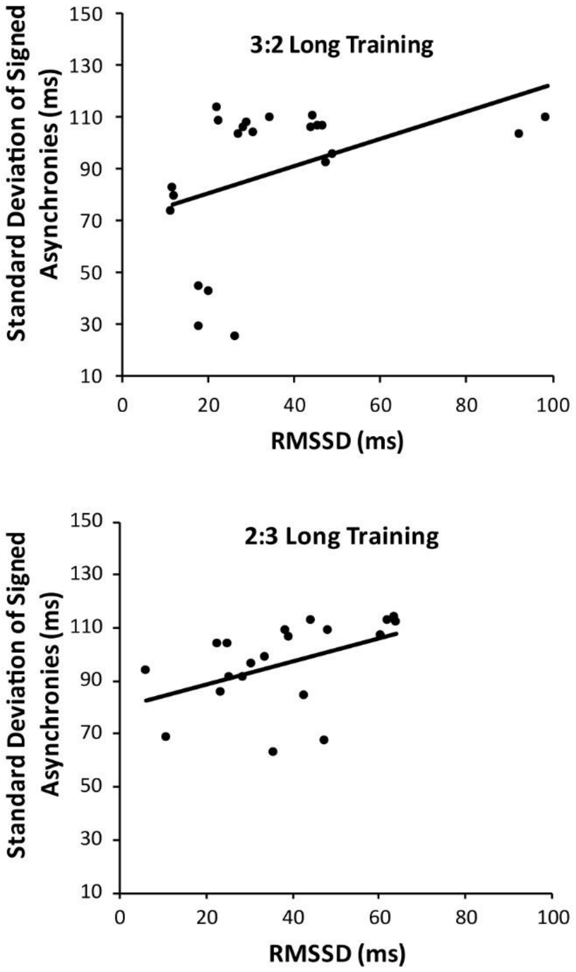

Figure 3. Correlations between mean heart rate variability (RMSSD, in ms) and mean tap synchronization variability (SD of signed asynchronies, in ms) in the Long Training condition. Top = 3:2 rhythm (*r* = .43, *p* = .043); Bottom = 2:3 rhythm (*r* = .47, *p* = .042).

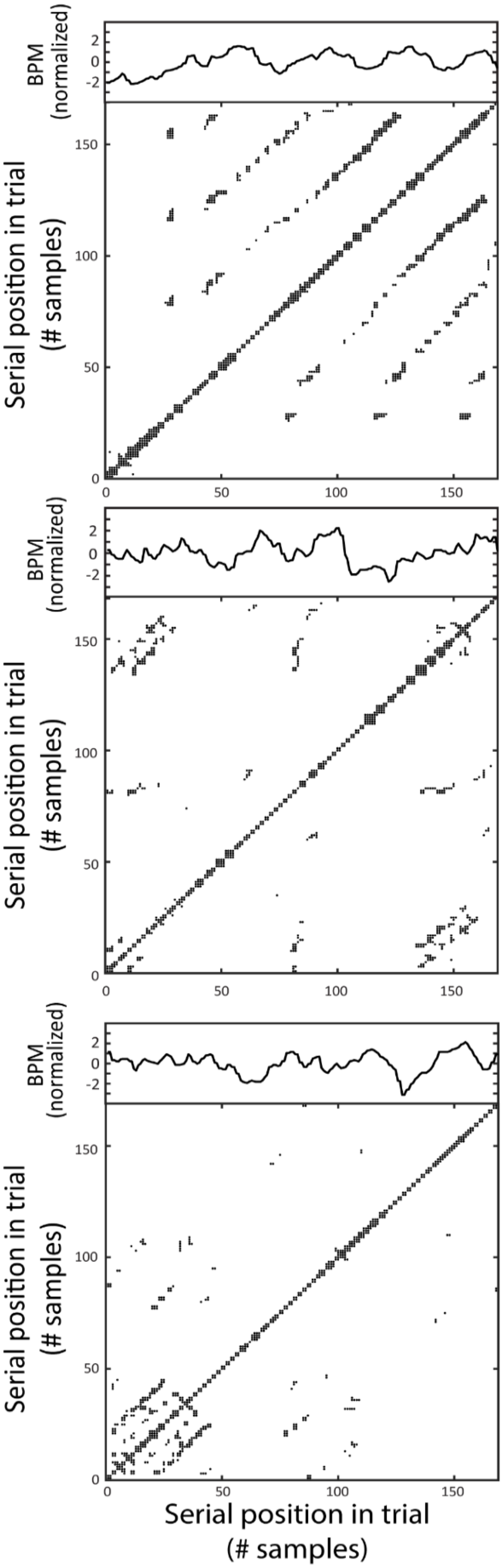
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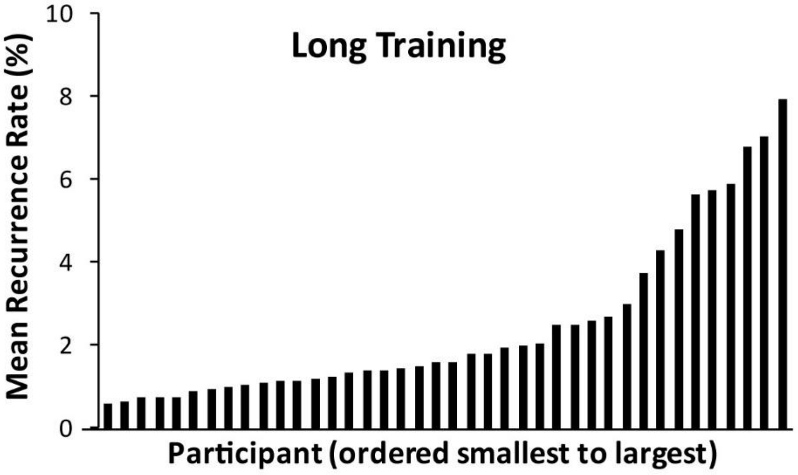
Figure 4. Auto-recurrence plots for one participant's sample trials of cardiac activity. Top = 2:3 rhythm synchronization (recurrence rate = 2.37%); Middle = 3:2 synchronization (recurrence rate = 1.40%); Bottom = silent baseline (recurrence rate = 1.37%).



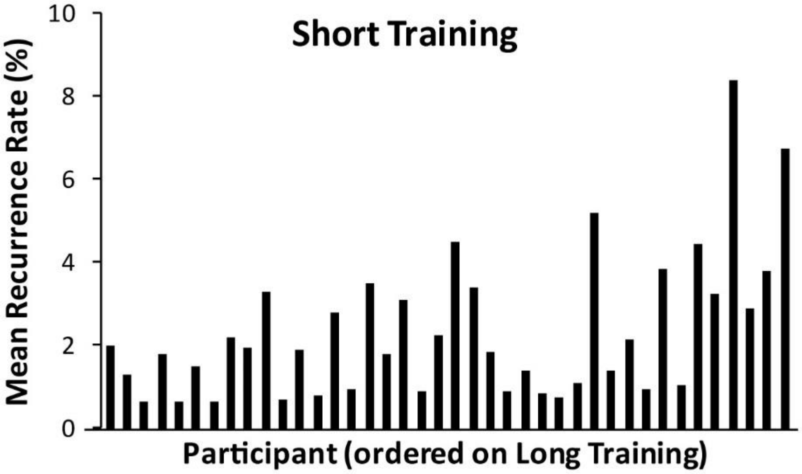


Figure 5. Individual differences in cardiac recurrence rates for Long (top) and Short (bottom) training conditions. Participant orderings from smallest to largest values in the Long Training (x-axis) are maintained from the top graph to the bottom graph.

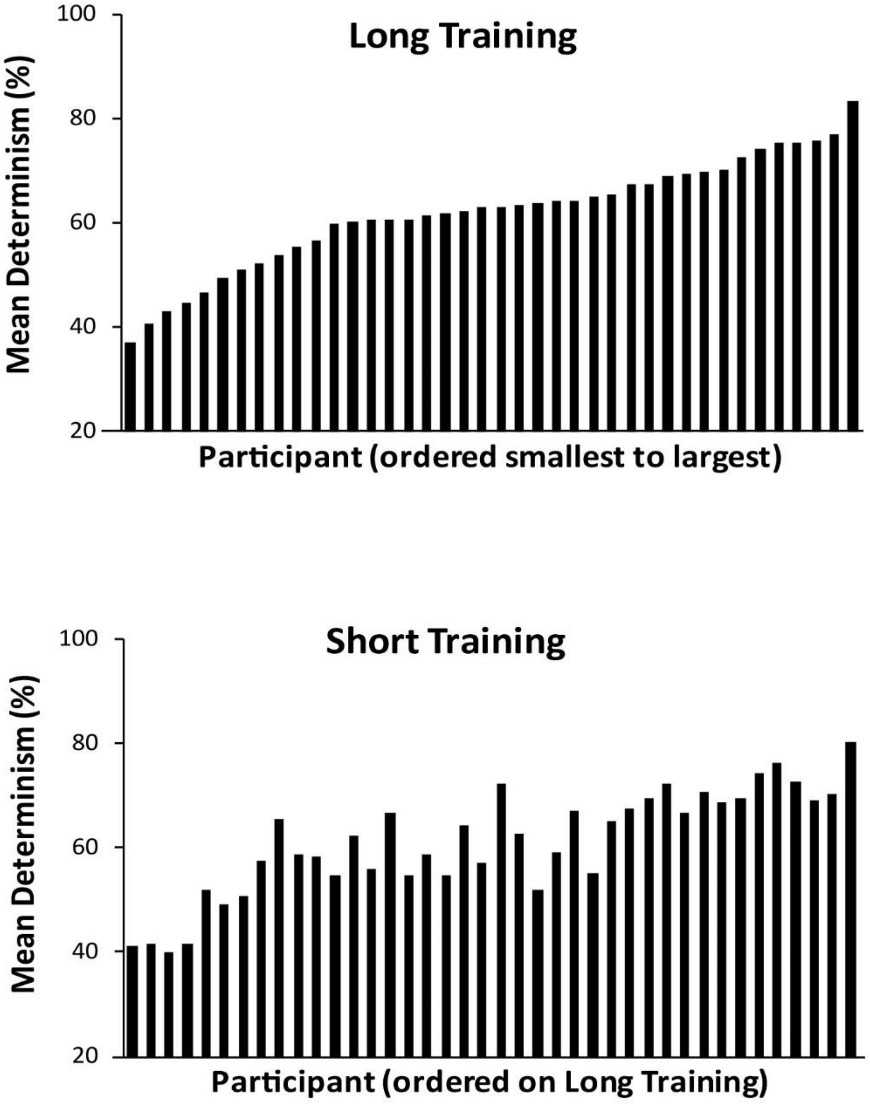


Figure 6. Individual differences in cardiac determinism for Long (top) and Short (bottom) training conditions. Participant orderings from smallest to largest values in the Long Training (x-axis) are maintained from the top graph to the bottom graph.

General Discussion

Humans perceive and produce a wide range of auditory rhythms, ranging from very simple to rather complex rhythms. The ability to rhythmically coordinate our actions with sound and to produce auditory rhythms gives rise to human behaviours such as dance and music making. These behaviours are not only enjoyable and present across cultures (Mehr et al., 2018), but are thought have adaptive significance in social bonding (Savage et al., 2021), group cohesion signalling (Hagen & Bryant, 2003), and interpersonal cooperation (Kirschner & Tomasello, 2010). The goal of this dissertation was to identify behavioural and physiological factors in rhythmic action-sound coordination. This constitutes an important step in understanding how auditory-motor synchronisation is achieved.

There were a number of behavioural aims in this dissertation. First, this dissertation tested individuals' consistency in rhythmic auditory sequence production. It was hypothesised that spontaneous production rates would increase and decrease in a manner consistent with circadian and cardiac activity influences, in line with previous research showing circadian and cardiac effects on rhythmic motor behaviour (Dosseville et al., 2002; Moussay et al., 2002). Second, this dissertation investigated synchronisation with simple and complex auditory rhythms. A direct comparison between perception and production of simple and complex rhythms was made; it was expected that synchronising with auditory rhythms would be more difficult than perceiving auditory rhythms, and effects would be further dependent on the complexity of the rhythm. This dissertation also tested the effects of short-term training (as opposed to long-term musical training) on synchronisation with complex auditory rhythms. The hypothesis was that synchronisation would be improved with short-term training for both musicians and non-musicians.

This dissertation also tested how cardiac activity is related to auditory rhythm perception and synchronisation. A large body of literature has investigated the neurophysiological underpinnings of auditory-motor synchronisation; equally, many studies have examined how music listening and performance of musical excerpts affect peripheral physiology, often with a focus on emotion (for example, see Swaminathan & Schellenberg, 2014) or how musical tempo affects cardiac activity during perception (see Wright et al., 2022). This dissertation examined basic questions of how listening to and synchronising with auditory rhythms affects cardiac activity. Guided by nonlinear dynamical systems principles of coupled oscillators (Large et al., 2015), a nonlinear analysis technique (recurrence quantification analysis, RQA) was used to capture cardiac dynamics while individuals listened to and produced rhythmic auditory sequences. It was hypothesised that cardiac dynamics would be differentially modulated by individual differences in auditory rhythm production, by perception and synchronisation, by the complexity of a rhythm, and by short-term experience/training with auditory rhythms.

The next section covers key findings and contributions of the experiments in this dissertation. Then, research themes will be highlighted and situated within the broader body of scientific literature. Finally, future research directions will be discussed with an eye to both basic and applied research contexts.

Key Findings and Research Contributions

Study 1: Circadian Rhythms and Music Performance

Chapter 1 was grounded in research showing influences of time of day and individual differences in circadian rhythms on motor and cognitive performance. Trained pianists performed simple melodies at a comfortable rate across four testing sessions in a 12h day. Cardiac activity was measured during a silent baseline and during melody performance. Pianists had slower and more variable natural performance rates in the morning compared to the afternoon and evening, yet remained relatively stable in their performance rate across times of day. Lower alertness and less musical training predicted slower production rates in the morning. Cardiac activity showed time of day and melody effects. Heart rate was faster during music performance, particularly when pianists performed unfamiliar melodies in the morning. Nonlinear measures of cardiac dynamics showed that cardiac activity was more predictable when pianists performed a familiar melody compared to an unfamiliar melody. Cardiac dynamics were also more predictable and changed more slowly during music performance compared to silent baseline in the morning.

The finding that auditory sequence production varies over the day, with mornings being slightly detrimental to performance, complement previous research showing optimal times of day for cognitive-motor performance (Edwards et al., 2007; Reilly et al., 2007; Van Vugt et al., 2013). Pianists who had fewer years of formal musical training and were less alert in the morning showed the slowest production rates, suggesting that the effect of time of day also depends on individual difference factors. Previous research has shown time of day effects on skilled motor performance (Reilly et al., 2007; Van Vugt et al., 2013), but has not considered the role of individual differences such as expertise in these effects. The current findings thus extend previous research by considering the influence of time of day and individual differences on auditory rhythm production.

These findings also contribute to previous research on individual differences in spontaneous production rates (Palmer et al., 2019; Scheurich et al., 2018; Tranchant et al., 2022; Zamm et al., 2018) by demonstrating that individual rates are relatively stable over the 12-hour day, independent of familiarity with a musical piece. Performances of familiar pieces, expected to elicit smaller practice effects, showed the same patterns as performances of unfamiliar pieces. This supports the nonlinear dynamical systems perspective that there are attractor rates for motor production to which an individual will converge (Kelso, 1995) and that natural production rates are optimally efficient states (Bereket et al., 2005; Hoyt & Taylor, 1981; Nessler et al., 2009).

Chapter 1 provides evidence that music performance impacts cardiac activity, with roles of familiarity and time of day. Given that all participants completed the same order of testing sessions (09h, 13h, 17h, 21h), it is difficult to disentangle whether the effects of music performance on cardiac activity were attributable to practice/experience effects, true time of day effects, or some combination of both. Faster heart rate (Fuentes-Garcia et al., 2019) and increased cardiac predictability and stability (Konvalinka et al., 2011; Schlenker et al., 2016) have been reported during more difficult behavioural tasks. The cardiac changes observed during music performance are consistent with an increase in physiological arousal when pianists performed an unfamiliar melody and when they performed at earlier times of day, possibly because it was a more difficult task under these conditions. Chapters 2 and 3 of this dissertation sought to disentangle effects of task difficulty and experience on cardiac dynamics during auditory rhythm performance.

Finally, these cardiac findings show that the nonlinear analysis technique of recurrence quantification analysis can be used to capture changes in cardiac dynamics during an auditory-motor synchronisation task, extending previous work that employed linear measures. This is significant because cardiac activity is known to show nonlinearities (Marwan et al., 2002). Employing an analysis technique that adequately captures this nonlinear behaviour helps to better “carve nature at its joints”, providing a more nuanced reflection of cardiac activity during behavioural tasks.

Study 2: Task and Rhythm Complexity Effects on Cardiac Dynamics

Chapter 2 of this dissertation built on Chapter 1 by focusing on task difficulty and testing the behavioural and cardiac effects of rhythm complexity. Chapter 2 also added an explicit test of perception and action on cardiac activity. Musically trained participants listened to and synchronised taps with a simple (1:2 duration ratio) and a complex (3:2 duration ratio) rhythm. In the perception condition, participants indicated whether they heard a missing tone in the rhythm; in the synchronisation condition, participants synchronised their taps (the "2" part of the 1:2 and 3:2 rhythm) with the stimulus tones (the "1" part of the 1:2 rhythm and the "3" part of the 3:2 rhythm) to form the intended rhythms. Cardiac activity was measured during the auditory rhythm tasks and an initial silent baseline. First, participants perceived the simple and complex rhythms equally well; synchronisation was more accurate and less variable with the simple rhythm than the complex rhythm. Second, heart rate was slowest and most variable during rhythm perception, and participants with greater heart rate variability had worse synchronisation performance for the complex rhythm. Nonlinear cardiac activity was more predictable during perception than synchronisation. Finally, nonlinear cardiac activity was more patterned during complex rhythm perception compared to simple rhythm perception, and during simple rhythm synchronisation compared to complex rhythm synchronisation.

The behavioural findings in Chapter 2 align with previous research showing better production of (Dotov & Trainor, 2021; Essens & Povel, 1985; Snyder et al., 2006) and synchronisation with (Mathias et al., 2020) simple vs complex auditory rhythms. These findings support the nonlinear dynamical systems perspective on simple and complex rhythms (Large et al., 2015; Large & Snyder, 2009; Treffner & Turvey, 1993). They also provide evidence that differences in synchronisation between simple and complex rhythms are not driven by differences in perception, as participants were equally good at perceiving missing tones in the simple and complex rhythms. This is important because it suggests that the difficulty of synchronising with complex auditory rhythms truly lies in the increased difficulty of coupling behaviour with sound, as predicted by coupled oscillator models in nonlinear dynamical systems theory.

The cardiac findings in Chapter 2 complement and extend those in Chapter 1 by showing that listening to and producing an auditory rhythm differentially affects cardiac activity. Chapter 2 thus disentangles the effects of rhythm perception and production on cardiac activity, demonstrating that cardiac activity is affected by rhythm synchronisation above and beyond the mere presence of an auditory rhythm. Recurrence quantification analysis also demonstrated for the first time that cardiac dynamics are sensitive to both perception/synchronisation and rhythm complexity, demonstrating the usefulness of applying nonlinear analysis techniques to cardiac data. Previous research has tied neural oscillations during complex rhythm perception (Stupacher et al., 2017) and production (Mathias et al., 2020) to behavioural performance. The findings in Chapter 2 are a first step towards identifying a potential role for oscillatory peripheral physiological activity in rhythm perception and synchronisation.

Study 3: Cardiac Dynamics with Short-term Training on Complex Rhythms

Chapter 3 investigated how short-term training on complex auditory rhythms affects behaviour and cardiac activity. Individuals with a range of musical experience synchronised finger taps with complex auditory rhythms (2:3 and 3:2 duration ratios). Participants received extra training on one rhythm (2 minutes), and their cardiac activity was recorded during a silent baseline as well as during the synchronisation task. Rhythm complexity effects were observed for synchronisation, with better synchronisation during the 2:3 rhythm than the 3:2 rhythm.

Overall heart rate variability was greater during silent baseline compared to rhythm synchronisation, and high-frequency heart rate variability was greater during the 2:3 rhythm than the 3:2 rhythm. After training, heart rate variability was also greater when participants showed more variable synchronisation with the rhythms. Nonlinear analyses showed more cardiac recurrence during the 2:3 rhythm synchronisation compared to silent baseline, but not compared to the 3:2 rhythm; large, stable individual differences were observed in cardiac recurrence and predictability that transcended training and rhythm.

Many studies address the role of long-term musical training on auditory-motor synchronisation, demonstrating that trained musicians tend to show more accurate, less variable synchronisation (Krause et al., 2010; Repp & Doggett, 2007; Scheurich et al., 2020), particularly with complex rhythms (Chen et al., 2008b). The general absence of a short-term training effect in Chapter 3 was somewhat surprising as previous research has indicated that both musicians and non-musicians can improve on auditory-motor synchronisation tasks after short practice (Drake & Palmer, 2000; Madison et al., 2013; Tajima & Choshi, 2000; Tillman et al., 2011). Nonetheless, testing short-term training effects on behaviour is an important contribution to understanding the timescale of practice and training effects.

In complement to Chapter 2, Chapter 3 refined our understanding of rhythm complexity effects on behaviour and cardiac activity. Whereas Chapter 2 compared a simple and a complex rhythm, Chapter 3 compared two complex rhythms (2:3 and 3:2). Better synchronisation with the 2:3 than the 3:2 rhythm was slightly unexpected, but is evidence in favour of recent nonlinear dynamical systems models of stable coupling between and a driver (stimulus) and a driven (human tapper) oscillator (Kim & Large, 2019). Similar to Chapter 2, there was greater heart rate variability and cardiac recurrence during the rhythm that was performed better (2:3). These behavioural and cardiac findings show that it is useful to conceptualise rhythm complexity in auditory-motor synchronisation tasks as a continuum rather than as discrete ‘simple’ or ‘complex’ rhythms. This conceptualisation fits with research showing that respiratory-motor coupling is easier for some complex rhythms (5:2) compared to others (5:3) after short-term training (Hessler & Amazeen, 2014), and is important to rhythm stimulus choices in future work.

Finally, RQA captured large individual differences in cardiac recurrence and predictability. Linear measures of cardiac activity have shown individual differences in response to musical tempo (Watanabe et al., 2017). This is the first evidence using a nonlinear analysis technique to show that individuals differ in their cardiac response during an auditory-motor synchronisation task and that individual responses are predictable and stable across rhythms and training. Greater recurrence and predictability in behaviour have been tied to less flexible, less temporally-adaptive behaviour (Schmit et al., 2005), particularly for non-musicians’ compared to musicians’ tapping behaviours (Scheurich et al., 2018; Tranchant et al., 2022). The finding that some individuals are consistently high in cardiac recurrence and predictability while others are consistently low raises an important question as to how these individual differences in cardiac dynamics contribute to auditory-motor synchronisation. Effects of long-term musical training and cardiac dynamics on auditory rhythm production have not been tested together. The findings in Chapter 3 suggest an additional source of individual variability in auditory-motor synchronisation that should be considered.

Research Themes and Key Concepts

Task Difficulty and Rhythm Complexity in Cardiac Dynamics

Task difficulty and rhythm complexity effects on behaviour and cardiac dynamics were central components of the three studies in this dissertation. Before delving into the ways in which this dissertation addressed task difficulty and rhythm complexity, consideration of the overlap between task difficulty and rhythm complexity is due.

This dissertation took a nonlinear dynamical systems perspective on rhythm complexity: Simple rhythms were defined as rhythms whose duration ratios form small integer ratios (ex. 1:2) whereas complex rhythms were rhythms whose duration ratios form large, non-integer ratios (ex. 3:2) (Large et al., 2015; Large & Snyder, 2009; Treffner & Turvey, 1993). For simple rhythms, stable temporal coupling is more likely to occur than for complex rhythms, which predicts better synchronisation with simple rhythms (Large et al., 2015). Implicit in this definition of rhythm complexity is task difficulty: Certain rhythms should be *easier* to synchronise with than others. It is thus a difficult task to distinguish separate influences of task difficulty from purely rhythm complexity and timing influences on behaviour and cardiac activity. One way to do this in the context of this dissertation is to consider how changes in cardiac activity were consistent with previous research on task difficulty.

There is some evidence of a shift towards greater sympathetic activation during more difficult cognitive and behavioural tasks (Richter et al., 2008), which corresponds to the "fight or flight" system: heart rate tends to increase (Fairclough et al., 2005) and heart rate variability tends to decrease (Fuentes-Garcia, 2019; Slade et al., 2020). Nonlinear measures of cardiac activity show that more difficult behavioural tasks (Konvalinka et al., 2011) and postures (Schlenker et al., 2016) produce more predictable, slowly changing cardiac activity. Chapter 1 provided evidence that auditory sequence production may be more difficult in the morning, and heart rate was faster and cardiac dynamics were more predictable for unfamiliar melodies in the morning. Similarly, cardiac dynamics were more predictable and stable during music performance compared to baseline rest in the morning. These changes in cardiac activity are consistent with the effect of music performance on cardiac dynamics being a result of task difficulty. However, given the complex nature of music as an acoustic stimulus, it seems unlikely that task difficulty could provide a full explanation of cardiac changes during music perception and production.

Chapters 2 and 3 of this dissertation built upon the findings of Chapter 1 by painting a more nuanced picture of the factors that may be driving cardiac changes during music perception and production. They did this by isolating a single acoustic feature, rhythm, and testing the effects of rhythm complexity on cardiac activity. Chapters 2 and 3 showed that more complex rhythms reduced synchronisation accuracy and precision, demonstrating that more complex rhythms are more difficult to synchronise with than simple rhythms, but cardiac activity was not modulated by rhythm complexity and synchronisation in a manner uniquely consistent with task difficulty. In contrast to the more difficult task in Chapter 1 (music performance) resulting in greater cardiac predictability and stability, Chapters 2 and 3 showed that cardiac activity was more predictable during rhythm perception than production, and more recurrent during simpler rhythm synchronisation than more complex rhythm synchronisation. Additionally, individuals with poorer synchronisation performance had greater heart rate variability.

Together, these findings suggest that task difficulty cannot fully explain the effects of an auditory-motor synchronisation task on cardiac dynamics. It is of course possible that the solo music performance task in Chapter 1 was more difficult than the rhythm synchronisation tasks in Chapters 2 and 3. This is however unlikely in the current context, as participants in Chapter 1 were trained musicians and melodies were very simple. Another possibility is that auditory rhythm and motor timing have a role in cardiac effects during perception and synchronisation. Notably, the unfamiliar melody in Chapter 1 showed lower tapping variance compared to the familiar melody, likely due to its fully isochronous structure. Across all three experiments in this dissertation, the auditory rhythm conditions that contained the least variability resulted in more recurrent and/or predictable cardiac dynamics. The complex interplay of how task difficulty and rhythmic structural complexity interact is highlighted by the set of studies in this dissertation and deserves further research attention.

Individual Differences

Temporal Stability in Behaviour and Cardiac Dynamics. A number of individual differences related to behaviour and cardiac activity were investigated and observed in this dissertation. Individual differences contributing to perception and action have a long history of investigation in psychology and provide a refined picture of human capacities (Revelle et al., 2011). In line with previous literature (McAuley et al., 2006; Palmer et al., 2019; Scheurich et al., 2018; Tranchant et al., 2022; Zamm et al., 2018), large, stable individual differences in spontaneous production rates were observed in Chapter 1 of this dissertation. Stability in behavioural individual differences are important to identify as individual differences in natural frequencies have been shown to shape how we coordinate actions with others (Nessler et al., 2009; Richardson et al., 2007; Tranchant et al., 2022; Zamm et al., 2016). Importantly, action coordination extends beyond music performance; basic communicatory behaviours like conversational speech require precise temporal coordination between partners, and moving in time with others affects perceptions of group cohesion (Fessler et al., 2016; Lakens, 2010; Lakens & Stel, 2011) and feelings of social affiliation (Hove & Risen, 2009). Identifying stable individual differences in natural production rates may ultimately help researchers understand variability in complex group behaviours.

Chapter 3 also revealed for the first time stable individual differences in nonlinear cardiac dynamics in an auditory-motor synchronisation context. These findings complement previous work showing large individual differences in respiratory rate during music performance (Sakaguchi et al., 2016). Individuals tend to show stable individual differences in neural activity over time, and these individual differences are related to performance on perceptual tasks (Charest et al., 2014). Stable individual differences in linear cardiac measures during behavioural tasks have been observed for a long time (for example, see Manuck et al., 1989), and age-related changes in nonlinear cardiac dynamics, as captured by RQA, have also been reported (Giuliani et al., 1998). Fluctuations in cardiac activity have been tied to neural activity patterns during music perception (Zhao & Kuhl, 2020). Identifying stable individual differences in cardiac dynamics is an important step towards understanding whether and how cardiac dynamics are related to auditory rhythm perception and production.

Circadian Rhythms. Chapter 1 tested circadian and time of day effects on spontaneous production rates and cardiac activity. Behavioural research paradigms that seek to tie circadian rhythms to behaviour and physiology present a particular challenge as daily confounding factors can prevent sound conclusions about circadian effects. In order to conclude that there is a true circadian effect on something, influences on circadian rhythms such as light-dark cycles, food, and social demands must be removed so that daily external factors can be uncoupled from true circadian rhythm effects (Golombek & Rosenstein, 2010). This is best achieved by placing individuals in constant conditions, meaning no light-dark cycle or predictable social or meal schedules that may entrain or mask an individual’s rhythm (Golombek & Rosenstein, 2010). Constant condition experiments with humans are extremely costly in time and financial resources as they require specialised laboratory set-ups in which individuals spend many days. The study in Chapter 1 follows established methods in the literature for investigating circadian and time of day effects in humans while compromising on the ability to draw a definitive conclusion about circadian effects on human behaviour. Rather, behavioural findings from Chapter 1 provide evidence that auditory production rates vary by time of day, which is inherently but not exclusively linked to circadian rhythms, and that individuals' natural production rates are relatively stable in the face of time of day and sleep influences.

Nonlinear Analysis Tools Applied to Cardiac Activity during Auditory-Motor Tasks

Cardiac data has an inherent time component – heartbeats unfold in time. Linear methods for analysing cardiac data, such as heart rate and heart rate variability, are aggregate snapshots of the cardiac signal, meaning they fail to capture the dynamic nature of cardiac activity. How heartbeats unfold in time contains important information about cardiac functioning (Marwan et al., 2002). The three studies contained in this dissertation applied a nonlinear analysis technique (recurrence quantification analysis) to cardiac data.

As noted in the General Introduction, nonlinear analysis approaches are well-suited to time series data for a number of reasons. They do not make assumptions about stationarity, they capture change or drift over time, and they are typically robust to outlier values (Webber & Marwan, 2015). For studying physiological systems, nonlinear analysis techniques also provide an accurate reflection of the type of system at hand. Research has demonstrated that biological activity can be modelled using nonlinear dynamical systems theory, from small-scale cellular activity to higher-level cognition and perception (Guastello et al., 2009). Cardiac activity is equally known to show nonlinear behaviour (Webber & Zbilut, 2005; Zbilut et al., 2002); the exclusive application of linear techniques to cardiac data limits information as to how the cardiac system behaves in a given context. The application of nonlinear analysis methods to cardiac activity in this dissertation is thus a step towards providing richer information on cardiac dynamics during behavioural tasks.

Recurrence quantification analysis (RQA), a nonlinear analysis technique applied to cardiac dynamics in this dissertation, was compared with traditional linear measures such as mean R-R intervals (heart rate) and heart rate variability (SDNN, RMSSD). RQA describes and quantifies the nonlinear repeating patterns in a signal of interest. There is a variety of nonlinear analysis techniques that have been used to capture cardiac activity during music performance (Chanwimalueang et al., 2017; Sebastiani et al., 2022; Williamon et al., 2013). RQA is a particularly strong approach for analysing cardiac signals during auditory rhythm perception and production tasks because these tasks involve periodic, oscillatory stimuli and behaviour, meaning there is strong repetition in the signals in time. This repetition in time is lost in linear cardiac metrics but accounted for in RQA. Chapter 1 showed that RQA was sensitive to differences in cardiac activity between performance of two simple melodies as well as time of day when a traditional measure of heart rate variability (SDNN) was not. Chapter 2 demonstrated that RQA was sensitive to rhythm complexity effects when linear cardiac measures of heart rate (mean R-R interval) and heart rate variability (RMSSD) were not. This dissertation showed that RQA is a useful analysis tool that is sensitive to different factors affecting cardiac activity during rhythm perception and production tasks.

Future Directions

Cross-Recurrence Quantification Analysis

Cross-RQA is an extension of auto-RQA that captures shared dynamics between two different time series and is particularly useful in characterising temporal coupling between two time series (Shockley, 2005). One potential use of cross-RQA is to capture the temporal coupling between physiological signals within an individual during auditory rhythm perception and production. The heart is embedded within a larger physiological system, meaning it receives input from various other physiological processes. One major connection is between the heart and the respiratory system: The respiratory sinus arrhythmia is the key example of this coupling, where changes in respiration rate and depth result in changes in heart rate and heart rate variability (Berntson et al., 1993; Marwan et al., 2013). RQA has previously shown that respiration rate affects cardio-respiratory coupling (Censi et al., 2002; Marwan et al., 2013). During perception, rhythm tempo can affect respiration rate (Mütze et al., 2018) and cardio-respiratory coupling (Wright et al., 2022); during production, trained musicians show individual differences in respiration rate changes when performing music (Sakaguchi et al., 2016). Given the close coupling between cardiac activity and respiration, future research should (1) incorporate measures of respiration rate to identify how auditory rhythms influence respiration and (2) utilize cross-RQA to capture the degree of coupling between the heart and respiration to understand interactions between cardiac and respiratory activity. This will provide a fuller picture of physiological effects of auditory rhythms.

A second future application of cross-RQA is to investigate how physiological signals couple to behavior during auditory-motor synchronization tasks. The research in this dissertation showed that there are changes in cardiac activity during rhythm perception and synchronization; cross-RQA can extend these findings when applied to tapping and cardiac time series to identify whether temporal coupling between rhythms and cardiac activity occurs. This would be a step towards further testing entrainment between physiological oscillators and behavior, as predicted by nonlinear dynamical systems theory, and how this supports auditory-motor synchronization.

Interpersonal Physiological Synchrony

Another novel direction for future research is to examine behavioural and physiological synchrony between individuals during music production. Nonlinear dynamical systems theory holds that oscillatory physiological activity underpins behavioural synchrony when oscillators entrain to one another; this has been investigated for neural activity where synchronised tappers show coupling in neural oscillations (Scheurich et al., 2019). RQA has also been used to demonstrate coupling between individuals' cardiac activity during live theatre performances (Ardizzi et al., 2020) and between musicians during live music performance (Høffding et al., 2023), but these studies have yet to link interpersonal cardiac coupling to behavioural synchrony. Future research could investigate interpersonal cardiac coupling during joint simple and complex rhythm performances.

General Conclusion

This dissertation provides evidence that auditory rhythms influence cardiac dynamics. Individual difference factors as well as rhythm complexity and practice/training were shown to have roles in how cardiac dynamics are affected during rhythm perception and production. These findings contribute to our understanding of how oscillatory peripheral physiology may influence successful auditory-motor synchronisation.

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