Timing, kinematics, and the cerebellum:

Tapping into differences between musicians and non-musicians

Lawrence H. Baer

A Thesis in the

Department of Psychology

Presented in Partial Fulfillment of the Requirements

For the Degree of Doctor of Philosophy at

Concordia University

Montréal, Québec, Canada

March, 2014

CONCORDIA UNIVERSITY
SCHOOL OF GRADUATE STUDIES

This is to certify that the thesis prepared

By: Lawrence Baer

Entitled: Timing, kinematics, and the cerebellum: Tapping into difference between musicians and non-musicians

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

Doctor of Philosophy (Psychology)

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

Signed by the final examining committee:

______________________________ Chair
Dr. R. Kilgour

______________________________ External Examiner
Dr. H.N. Zelaznik

______________________________ External to Program
Dr. R. Courtemanche

______________________________ Examiner
Dr. A. Johnson

______________________________ Examiner
Dr. V. Penhune

______________________________ Thesis Supervisor
Dr. K. Li

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

May 2, 2014 ______________________________
Interim Dean J. Locke, Faculty of Arts & Science

ABSTRACT

Timing, kinematics, and the cerebellum: Tapping into differences between musicians and non-musicians

Lawrence H. Baer, Ph.D.

Concordia University, 2014

Musical performance relies on basic processes such as timing, and the synchronization of motor responses with environmental stimuli. The study of the effects of musical training on behaviour and the brain provides an opportunity to understand these processes and their neural correlates, particularly in relation to the cerebellum, a brain region implicated in timing.

The first study presented here compared musicians and non-musicians on the standard sensorimotor synchronization task of finger tapping to a metronome, with and without tactile feedback. The results indicated that musicians differed from non-musicians in their use of kinematics and sensory information for synchronization.

The second study focused on how musical training affects event-based and emergent timing in repetitive rhythmic tapping and drawing. Event-based timing has been shown to rely on an internal clock-like process that is independent of the motor response. Conversely, emergent timing establishes regular rhythmic movement by stabilizing kinematic parameters without reference to an explicit internal representation of time intervals. Musical training was associated with improved precision in event-based timing but not in emergent timing. For musicians only, the kinematic parameter of movement jerk was decoupled from timing variability in both event-based and emergent timing. These results support the dissociability of the two timing modes, highlight the limits of musical training, and show that the relationship between kinematics and timing is affected by musical expertise.

The third study examined differences between musicians and non-musicians in a finger-tapping task, and in regional cerebellar volumes measured from magnetic resonance imaging data. Smaller volumes were associated with an earlier age of start of musical training, and with better timing performance. These findings are evidence for a sensitive period, before seven years, for initiation of musical training. Timing variability was associated with the volume of right Lobule VI, indicating localization of event-based timing to this region.

The overall pattern of results suggests that musicians may be using sensory information to maintain timing in a more efficient and parsimonious manner compared to non-musicians. This is interpreted as evidence that musicians are using a top-down approach for many music-related tasks, in contrast to the bottom-up approach of non-musicians.

In memory of my parents, Evelyn and Lucian Baer.

Acknowledgements

First and foremost, I would like to thank Dr. Virginia Penhune for giving me the life-changing opportunity to take the leap into a second career, clinical psychology, where the mix of research and clinical work makes every day interesting, and challenging, and meaningful. I would also like to thank Virginia and my co-supervisor, Dr. Karen Li, for their guidance, good humour, expertise, and encouragement all these years. I would also like to acknowledge Karen for giving me the opportunity to work on another challenging project, a longitudinal study of cognitive function in retirement, that has led to many good and interesting things. It has been an absolute pleasure to work with them both and I know that I will miss our discussions -- as well as the lab parties.

I will also miss the camaraderie of the lab and the tolerance of my labmates for my horrific puns. If there is a tapping pun that I failed to put my finger on, please don't point it out. I thank them for that, as well as for moral support and many stimulating discussions, writing sessions, and various adventures around town: Anne Bailey, Alejandro Endo, Laura Fontil, Sarah Fraser, Tara Gralnick, Avrum Hollinger, Clarisse Longo dos Santos, Tal Savion-Lemieux, Mike Spilka, Chris Steele, Dilini Sumanapala, Joe Thibodeau, Kevin Trewartha.

I would like to thank my internal committee members, Dr. Richard Courtemanche and Dr. Aaron Johnson, for their helpful feedback. I am grateful for the time they have taken to help me improve this dissertation.

I would like to thank Dr. Mallar Chakravarty and his team, especially Jon Pipitone, for making me feel so welcome in the Kimel Family Translational Imaging-Genetics Laboratory at the Centre for Addiction and Mental Health in Toronto. Mallar, I have always had an

appreciation for how life can turn on a dime but even I was impressed at how our collaboration grew out of a chance encounter with you on an elevator, just as I was leaving my internship interview at CAMH. Thank you so much for letting me spend my pre-internship summer in your lab. Matt Park, thank you for all your hard work in processing the MRI data – it has been a real pleasure to work with you.

I would also like to thank the undergraduate students with whom I worked, for their help with data collection: Eva Best, Joannie Huberdeau, Emilie Sheppard, Wai Yen Tang. It was a particular pleasure to supervise Marc-Oliver Hamel-Doyon on his undergraduate thesis and I also thank him for his efforts at data collection.

I am very aware of how blessed and fortunate I have been to have this opportunity to pursue a second career, particularly one as intellectually stimulating and as meaningful as psychology. No challenge as great as the pursuit of a Ph.D. can be met alone and I would like to thank my partner, Randall Cochrell, and my sister, Bev, for their wonderful support these past years. Bev, you have no choice but to put up with me. Randall, I feel very lucky that you have chosen to put up with me.

CONTRIBUTIONS OF AUTHOR

This dissertation consists of a general introduction, three studies and a general discussion. I wrote the general introduction and general discussion with feedback from my supervisors, Dr. Virginia Penhune and Dr. Karen Li, and from my internal committee members. The contributions of myself and others to the three studies are described below.

Study 1: Chapter 2

I developed the goals of the study and designed the experimental method and planned the analyses collaboratively with Dr. Penhune and Dr. Li. I worked with research assistant Alejandro Endo to design the software for data collection, which Mr. Endo wrote. I worked with Mr. Endo on the design and coding of MATLAB® software to analyze the motion capture data. I recruited and tested participants with the help of undergraduates Wai Yen Tang and Emilie Sheppard. I carried out the statistical analyses in the SPSS statistical software package and wrote all sections of the manuscript with guidance and feedback from Dr. Penhune and Dr. Li.

Study 2: Chapter 3

I developed the goals of the study, designed the experimental method and planned the analyses collaboratively with Dr. Penhune and Dr. Li. Research assistants Ricco Boma, Luis Da Costa and Joseph Thibodeau refined the existing customized software for data collection. Mr. Thibodeau wrote customized scoring software in MATLAB® after consulting with me on the design. I recruited and tested participants with the help of undergraduate student Marc-Olivier Hamel Doyon and research assistant Tara Gralnick. I carried out the statistical analyses in the SPSS statistical software package. I wrote all sections of the manuscript with guidance and feedback from Dr. Penhune and Dr. Li and with contributions from Mr. Thibodeau and Ms. Gralnick in the Methods.

Study 3: Chapter 4

I designed the behavioural task under the guidance of Dr. Penhune and Dr. Li. The task was part of a larger study conducted by doctoral student (now Ph.D.) Anne Bailey. The data collection and scoring software were re-used from Study 2. Dr. Bailey coordinated the recruitment and brain imaging of participants. Undergraduate student Eva Best and research assistants Michael Spilka and Tara Gralnick tested participants on the behavioural task. Brain imaging data was analyzed at the Kimel Family Translational Imaging-Genetics Laboratory at the Centre for Addiction and Mental Health in Toronto, where I wrote the beta version of the imaging pipeline under the guidance of Dr. Mallar Chakravarty and Jon Pipitone. Matt Park wrote the final version of the pipeline. Magnetic resonance image processing computations were performed on the GPC supercomputer at the SciNet HPC Consortium. SciNet is funded by: the Canada Foundation for Innovation under the auspices of Compute Canada; the Government of Ontario; Ontario Research Fund - Research Excellence; and the University of Toronto. I carried out all statistical analyses in the SPSS statistical software package, with the exception of the calculations of effect sizes, for which I used software provided by my internal committee member, Dr. Aaron Johnson. I wrote all sections of the manuscript with guidance and feedback from Dr. Penhune and Dr. Li and with contributions from Dr. Chakravarty and Mr. Park in the Methods section.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Chapter 1: General Introduction

Great musical performance is achieved after thousands of hours of practice over many years. It is the result of numerous complex brain processes working in synchrony and refined after extensive training, the effects of which are reflected in both behavioural and brain differences between musicians and non-musicians (Peretz & Zatorre, 2005; Schlaug, 2001; Zatorre, Chen, & Penhune, 2007). This dissertation focuses on the effects of musical training for the purpose of understanding the processes involved in sensorimotor synchronization, in particular the timing of voluntary repetitive movement on the millisecond scale. Musical training effects are also studied in order to address the question of how kinematics and timing interact to produce precisely timed movement. The work presented here also explores the neural correlates of musical training and of timing within the cerebellum, a brain region known to be involved in both music and timing (E, Chen, Ho, & Desmond, 2012; Manto et al., 2012). Finally, the work presented here extends research on a sensitive period, up to the age of seven years, for the initiation of musical training, to include effects on the cerebellum. Three studies are presented that contribute to our understanding of these issues.

As a means of comprehending and localizing brain function in humans, we may investigate expert populations, whose members excel at a given task, and correlate performance with brain differences, in comparison to a control group. A well-known example is the series of studies of London cab drivers, and the effects of drivers' training on spatial memory and the hippocampus (e.g., Maguire et al., 2000; Woollett & Maguire, 2011). In line with this approach, the research presented here examines the role of musical expertise in repetitive rhythmic movement tasks and analyzes associations of musical experience with timing, kinematics, and cerebellar volumes.

The brain processes time intervals on multiple scales, from circadian rhythms to microseconds (Mauk & Buonomano, 2004). The millisecond timescale plays a critical role in our interactions with the world around us. A sense of time at the millisecond scale is needed for language, where syllable production occurs every few hundred milliseconds, and for music, with the interval between beats of most tempi falling in the range of about 250 to 1500 ms (Shannon, Zeng, Kamath, & Wygonski, 1995; Zatorre, Chen, & Penhune, 2007). Further, in associative learning, conditioned eye blink responses are learned only when the interval between conditioned stimulus and unconditioned stimulus falls in the range of 100 to 3000 ms and the millisecond scale is also used for coordinated movement, for which muscle activations must be accurately timed to within tens of milliseconds (Mauk & Buonomano, 2004). The means by which the brain is able to estimate interval durations on this time scale is not completely understood. However, two modes of millisecond timing have been identified: Event-based timing, which relies on an explicit internal representation of interval duration (Wing & Kristofferson, 1973; Wing, 2002), and emergent timing, which does not appear to use such an internal representation but relies on the kinematics of movement to maintain timing (Robertson et al., 1999; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Zelaznik & Rosenbaum, 2010; Zelaznik, Spencer & Ivry, 2002). There is a large body of evidence pointing to a role for the cerebellum in event-based timing (E, Chen, Ho, & Desmond, 2012; Ivry, Keele, & Diener, 1988; Koch et al., 2007), but not in emergent timing (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). This dissertation focuses on how the brain executes repetitive rhythmic movement tasks whose periodicity lies on the millisecond scale. Both modes of timing are investigated and associations between regional cerebellar volumes and event-based timing are analyzed.

Several questions guided the research in the experimental studies that are presented here: (1) How will musical training affect the kinematics of repetitive, rhythmic movement and the relation between kinematics and timing; (2) Will musical expertise affect performance on event-based and emergently timed tasks differently, supporting the dissociability of the two timing modes; (3) Are there brain differences between musicians and non-musicians that are related to timing performance; (4) Is the cerebellum affected by a sensitive period for the initiation of musical training?

1.1 Neural correlates of music

Musical performance results from numerous brain processes acting in concert. These include the perception and production of rhythm and pitch, the planning, timing and execution of sequences of fine motor movements, auditory working memory, attention, and the processing of emotional aspects of music (James et al., 2013; Peretz & Zatorre, 1995). Thus, it is not surprising that plasticity related to musical training is observed across numerous brain regions, indicated, for example, by larger volume of the anterior corpus callosum, part of the bundle of nerve fibers connecting the two hemispheres (Schlaug, 2001), and greater grey matter volume in motor and parietal areas (Gaser & Schlaug, 2003).

The cerebellum is of particular interest as a site of music-related plasticity, given the evidence for its role in both lower level aspects of timing and motor control (Manto et al., 2012), and higher level cognitive processes (E et al., 2012; Stoodley & Schmahmann, 2009; Stoodley, Valera, & Schmahmann, 2012) that are recruited for musical performance. This brain region, located inferior and posterior to the cerebrum, and holding more than half the neurons of the brain packed into a tenth of the brain's total volume (Bear, Connors, & Paradiso, 2001), has been found to be of larger volume in musicians compared to non-musicians (Hutchinson, Lee, Gaab, & Schlaug, 2003). Additional evidence for music-related plasticity in the cerebellum includes the finding that a major input tract of nerve fibers from cortical sensorimotor areas, the middle cerebellar peduncle, and a major output tract to these same areas, the superior cerebellar peduncle, are also larger in musicians than in non-musicians (Abdul-Kareem et al., 2011). Functionally, the cerebellum has been shown to be active in music-related tasks, including rhythm perception and production (Chen, Penhune, & Zatorre, 2008; Karabanov, Blom, Forsman, & Ullén, 2009). The cerebellum is also involved in other processes that are crucial to musical performance, including sensorimotor integration and error correction of motor responses (Zatorre, Chen, & Penhune, 2007). Therefore, as part of the research presented here, the cerebellum is investigated as a site of plasticity related to musical training.

1.2 A sensitive period for musical training

Various aspects of musical training may affect the brain and behavior, the most obvious being duration and intensity of training. The age at which training begins has also been identified as a parameter of musical training that may moderate its effects. Recent research has identified a *sensitive period*, before the age of seven years, for musical training, such that training initiated during this period is associated with enhanced performance and grey and white matter differences later in life, compared to late-trained musicians (Penhune, 2011). This is comparable to a sensitive period for second-language learning before the age of 13 years (Johnson & Newport, 1989; Kuhl, 2010), but is distinct from a *critical period* for learning during development (Knudsen, 2004), such as has been observed, for example, with congenitally deaf cochlear implant recipients who do not show normal responses to auditory stimuli if the implantations take place after the age of about four years (Kral & Eggermont 2007). In the case of a critical period for acquisition of a skill, learning must be initiated during this period in order for normal skill development to occur. In contrast, for some skills, such as music or second-language acquisition, initiation of learning during the sensitive period is not necessary for normal performance but it does appear to facilitate enhanced performance such that effects endure well beyond the sensitive period.

In the case of early-trained musicians, when tested as adults in the reproduction of complex rhythmic sequences, they exhibit sensorimotor synchronization performance that is superior to that of late-trained musicians (Bailey & Penhune, 2010; Watanabe, Savion-Lemieux, & Penhune, 2007). Absolute pitch is also far more likely to occur in musicians who began training before the age of six years, and is quite rare in musicians who began their training after the age of nine years (Baharloo et al., 1998). With regard to neural plasticity related to musical training, the right ventral pre-motor cortex has been shown to have a greater amount of grey matter in early-trained musicians (Bailey, Zatorre, & Penhune, 2013), and the corpus callosum exhibits greater connectivity (Steele, Bailey, Zatorre & Penhune, 2013), even after controlling for total years of musical experience. These differences related to the age of initiation of musical training have been explained in the context of the developmental trajectories of brain regions known to be involved in musical performance, such that initiation must happen before full maturation in order for sensitive period effects to occur. The primary motor areas mature at about the age of five years, while other cortical areas, such as auditory regions, continue to develop over the next 15 years (Bailey et al., 2013). Because multiple brain regions interact during the execution of music production tasks, it may be that the regions with the earliest maturations determine the temporal limits of the sensitive period.

Given the cerebellum's role in music-related tasks, it would help our understanding of sensitive-period effects to investigate the connection between the age of initiation of training and cerebellar structure. Additionally, the basic timing processes involving the cerebellum are generally affected by musical training and so may also be affected by a sensitive period. For these reasons, both cerebellar structure and timing performance are investigated in the studies that comprise this dissertation.

1.3 Timing

In any repetitive movement task where the sequence of motor responses is required to adhere to a specific rhythm, the accuracy and precision of the responses are indicators of timing ability. The classic experimental paradigm for studying timing in this way is finger tapping to a metronome beat (Stevens, 1886). This finger-tapping task consists of two parts. In the paced phase, an individual taps in synchrony with a metronome beat. In the unpaced phase, the individual is instructed to continue tapping without the aid of a metronome but at the same rhythm established in the paced phase. The sequence of responses for each phase forms a time series from which measures of accuracy and precision can be extracted, and whose patterns can be studied to infer properties of the neural timing process that was used to generate the responses.

In the paced phase, a measure of timing accuracy is mean asynchrony, or the difference between the onset of the auditory stimulus of the beat and the onset of the tap response. This has been observed to be negative across many studies, indicating that individuals generally respond tens of milliseconds before stimulus onset (Repp, 2005). Negative mean asynchrony is still not well explained (Repp & Su, 2013), but theories include the sensory accumulation model in which tactile information is thought to be processed less efficiently than auditory information so that a tap must precede a tone in order to maintain an internal representation of synchrony

(Aschersleben, 2002). In the unpaced phase, the mean of the inter-response interval (IRI) of taps reflects timing accuracy and the variability of the IRI measures timing precision.

Intra-individual correlation of temporal performance across tasks is considered evidence of a common underlying timing process (Ivry & Hazeltine, 1995). In a series of experiments, Robertson et al. (1999) established that IRI variability in unpaced finger tapping did not correlate with IRI variability in unpaced continuous rhythmic circle drawing within individuals. They concluded that distinct timing processes were being engaged by these two tasks, so-called event-based timing for finger tapping and emergent timing for circle drawing. They further concluded that it was the movement style, discrete versus continuous, that determined which timing mode was used, although numerous counterexamples to this categorization have since been demonstrated (Delignières & Torre, 2011; Studenka & Zelaznik, 2008; Studenka, Zelaznik, & Balasubramaniam, 2011; Zelaznik & Rosenbaum, 2010). Each of these two timing mechanisms is reviewed next.

1.3.1 Event-based timing

Event-based timing is hypothesized to consist of a central clock-like timer distinct and independent from the motor response, as exemplified by the Wing-Kristofferson timing model (Wing & Kristofferson, 1973) for the unpaced phase of finger tapping. This central timekeeper could be either deterministic, such that any observed variability is fully accounted for by non-clock sources, or it could be stochastic, such that its error is a random variable, the sub-intervals between “clock ticks” will have a certain probability distribution, and variability will grow with the mean IRI. The Wing-Kristofferson model supports the latter formulation. Total variability in response timing is completely accounted for in an open loop (i.e., no feedback) system by two independent sources: a central timer process that is conceptualized as triggering each motor response, and the execution of the motor response. The variability of the central timer has a global effect on timing and is dependent on target interval duration, increasing with increasing length of mean IRI, while the variability of the motor execution has a local effect on adjacent responses only. Wing and Kristofferson (1973) showed how to obtain estimates of timer and motor variability from the covariance of adjacent tapping intervals. In the paced phase, the presence of the metronome signal means that "real-time" estimates of the accuracy of previous responses are possible. The model has been extended to account for this asynchrony feedback in the paced phase by the addition of error correction terms from the previous two tapping cycles, forming a linear second-order error correction model (Semjen, Schulze, and Vorberg, 2000).

Evidence for the independence of the timer and motor components of the Wing-Kristofferson model can be found in brain lesion studies and dual task studies. Cerebellar patients with lateral cerebellar damage ipsilateral to the tapping finger showed greater timer variability, while those with ipsilateral medial damage had greater variability in response execution (Ivry, Keele, & Diener, 1988). Silently solving anagrams while tapping increased timer variability but left motor variability unchanged (Sergent et al., 1993). In contrast, transcranial magnetic stimulation of the primary motor cortex while tapping increased motor variability and left timer variability unaffected (Verstynen, Konkle, & Ivry, 2006).

The Wing-Kristofferson model continues to be the dominant model of event-based timing but it has some important limitations. The model assumes that the timing system does not incorporate feedback during the unpaced phase, but perhaps not surprisingly, evidence suggests this is not necessarily the case. For example, when auditory feedback is present, it may be used for error correction, as evidenced by response adjustment after deliberate perturbations in feedback (Wing 1977). It has also been shown that the central timer more likely controls the timing of the arrival of the finger at the tapping point rather than the timing of the initiation of downward flexion as the original model assumed (Billon, Semjen, & Stelmach, 1996). The "sensory-goals model" accounts for these findings by suggesting that the central timer, while still independent of the motor system, is signaling to it when a tap should occur and using sensory feedback to make this prediction (Drewing, 2013; Drewing & Aschersleben, 2003).

Another limitation of the Wing-Kristofferson model is related to the estimation of timer variance in time interval discrimination tasks, where there is no timed motor response. In such cases, Wing-Kristofferson timer variance may include additional sources of variance that are not present in a motor response task and may exclude other sources that are specific to interval discrimination. Ivry and Hazeltine (1995) used the generalized Weber law equation of Getty (1975) as the basis of their "slope analysis" for partitioning the total variance of a timing task into duration-dependent and duration-independent sources, such that total variance changes linearly with the square of the interval duration. The slope of this line is an indication of duration-dependent variability and the intercept represents duration-independent variability. This approach has turned out to be a useful way to compare timing across tasks that may use different timing mechanisms. It is employed in Study II of this dissertation to compare musicians and non-musicians on different kinds of timing tasks.

1.3.2 Emergent timing

In an emergently timed task, timing is thought to derive from the optimization of motor control parameters specific to the task, resulting in an observable temporal regularity to the movement that does not rely on an explicit time interval representation. In other words, timing emerges from movement, in contrast to event-based timing, where a time interval is explicitly represented independently of movement. Using the slope analysis described above, Robertson and colleagues (1999) showed that discrete finger tapping and continuous circle drawing had uncorrelated intra-individual duration-dependent variability, and were therefore using different timing mechanisms. Tapping, with distinct stop and start events in each cycle of movement, was thought to require an explicit internal representation of a time interval, while circle drawing, characterized by continuous movement, was thought to use emergent timing.

This initial finding of distinct timing processes was supported by later studies, including one that ruled out the possibility that the greater kinematic complexity of circle drawing compared to finger tapping was what was responsible for the observed differences (Zelaznik, Spencer, & Ivry, 2002). The study found that intermittent circle drawing correlated with finger tapping but not with continuous circle drawing. Spencer and Zelaznik (2003) showed that for tapping, the variability of timing performance at the tapping point was minimal compared to other points on the finger trajectory, consistent with control by a central timer that signals the motor system at one moment in time. On the other hand, in circle drawing, timing variability was more or less constant throughout the trajectory no matter where the synchronization point occurred, suggesting that timing was not related to a specific event but to the entire movement cycle.

Zelaznik and colleagues (2005) proposed the *transformation hypothesis* to explain how timing emerges from movement in circle drawing. They suggested that continuous movement begins with an explicit internal interval representation in the paced phase, much as tapping movement does. Then, once motor control is stabilized, timing becomes emergent. In testing this, they found that timing variability in the first circle drawing interval correlated more strongly with tapping than with subsequent circle drawing intervals.

1.3.3 The relationship between event-based and emergent timing

The disassociation between event-based and emergent timing is supported by brain lesion and neuroimaging studies. Compared to healthy controls, patients with cerebellar damage showed disrupted timing (i.e., measured by the coefficient of variation of temporal accuracy), when tapping, and when drawing circles intermittently, but not when drawing circles continuously (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). An fMRI study of discrete and continuous finger tapping in healthy participants showed increased cerebellar activation (specifically lobule V/VI) in the discrete tapping condition only (Spencer, Verstynen, Brett, & Ivry, 2007). Spencer and Ivry (2005) examined the role of the basal ganglia in millisecond interval timing by studying Parkinson's disease patients. They found no difference between patients and healthy controls for tapping or intermittent circle drawing but did report that patients were slightly more variable on continuous circle drawing, suggesting that the basal ganglia may play a role in emergent timing.

Examining intra-individual correlations of timing variability can help establish whether or not two tasks share a common timing mechanism but to identify the specific timing mode used, the autocorrelation pattern of adjacent intervals in a given time series can be analyzed. An interesting pattern that is observed in the time series of responses in a task using event-based timing is an alternating sequence of short and long intervals (Stevens, 1886; Vorberg & Wing, 1996). This is accounted for mathematically by Wing & Kristofferson (1973), who showed that the lag-one autocorrelation of IRIs is bounded by negative one-half and zero and that it depends solely on the variability of the motor response delay. For example, a shorter than average delay will tend to shorten the previous IRI and lengthen the next IRI and, in general, the delay of the jth response in a time series will affect the length of the two IRIs that it demarcates. Said differently, a single IRI is affected by the motor error of the two adjacent responses. Negative lag one autocorrelation is considered a signature of event-based timing in both paced and unpaced phases (Delignières & Torre, 2011; Torre & Balasubramaniam, 2009). Autocorrelations at lags greater than one are predicted to be zero (Vorberg & Wing, 1996).

In contrast with event-based timing, the time series of IRIs in an emergently timed task exhibits a nonnegative lag one autocorrelation (Delignières & Torre, 2011; Torre & Balasubramaniam, 2009). A single response cycle in an emergently timed task is affected by the motor error for that cycle only and it is affected throughout the cycle. If the motor error is modeled as white noise, then it can be shown that a single white noise term in the equation defining the IRI implies that the lag one autocorrelation cannot be negative (Delignières & Torre, 2011; Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008; Torre & Balasubramaniam, 2009). Examining the lag one autocorrelation of a time series can help to identify the mode of timing that is employed for a given task.

It was originally thought that the event-based versus emergent dichotomy was based solely on the style of movement, discrete versus continuous, respectively. More recent studies have maintained the distinction between the two modes of timing but uncovered exceptions to this categorization based on movement style. Giving participants auditory or tactile feedback at the synchronization point in a continuous circle drawing task induced event-based timing (Studenka, Zelaznik, & Balasubramaniam, 2011; Zelaznik & Rosenbaum, 2010), as did getting participants to draw circles with their nondominant hand (Studenka & Zelaznik, 2008). It has been suggested that both event-based and emergent timing can be simultaneously active and contributing to timing within a response cycle (Repp & Steinman, 2010) but this has been refuted by Delignières & Torre (2011) who showed that control can alternate between the two timing modes between, but not within, response cycles. By calculating a sequence of lag one autocorrelations within a window moving along the time series of responses for a given individual, they demonstrated that an overall lag one autocorrelation value near zero is the result of sub-series of event-based and emergently timed responses. At the group level, a mean close to zero may mean that some individuals are using mostly or exclusively event-based timing and others are using emergent timing. Thus, the circumstances under which one or the other timing mode may be used are not yet well defined. Studying an expert group such as musicians, who use timing as a fundamental part of musical performance, may help to shed further light on this.

1.4 Timing and musical training

Given the role that sensorimotor synchronization plays in musical performance, it should not be surprising that musical training has been associated with reduced negative mean asynchrony in paced tapping and reduced variability in unpaced tapping (Franěk, Mates, Radil, & Beck,1991; Repp, 2010). A certain minimal level of training seems necessary in order for timing ability to benefit, as amateur musicians perform as well as non-musicians on tapping tasks (Repp & Su, 2013). Amongst professional musicians, the instrument that a musician plays also has an effect on timing, with percussionists exhibiting smaller negative mean asynchrony than pianists (Krause, Pollok, & Schnitzler, 2010) and less variability (Gérard & Rosenfeld, 1995).

An interesting question is which aspects of tapping performance are related to which aspects of music-related plasticity. The neural correlates of paced finger tapping include primary motor, somatosensory, and auditory cortices, as well as premotor areas and the posterior parietal cortex (PPC), cerebellum and thalamus and connections between these regions (Müller, et al., 2000; Pollok, Gross, & Schnitzler, 2006). The inferior parietal region has also been implicated in paced tapping (Jäncke, Loose, Lutz, Specht, & Shah, 2000). In terms of the time course of neural activations within a tap cycle, activations in primary somatosensory areas that occur on the order of 100 ms after finger movement onset and after tap onset are thought to represent proprioceptive and tactile feedback, respectively (Pollok et al.). Meanwhile, repetitive transcranial magnetic stimulation of the contralateral PPC, a region involved in multisensory integration, reduces negative mean asynchrony but has no effect on IRI variability, indicating that this region may have a role in maintaining timing accuracy but not precision (Krause et al., 2012). Krause and colleagues (2012) suggested that the reduction in asynchrony could be due to inhibition of motor areas because of disrupted input from the PPC, leading to delayed movement.

With regard to how musical training may affect this network for paced tapping, musicians showed enhanced connectivity between the thalamus and premotor region, suggesting enhanced sensorimotor integration (Krause, Schnitzler, & Pollok, 2010). Drummers also exhibited enhanced connectivity between the thalamus and the PPC, which may be related to reduced IRI variability (Krause, Schnitzler, & Pollok). It is plausible that the reduced negative mean asynchrony of musicians partially stems from more efficient processing in and communication of sensory information from primary somatosensory areas, which have greater volumes of grey matter in musicians compared to non-musicians (Gaser and Schlaug, 2003). With regard to motoric sources of response variance in finger tapping, it is possible that these are linked to observed differences in motor areas (Gaser and Schlaug). The increased volume in the corpus callosum of musicians' brains (Schlaug, 2001) may also be implicated in reduced motor variability, given the bilateral activations seen in motor areas for unimanual tapping (Pollok et al., 2006). Both reduced timer and motor variability may be related to cerebellar differences that have been observed between musicians and non-musicians (Hutchinson et al., 2003). This dissertation is concerned specifically with music-related plasticity in the cerebellum and how it may be related to finger tapping performance.

1.5 Current studies

The overarching theme of this dissertation is that the study of musicians offers a path to understanding how the brain estimates time intervals, and how it produces accurately and precisely timed rhythmic movement on the millisecond scale. It is clear that musical training conveys an advantage in rhythmic movement tasks. However, what is less clear is the underlying nature of this difference between musicians and non-musicians. Musicians may perform better because of more accurate and precise timing abilities, but they may also be performing the tasks in different ways compared to non-musicians. If the latter turns out to be the case, then it would indicate that neural plasticity related to musical training is not just a matter of increasing efficiency of neural processes, but of reorganization of some of these processes.

In pursuit of the answer to whether musicians and non-musicians perform the same timing tasks in different ways, the first study presented here examined the relationship between kinematics, timing and tactile information in the paced phase of a tapping task. Musical training has been associated with improved timing (Franek, et al., 1991; Repp, 2005; Repp & Doggett, 2007; Repp, 2010), with structural and functional brain differences in areas related to sensorimotor integration and synchronization (Gaser & Schlaug, 2003; Krause, Schnitzler, & Pollok, 2010), and with greater tactile sensitivity in the fingers (Ragert, Schmidt, Altenmüller, & Dinse, 2004). In light of these differences between musicians and non-musicians, the study focused on the question of whether musical training moderates the relationship between timing, motion, and tactile information.

Another unknown is whether musical training will convey an advantage in emergently timed tasks. Therefore, in the second study, we compared the performance of musicians and non-musicians on tapping and drawing tasks. We hypothesized that musical performance primarily uses event-based timing and predicted that musical training would be associated with better timing in finger tapping but not in circle drawing. We also examined the effects of musical training and of task on the relationship between movement smoothness and precision of timing.

Finally, given what we know about sensitive period effects on other brain regions, we sought evidence that the cerebellum is also sensitive to the age of onset of musical training. Another goal was to localize event-based timing to specific cerebellar lobules. Therefore, the third study compared musicians to non-musicians using timing data from a finger-tapping task and structural brain imaging data, with the goal of exploring the effects on the cerebellum of musical training and, in particular, of a sensitive period for the initiation of musical training. Regional cerebellar volumes were calculated from magnetic resonance data using a novel automatic segmentation algorithm and cerebellar atlas (Chakravarty et al., 2013; Park et al., in press). Automatic segmentation is more efficient than manual segmentation and allows for straightforward comparisons of and correlations with volumes of the individual lobules and white matter of the cerebellum. It complements the other techniques that have been used in our lab, including diffusion tensor imaging to examine white matter in the whole brain (Steele, Bailey, Zatorre, & Penhune, 2013), and voxel-based morphometry to examine cortical grey matter (Bailey et al., 2013).

Chapter 2: The use of tactile and proprioceptive information in paced finger tapping

2.1 Abstract

Finger tapping to a metronome beat is a classic experimental paradigm for studying sensorimotor synchronization. Previous work studying tapping in the absence of tactile feedback suggests that asymmetric finger trajectories play a functional role in reducing asynchrony. We tested whether this relationship would be observed in the presence of tactile feedback by varying the tapping surface and measuring participants' timing and finger trajectory. It was also hypothesized that the level of expertise in sensorimotor integration and synchronization could moderate the association between asynchrony and asymmetry relationship. To test this hypothesis, we compared musicians and non-musicians in the finger-tapping task in the presence or absence of tactile information. We found that non-musicians became more asynchronous in the presence of increased tactile information, suggesting that they were less efficient at integrating tactile information to benefit performance while musicians appeared to be using somatosensory information in a way that suggests better sensory integration compared to non-musicians. Furthermore, we found a difference between musicians and non-musicians in their patterns of asynchrony-asymmetry correlations across tapping surfaces, indicating that the two groups may have been using proprioceptive information in different ways. Our results inform kinematically-oriented explanations of sensorimotor synchronization, extending what is known about the role of sensory input and showing that there are limits to its facilitative role in synchronization.

2.2 Introduction

The ability to synchronize motor responses with regular auditory stimuli is a critical component of behavioural phenomena ranging from simply tapping along to a favourite song to ensemble musical performance. The classic experimental paradigm for studying auditory synchronization is finger tapping to a metronome beat (see Repp, 2005 for review). Previous researchers have focused on the temporal accuracy and variability of the responses (Wing and Kristofferson, 1973; Wing, 2002). More recently, it has been suggested that the kinematics of the motor response play a role in timing accuracy (Balasubramaniam, 2006; Doumas and Wing, 2007; Elliott, et al., 2009; Goebl and Palmer, 2008). In a study examining movement kinematics during tapping in the air without tactile feedback, Balasubramaniam et al. (2004) showed that accurate timing during a synchronization task was associated with asymmetric movement trajectories, such that less time was spent in flexion compared to extension. They hypothesized that an asymmetrical trajectory would result in greater proprioceptive feedback that would be useful in correcting errors, resulting in more accurate timing. While the exact nature of this error correction process is left unspecified, Balasubramaniam and colleagues suggested that the high velocity of the flexion phase could be a source of proprioceptive information that is used to maintain accuracy. This phenomenon poses an interesting problem for motor control, as it shows that synchronized tapping appears to yield kinematic patterns different from those that emerge from unsynchronized repetitive motion. This suggests that models of motor control that predict that efficient movement is smooth and symmetrical (Flash and Hogan, 1985) may not apply to all types of movement. Balasubramaniam and colleagues based their hypothesis on data from participants tapping in the air but in most synchronization tasks, participants tap on a surface, so tactile information is also available, and therefore tactile and proprioceptive information are likely both used to control and monitor performance. In fact, tactile information has been shown to be important in maintaining temporal accuracy (Goebl and Palmer, 2008), and these same authors suggest that the relative contributions of tactile and proprioceptive information to timing be further investigated. Therefore, the central question we addressed in the current experiment is how the information from these two sensory modalities is used in sensorimotor synchronization performance. We examined this issue by manipulating the level of available tactile information during an auditory synchronization task in order to see how it affected the asymmetry of the tapping movement.

An association between sensory input and temporal accuracy and precision has been observed in various synchronization studies (Aschersleben, et al., 2001; Aschersleben & Prinz, 1995; Drewing & Aschersleben, 2003). A basic measure of temporal accuracy is the difference in time between tap onset and stimulus onset. A consistently observed pattern related to this measure is negative mean asynchrony (NMA), such that the tap generally precedes stimulus onset by several tens of milliseconds, with NMA increasing as tempo slows (Repp, 2005). Reducing tactile input by anaesthetizing the finger results in increased NMA (Aschersleben et al., 2001). Meanwhile, increased auditory, tactile, and proprioceptive information are associated with reduced NMA (Aschersleben and Prinz, 1995).

As described above, a recent study measured both temporal accuracy and movement kinematics during an auditory synchronization task (Balasubramaniam et al., 2004). They found that participants showed an asymmetrical movement trajectory when tapping in the air without tactile feedback, such that the downward flexion time was shorter than upward extension time. Importantly, on a cycle-by-cycle basis, greater asymmetry was associated with smaller asynchrony. It was further found that this asymmetry was greatest at the slowest tapping rates, when response variability was also greatest, and was not present when there was no auditory cue. Based on these results, it was proposed that participants use the relatively high velocity of the flexion phase to acquire greater proprioceptive information that aids in error correction, particularly at the more challenging slower tempi. This finding is notable because it contrasts with existing models of motor control, which suggest that efficient movements - such as periodic movements with no specific temporal goal - typically exhibit symmetrical, smooth trajectories. For example, in planar hand and arm movements tasks, it has been shown that the resulting motion is maximally smooth (Flash & Hogan, 1985). The observed deviation from symmetry of repeated flexion and extension of the finger in the presence of a timing constraint occurred when tapping without tactile information. Therefore, we propose that increasing the available tactile information should reduce the dependence on proprioceptive feedback, as indexed with trajectory asymmetry. More specifically, we would expect the correlation between movement asymmetry and asynchrony to weaken as tactile feedback from the tapping surface increases. In addition, we would expect this effect to be most pronounced at the slowest tapping rates, when trajectory asymmetry has been found to be greatest.

Another factor that is known to affect temporal accuracy in auditory synchronization tasks is expertise. Musicians are known to be more accurate and less variable on these tasks (Franek, et al., 1991; Repp, 2005; Repp & Doggett, 2007; Repp, 2010). Moreover, musicians show differences in brain structure (Schlaug, 2001; Gaser & Schlaug, 2003), and function (Chen, et al., 2009) in regions thought to be involved in motor synchronization and timing. Therefore, given these differences and given the proposed role of kinematics in synchronization timing (Balasubramaniam et al., 2004), we hypothesized that musicians would show differences in the relationship between movement asymmetry and timing, compared to non-musicians.

Behaviorally, musicians are known to have substantially smaller NMA than non-musicians (Repp, 2005), and smaller variability of the inter-tap interval (Franek et al., 1991; Repp and Doggett, 2007; Repp, 2010). Experimental evidence suggests that musicians process and integrate sensory input more quickly than non-musicians. Neuroimaging studies depict the musically trained brain as one with larger anterior corpus callosum (Schlaug, 2001), and greater grey matter volume in cerebellar, motor, and parietal areas. The parietal area includes the anterior superior parietal area (i.e., primary somatosensory cortex), a region that has been implicated in the integration of sensory information (Gaser and Schlaug, 2003). There is commonality between brain regions known to be of greater volume in musicians, and brain regions known to be recruited during finger tapping. We know that primary motor and auditory areas are recruited bilaterally during finger tapping, as well as contralateral somatosensory and ipsilateral cerebellar regions (Pollok, Gross, and Schnitzler, 2006). In particular, the primary somatosensory cortex is active about 100 ms after the initiation of finger motion, and about the same amount of time after a finger tap (Müller, et al., 2000). This activation of the primary somatosensory cortex may represent proprioceptive and tactile feedback from the finger (Müller, et al., 2000). Thus, it may be that these structural brain differences between musicians and non-musicians are directly related to the differences in finger-tapping performance observed between these two groups. It is also worth noting that piano players exhibit finer tactile sensitivity of the finger compared to non-musicians (Ragert, et al., 2004). Based on these findings, we predicted that musicians would be more sensitive to tactile feedback and that the relationship between movement asymmetry and temporal accuracy would be stronger for musicians than for non-musicians.

Taken together, previous findings show a correlation between finger trajectory asymmetry and temporal accuracy in the absence of tactile feedback, such that increased trajectory asymmetry likely provides greater proprioceptive information, which aids in synchronization. We also know that musical training is associated with superior sensorimotor integration and synchronization. However, it is less clear if the asymmetry-asynchrony relationship will hold in the presence of tactile feedback, or if the level of participants' synchronization expertise influences this relationship. Hence, our first hypothesis was that the presence of tactile information would reduce trajectory asymmetry. Our second hypothesis was that musical training would moderate the relationship between timing, motion, and tactile information such that increased tactile feedback would be associated with a larger reduction of asymmetry and asynchrony for musicians than for non-musicians and such that the relationship between asynchrony and asymmetry would be stronger for musicians than for non-musicians. To test this, we compared the behaviour of musicians and non-musicians on a paced finger-tapping task under varying levels of tactile feedback and at varying tapping rates, recording participants' finger motion in order to measure trajectory asymmetry.

2.3 Methods

2.3.1 Participants

Twelve musicians (7 males) and twelve non-musicians (3 males), all neurologically healthy, were recruited, primarily from the undergraduate student population of Concordia University in Montréal, Québec. Musicians had to be actively engaged in practicing at least one musical instrument while non-musicians could not be currently practicing any instrument and had to have less than three years of musical training or experience. The years of training of musicians (*M* = 16.4 years; *SD* = 5.7) and non-musicians (*M* = 0.4 years; *SD* = 0.7) differed substantially, and seven non-musicians had no musical training whatsoever. Musicians played a range of instruments including guitar, drums, piano, and saxophone. The age of the musicians (*M* = 25.1 years; *SD* = 5.0) and non-musicians (*M* = 23.5; *SD* = 4.1) did not differ significantly (*t*(22) = 0.850, *p* = .404). Handedness was determined by administering the Crovitz and Zener (1962) questionnaire. The handedness scores of musicians (*M* = 25.9; *SD* = 5.5) and non-musicians (*M* = 24.3; *SD* = 3.5) did not differ significantly (*t*(22) = 0.836, *p* = .414), indicating that both groups were strongly right-handed. The study was approved by the Concordia University Human Research Ethics Committee, and informed consent was given by all participants. Participants were debriefed about the goals of the experiment following their testing.

2.3.2 Apparatus

Finger motion was recorded using the Visualeyez VZ3000 3D motion tracking system, manufactured by Phoenix Technologies. For each participant, data were collected from a small light-emitting diode (LED), attached by thin copper wire to a central controller, and affixed with Velcro tape to the tip of the fingernail of the right index finger. Nine infrared-sensitive cameras tracked the position of the marker in three-dimensional space at a sampling rate of 200 Hz and to a spatial resolution of 0.015 mm. A National Instruments 6221 Data Acquisition board was used to synchronize motion capture with a computer-generated 1 KHz 20 ms metronome tone. All participants heard the same metronome tone through a pair of ear bud headphones fitted with sound insulating caps to block the sound of their finger taps. Each participant was seated on a desk chair facing a Yamaha PSR-290 keyboard. The chair's seat and armrest heights were independently adjustable. The right armrest was reinforced and extended so that participants could comfortably keep their entire forearm, wrist, and most of their right hand supported and immobile during the experiment. The LED marker wires had sufficient slack to allow for complete freedom of movement of the right index finger. Different tapping surfaces corresponded to different levels of tactile feedback.

2.3.3 Design and Procedure

To manipulate the level of tactile feedback during tapping, we implemented three conditions: tapping in the air (Air), tapping on a piano key that was blocked from descending by a wooden block inserted under the key (Blocked), and tapping on a regular piano key that descended to a depth of 1 cm (Piano). The regular piano key provides tactile feedback from the point of initial key contact until the point of synchronization at key bottom. Thus, compared to the Blocked condition, the Piano condition provides greater tactile information during the downward flexion phase. In the former condition, the fingertip makes contact with the surface of the piano key before the synchronization target is reached, and while the finger is still moving in downward flexion. This means that tactile information is available earlier in the tapping cycle and has the potential to be used to aid synchronization during this flexion phase. Thus, the Air condition provided no tactile feedback, the Piano key condition provided a high level of tactile feedback because of the early key contact before key descent, and the Blocked condition provided an intermediate level of tactile information because it consisted of contact only at the point of synchronization.

Participants tapped on each surface at four tapping rates: 1 Hz, 1.5 Hz, 2 Hz, and 3 Hz. These rates were selected in order to cover a typical but broad range of rates used in finger tapping experiments. The ordering of the twelve conditions was determined by using a Latin square for counterbalancing of the different levels of independent variables. Each condition consisted of three trials of forty presentations of the auditory stimulus at the given rate, and participants were instructed to tap on the beat using only their right index finger. Within each test session, participants completed a consent form, the Crovitz-Zener handedness questionnaire, a musical training questionnaire, and the main experimental task. They were then debriefed and compensated for their time. Each session lasted approximately 90 minutes.

2.3.4 Data analysis

We measured temporal asynchrony, inter-response interval (IRI) variability, and trajectory asymmetry. All analyses were carried out using the z coordinate of the fingertip marker, corresponding to vertical finger motion. In order to compute the dependent variables from the kinematic/motion capture data, a number of steps were required. First, the initial ten tapping cycles of each trial were discarded from the analysis. Then the kinematic landmarks of each finger tap, including movement onset and tap onset, were found automatically using the following algorithm that we designed and implemented in the MATLAB® (The MathWorks, Inc., MA, USA) programming environment. For each stimulus presentation, a temporal window was defined, such that its centre was the stimulus onset, and its width depended on the prescribed tapping frequency. In each window, the absolute maximum and minimum values were then identified, corresponding to the maximum and minimum finger heights (points of maximum finger extension and maximum finger flexion, respectively) within that time period. Next, a sub-window delimited by these two extrema was searched for the point of movement onset, defined as the point at which 5% of the minimum velocity (recalling that velocity will be negative during finger descent) was first attained. Finally, candidates for the tap onset were found by searching for local minima between the point of movement onset and the absolute minimum by applying the first derivative test to the velocity curve derived from the unfiltered motion capture data. If more than one local minimum was found, then the one closest in time to the stimulus onset was taken as the tap onset. Any cycles in which a tap onset was not found were discarded from further analysis.

The trajectory asymmetry dependent measure was defined as the ratio of time spent in downward flexion to the time spent in upward extension for a given tap. Thus, a value of 1.0 indicates perfect symmetry, and values less than 1.0 indicate asymmetry such that more time was spent in extension than in flexion. The period of downward flexion was defined as beginning at the first point at which 5% of minimum velocity was first reached, and ending at tap onset. The period of upward extension was defined based on the maximum velocity of that phase of movement, beginning at the initial point beyond tap onset at which 5% of this maximum was reached and ending at the final point at which this same velocity value was attained.

Temporal asynchrony was calculated as the difference in time between tap onset and corresponding stimulus onset for each tapping cycle. The inter-response interval (IRI) was calculated as the difference in time between the onsets of adjacent taps. In order to normalize for different tapping rates, we used the coefficient of variation of the IRI in our statistical analyses. Finally, the correlation between asynchrony and asymmetry was calculated for each level of tactile feedback pooled across tapping rates by computing the correlation within each trial and then taking the average correlation value across trials for all participants at all tapping rates.

2.4 Results

2.4.1 Kinematics

In order to assess expected differences in kinematics between musicians and non-musicians, we first examined finger motion trajectories qualitatively. Figures 2.1 and 2.2 portray the vertical finger motion for a musician and a non-musician tapping in the Blocked condition at 2 Hz. The graphs suggest that non-musicians move in a more variable, and in less of a smooth fashion than musicians. The greater regularity of finger amplitude of the musician over the non-musician that is evident in Figure 2.1 is also seen in the corresponding phase plots of Figure 2.2. These figures illustrate the differences in motor control between musicians and non-musicians, with greater cycle-to-cycle variability in the finger trajectory of non-musicians. In particular, the phase plots show that the non-musician exhibits the greatest variability at the transition from the extension of one tap cycle to the flexion on the subsequent tap cycle.

To address our hypothesis that increasing available tactile information would result in a reduction of finger trajectory asymmetry, we analyzed the kinematic data as a function of available tactile feedback and rate. As predicted, trajectory asymmetry was affected by the level of tactile feedback, $F(2, 21) = 18.05$, $p < .001$, $\eta_p^2 = 0.451$, such that the Blocked condition was more asymmetric than the other two. However, recalling that the Blocked condition corresponds to tapping on a hard surface, it may simply be that the collision with the surface, rather than the level of tactile information, was responsible for the change in kinematics. The effect of tapping rate on asymmetry was marginally non-significant after Greenhouse-Geisser correction, such that asymmetry decreased as rate increased, $F(2, 20) = 2.97$, $p = .069$, $\eta_p^2 = 0.119$ ($p = .038$ before Greenhouse-Geisser correction).

In relation to our second hypothesis concerning the moderating effects of musical training on asymmetry, we found that the difference in asymmetry between musicians and non-musicians was marginally non-significant, $F(1, 22) = 3.56$, $p = .072$, $\eta_p^2 = 0.139$ ($M = 0.452$ and 0.531 respectively). The interaction between musical training and tapping rate was also marginally non-significant, $F(3, 20) = 2.97$, $p = .069$, $\eta_p^2 = 0.119$ ($p = .038$ before Greenhouse-Geisser correction). Post-hoc comparisons revealed that musicians were more symmetric at the fastest rate of 3 Hz compared to the 2 Hz and 1.5 Hz rates ($p < .05$ and .01 respectively). Contrary to expectation however, the interaction of musical training and level of tactile information was non-significant, $p = .472$.

2.4.2 Timing

In support of our hypothesis about the effect of musical training on the use of sensory information and temporal asynchrony, we found a significant interaction between level of tactile feedback and musical training, $F(2, 21) = 3.90$, $p < .05$, $\eta_p^2 = 0.151$. Post-hoc comparisons with a Bonferroni correction revealed that non-musicians were significantly more asynchronous when tapping in the Piano condition compared to the Air condition, $p < .05$, whereas musicians did not differ significantly in their asynchrony across levels of tactile feedback (p's $\geq .244$). There was also a significant difference between the two groups such that in the Piano condition, musicians were significantly less asynchronous than non-musicians, $p < .05$ after Bonferroni correction. These results suggest that the level of available tactile information affected the temporal accuracy of musicians and non-musicians in different ways, with non- musicians showing an unexpected increase in asynchrony as sensory information increases. No significant main effect of group ($p = .144$; observed power = .305), level of tactile feedback ($p = .066$; power = .537) or tapping rate ($p = .058$; power = .617; $p = .098$ after Greenhouse-Geisser correction; power = .434) was observed (see Figures 2.3 and 2.4).

The variability of asynchrony was affected by both musical training and tapping rate, but not tapping surface. Asynchrony variability was significantly smaller for musicians ($M = 29.2$ ms) than for non-musicians ($M = 54.5$ ms), $F(1,22) = 10.546$, $p < .004$, $\eta_p^2 = .324$. Variability also significantly decreased as tapping rate increased, $F(2,20) = 32.475$, $p < .001$., $\eta_p^2 = .596$. However, neither the effect of tapping surface ($p = .126$) nor the interaction between musical training and tapping surface ($p = .660$) were significant. Taken together with the effects on mean asynchrony, this suggests that tapping surface affected temporal accuracy, but not precision.

In order to further analyze the effects of tactile feedback and musical training on temporal performance, we examined the coefficient of variation of the IRI. An interaction between tapping rate and musical training shows that non-musicians became significantly more variable in their IRI as tapping rate increased, $F(3, 20) = 3.91$, $p < 0.05$, $\eta_p^2 = = 0.151$ (Figures 2.5 and 2.6) while musicians' variability did not change across rates ($p > .482$). We did not find an effect of tactile information but a main effect of musical training indicates that musicians were significantly less variable than non-musicians in their IRI, $F(1, 22) = 9.78$, $p < 0.05$, $\eta_p^2 = 0.308$. In summary, the effect of rate on non-musicians only and the smaller variability in musicians' IRI illustrate the superior synchronization performance of musicians.

2.4.3 Kinematics and Timing

In order to verify our prediction that tactile feedback and musical training would interact to affect the relationship between asynchrony and asymmetry, we computed the correlations between asynchrony and asymmetry for each tactile feedback condition, pooled across tapping rates (Figure 2.7). The largely significant negative correlations show that participants were less asynchronous as their trajectories became more asymmetric, supporting the notion that asymmetry facilitates temporal accuracy (Balasubramaniam et al., 2004). An ANOVA of the asynchrony-asymmetry correlations revealed an interaction between tactile condition and musical training, $F(2, 21) = 5.08$, $p < .05$. Subsequent pairwise comparisons showed that musicians had a marginally weaker correlation in the Piano condition compared to non-musicians ($p = .08$). Within the non-musician group, participants displayed a significantly stronger correlation in the Piano condition compared to the Air condition ($p < .05$), while musicians had a stronger association between asymmetry and asynchrony in the Blocked condition compared to the Piano condition ($p < .01$). These differences suggest that the varying levels of tactile feedback had different effects on the synchronization strategies employed by the two groups of participants. It may be that musicians relied less on the proprioceptive information of a fast flexion phase in the presence of rich tactile information.

2.5 Discussion

The goal of this study was to examine the relationship between expertise in sensorimotor synchronization, as exemplified by musical training, and the use of tactile and proprioceptive information in a paced finger-tapping task. Our first hypothesis was that as tactile information increased, the reliance on proprioceptive input as represented by trajectory asymmetry would decrease. We further hypothesized that musicians would be better able to use tactile information than non-musicians, and that the previously observed correlation between asynchrony and asymmetry would be greater for musicians than for non-musicians. We found clear differences between musicians and non-musicians in terms of tapping synchronization and variability, consistent with previous findings of superior synchronization performance in musicians (Franek, et al., 1991; Repp, 2005; Repp and Doggett, 2007; Repp, 2010). We further found that when additional tactile information was available, non-musicians became more asynchronous but musicians' asynchrony did not change. This suggests that non-musicians do not use tactile information as efficiently as musicians do. Finally, we found a different pattern of correlations between asynchrony and trajectory asymmetry for musicians and non-musicians across different levels of tactile information, indicating that musicians appeared to be using tactile and proprioceptive information in a way that suggests better sensory integration compared to non-musicians.

Exploring the effect of tactile feedback, we found that the impact of increasing tactile information differed between the two groups, suggesting that it plays a different functional role depending on expertise. Previous synchronization tapping findings have shown that better synchronization is associated with more asymmetrical movement trajectory, leading to the hypothesis that, at least when tapping in the absence of tactile feedback, an asymmetrical movement allows participants to gain more proprioceptive feedback to make a more temporally accurate tap (Balasubramaniam et al., 2004). Our current findings show that this association cannot be generalized across varying levels of tactile feedback, or to non-musicians. If we compare the two extremes of tactile feedback, the Air and Piano conditions, clear and consistent differences emerge between the two groups along several dependent measures. In the Air condition, there were no group differences in the asynchrony measure, but importantly, musicians showed the expected correlation between asynchrony and asymmetry whereas non-musicians did not. In contrast, in the Piano condition, musicians were significantly more temporally accurate, but did not show the expected correlation between asynchrony and asymmetry. This suggests that musicians used a different strategy to synchronize their motor responses, relying less on proprioceptive information when sufficient tactile information was available. It remains an open question as to whether trajectory asymmetry plays a functional role in error correction, or is merely the kinematic manifestation of an error correction process. We and others (Balasubramaniam et al., 2004; Doumas and Wing, 2007; Goebl and Palmer, 2008) endorse the former explanation, as it offers a reason for the departure from the efficient, symmetric, and smooth trajectory predicted by some models of motor control (Balasubramaniam et al., 2004; Flash and Hogan, 1985). Therefore we have interpreted our results in the context of this functional interpretation of the asynchrony-symmetry association.

In order to test the hypothesis that greater tactile feedback during tapping would result in reduced trajectory asymmetry, we manipulated the tapping surface. In the Blocked key condition compared to the Air condition, participants receive more tactile feedback at the end of the flexion cycle. In the Piano condition, participants receive additional tactile feedback throughout the flexion phase of tapping. The effect of this manipulation showed that musicians were effectively able to use the additional sensory information to improve their synchronization accuracy, but non-musicians were not. While our manipulation of tapping surface is not a scalar or parametric manipulation of tactile feedback, our results do allow us to conclude that additional sensory information did not contribute to synchrony in non-experts, suggesting that expert training is necessary to take advantage of the earlier availability of tactile feedback during the synchronization process. Future experiments could use a parametric manipulation of the amount of tactile information available during the tapping cycle in order to further address the role of this sensory modality in synchronization and corroborate our more qualitative manipulation of this variable.

A number of factors might contribute to musicians' superior ability to use tactile information. Previous studies have shown that musicians are better able to synchronize with both auditory and visual rhythms, suggesting a superior ability to integrate sensory and motor information (Watanabe, et al., 2007; Chen, et al., 2008). Differences in brain structure between musicians and non-musicians may underlie these performance advantages. The larger corpus callosum of musicians (Schlaug, 2001) may facilitate inter-hemispheric communication between bilateral auditory and motor areas that are active during finger tapping (Müller, et al., 2000; Pollok et al., 2006). Together with the greater grey matter volume of the primary somatosensory areas (Gaser and Schlaug, 2003), this may allow for multimodal sensory information to be processed more quickly. Additionally, the finer tactile sensitivity of pianists (Ragert et al., 2004) indicates that in general, musicians may be able to more efficiently acquire tactile information. Finally, greater experience with musical instruments may contribute to musicians' superior performance in the Piano condition, and their apparent ability to relax their dependence on proprioceptive information in this context. In fact, even non-pianist musicians have been found to be more temporally accurate than non-musicians in bimanual multi-finger tapping on a piano keyboard, suggesting that training on another instrument can transfer to performance on the keyboard (Kincaid, et al., 2002) and result in superior synchronization performance.

A second factor distinguishing musicians and non-musicians was that non-musicians showed less accurate timing in the presence of greater tactile input, suggesting that they were less able to integrate information from the two modalities. This pattern may appear counter-intuitive because one might assume that having both proprioceptive and tactile feedback would result in better synchronization performance. However, this finding is consistent with models of tapping performance that emphasize the role of sensory processing (Aschersleben, et al., 2001; Aschersleben and Prinz, 1995; Drewing and Aschersleben, 2003). As described in the introduction to this chapter, a common finding in sensorimotor synchronization tasks is negative mean asynchrony, where participants' taps precede the auditory signal. These models interpret negative asynchrony as the difference in time that it takes to process somatosensory information from the finger versus the more efficiently processed auditory information of the metronome (Aschersleben, 2002; Fraisse, 1980; Paillard, 1949). Therefore, we view the non-musicians' poorer performance with greater tactile feedback as indicating that non-musicians process tactile input less efficiently, and tactile and proprioceptive information are integrated together less effectively. This is also consistent with previously noted expertise effects in tactile sensitivity and brain structure and function (Gaser and Schlaug, 2003; Ragert, et al., 2004; Schlaug, 2001).

Our results extend previous findings showing a connection between kinematics and synchronization performance. The original finding that as trajectory asymmetry increased, temporal asynchrony decreased was interpreted as evidence for the role of trajectory asymmetry in timing accuracy (Balasubramaniam et al., 2004). However, as described above, we have shown that the coupling between kinematics and synchronization is moderated by multiple factors, including expertise and somatosensory information. An open question is why we might observe asymmetric trajectories in conditions where asymmetry is not correlated with greater accuracy. Traditional models of motor control propose that efficient movement is smooth and symmetrical (Flash and Hogan, 1985). So why would we observe the less efficient asymmetrical movement trajectory even when it does not benefit accuracy? It could be that trajectory asymmetry is simply characteristic of timed movement (Balasubramaniam et al., 2004). Other recent studies have also suggested that a variety of aspects of movement kinematics can affect synchronization performance (Elliott, et al., 2009; Goebl and Palmer, 2008; Zelaznik, et al., 2002).

2.6 Conclusions

The present study explored the generalizability of the relationship between temporal accuracy and trajectory asymmetry and demonstrated that other factors, such as multimodal sensory integration and individual differences related to expertise, must be considered. We showed that for non-musicians, greater sensory information from tactile and proprioceptive modalities is not always helpful in synchronizing motor responses and, in fact, can interfere. However, for musicians, training appears to lead to more efficient sensorimotor integration and more accurate synchronization performance. Taken together, our results inform kinematically-oriented explanations of sensorimotor synchronization, extending what is known about the role of sensory input and showing that there are limits to its facilitative role in synchronization.

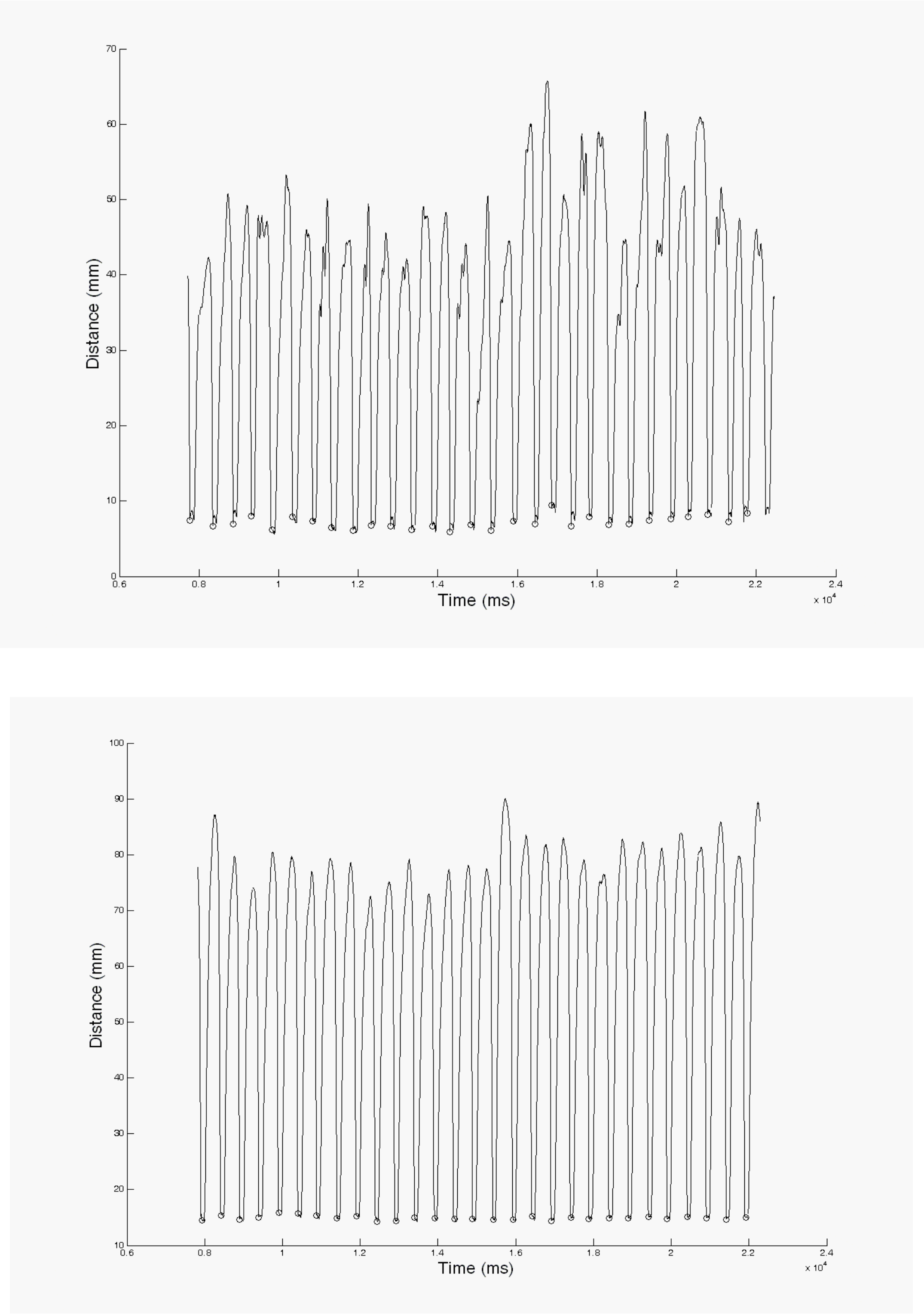

Figure 2.1. Z-coordinate of finger trajectory of a non-musician (top) and musician tapping at 2Hz in the Blocked condition. Circles indicate tapping points.

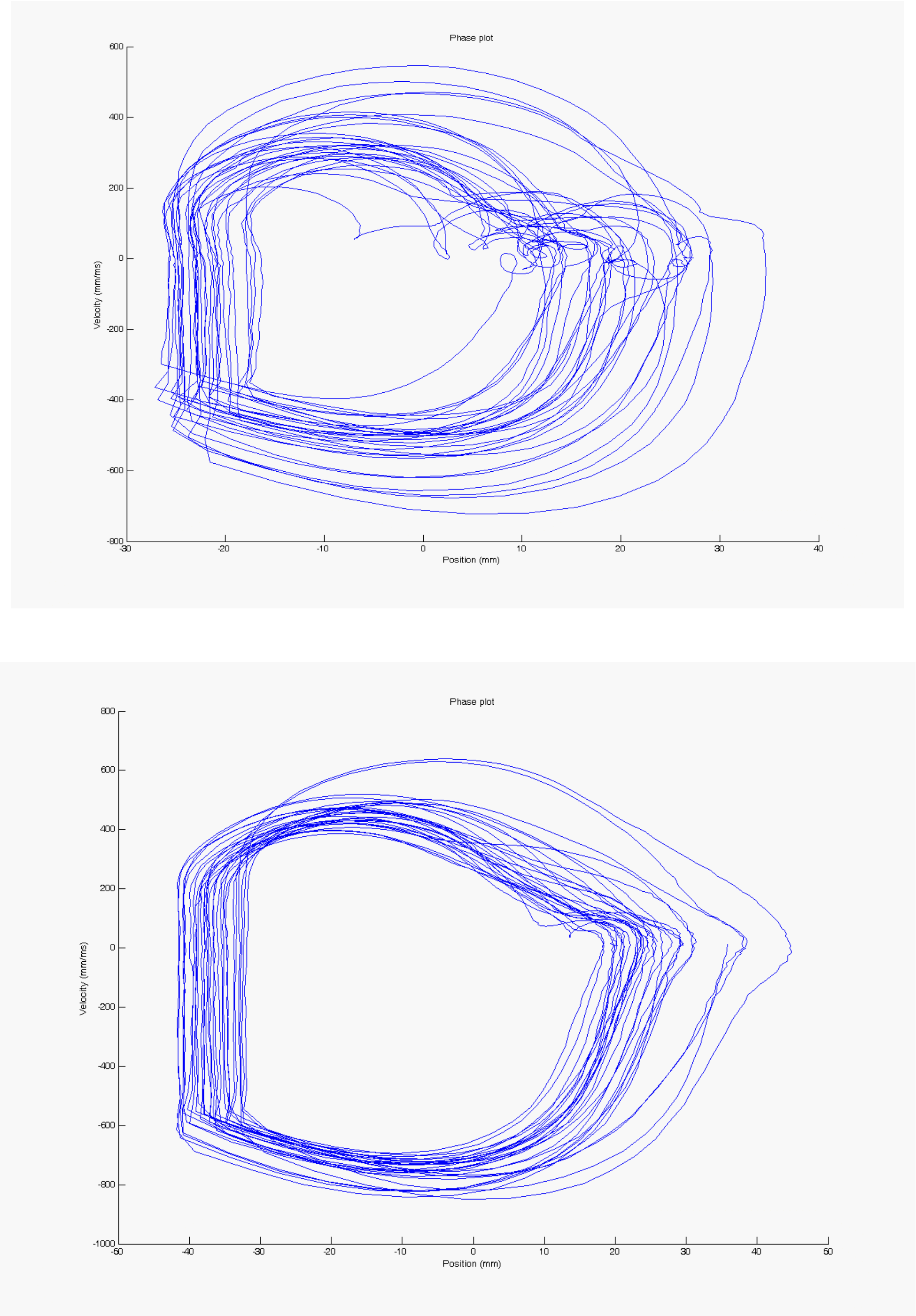

Figure 2.2. Position by velocity phase plots of a non-musician (top) and musician tapping at 2Hz in the Blocked condition. All tap cycles of a single block of trials are overlaid in the graphs.

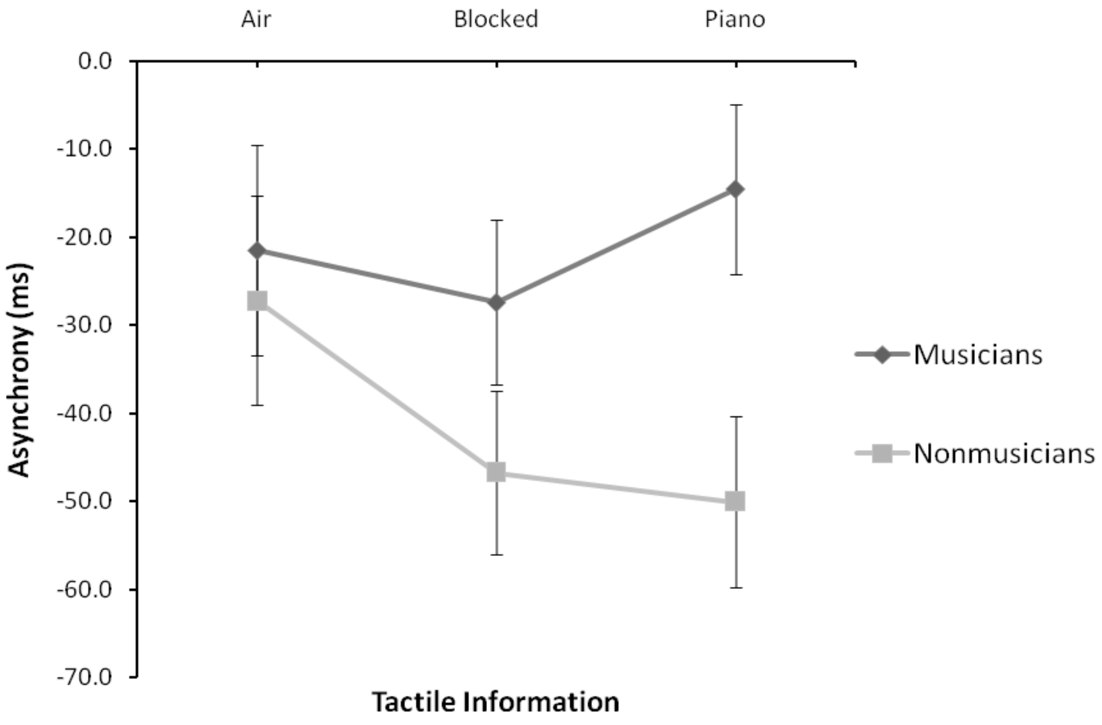

Figure 2.3. Mean asynchrony across levels of tactile feedback. Error bars represent standard error of the mean. X-axis labels indicate level of tactile information as follows. Air: No tactile information; Blocked: Intermediate tactile information; Piano: High tactile information.

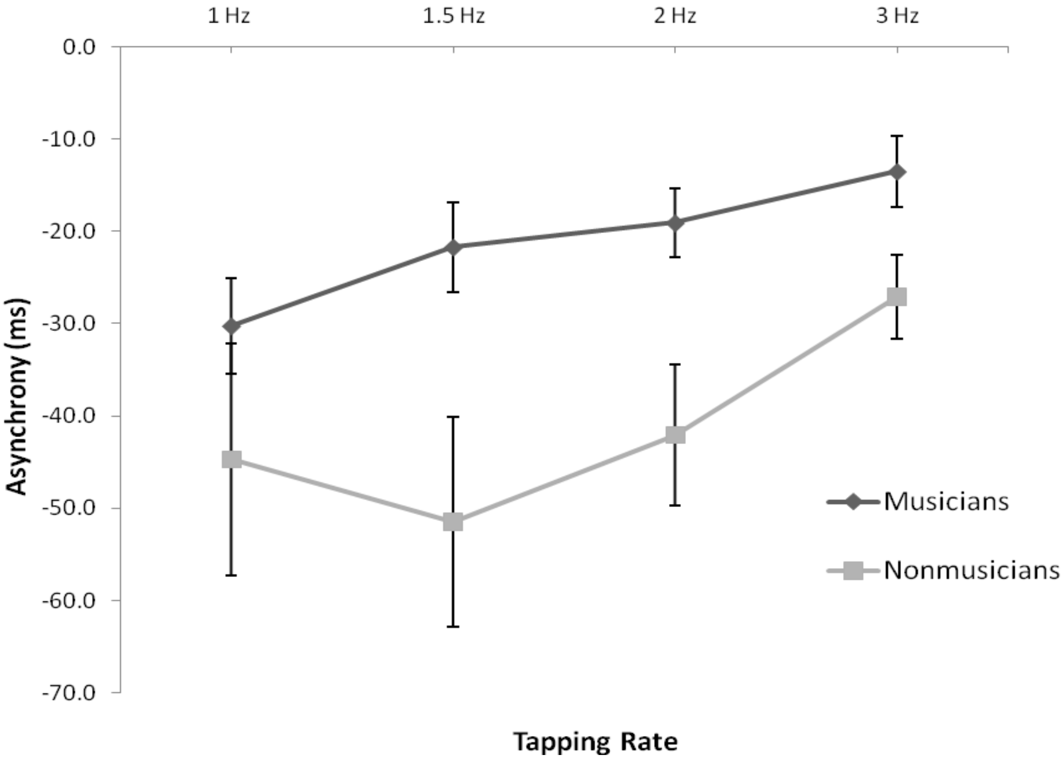

Figure 2.4. Mean asynchrony across tapping rates. Error bars represent standard error of the mean.

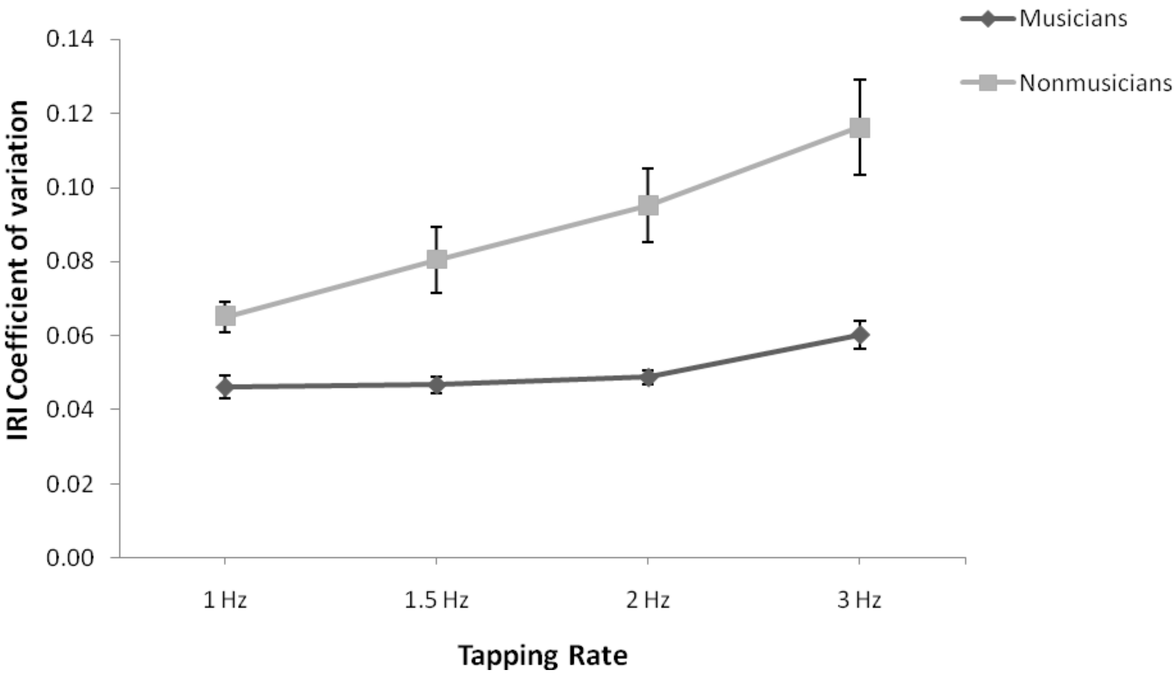

Figure 2.5. IRI coefficient of variation pooled across tapping rates. Error bars represent standard error of the mean.

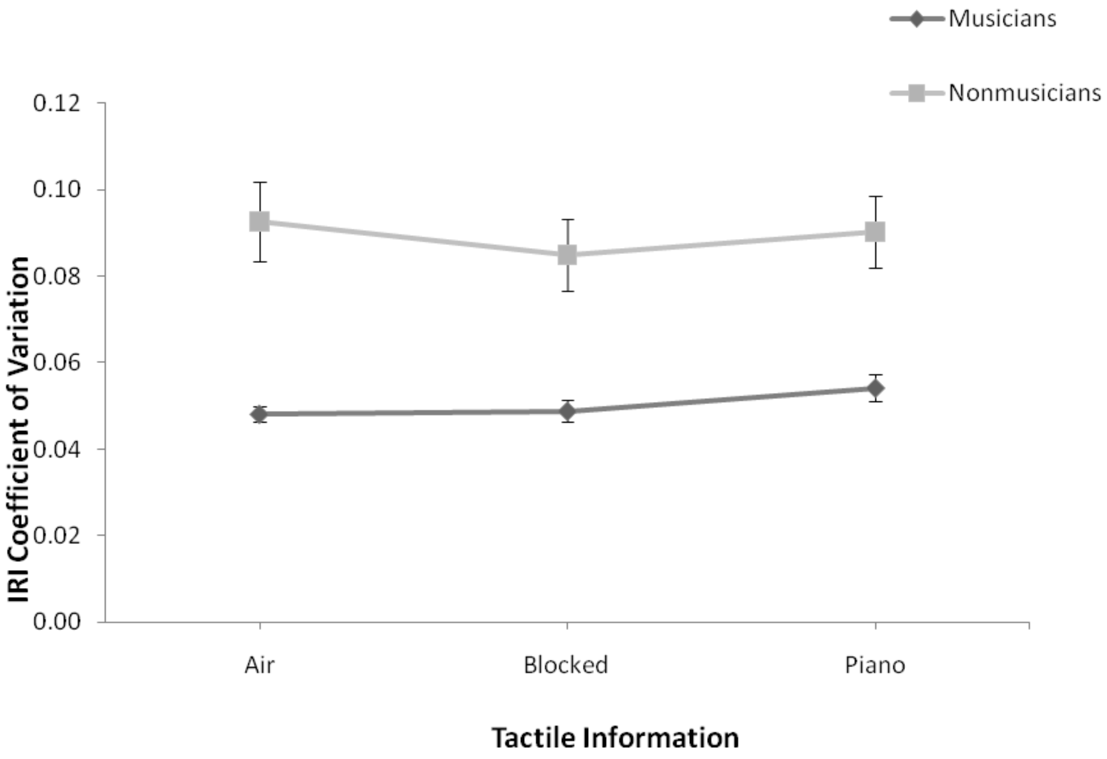

Figure 2.6. IRI coefficient of variation pooled across levels of tactile feedback. Error bars represent standard error of the mean.

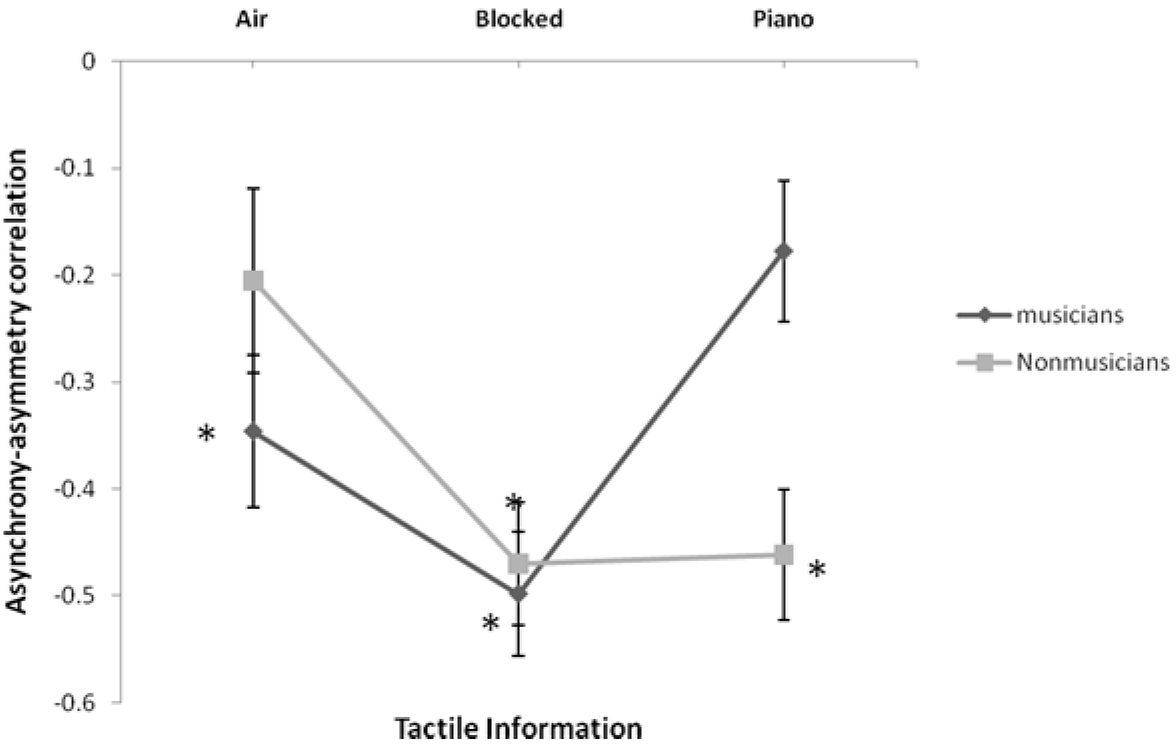

Figure 2.7. Correlations between asynchrony and trajectory asymmetry. Significant correlations ($p < 0.05$) are marked with an asterisk. Error bars represent standard error of the mean.

Chapter 3: The role of musical training in emergent and event-based timing

[Published as Baer, L. H., Thibodeau, J. L. N., Gralnick, T. M., Li, K. Z. H., & Penhune, V. B. (2013). The role of musical training in emergent and event-based timing. Frontiers in Human Neuroscience, 7, 191. doi:10.3389/fnhum.2013.00191]

3.1 Abstract

Musical performance is thought to rely predominantly on event-based timing involving a clock-like neural process and an explicit internal representation of the time interval. Some aspects of musical performance may rely on emergent timing, which is established through the optimization of movement kinematics, and can be maintained without reference to any explicit representation of the time interval. We predicted that musical training would have its largest effect on event-based timing, supporting the dissociability of these timing processes, and the dominance of event-based timing in musical performance. We compared 22 musicians and 17 non-musicians on the prototypical event-based timing task of finger tapping and on the typically emergently timed task of circle drawing. For each task, participants first responded in synchrony with a metronome (paced phase) and then responded at the same rate without the metronome (unpaced phase). Analyses of the unpaced phase revealed that non-musicians were more variable in their inter-response intervals for finger tapping compared to circle drawing. Musicians did not differ between the two tasks. Between groups, non-musicians were more variable than musicians for tapping but not for drawing. We were able to show that the differences were due to less timer variability in musicians on the tapping task. Correlational analyses of movement jerk and inter-response interval variability revealed a negative association for tapping and a positive association for drawing in non-musicians only. These results suggest that musical training affects temporal

variability in tapping but not drawing. Additionally, musicians and non-musicians may be employing different movement strategies to maintain accurate timing in the two tasks. These findings add to our understanding of how musical training affects timing and support the dissociability of event-based and emergent timing modes.

3.2 Introduction

The production of accurately and precisely timed movement is a key aspect of many activities. Many forms of musical performance, such as drumming in a jazz ensemble, are characterized by mostly discrete movements with explicit start and stop events. This kind of behavior is thought to generally rely on event-based timing, which involves a clock-like neural process and an explicit internal representation of the time interval (Wing & Kristofferson, 1973). In contrast, other activities, such as the laboratory task of repetitive, continuous circle drawing, are characterized by smoothly produced movement and are thought to normally engage emergent timing in which timing can be maintained without reference to any explicit representation of the time interval (Robertson et al., 1999; Turvey, 1977). It has been proposed that event-based and emergent timing are dissociable systems, both cognitively (Delignière & Torre, 2011; Zelaznik & Rosenbaum, 2010; Zelaznik, Spencer, & Ivry, 2002) and neurophysiologically (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). However, the circumstances under which a given timing mode is engaged are less clear, with recent studies showing that tasks typically thought to use event-based timing can exhibit emergent timing behaviour and vice versa (Delignière & Torre, 2011; Studenka & Zelaznik, 2008; Zelaznik & Rosenbaum, 2010). Musicians are known to excel at event-based timing tasks (Bailey & Penhune, 2012; Collier & Ogden, 2004; Franěk, Mates, Radil, Beck, & Pöppel, 1991; Repp, 2005, 2010; Repp & Doggett, 2007) but, to the best of our knowledge, musicians and non-musicians have never been compared on both event-based and emergent timing tasks. It may be the case that some musical performance, such as the movement involved in controlling a violin bow, involves emergent timing and, therefore, the skills gained by musicians via years of practicing timing tasks may improve both event and emergent timing. In the present study, we compared musicians and non-musicians on finger tapping and circle drawing, the prototypical event-based and emergent timing tasks respectively. We predicted that musical training would have its largest effect on event-based timing behaviour, supporting the dissociability of these timing processes and the dominance of event-based timing in musical performance, and informing us as to the limits of transferability of musical skill.

The experimental paradigm most often used to study event-based timing is the finger-tapping task (for review, see Repp, 2005). Participants first tap in synchrony with an auditory metronome (paced phase); when the metronome stops, they are asked to continue tapping at the same rate (unpaced phase). Wing and Kristofferson (1973) proposed the classic model of event-based timing for the unpaced phase of the task, in which participants presumably rely on an internal timing process in the absence of external cues. The model assumes a central stochastic timer operating independently of the motor response and partitions the variability of the inter-response interval (IRI) into timer and motor sources. Timer variability increases linearly with mean IRI while motor variability is independent of the IRI (Wing, 2002). It has also been shown that lesions to lateral cerebellar regions increase timer but not motor variability, while medial cerebellar lesions have the converse effect (Ivry, Keele, & Diener, 1988). Overall, there is extensive empirical support for the independence of timer and motor processes in the Wing-Kristofferson model (for full review see Wing, 2002).

The effects of musical expertise on event-based timing have been well studied. Musicians exhibit greater accuracy and less variability in both the paced and unpaced phases of the tapping task compared to non-musicians (Franek, et al., 1991; Repp, 2005, 2010; Repp and Doggett, 2007). Collier and Ogden (2004) developed an extension to the Wing-Kristofferson model that accounts for clock drift and showed that musical experience is related to lower motor variance, clock variance and clock drift.

In contrast to event-based finger tapping, the task that has most commonly been used to investigate emergent timing is continuous circle drawing. In the paced phase of this task, participants continuously trace a circle in time with a metronome such that on each cycle, the drawing instrument must pass through an anchor point in synchrony with the metronome. In the unpaced Phase, participants keep drawing at the same rate but without a metronome. Evidence for a separate "emergent timing" system based on circle-drawing results was first put forward by Robertson et al. (1999), who showed that intra-individual variability of timing on a tapping task was unrelated to timing variability on the circle drawing task. These results indicated that tapping and circle drawing engaged different timing processes, and it was suggested that the class of movement, discrete or smoothly produced, determined which process was engaged.

In emergent timing, the target interval has no explicit internal representation. Instead, timing is thought to emerge from the kinematics of the required movements (Robertson et al., 1999; Turvey, 1977). For example, in the case of continuous circle drawing, a kinematic profile will be established after the first iterations. This may be manifested by minimal cycle-to-cycle variability in acceleration, or some other kinematic parameter, and will presumably also be evident in the establishment of patterns of physiological measures such as muscle activation in the drawing hand. Timing, which begins as a constraint for the optimization of kinematics, becomes an epiphenomenon or an emergent property of the kinematics once optimization is achieved.

Continuous circle drawing performance has been shown to be similar to finger tapping performance for the initial few cycles only, presumably when kinematic parameters are still being stabilized (Zelaznik et al., 2005). It has also been shown that the temporal variability of intermittent circle drawing is related to that of tapping but not to that of continuous circle drawing, suggesting that differences in timing performance are not due to differences in task complexity (Zelaznik et al., 2002). Furthermore, cerebellar lesions disrupted timing in finger tapping, but not circle drawing (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). An fMRI study of discrete versus smoothly produced air tapping found that the cerebellum was not involved in smoothly produced tapping (Spencer, Verstynen, Brett, & Ivry, 2007). In sum, since the Robertson et al. (1999) studies, a number of other studies have consistently supported the idea of emergent timing as a distinct mode of timing.

The specific conditions under which an individual will use event-based or emergent timing are largely unclear. Until recently, it was thought that the style of movement (discrete, with distinct start and stop landmarks, or smoothly produced) determined which timing process (event-based or emergent) was engaged (Zelaznik et al., 2002), but there is some evidence that the presence of a regularly occurring sensory event may engage event-based timing even for tasks performed with smoothly produced movement (Studenka & Zelaznik, 2011; Studenka, Zelaznik & Balasubramaniam, 2012; Zelaznik & Rosenbaum, 2010). For example, hearing an auditory tone after completing a cycle of circle drawing can "eventize" timing behavior (Zelaznik & Rosenbaum, 2010). Delignière and Torre (2011) demonstrated that, while the two modes of timing are mutually exclusive in the performance of a task, individuals may alternate between event-based and emergent timing on the same task. It has been suggested that rate (Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008), learning, and practice, including experience with a given mode of timing, (Studenka & Zelaznik, 2008; Studenka et al., 2012) could play roles in determining which mode of timing is used.

In sum, previous research supports the existence of two separable and mutually exclusive timing modes but the conditions under which a specific mode is engaged are not clear. We know that musicians perform better than non-musicians on the event-based finger-tapping task and that musical training focuses largely on discrete movements, although smoothly produced movement may be a component of training depending on instrument type. To the best of our knowledge, musicians have not been compared to non-musicians on both discrete and continuous tasks. In the present experiment, we hypothesized that if event-based and emergent timing modes are dissociable, then musical training should be predominantly associated with superior temporal control in finger tapping. If musicians also perform better than non-musicians on circle drawing, this would suggest that either the two modalities are less separable than previously thought, or that musical training affects both event-based and emergent timing. To test this, we assessed performance on these tasks by measuring variability in the temporal domain, the smoothness of movement in the spatial domain and the relationship between the two.

3.3 Material and Methods

3.3.1 Participants

Twenty-two musicians (seven males) and 17 non-musicians (four males) were recruited through the departments of Psychology and Music of local universities in Montréal, Québec, as well as in between late night sets at various local jazz clubs. The age of musicians ($M = 23$ years, range = 18 to 33 years) and non-musicians ($M = 22.2$ years, range = 19 to 31 years) did not differ significantly ($t(37) = -.657, p > .05$). Psychology undergraduate students were compensated with a one per cent credit applicable to a course grade. All other participants received 15 dollars. The Concordia University Human Research Ethics Committee approved the study, and all participants gave informed consent. Participants were debriefed about the goals of the experiment following their testing.

Non-musicians had minimal musical training (*M* = 2.2 years, *SD* = 1.6) and none were currently practicing. Musicians played a range of instruments, including guitar, piano and violin, were all currently practicing and had at least 6 years of musical training (*M* = 13.9 years, *SD* = 4.3). All participants were strongly right-handed (*M* = 9.59, *SD* = 0.67 for musicians and *M* = 9.71, *SD* = 0.47 for non-musicians), as evaluated using the Edinburgh Handedness Inventory (Oldfield, 1971). Data from two additional non-musician participants were excluded based on poor performance of more than three standard deviations from the mean paced or unpaced IRI.

3.3.2 Apparatus

Motion was recorded with the Visualeyez VZ3000 3D motion tracking system, manufactured by Phoenix Technologies. The markers consist of infrared light emitting diodes (LED), each mounted on hard round plastic casing of 0.5 cm diameter and attached by thin copper wire to a central controller. For the finger-tapping task, a single marker was affixed with Velcro tape to the nail of the right index finger. For the circle-drawing task, three markers were attached with Velcro tape to the surface of a pen of diameter 1.1 cm. The pen had a rounded plastic tip that participants used to trace circles. The LED wires had sufficient slack to allow for complete freedom of movement. Infrared-sensitive cameras tracked the position of the markers in three-dimensional space at a sampling rate of 200 Hz and to a spatial resolution of 0.015 mm. A National Instruments 6221 Data Acquisition board was used to synchronize the Visualeyez system with a computer-generated 1 KHz 20 ms metronome tone. Participants heard the metronome tone through a pair of Sony MDR-7506 headphones. Each participant was seated on a chair with independently adjustable seat and armrest heights.

Participants tapped and drew on a table of height 70.0 cm. For the circle drawing task, they traced a circle (7.0 cm diameter, 0.5 cm line thickness) printed in black on a white sheet of paper covered in a clear plastic sleeve affixed securely to the tabletop. A smaller (1.0 cm diameter) circle was printed on the larger circle's perimeter at the twelve o'clock position and served as the spatial target which participants were instructed to move the pen through in synchrony with the metronome.

3.3.3 Stimuli, Task, Conditions and Procedure

Participants tapped and drew at four different rates (400, 550, 700, and 850 ms) for a total of eight different conditions, the order of which was counterbalanced across participants such that tapping and drawing conditions were intermixed as determined by a Latin Square design. We tested across a range of metronome rates to assess the rate of change in IRI variability as a function of interval duration. The fastest rate at which both musician and non-musician participants could perform both tasks was determined by pilot testing. The slowest rate was set well below the limit of 1800 ms beyond which sensorimotor synchronization breaks down (Repp, 2005). Each condition consisted of six trials of 30 cycles of tapping or drawing paced by an auditory metronome. This was followed by sufficient time to complete 30 cycles of unpaced tapping or drawing, assuming that a participant stayed reasonably close to the target rate. A final 1 KHz 20 ms tone indicated the end of each trial. All trials of a condition were performed one after another with a rest period of 30 seconds in between each trial.

For the tapping task, participants were told to tap their right index finger in synchrony with the metronome and use their full range of motion, without moving any other part of their body. They were then told that once the metronome stopped they should continue tapping at the same pace until hearing the final tone. For the circle drawing task, participants were instructed to hold the pen in their right hand and trace the 7.0 cm circle template in the counter clockwise direction without stopping and such that the pen passed over the smaller 1.0 cm circle on the beat of the metronome. Identically to the tapping task, they were instructed to keep tracing at the same rate after the metronome stopped. At the beginning of the session, single practice trials of tapping and of circle drawing at 425 ms (a pace not used during the real test session) were administered to familiarize participants with the task.

Participants were also administered the Musical Experience Questionnaire (Bailey & Penhune, 2010) to assess age of initiation of musical training, years of musical training and hours of current practice. They were also given the Digit Symbol subtest of the Wechsler Adult Intelligence Scale-III (Wechsler, 1997) in order to evaluate processing speed and visuomotor coordination (Joy, Fein, & Kaplan, 2003; Kaplan, Fein, Morris, & Delis, 1991). Finally, they were given the Grooved Pegboard test (Lafayette Instrument Company) of fine motor control (Mathews & Klove, 1964). A testing session lasted approximately two hours.

3.3.4 Data analysis

3.3.4.1 Preprocessing

All temporal and kinematic measures were derived from the motion capture data synchronized with the digital metronome data. The data were analyzed using custom software written in Matlab (release R2007b, The MathWorks). The motion capture system permitted us to arbitrarily set a local coordinate reference frame and we did so using the tabletop as the xy-plane. This allowed us to examine the z-coordinate for finger height in tapping and the x and y coordinates for drawing.

To automatically detect cycle end points for tapping, we first filtered the motion capture data using a forward and reverse second-order low pass Butterworth filter with a cutoff set at 50Hz. The reverse filter compensated for any time shifts that might have been introduced by the forward filter. A high cut-off value allowed us to filter out noise inherent in the motion capture signal without removing the natural jitter of finger motion. Next, all local maxima, corresponding to the peak finger position for each cycle, were identified through an iterative search method. The acceleration curve was then calculated from the position curve and, next, the points of maximum acceleration between successive peaks were identified. These local maxima on the acceleration curve were prominent in all data, despite individual variations in tapping style, and they corresponded closely to the points at which the finger hit the tabletop because of the rapid change in velocity. In a final step, each point on the position curve that corresponded to a local acceleration maximum was automatically adjusted so that it coincided with the closest local minimum on the position curve. Thus, each identified tapping point closely coincided with the point of initial finger compression on the tabletop.

Circle drawing data was filtered using a forward and reverse second-order low pass Butterworth filter with a cutoff set at 7Hz (Roithner, Schameder, & Meuller, 2000) in order to more easily detect cycle end points (the 12 o'clock position) in smoothed data. The trajectory data were then linearly transformed such that the origin of the coordinate reference frame was translated to the centre of the circle template. Then all points in the trajectory where the x coordinate changed sign from positive to negative (negative zero crossings) were identified as the cycle end points, where the pen crossed the anchor point at the top of the circle. To be considered valid crossings, the pen had to be on the table as indicated by the z-coordinate.

Once all tapping and drawing cycle end points were identified, further analysis focused on the unpaced phases of tapping and drawing. The IRIs were calculated as the duration in time between adjacent points. For this and for all other measures, the first 2 cycles of the unpaced phase of a trial were not used in the analysis (Zelaznik & Rosenbaum, 2010). Trials with fewer than 20 consecutive successfully identified cycle end points were excluded from analysis. We excluded 0.76 % and 0.98% of tapping sequences for musicians and non-musicians, respectively. In the case of circle drawing, 4.17 % of musicians' sequences and 3.68% of non-musicians' sequences were excluded. Amongst those sequences included in the analysis, the average sequence lengths for tapping (26.7 for musicians; 27.4 for non-musicians) and circle drawing (26.6 for musicians; 26.7 for non-musicians) were close to the maximum possible length, indicating that the detection algorithm successfully identified most taps and draws.

3.3.4.2 Basic performance measures

The coefficient of variation (standard deviation divided by the mean) was calculated for the unpaced IRIs of each trial. The average coefficient of variation was then calculated across all trials of a condition for a given individual. This measure provides an overall view of the combination of all sources of IRI variability, including long-term drift away from the target tempo and motor, as well as timer, variability. To better isolate timer variability, we next removed linear drift from the time series of responses for each trial and examined the remaining variance. We carried out mixed-type ANOVA analyses for all dependent variables, using musical training as the between-groups variable and task and rate as within-subjects variables. We used the Bonferroni correction for multiple comparisons.

3.3.4.3 Analysis of timing modes and kinematics

To further analyze the IRI variability, we employed slope analysis (Ivry & Hazeltine, 1995). It can be shown that by plotting the variance against the square of the interval duration, the slope of the resulting line gives an estimate of the variance that is related to timing and the intercept is related to variability independent of interval duration, such as that stemming from execution of the motor response. Therefore, if two tasks share a common timing process, then the slopes related to each task should be equal, or at least correlated, within individuals. Equality of slopes is a necessary but not a sufficient condition for commonality of timing processes across tasks. However, if tapping and drawing slopes are unequal or, at the very least, uncorrelated, and if musical expertise affects only tapping slopes but not drawing slopes, this would be strong evidence in support of distinct timing processes. We used t-tests to assess the significance of slope correlations.

Another approach to demonstrating that tapping and drawing are associated with distinct timing processes is to determine whether or not task performance adheres to the Wing-Kristofferson open-loop model of event-based timing (Wing & Kristofferson, 1973), which partitions the response variability into two independent components: central (clock) and peripheral (motor). It follows from their model that the lag one covariances of the time series of responses will be negative (Zelaznik & Rosenbaum, 2010). In contrast, emergent timing is associated with a non-negative lag one covariance (Delignière & Torre, 2011). Therefore, the lag one covariance offers a means of verifying the kind of timing mode used in the execution of a task. To that end, we calculated the lag one covariance for the detrended IRI time series (Zelaznik & Rosenbaum, 2010).

We also examined the kinematic data with the goal of measuring the smoothness of movement. The more continuous motion is, the smoother we would expect it to be and a common measure of smoothness is mean squared jerk (Flash & Hogan, 1985). Mean squared jerk calculations were extracted from the motion capture data filtered at 50Hz – the original circle data were re-filtered at this threshold. The normalized mean squared jerk was calculated per cycle by taking half the integral of squared jerk and multiplying this by a normalizing factor of duration to the fifth power divided by distance squared (Teulings, Contreras-Vidal, Stelmach, & Adler, 1997). The square root of this value was used as the per-cycle normalized mean squared jerk. The average normalized mean squared jerk for a single trial was calculated from the per-cycle values.

3.4 Results

3.4.1 Cognitive measures

On the Digit Symbol test, musicians (*M* = 101.2; *SD* = 14.0) scored significantly higher than non-musicians (*M* = 92.1; *SD* = 10.1), *t*(37) = -2.260, $p < .05$. Musicians were also faster (*M* = 53.9 s; *SD* = 4.3) than non-musicians (*M* = 59.0 s; *SD* = 9.0) when using their dominant (right) hand to complete the Grooved Pegboard test, *t*(37) = 2.377, $p < .05$. These results suggest that the sample of musicians possessed superior fine motor control compared to the sample of non-musicians.

3.4.2 Temporal measures

To determine if participants were able to carry out both tasks, we measured the mean IRI of the paced and unpaced phases separately for all conditions (Table 3.1). Mean IRI values were close to the target interval durations for both paced and unpaced phases, indicating that both groups of participants were generally able to produce accurately timed movements with and without the aid of a metronome. A 2 (musical training) x 2 (phase) x 2 (task) x 4 (rate) repeated measures ANOVA of mean IRI revealed an interaction of phase and task (*F*(1,37) = 11.882, $p < .01$) such that participants generally had shorter paced IRIs for drawing compared to tapping ($p < .05$). Furthermore, participants' mean IRIs for tapping were shorter in the unpaced compared to paced phases ($p < .05$). However, there was no main effect of musical training nor were there any significant interactions involving musical training. In sum, there were no differences in the mean IRI of either the paced or unpaced phases that were related to musical training.

As a first step in assessing variability of performance in the unpaced phase, we compared the coefficient of variation of the IRI for musicians and non-musicians across tasks and rates using a 2 (musical training) x 2 (task) x 4 (rate) repeated measures ANOVA (Figure 3.1). There was a significant interaction between task and musical expertise ($F(1,37) = 10.207$, $p < .05$; *partial* $\eta^2 = .216$) such that non-musicians were significantly more variable in tapping compared to musicians ($p < .01$) but the two groups did not differ in drawing ($p = .454$). Furthermore, while non-musicians were more variable in tapping than in drawing ($p < .01$), musicians did not differ on these tasks ($p = .587$).

To better isolate timer variability we analyzed the variance of the unpaced IRI sequences after linear detrending. Musicians were less variable than non-musicians overall, $F(1, 37) = 8.691$, $p < .01$, *partial* $\eta^2 = .190$. For both groups, variability increased with interval duration , $F(3,111) =88.32$, $p < .01$; *partial* $\eta^2 = .705$, consistent with previous studies (Robertson et al., 1999). Consistent with the analysis of the coefficient of variation, there was an interaction between task and musical expertise, $F(1,37) =7.325$, $p < .05$; *partial* $\eta^2 = .165$. Pairwise comparisons showed that musicians were less variable than non-musicians for tapping ($p < .01$) but not for drawing ($p = .425$). Furthermore, while non-musicians were more variable in tapping than in drawing ($p < .01$), musicians did not differ between these two tasks ($p = .421$). Taken together, the results of both the coefficient of variation and the detrended variance analyses suggest that musical training is associated with greater regularity of unpaced tapping but has no effect on unpaced drawing.

It may be the case that the observed differences in variability are due to better motor control by musicians in the tapping task, but that underlying timing processes are unaffected by expertise. To test this possibility, we used slope analysis to partition the IRI variability into timer-related and non-timer-related (e.g., motor) components (Ivry & Hazeltine, 1995; Robertson et al., 1999). Timer variability is expected to increase with IRI, resulting in positive slope values across rates (Robertson et al., 1999). A 2 (group) by 2 (task) repeated measures ANOVA for the slope values showed a marginally significant interaction between task and musical training ($F(1,37) = 3.940$, $p = .055$, *partial* $\eta^2 = .096$). Pairwise comparisons showed that musicians had significantly smaller slopes than non-musicians for tapping ($M = 0.00124$ and 0.00236 respectively; $p < .05$; see Figures 3.2 and 3.3) but there were no differences between groups for drawing ($M = 0.00167$ and 0.00179 respectively; $p = .75$). Within groups, there were no statistically significant differences between tasks. For both musicians and non-musicians, tapping and drawing slopes were not correlated, suggesting that these tasks were using unrelated timing processes (Ivry & Hazeltine, 1995). Overall, these results further suggest that musical training only affected timing for the tapping task.

To further investigate the timing processes used by each group on the tapping and drawing tasks, we examined whether performance on each task adhered to the Wing-Kristofferson (1973) event-based model of timing. The Wing-Kristofferson model predicts significantly negative lag one covariance for tapping (Wing & Kristofferson, 1973; Zelaznik & Rosenbaum, 2010). In contrast, emergent timing is characterized by non-negative lag one covariance (Delignière & Torre, 2011). A series of one-sample t-tests were carried out on individual lag values with a significance level set at .01 to correct for multiple comparisons (Zelaznik & Rosenbaum, 2010). They revealed that most lag one covariances were negative (Figure 3.4), with the exception of musicians tapping at 850 ms ($p < .05$) and non-musicians drawing at 700 and 850 ms ($p = .486$ and .131 respectively). Overall these results suggest that musicians were largely using event-based timing for tapping and drawing while non-musicians were engaging event-based timing processes for tapping and emergent timing processes for drawing.

3.4.3 Kinematic measures

To analyze smoothness of movement, we compared the average normalized mean squared jerk per cycle between groups for a given task (Zelaznik & Rosenbaum, 2010). For tapping, we examined mean squared jerk of the z coordinate of movement and for circle drawing, we analyzed mean squared jerk in the x (6 o'clock to 12 o'clock) direction. A 2 (musical training) x 2 (task) x 4 (rate) repeated measures ANOVA showed a main effect of task ($F(1, 111) = 272.311$, $p < .001$, *partial* $\eta^2 = .880$) such that tapping is significantly less smooth than circle drawing (Figure 3.5). There was a main effect of rate ($F(3, 111) = 244.019$, $p < .001$) but no effect of musical training ($p = .640$) or interaction between musical training and either task ($p = .498$) or rate ($p = .966$). In sum, tapping was significantly jerkier than circle drawing and musicians and non-musicians did not differ in their movement smoothness for either task.

We examined the relationship between an individual's movement kinematics and their timing variability by analyzing the bivariate correlations between mean squared jerk and detrended IRI variance (Table 3.2). It has been suggested that jerkiness aids timing in a tapping task (Balasubramaniam, Wing, & Daffertshofer, 2004). Therefore we expected to find negative correlations between jerkiness and IRI variability for tapping. In the case of circle drawing, given that timing emerges from movement once kinematic parameters are stabilized, it seemed reasonable to expect that the less jerky movement becomes, the less variable timing would be. Musicians exhibited no significant correlations between jerkiness and IRI variability for either task. However, non-musicians displayed significant or marginally significant negative correlations at the three slowest tapping rates, suggesting that jerkier movement is associated with decreased IRI variability in tapping. On the other hand, when it came to drawing, non-musicians had significant positive correlations between jerk and IRI variability at most rates. The same pattern of correlations was found for the drawing conditions when basing the jerk calculations on either the X or Y coordinate of movement. To sum up, musicians unexpectedly showed no relationship between jerk and IRI variability, while non-musicians showed a negative association for tapping and a positive association for drawing.

3.5 Discussion

The main purpose of this study was to test the dissociability of event-based and emergent timing mechanisms in trained musicians. We know that musicians excel at tasks that typically engage event-based timing, such that musical training has been associated with greater temporal accuracy and precision in rhythmic tapping tasks (Bailey & Penhune, 2012; Franěk et al.,1991; Repp, 2010). We therefore reasoned that if the two modes of timing are dissociable, then expertise in predominantly event-based timing would not affect performance on tasks associated with emergent timing. We investigated this by examining both temporal and kinematic measures of performance for finger tapping and circle drawing.

Consistent with our hypothesis that event-based and emergent timing are dissociable, we found that musical training affects temporal variability in tapping but not drawing. This result is borne out across three different measures. When we examined the coefficient of variation of the IRI, the detrended IRI variance, and the variance related exclusively to timing as estimated from a slope analysis, we consistently found that musicians were less variable than non-musicians in tapping but did not differ in drawing. This set of results suggests that the effects of musical training do not transfer to continuous circle drawing and lends support to the hypothesis that event-based and emergent timing are dissociable processes.

Another piece of evidence supporting the dissociability of the two timekeeping processes is that the sign of the relationship between movement jerk and timing variability appears to be a function of task, but only for non-musicians. It has been suggested that greater jerk may result in a greater volume of proprioceptive information which may aid in maintaining the regularity of movement in an event-based task (Balasubramaniam et al., 2004). In our analysis, the control group of non-musicians generally showed a negative correlation between jerk and IRI variance for tapping, as expected. However, musicians did not show any relationship between movement jerk and IRI variance for either task. It may be that the event-based timing of musicians is precise and accurate enough that the additional information garnered from jerky movement is not needed to successfully perform event-based timing tasks. Indeed, our slope analysis of tapping showed that the timer-related variance of musicians was only 52% of that of non-musicians. Thus, the difference between musicians and non-musicians in how timing related to movement in tapping could be explained by the more precise timekeeping of musicians.

In a repetitive, smoothly produced movement task that uses emergent timing, less jerk indicates more regular movement which should lead to less variability in timing if timing emerges from movement kinematics. Once again, musicians did not show any relationship between jerk and IRI variance but non-musicians generally showed the expected positive correlation for drawing. Although musicians were not better than non-musicians at the drawing task, our results indicate that musicians did not rely on a kinematic strategy, similar to their results for tapping. In sum, musical training was associated with a decoupling of movement jerk and IRI variability for both tasks. These group differences for tapping and drawing suggest that any relationships that may exist between kinematics and timing are malleable through experience and not a requirement of the timing system.

The analyses of IRI variability discussed so far help to determine if timing modes are the same or different across tasks. The lag one covariance of the IRI can help us to identify which mode of timing is being used in a given task. Lag one covariances are predicted to be negative for event-based timing and nonnegative for emergent timing (Delignière & Torre, 2011; Wing & Kristofferson, 1973; Zelaznik & Rosenbaum, 2010). In the present study, analysis of the lag one covariances revealed additional differences in how musicians and non-musicians executed both tasks. Lag one covariances were almost uniformly negative for musicians across both tasks, suggesting that they were using event-based timing for tapping and drawing. This result is inconsistent with the results of the slope analysis for musicians, which did not yield any significant correlation between slopes for these two tasks, implying the use of different timing modes in the two tasks. Non-musicians exhibited lag one covariances that were negative for tapping and nonnegative for drawing at the two slowest rates. This pattern of results is closer to the expected patterns for event-based tapping and emergent drawing.

What could account for the inconsistency between musicians' lag one IRI covariances and their IRI variance slopes? Using lag one covariances to identify the mode of timing comes with a risk of misidentifying event-based timing as emergent (Lemoine & Delignière, 2009). This caveat may not apply to the present study, for which a misidentification of emergent timing as event-based seems the more likely scenario. Another possible explanation is that a relationship between tapping and drawing slopes for musicians is being suppressed by some other factor. For musicians with greater than the median amount of 13.5 years of experience there was a marginally significant correlation between tapping and drawing slopes ($r(9) = .570$, $p = .067$, $r^2=.325$). We speculate that the most experienced musicians in our study may have been using event-based timing for circle drawing but additional experiments with a larger sample size and a more uniform distribution of years of musical training are needed to resolve this issue.

If a subset of our musician group did use event-based timing on the drawing task, then it would be consistent with recent studies that show that priming effects may play a role in the use of event-based timing when emergent timing would normally be used. When intermixing tapping and drawing conditions in a fixed order for all participants, unexpected significant correlations of the IRI coefficient of variation have been observed between the final circle drawing condition that was expected to exhibit emergent timing and previous conditions that were event-like (Studenka et al., 2012; Zelaznik & Rosenbaum, 2010). It has been suggested that the previous event-timed conditions in the fixed ordering led to a practice effect that primed participants to use event-based timing on the final condition that might otherwise have shown the signature of emergent timing (Studenka et al., 2012). Similarly, in the present study, the event-based timing that at least some musicians may be using for circle drawing could be the result of years of extensive musical training -- long-term practice effects that primed participants to use event-based timing.

In general, a target for future study is the identification of the aspects of musical training that are responsible for the relationships observed in the present study. Intensity of musical practice, rather than total years of musical training, has been found to be associated with superior ability to improve tactile discrimination in the index fingers of pianists (Ragert, Schmidt, Altenmüller, & Dinse, 2004). In a comparison of percussionists, pianists, singers, and non-musicians, the type of musical instrument was found to affect timing variability such that drummers were the least variable (Krause, Pollok, & Schnitzler, 2010). In the present study, we did not have a sufficiently large sample size to address these issues. These or other parameters of musical experience, such as the age of onset of training (Bailey & Penhune, 2012) could be contributing to the results of the present study and could become the focus of future studies.

Our study is novel for its comparison of musicians and non-musicians on event-based and emergent timing tasks. Most importantly, our results add to the body of research supporting the dissociability of event-based and emergent timing. Our results also suggest that the effects of musical training on timer variability may be limited to the kinds of tasks and modes of timing used in musical performance. They also demonstrate that the relationship between movement and timing may depend on experience. Further investigation is needed to identify the aspects of musical training that contribute to these differences between musicians and non-musicians.

Table 3.1. Mean Inter-response Intervals of the paced and unpaced phases.

	Prescribed interval duration							
	400 ms		550 ms		700 ms		850 ms	
	Paced	Unpaced	Paced	Unpaced	Paced	Unpaced	Paced	Unpaced
Musicians								
Tapping	400.06 (0.93)	401.79 (10.06)	549.95 (1.10)	550.47 (14.23)	699.85 (0.95)	689.74 (16.00)	847.34 (10.82)	844.97 (34.53)
Drawing	395.53 (13.63)	407.16 (12.82)	538.04 (16.31)	544.17 (19.20)	687.30 (9.82)	686.48 (19.88)	836.70 (16.31)	837.09 (34.68)
Non-musicians								
Tapping	395.31 (12.09)	390.54 (22.55)	548.52 (3.86)	539.68 (22.41)	697.96 (2.68)	675.18 (34.88)	846.61 (5.02)	827.05 (51.72)
Drawing	396.53 (20.96)	408.16 (25.20)	541.3 (23.63)	546.95 (28.38)	684.28 (43.51)	679.22 (56.36)	841.52 (36.58)	837.74 (41.47)

Note. All values in milliseconds. Standard deviations in parentheses.

Table 3.2. Correlations between normalized mean squared jerk (Z-coordinate for tapping; X coordinate for drawing) and detrended IRI variance.

	Prescribed interval duration							
	Tapping				Drawing			
	400 ms	550 ms	700 ms	850 ms	400 ms	550 ms	700 ms	850 ms
Musicians	-.217	-.345	.309	.022	-.003	-.266	-.299	-.006
Non-musicians	-.586*	-.461^{+}	-.456^{++}	-.310	.608*	.540*	.624*$^{+++}$	.103

Note. *p < .05. ^{+}p = .063. ^{++}p = .066. $^{+++}$after removing a single outlier.

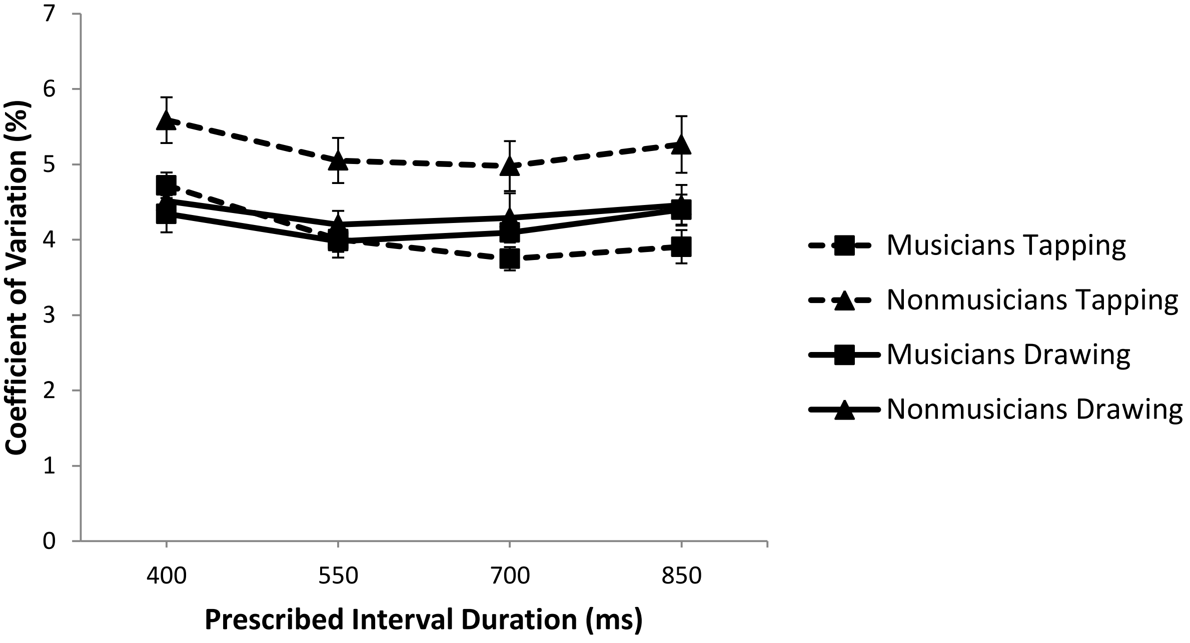

Figure 3.1. Coefficient of variation of the unpaced IRI, plotted against prescribed interval duration and with standard error bars.

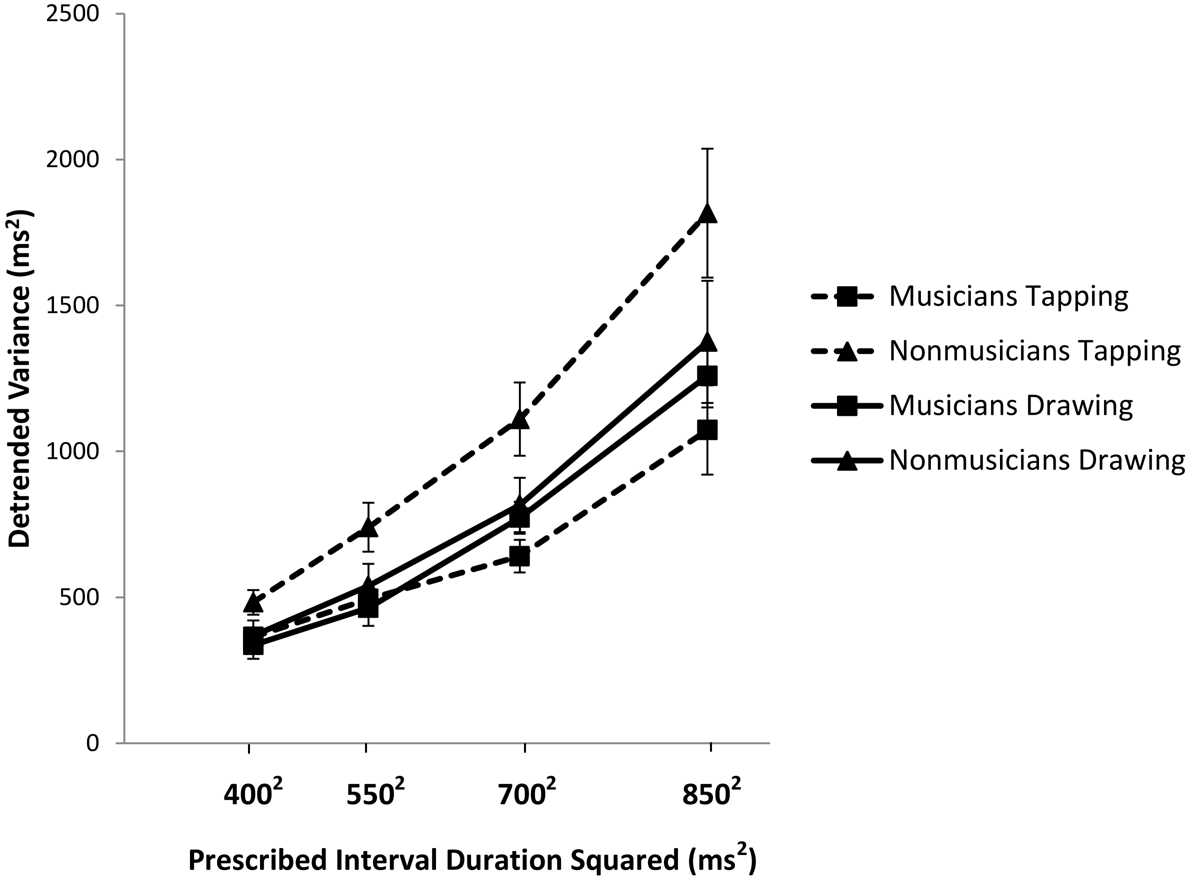

Figure 3.2. Detrended variance of the unpaced IRI plotted against the square of the prescribed interval duration and with standard error bars.

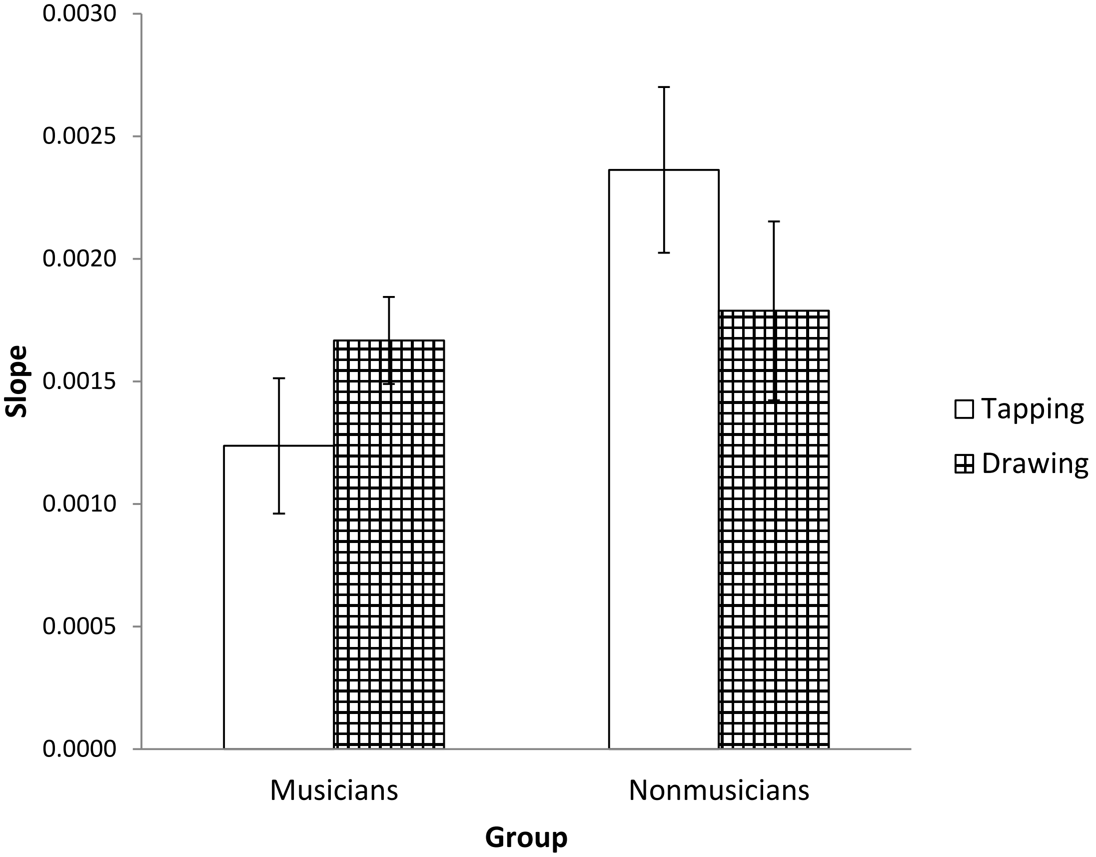

Figure 3.3. Average slopes of the lines formed from plotting unpaced IRI variance against the square of the prescribed interval duration. Standard error bars are shown.

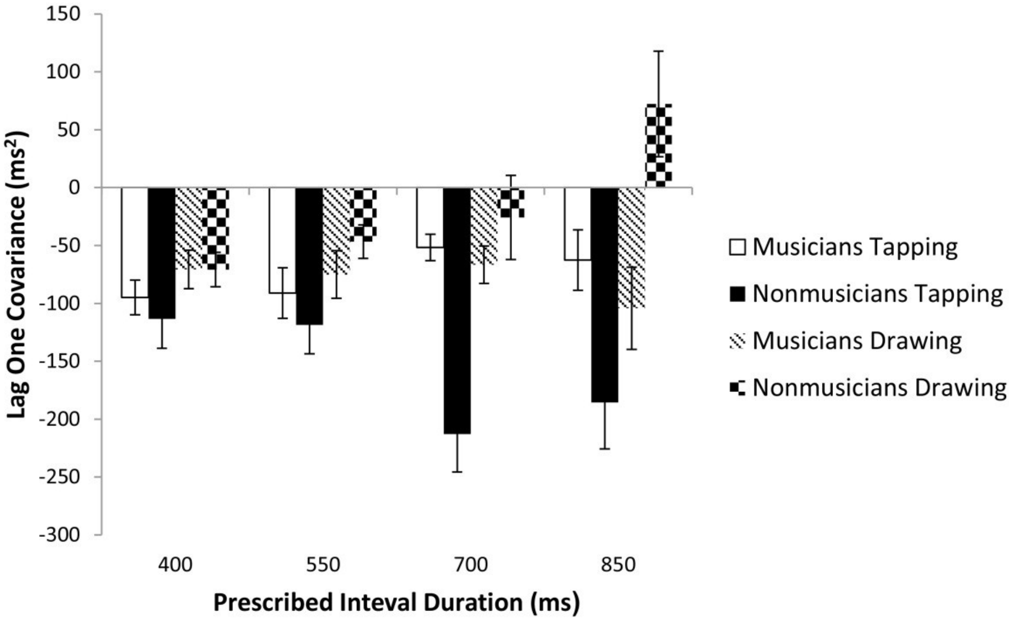

Figure 3.4. Lag one covariances of the IRI for the four prescribed interval durations. Standard error bars are shown.

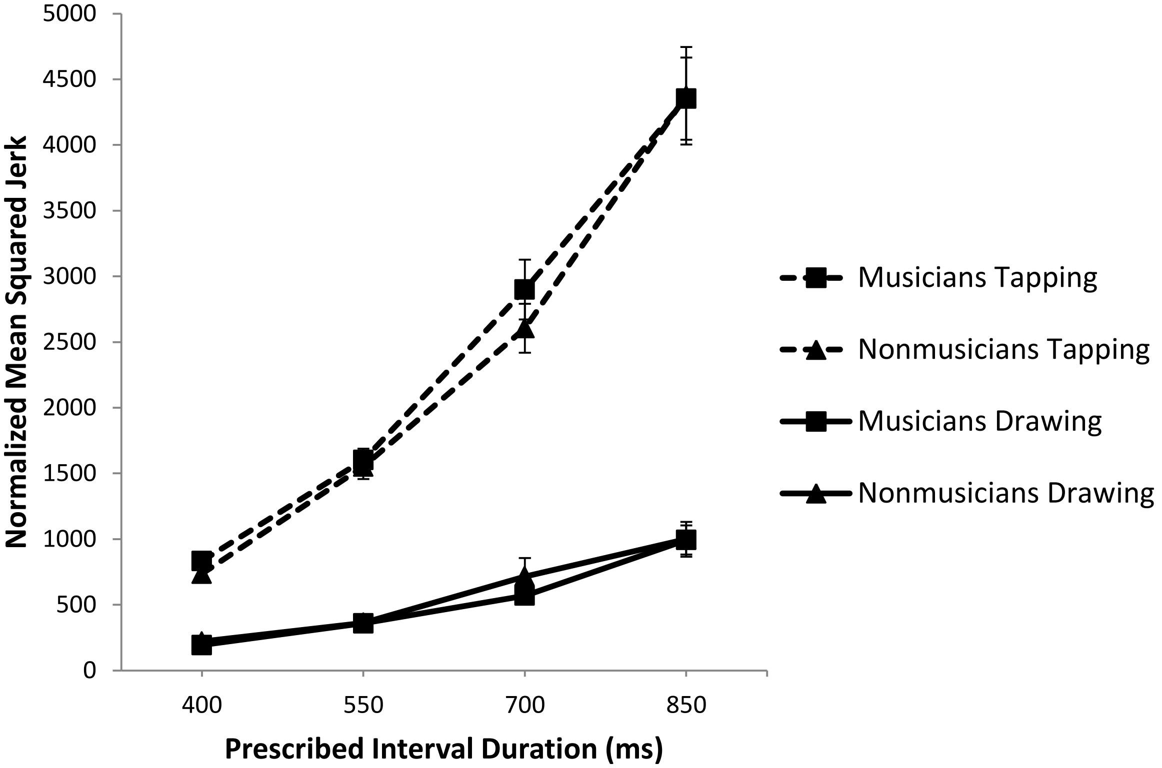

Figure 3.5. Normalized mean squared jerk plotted against prescribed interval duration and with standard error bars.

Chapter 4: Regional cerebellar volumes are related to early musical training and finger tapping performance

4.1 Abstract

The cerebellum has been associated with music-related tasks, including timing on the millisecond scale. Initiation of musical training during a sensitive period up to the age of seven years is associated with enhanced performance and significant brain differences compared to later trained musicians. In the present study, we examined the relationships between regional cerebellar volumes, musical experience, and timing performance and sought to establish whether or not a sensitive period for musical training affects the cerebellum. We collected MRI data from 38 musicians and 20 non-musicians, all right-handed adults, and compared volumes of cerebellar lobules previously identified as being involved in music-related tasks. A subset of 31 of these participants (20 musicians) also performed the classic task of finger tapping to an isochronous rhythm. We found that early-trained musicians had reduced volume in bilateral cerebellar white matter and right Lobules IV, V and VI, compared to late-trained musicians. Strikingly, better timing performance, greater musical experience and an earlier age of start of musical training were associated with smaller cerebellar volumes. Timing performance was specifically associated with smaller volumes of right lobule VI. Collectively, these findings support the sensitivity of the cerebellum to the age of initiation of musical training and suggest that Lobule VI plays a role in timing. Our results also add to a growing body of evidence indicating that training and expertise can be associated with smaller regional brain volumes.

4.2 Introduction

Musical performance relies on accurate timing and nuanced rhythm production as vital parts of its power to communicate. The neural correlates of these processes are thought to at least partially involve the cerebellum (E, Chen, Ho, & Desmond, 2012; Zatorre, Chen, & Penhune, 2007; Ivry, Keele, & Diener, 1988; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Koch et al., 2007) a brain region that has also been associated with plasticity related to musical training, observable when comparing the cerebellar volumes of musicians with those of non-musicians (e.g. Hutchinson, Lee, Gaab, & Schlaug, 2003). Musical-training related plasticity in other brain areas has been shown to be moderated by the age of initiation of musical training, with evidence pointing to a sensitive period before the age of seven years (Penhune, 2011). However, to the best of our knowledge, it is not known whether cerebellar lobular volumes or the timing processes associated with the cerebellum are affected by training during this sensitive period. In the present study, we used a novel magnetic resonance imaging (MRI) segmentation algorithm (Chakravarty et al., 2013) to calculate regional volumes within the cerebellum and then examined the associations between the volumes of specific cerebellar regions, musical training experience and timing data from a finger-tapping task in musicians and non-musicians. The goal of the study was to better understand the relationships between age of start of training, cerebellar volume and timing variability. In addition, we hoped to more precisely link timing variability with structure in specific cerebellar regions.

Previous work in our lab suggests there is a sensitive period for musical training, such that acquisition of musical skill before age seven is associated with long-lasting behavioural and structural brain differences. The differences between early- and late-trained adult musicians include superior performance in sensorimotor synchronization tasks (Bailey & Penhune, 2010;

Watanabe, Savion-Lemieux, & Penhune, 2007), greater connectivity in the region of the corpus callosum that links sensorimotor cortices of the two hemispheres (Steele, Bailey, Zatorre & Penhune, 2013), and greater grey matter density in the premotor cortex (Bailey et al., 2013). Both behavioral and brain differences are significant even after controlling for total years of musical experience. Overall, these results suggest that sensorimotor integration and timing may be sensitive to early training (Penhune, 2011).

Given the evidence linking the cerebellum to musical training and the hypothesized role for the cerebellum in timing and other music-related processes, it may be the case that cerebellar structure and function are also affected by early age of start. Musicians have been found to have larger cerebellar volumes than non-musicians and volume was correlated with lifelong intensity of practice (Hutchinson, Lee, Gaab, & Schlaug, 2003). In a study of mostly right-handed participants, musicians were found to have greater volume of right cerebellar white matter and right superior and middle cerebellar peduncles (Abdul-Kareem et al., 2011). Functionally, the cerebellum is likely involved in the perception and production of musical rhythm. A recent meta-analysis (E, Chen, Ho, & Desmond, 2012) identified two PET and five fMRI studies that used rhythm perception and production tasks. The musical rhythm tasks involved right Lobules IV and V and bilateral Lobules VI and VIIIA/B. Lobule V has also been associated with hand movement while lobules VIIIA/B have been linked to motor tasks (Stoodley & Schmahmann, 2009).

Substantial evidence also points to the cerebellum's involvement in timing on the millisecond scale. Event-based timing, a form of sub-second timing modeled as a central clock process operating independently of the motor response that is being timed (Wing & Kristofferson, 1973) likely underlies the time-based components of musical performance (Baer, Thibodeau, Gralnick, Li, & Penhune, 2013). It is typically evaluated using the finger-tapping task (Repp & Su, 2013; Repp, 2005), in which participants first tap in synchrony with an auditory metronome (paced phase); when the metronome stops, they are asked to continue tapping at the same rate (unpaced phase). Timing ability is measured by analyzing the time series of inter-response intervals (IRIs) of the unpaced phase, such that an IRI is defined by the time interval between adjacent taps. The tapping paradigm employed in the present study was also used in a recent study from our group that showed that musicians are substantially less variable in the timing of their unpaced responses compared to non-musicians (Baer et al., 2013). This is consistent with other studies that have demonstrated that musicians are less variable (Franěk, Mates, Radil, Beck, & Pöppel, 1991; Repp, 2010; Repp & Doggett, 2007), and show less drift away from the prescribed tapping rate compared to non-musicians (Collier & Ogden, 2004).

There is some debate about the precise localization of timing-related processes within the cerebellum. Timing has been shown to be disrupted by repetitive transcranial magnetic stimulation (TMS) of (Koch et al., 2007), and by lesions to, the lateral cerebellar hemispheres (Ivry, Keele, & Diener, 1988). However, a recent study that examined the relationship between finger tapping performance and cerebellar volume showed that the variability of tapping in the unpaced phase was negatively associated with volume of the vermis (Bernard & Seidler, 2013). At least one TMS study has also implicated the vermis in sub-second timing (Théoret, Haque, & Pascual-Leone, 2001). Thus, while overall evidence points to a role for the cerebellum in sub-second timing, it is less clear, from structural, lesion and TMS studies, which specific regions of the cerebellum are involved.

Functional neuroimaging studies of the cerebellum point to the involvement of lobule VI in timing. In a meta-analysis (E, Chen, Ho, & Desmond, 2012), nine fMRI studies related to timing were identified. The timing tasks were most likely to be associated with activity in right Lobule VI. Other functional studies related to timing that were not included in this meta-analysis include a PET study of paced finger tapping at a baseline interval of 1250 ms and ranging from 1000 – 1500 ms, which showed activation in bilateral Lobule VI that increased with the magnitude of perturbations in interval duration (Thaut et al., 2009). Lobule VI lies between the primary and superior posterior fissures (Schmahmann et al., 1999), in the superior-posterior lobe (Tiemeier et al., 2010). In relation to other classifications of cerebellar anatomy, Lobule VI has both vermal and hemispheric regions. Therefore, previous studies that have linked either vermal or lateral regions to timing may not necessarily be in conflict with each other but further clarification is needed.

To the best of our knowledge, volumetric differences between musicians and non-musicians have not been investigated at the level of individual lobules of the cerebellum, nor has the age of initiation of musical training been considered when investigating cerebellar volumes. In the present study, we analyzed finger tapping data and structural cerebellar imaging data from musicians and non-musicians. We examined the relationships of the volumes of cerebellar lobules with the age of start of musical training, years of training, and timing variability exhibited in the tapping task. We expected to find associations between musical training and the volumes of right Lobules IV and V and bilateral Lobules VI and VIII, in support of functional imaging studies that have implicated these regions in musical tasks. We also predicted that the volume of Lobule VI would be negatively associated with timing variability. Finally, we predicted that earlier age of start of musical training and greater number of years of musical training would be associated with smaller timer variability.

4.3 Materials and Methods

4.3.1 Participants

Fifty-eight participants were included in this study (thirty-eight musicians and twenty controls selected to have less than three years of musical training or experience). All had high-resolution T1 MRI scans as part of a larger study (Bailey, Zatorre & Penhune, 2013; Steele, Bailey, Zatorre, & Penhune, 2013). Thirty-one participants (twenty musicians) returned for behavioral testing on the finger-tapping task. Demographic and musical experience data for both sets of participants are presented in Table 4.1. All were right-handed, neurologically healthy, and gave informed written consent to participate. They were also administered the Musical Experience Questionnaire (Bailey & Penhune, 2010), from which we extracted the age at which they first began to play an instrument, and the total years of musical experience, including practice and formal training. The Concordia University Human Research Ethics Committee and the McGill University/Montreal Neurological Hospital and Institute Research Ethics Board approved the experimental protocol.

4.3.2 Image acquisition and processing.

Structural MRI scans were acquired using a Siemens Trio 3T MRI scanner with a 32-channel head coil (TR = 2300ms, TE = 2.98ms, voxel size = 1x1x1mm^3). All MRI processing was done on the General Purpose Cluster at the SciNet supercomputer centre. Total brain volume was estimated from the grey and white matter of the cerebrum and the cerebellum, calculated using parts of the CIVET pipeline (Ad-Dab'bagh et al., 2006). The cerebellum was segmented in native space using the method of multiple automatically generated templates of different brains

(MAGeT Brain; Chakravarty et al., 2013). The MAGeT algorithm is a multi-atlas label fusion technique that is ideal when confronted with the challenge of using a limited number of atlases as input for the segmentation of a dataset. The algorithm first matches a subset of the input images to a set of expertly labeled atlases. The newly labeled images are now referred to as "templates". The atlases, supplemented by this subset of segmented input, form the template library, where each template now has as many possible candidate labels as there are atlases. For example, in the present study, we used five atlases and randomly chose 20 input images for the template library (evenly split between male and female and between musician and non-musician, with the musicians evenly split between early- and late-trained). This generated a template library of 100 different segmentations. MAGeT then matches each input image to each of the templates, to generate all possible candidate segmentations for each input image. In a final step, the label of each voxel in an input image is determined by voxel voting, such that the most frequently occurring label amongst all the candidate segmentations becomes the final label. In the present study, the high-resolution atlases, produced from five healthy participants not part of our study (but previously described in Winterburn et al., 2013 for their use in the construction of a hippocampal atlas), were manually segmented based on the atlas of Schmahmann et al. (1999). We used the Schmahmann nomenclature to refer to subregions of the cerebellum, wherever possible. The deep cerebellar nuclei were included in the volumes of left and right white matter that were estimated from the MAGeT segmentations as it is difficult to identify these nuclei in our T1-weighted MRI data.

The generation of the high-resolution cerebellar atlases (Figure 4.1a) used for MAGeT and the validation of the MAGeT algorithm on the cerebellum are described elsewhere (Park et al., in press). The segmentations used in the present study (Figure 4.1b) were manually checked for quality. All cerebellar volumes were normalized with respect to total brain volume. We focused our analysis on those lobules for which we hypothesized associations with musical experience and timing (right Lobules IV and V, bilateral Lobules VI and VIII), as well as on bilateral white matter.

4.3.3 Behavioural Stimuli, Task Conditions and Procedure

The experimental set-up for the finger-tapping task was identical to that used in a previous study (Baer et al., 2013), including the use of motion capture equipment to record finger movement. Participants used their right index finger to tap on a tabletop in synchrony with an auditory metronome (1 *KHz* 20 ms tone) for 35 cycles (paced phase). The metronome then stopped and they were asked to continue tapping at the same rate for approximately 35 additional cycles (unpaced phase) until a final tone sounded to indicate the end of the trial. Participants performed a block of six such trials for each of three different rates (250, 500 and 750 ms inter-stimulus intervals), with a 30 *s* rest between trials. The order of tapping rates was counterbalanced across participants.

4.3.4 Behavioural apparatus

Finger movement was recorded with the Visualeyez VZ3000 3D motion tracking system, manufactured by Phoenix Technologies. An infrared light emitting diode (LED) was attached with Velcro tape to the nail of the right index finger. Infrared-sensitive cameras tracked the position of the marker in three-dimensional space at a sampling rate of 200 Hz and to a spatial resolution of 0.015 mm. A National Instruments 6221 Data Acquisition board was used to synchronize the Visualeyez system with a computer-generated 1 *KHz* 20 ms metronome tone, which was heard through a pair of Sony MDR-7506 headphones. Each participant was seated at a table of height 70.0 cm, on a chair with independently adjustable seat and armrests.

4.3.5 Behavioural data analysis

Adjusting the local coordinate reference frame of the 3D motion capture data so that the xy-plane coincided with the tabletop, we analyzed the z-coordinate of motion, corresponding to finger height, to automatically detect the onset of each tap, using custom software written in Matlab. As described in detail elsewhere (Baer et al., 2013), our algorithm first identified local maxima on the acceleration curve of finger motion and then adjusted the corresponding points on the position curve so that they coincided with nearby local minima. This was a more reliable method of detecting tap onset points than examining the position curve directly for local minima. We then focused on data from the unpaced phase, when internal timing processes, rather than synchronization with external stimuli, were likely to predominate. The inter-response intervals (IRIs) of the tapping cycles of the unpaced phase, defined as the duration in time between adjacent taps, were calculated. We excluded the first two cycles of the unpaced phase from all analyses (Zelaznik and Rosenbaum, 2010).

Several measures of temporal variability in the unpaced phase were calculated. The average coefficient of variation (standard deviation divided by the mean) of the IRI across all trials of a condition is a general measure of tapping variability, normalized by interval duration. We next separated out long-term drift away from the prescribed rate by estimating drift as a linear trend in the time series of responses of the unpaced phase. We calculated the slope of this trend line as an estimate of drift and also calculated the variance of the linearly detrended IRI time series. Next, we broke down this remaining variance into timer and motor sources, using the Wing-Kristofferson (1973) model.

Group differences were analyzed using repeated-measures ANOVAs. The Greenhouse-Geisser correction was applied where necessary, based on the results of Mauchly's test of sphericity. The results of multiple pairwise comparisons are reported using Bonferroni-adjusted *p*-values.

4.4 Results

4.4.1 Differences in cerebellar volume between musicians and non-musicians

These analyses compared the total brain volume, total cerebellar volume, and regional cerebellar volumes of musicians and non-musicians. The two groups did not differ significantly in age, $t(56) = .511$, $p = .61$. The non-musicians' duration of musical experience ranged from 0 to 2 years ($M = 1.0$) and none were currently playing an instrument. Musicians' musical experience ranged from 9.5 to 25 years ($M = 16.3$) and all were currently playing (Table 4.1). Musicians practiced an average of 13.9 hours per week.

The cerebellar lobule segmentation that MAGeT produces uses images that are not normalized by transformation to standardized space. To control for known sex differences in cerebellar volume, we planned to normalize our measures with respect to total brain volume (Hutchinson, Lee, Gaub & Schlaug, 2003). To confirm the appropriateness of this control, we compared total brain volume in a 2 (sex) x 2 (musician/non-musician) ANOVA. There was a main effect of sex ($F(1, 54) = 23.105$, $p < .001$), with females having smaller total brain volume, but no effect of musical training and no interaction (Figure 4.2). We also evaluated the effect of sex on absolute cerebellar volume with a 2 (sex) x 2 (musician/non-musician) ANOVA and found a significant effect, $F(1, 54) = 21.081$, $p < .001$), such that females had smaller cerebellar volumes, but no effect of musical experience and no interaction. Based on these results, all subsequent analyses used cerebellar volumes normalized with respect to total brain volume.

Comparing musicians and non-musicians on total cerebellar volume, which averaged 10.92 % of total brain volume ($SD = 0.90$), there were no significant differences ($F(1,56) = .011$,

$p > .05$). Further, no significant differences were found when we compared the two groups on volumes of bilateral Lobules IV, V, VI and VIIIA/B and bilateral white matter.

4.4.2 Relationship of cerebellar volumes to age of start of training and years of musical experience

Based on previous work identifying a sensitive period for initiation of musical training (Bailey & Penhune, 2010; Steele, Bailey, Zatorre & Penhune, 2013; Watanabe, Savion-Lemieux, & Penhune, 2007), we split the musicians into two groups: early-trained musicians (ET; N=18) who started at or before the age of 7 years and late-trained (LT; N=20) who started after the age of 7 years. Their demographic and musical experience data are also presented in Table 4.1. These groups did not differ in their total years of musical experience ($t(36) = -0.146$, $p > .05$).

Comparisons between ET and LT groups showed that ET musicians had significantly smaller normalized volumes of Lobules IV, V and VI in the right hemisphere, smaller white matter volume in both hemispheres, and smaller total cerebellar volume, compared to LT musicians. ET musicians also had significantly smaller white matter volume in both hemispheres compared to non-musicians. There were no significant differences between LT and non-musicians. These findings are summarized in Table 4.2. The unbiased Hedges's g effect size values indicate that early musical training had a large effect on regional cerebellar volumes. Because ET musicians significantly differed from LT musicians in age ($M = 22.6$ and 27.8 respectively; $t(36) = -3.417$, $p < .01$) we examined possible correlations between age and either total or regional cerebellar volumes. No significant correlations were found, indicating that any differences in cerebellar volumes between the ET and LT groups were not due to a difference in current age.

We next examined correlations between the normalized volumes of the same cerebellar regions and the age at which musicians began playing and their total years of musical experience. We found significant positive correlations between the age of start of musical training and the volumes of left, r(36) = .489, p < .01, and right, r(36) = .456, p < .01, white matter and left Lobule VIIIA, r(36) = .346, p < .05. This indicates that later start of training was associated with larger volume in these regions (Table 4.3 and Figure 4.3). We also found significant negative correlations between years of musical experience and right Lobule VI, r(36) = -.335, p < .05, and left Lobule VIIIA, r(36) = -.365, p < .05. These data indicate that greater experience was associated with smaller volumes. The correlations with both age of start and years of musical experience remained significant even after controlling for one against the other, indicating that each variable accounted for distinct portions of the variance of these regional volumes.

4.4.3 Finger tapping performance

To assess the accuracy with which both groups could synchronize to the target metronome rates, we calculated the mean IRI of the paced and unpaced phases. The musician and non-musician groups both had mean IRI values that were close to the intervals defined by the metronome (Table 4.4). Musicians were significantly more accurate than non-musicians in the paced phase of the two slowest rates ($p < .05$ at 500 and 750 ms). In the unpaced phase, non-musicians had significantly shorter IRIs than musicians at the two slowest rates ($p < .001$ at 500 ms and at 750 ms) but overall both groups of participants were able to carry out the tapping task.

Focusing on the unpaced phase in order to examine internal timing processes, we first examined the coefficient of variation of the IRI. A 2 (musical training) x 3 (rate) repeated measures ANOVA indicated a main effect of musical training, ($F(1, 29) = 11.123$, $p < .01$), such that musicians had a smaller coefficient of variation across all rates (Figure 4.4). Further, the unbiased Hedges's effect size value (*g* = 1.22) indicated a large practical significance of musical training. Next, we focused on the linearly detrended variability of the IRI. Again, a significant main effect of musical training was found (*F*(1, 29) = 6.670, *p* < .05), indicating that musicians were less variable and that musical training had a large effect (*g* = 0.94). As expected (Wing, 2002), there was also a significant main effect of tapping rate, such that variability increased with interval duration, *F*(2, 58) = 45.339, *p* < .001. An interaction between musical training and rate did not reach significance, *F*(2, 58) = 3.136, *p* = .082, but pairwise comparisons revealed that musicians had significantly smaller IRI variability at the 500 ms (*p* < .01) and 750 ms (*p* < .05) rates, compared to non-musicians. Further, musical training had large effects on IRI variability at these two rates (*g* = 1.03 at 500 ms and 0.79 at 750 ms).

To assess long-term drift away from the target tapping rate, we examined the absolute value of the slope of the linear trend that was removed from the IRI time series of the unpaced phase. We found a significant main effect of musical training, *F*(1, 29) = 6.514, *p* < .05, with musicians exhibiting significantly less drift than non-musicians (Figure 4.5), and a large effect of musical training (*g* = 0.93). There was also a significant main effect of rate, *F*(2, 58) = 14.105, *p* < .001, such that drift increased with interval duration. No significant interaction between rate and musical training was found, F(2, 58) = 1.254, p = .293.

To test whether musicians' less variable tapping performance was due to reduced timer variability or to reduced motor variability or a combination of the two, we used the Wing and Kristofferson (1973) model to estimate the portion of the total unpaced IRI variability attributable to central timer and to motor functions. Consistent with the prediction of the model, we found a main effect of rate, *F*(2, 58) = 52.255, *p* < .001, such that timer variability increased with interval duration (Figure 4.6), but we did not find any significant effect of musical training or interaction between the two independent variables. Nevertheless, post hoc pairwise comparisons showed that musicians were less variable at the 250 and 500 ms rates compared to non-musicians ($p < .05$), with large effect sizes for musical training ($g = 0.75$ and 0.98 at 250 and 500 ms rates, respectively).

In contrast, for the motor component of variability, we found main effects of musical training, F(1, 29) = 11.905, p < .01, and rate, $F(2, 58) = 18.084$, $p < .001$, such that motor variability was smaller in musicians and larger as interval duration increased. Further, the effect size of musical training on motor variability ($g = 1.26$) suggested high practical significance for musical training on this aspect of performance. We also found an interaction between musical training and rate, $F(2, 58) = 10.005$, $p < .01$, such that musicians had significantly less motor variability at the 500 ms ($p < .05$) and 750 ms ($p < .01$) rates. Within the group of musicians, motor variability did not differ significantly between rates, consistent with the prediction of the Wing and Kristofferson model. However, motor variability of the non-musicians increased significantly as interval duration increased (Figure 4.7).

When we split the group of musicians into ET ($n = 7$) and LT ($n = 13$) subgroups, no significant differences were found for any of the timing measures. We examined the correlations of both the age at which musical training began and the total number of years of musical experience, with the timing of finger tapping. A marginally significant correlation between years of experience and Wing-Kristofferson timer variability at 500 ms ($r = -.435$, $p = .055$) was found. Additionally, the correlation between years of experience and the absolute value of the slope of the linear trend at 750 ms was marginally significant ($r = -.413$, $p = .07$). No significant correlations with motor variability were found. Thus, there was some evidence indicating that greater years of training may be associated with smaller timer variability and less drift.

4.4.4 Relationship between cerebellar volumes, timing and musical experience

Using the subset of participants with both behavioral and MRI data, we examined the relationships between cerebellar volumes, timing measures and musical experience. This subset of participants did not differ from the larger sample in age ($t(87) = .417$, $p = .678$), total brain volume ($t(87) = .639$, $p = .524$) or normalized total cerebellar volume ($t(87) = -.459$, $p = .648$). Furthermore, the musicians from these two groups did not differ in their years of musical experience ($t(56) = .760$, $p = .450$).

To limit the number of separate analyses, we only examined the correlations for regions previously found to be associated with musical experience for the larger group (bilateral white matter, right VI and left VIIIA). Significant correlations were found between the coefficient of variation of the unpaced IRI and right Lobule VI (Table 4.5; Figure 4.8). Interestingly, breaking down this variability into timer and motor components using the Wing-Kristofferson (1973) model, we found that timer variability correlated significantly with right Lobule VI ($r = .409$ at 250 ms, .400 at 500 ms, .381 at 750 ms; Table 4.5; Figure 4.8) while motor variability did not. This indicates that lower timer variability is related to smaller volumes of right Lobule VI.

4.5 Discussion

The goal of the present study was to illuminate the relationships between musical experience, timing, and regional cerebellar volumes. We used a novel automatic segmentation pipeline to measure cerebellar regional volumes in structural MR images and combined this with measures of musical experience and finger tapping variability in musicians and non-musicians. We found that ET musicians had smaller total and regional cerebellar volumes compared to LT musicians but found no differences between LT musicians and non-musicians. We found that the earlier in life that musicians began playing, the smaller were the volumes of their bilateral white matter and left Lobule VIIIA. We also found that greater duration of musical experience was associated with smaller volumes of right Lobule VI and left Lobule VIIIA. In terms of tapping performance, we found that musicians showed less long-term drift than non-musicians and were less variable, due to both reduced timer variability and reduced motor variability. We also found evidence that timing performance is related to the volume of right Lobule VI.

Overall, there are several inter-related findings stemming from these results. The first related to the idea of a sensitive period, before the age of seven years, for musical training. It is supported by results showing that ET musicians had reduced volume in bilateral cerebellar white matter and right Lobules IV, V and VI. There were no differences in tapping performance between the groups, which may indicate that LT musicians can achieve the same level of timing performance as ET musicians but with different underlying brain structure. A striking aspect of this finding is that better timing performance, greater musical experience and an earlier age of start of musical training were unexpectedly associated with smaller, not larger, cerebellar volumes. Finally, we found that both timing performance and years of musical experience were specifically associated smaller volumes of right lobule VI.

Our first key finding of cerebellar volumetric differences between ET musicians and both LT and non-musicians adds to the body of evidence supporting a sensitive period for the initiation of musical training (Bailey & Penhune, 2010; Penhune, 2011; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995; Watanabe, Savion-Lemieux, & Penhune, 2007). Interestingly, these volumetric differences between ET and LT musicians were not accompanied by performance differences on the tapping task. However, performance differences between ET and LT musicians have been observed in motor sequence learning and rhythm reproduction tasks in other studies in our lab (Bailey, Zatorre, & Penhune, 2014; Watanabe, Savion-Lemieux, &

Penhune, 2007). It may be that timing performance is less affected by a sensitive period and more strongly related to years of experience, given the correlations we found between this aspect of musicianship and both timer variability and right lobule VI volume.

Our second key finding showed that smaller volumes of cerebellar grey and white matter were related to better timing performance, greater musical experience and an earlier age of start of musical training . Timer variability positively correlated with right VI volume, years of experience negatively correlated with right VI and left VIIIA volumes and the age of start of musical experience positively correlated with bilateral white matter and left VIIIA volumes. The overall pattern of results suggests that musical skill, specifically timing ability, and the age of initiation into musical training, are associated with smaller volumes of grey and white matter in the cerebellum. This result is counter to the more typical pattern of musical or other skill being associated with larger volumes of brain regions (e.g. Hutchinson, Lee, Gaab, & Schlaug, 2003; Maguire et al., 2000), but it is consistent with a recent study of pianists that found reduced variability in piano playing was associated with smaller putamen volume (Granert, Peller, Jabusch, Altenmüller, & Siebner, 2011). Expertise in other fields has also been associated with reduced cerebellar volumes. Female ballet dancers had smaller bilateral lobules VIII and IX compared to controls, such that the volumes of these lobules were negatively associated with years of dance experience (Nigmatullina, Hellyer, Nachev, Sharp, & Seemungal, 2013). Additionally, it has been suggested that reduced volume is consistent with the reduced activations that have been observed to be associated with skill mastery (Hänggi, Koeneke, Bezzola, & Jäncke, 2010). For example, professional pianists, compared to controls, have shown reduced activation in motor areas in fMRI studies of tapping (Jäncke, Shah, & Peters, 2000; Krings et al., 2000). To sum up, our finding that smaller cerebellar volumes are associated with an earlier initiation of musical experience, a longer duration of musical experience, and more precise timing, is consistent with other studies that have associated smaller volumes and diminished activation with expertise.

The unexpected direction of these correlations of measures of experience and expertise with brain volumes could be explained by neural processes that are more efficiently and elegantly implemented during the sensitive period and consequently use less grey and white matter. Grey matter density has been found to increase in relation to musical expertise in areas related to cognitive functions used in musical performance but to decrease in areas related to sensorimotor processes, with the suggestion that decreases could be related to more efficient motor control processes that may require fewer neurons and less sensory feedback (James et al., 2013) and similar factors may be responsible for the volume decreases observed here. In support of this explanation, we found in a previous study that non-musicians exhibited a negative association between movement jerk and timer variability on a tapping task, while musicians' jerk and timing were decoupled, indicating that musicians were able to achieve superior timing with less sensory feedback (Baer et al., 2013), as jerk is a source of proprioceptive information (Balasubramaniam et al., 2004).

The effect on the cerebellum of a sensitive period for musical training is somewhat surprising given what we know of the developmental trajectory of this brain region. The relatively late peak in total cerebellar volume (11.8 – 15.5 years) and, in particular, the superior posterior lobe (15.8 – 18.2 years), which includes Lobule VI (Tiemeier et al., 2010), might suggest a later cut-off than seven years for the sensitive period. Instead, it may be that cerebellar development is at least partially yoked to development in connected brain regions that are also affected by musical training but with shorter maturational trajectories.

Our third key finding of an association between the volume of right Lobule VI and both the variability of the tapping IRI and years of musical experience is consistent with the evidence from functional imaging and TMS studies (E, Chen, Ho, & Desmond, 2012; Thaut et al., 2009) that indicate a role for this region in timing. Furthermore, when we broke down the total IRI variability into timer and motor sources, we found that timer variability correlated with the volume of right Lobule VI, but motor variability did not. This suggests that Lobule VI is tied more closely to the timing aspects of finger tapping, rather than the motoric aspects of this task and supports the dissociability of timer and motor variability predicted by the Wing-Kristofferson (1973) model In sum, our key finding of an association of timer variability with right Lobule VI volume further contributes to the localization of timing, in a repetitive auditory-motor synchronization task, by adding to the precision of cerebellar localization to a specific lobule.

The results of this study contribute supporting evidence for a sensitive period for initiation of musical experience. Our study also adds to a small but growing body of evidence that links skill mastery with smaller grey and white matter volumes. Finally, a major contribution of this study was to add to the body of evidence suggesting a role for cerebellar lobule VI in event-based timing for repetitive auditory-motor synchronization tasks.

Table 4.1. Demographic and musical training data

	N	Mean Age (years)	Age of Start of Training (years)	Years of Training
MRI data				
Musicians	38 (15 female)	25.3 (5.3)	8.6 (3.4)	16.3 (4.3)
ET	18 (10 female)	22.6 (4.1)	5.8 (1.1)	16.2 (4.1)
LT	20 (5 female)	27.8 (5.2)	11.2 (2.7)	16.4 (4.7)
Non-musicians	20 (10 female)	26.0 (4.4)	10.6[+] (4.2)	1.0[+] (0.5)
Tapping & MRI Data				
Musicians	20 (6 female)	26.3(6.3)	9.0 (3.5)	16.9 (4.4)
Non-musicians	11 (7 female)	25.6 (4.1)	11.6[++] (5.1)	1.2[++] (0.4)

Note: Parenthesized values are standard deviations, unless otherwise noted. [+]Four participants had no musical training, [++]Three participants had no musical training.

Table 4.2. ANOVA results for cerebellar regions predicted to differ in musicians. All volumes were normalized with respect to total brain volume. Between-subjects factor was group, with three levels: ET, LT, non-musician (NM).

Region	*F*(2,55)	*p*	Significant pairwise comparisons (p values in parentheses)	Bias-corrected Hedges's *g* effect size (95% CI in parentheses)
Total cerebellum	4.300	.018	ET < LT (.015)	0.87, [0.21, 1.54]
right Lobule IV	4.128	.021	ET < LT (.018)	0.95, [0.28, 1.63]
right Lobule V	3.286	.045	ET < LT (.039)	0.76, [0.10, 1.42]
right Lobule VI	3.413$^+$	.04$^+$	ET < LT (.041)	0.80, [0.12, 1.47]
right Lobule VIIIA	0.246	.783	None	/
right Lobule VIIIB	1.448	.244	None	/
right white matter	6.053	.004	ET < LT (.005); ET < NM (.036)	1.01, [0.33, 1.69]; 0.89, [0.22, 1.56]
left Lobule VI	2.247	.115	None	/
left Lobule VIIIA	2.565	.086	None	/
left Lobule VIIIB	1.227	.301	None	/
left white matter	6.909	.002	ET < LT (.002); ET < NM (.020)	1.07, [0.39,1.75]; 0.98, [0.31,1.65]

Note. $^+$Significant after removing a single outlier from the ET group (*Z* score = 2.7 with respect to the mean of the ET group), *F*(2, 54) = 3.413, *p* = .04.

Table 4.3. Bivariate Pearson coefficients of normalized regional cerebellar volumes with musical experience (*p* values in parentheses) for the 38 musicians pooled together. Partial correlations for age of start, after controlling for years of experience, and years of experience, after controlling for age of start, are also shown for the significant bivariate correlations.

Region	Age of start		Years of experience	
	Bivariate	Partial	Bivariate	Partial
total cerebellum	.273 (.097)	/	-.296 (.071)	/
right Lobule IV	.275 (.095)	/	-.015 (.927)	/
right Lobule V	.222 (.180)	/	-.239 (.149)	/
right Lobule VI	.260 (.115)	/	-.335* (.040)	-.350* (.034)
right Lobule VIIIA	.270 (.101)	/	-.061 (.715)	/
right Lobule VIIIB	.230 (.164)	/	.099 (.552)	/
right white matter	.456** (.004)[+]	.474** (.003)	-.251 (.128)	/
left Lobule VI	.314 (.055)	/	-.295 (.072)	/
left Lobule VIIIA	.346* (.033)	.376* (.022)	-.365* (.024)	-.393* (.016)
left Lobule VIIIB	.131 (.432)	/	.141 (.399)	/
left white matter	.489** (.002)[++]	.505** (.001)	-.231 (.163)	/

Note. *Significant at p < .05. **Significant at p <.01. [+]Marginally significant after removal of a single outlier, r = .295, p = .077. [++]Significant after removal of the same single outlier, r = .337, p = .041.

Table 4.4. Mean Inter-response Intervals of the paced and unpaced phases.

	Interval duration					
	250 ms		500 ms		750 ms	
	Paced	Unpaced	Paced	Unpaced	Paced	Unpaced
Musicians	249.69	254.01	499.91	509.41	749.86	765.31
	(0.76)	(6.40)	(0.71)	(11.64)	(.84)	(22.89)
Non-musicians	246.46	252.78	498.44	492.42	747.45	725.28
	(8.58)	(8.49)	(2.76)	(11.31)	(5.02)	(35.40)

Note. All values in milliseconds. Standard deviations in parentheses.

Table 4.5. Bivariate Pearson correlation coefficients of normalized regional cerebellar volumes with measures of unpaced IRI variability (*p* values in parentheses) for 31 participants.

	right Lobule VI	right white matter	left Lobule VIIIA	left white matter
Coefficient of Variation				
250 ms	.037 (.842)	.075 (.688)	.033 (.860)	.037 (.844)
500 ms	.407* (.023)	.189 (.308)	.119 (.524)	.156 (.401)
750 ms	.394* (.028)	.153 (.412)	.049 (.795)	.129 (.489)
Wing-Kristofferson Timer variability				
250 ms	.409* (.022)	.265 (.149)	.294 (.108)	.226 (.222)
500 ms	.400* (.026)	.009 (.964)	.295 (.107)	-.022 (.904)
750 ms	.381* (.034)	.116 (.534)	.057 (.760)	.094 (.617)
Wing-Kristofferson Motor variability				
250 ms	-.051 (.786)	-.084 (.652)	-.093 (.620)	-.082 (.660)
500 ms	.312 (.087)	.205 (.268)	-.193 (.297)	.190 (.305)
750 ms	.317 (.082)	.153 (.410)	-.055 (.769)	.144 (.440)

Note. *Significant at $p < .05$

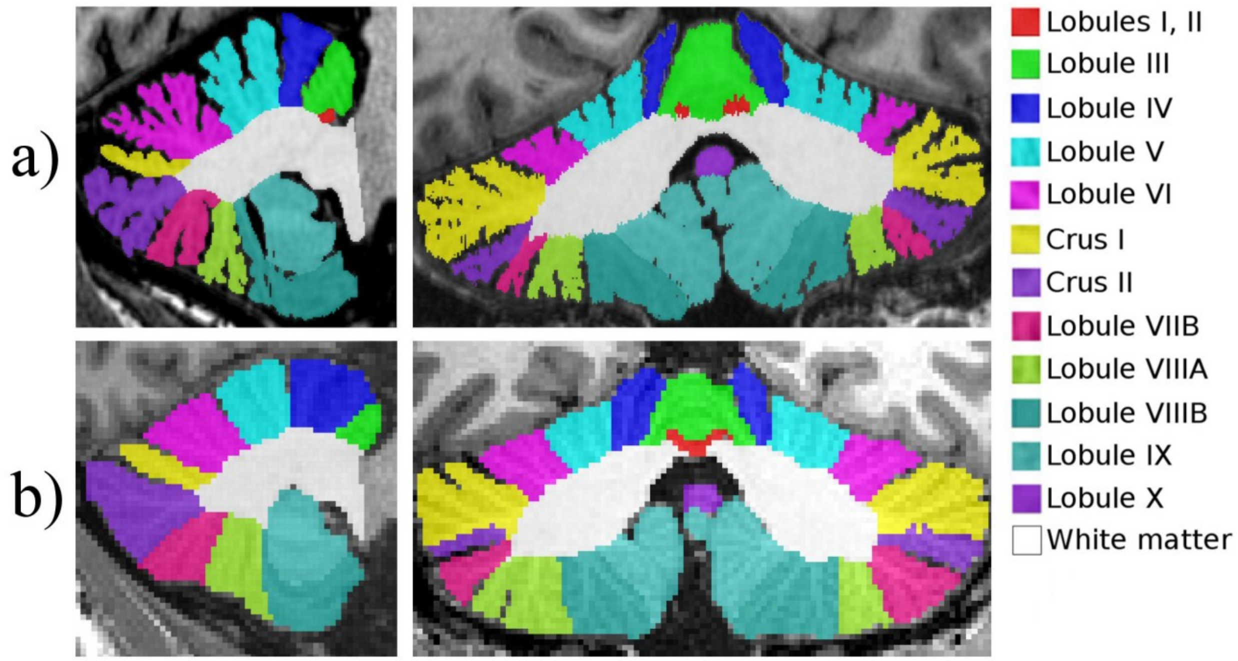

Figure 4.1. Midline cerebellar sagittal and coronal slices. (a) Manually segmented high-resolution cerebellar atlases acquired from super-sampling 3 T images from 5 healthy participants who were not part of this study. 0.3 mm isotropic voxels. (b) MAGeT-labeled cerebellum of a musician, 1mm isotropic voxels.

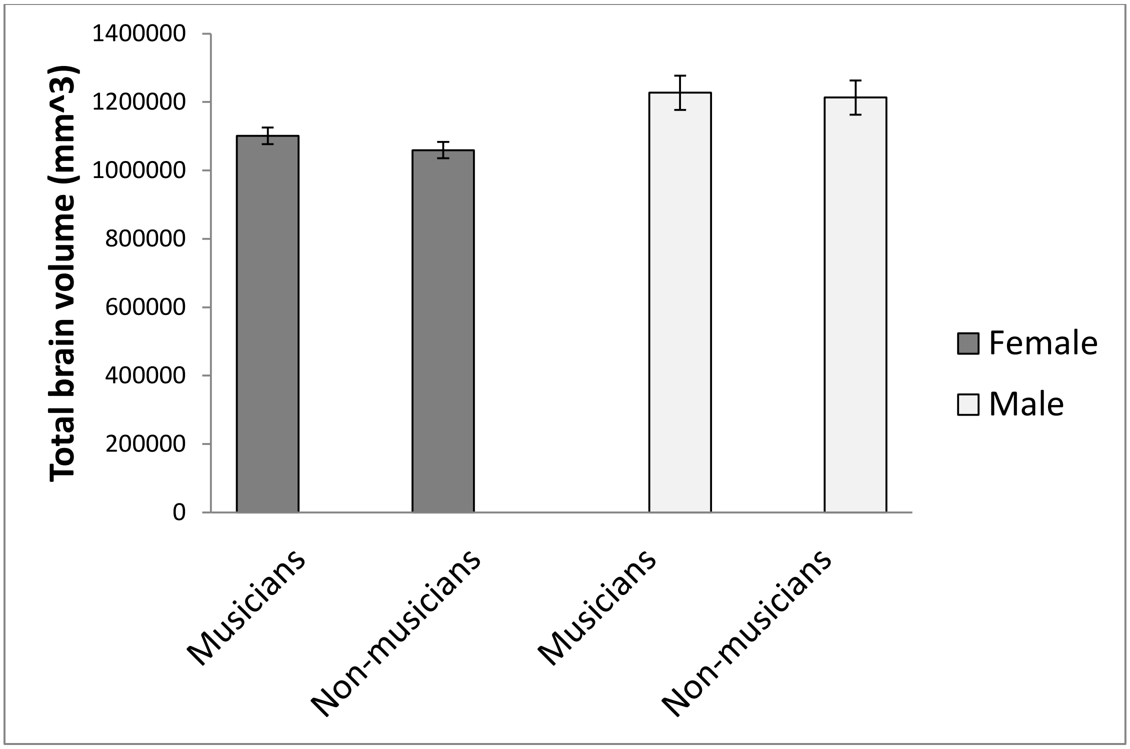

Figure 4.2. Total brain volume, showing a significant main effect of gender. Standard error bars are shown.

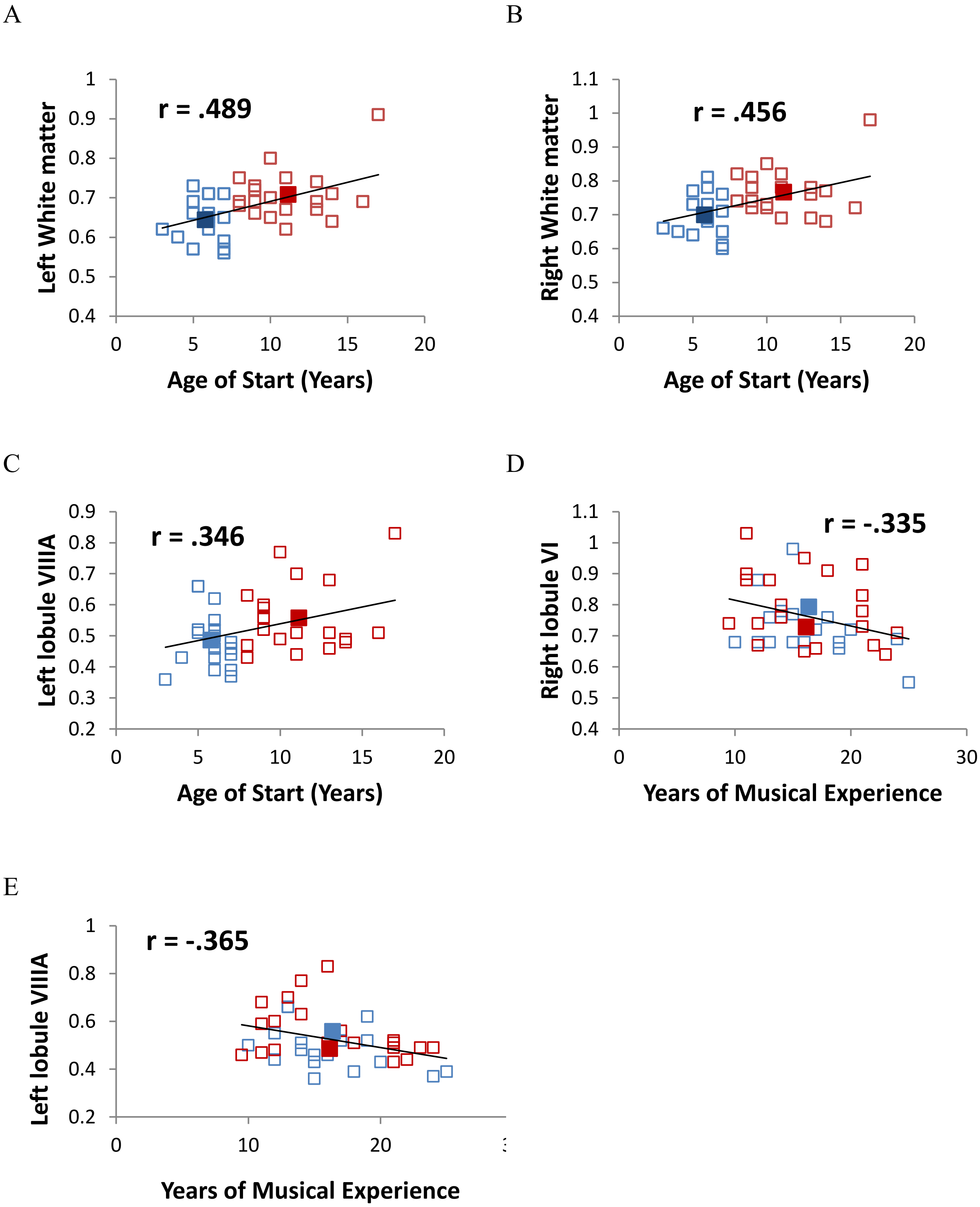

Figure 4.3. Scatter plots for 38 musicians showing correlations between the age of start of musical experience and normalized volumes of (A) Left cerebellar white matter, (B) right cerebellar white matter, and (C) left Lobule VIIIA, and between the years of musical experience and normalized volumes of (D) right lobule VI and (E) left lobule VIIIA. ET musicians are shown in blue, LT musicians in red. Filled squares represent subgroup means.

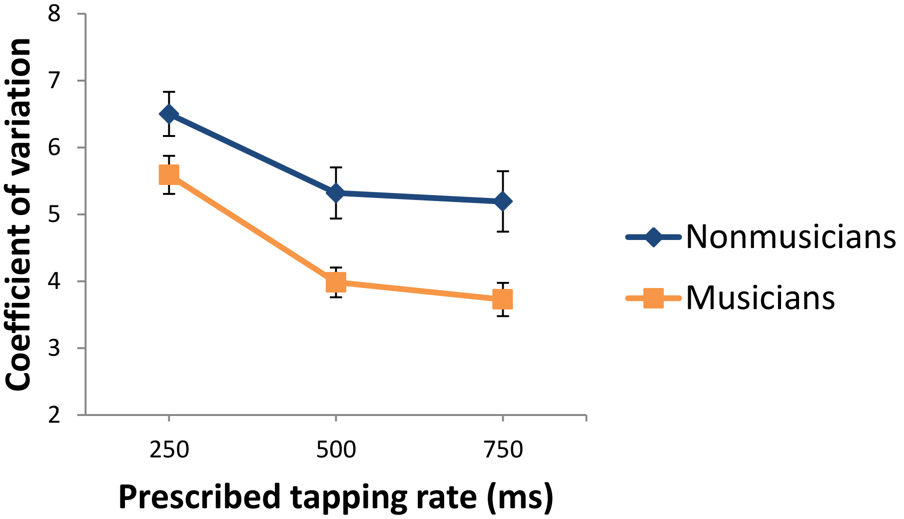

Figure 4.4. Coefficient of variation of the unpaced phase plotted against the prescribed tapping rate. Standard error bars are shown.

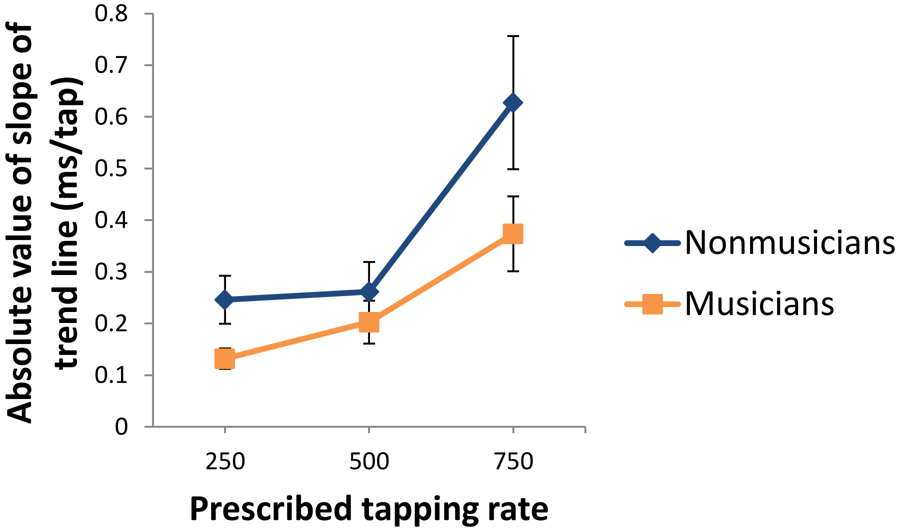

Figure 4.5. Linear drift in the unpaced phase, represented by the absolute value of the slope of the linear trend line of the IRI time series. Bars represent standard error.

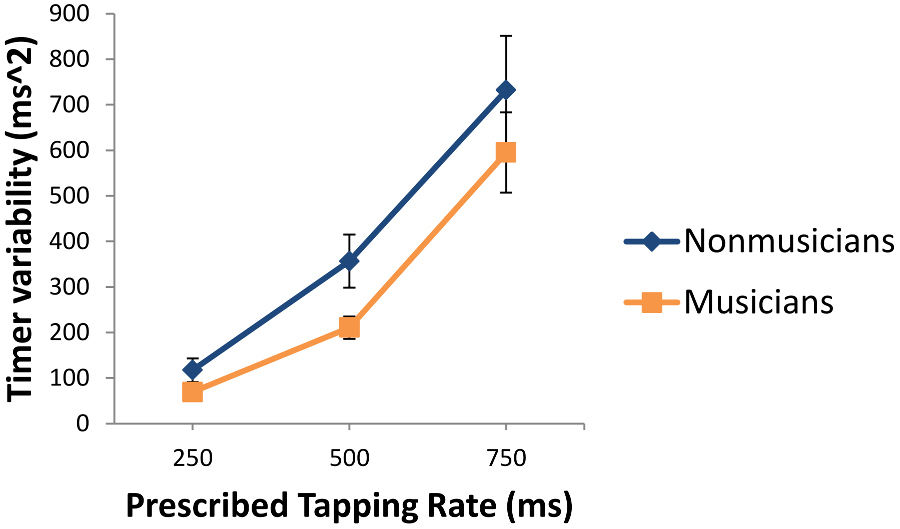

Figure 4.6. Timer variability in the unpaced phase, estimated using the Wing-Kristofferson model. Bars represent standard error.

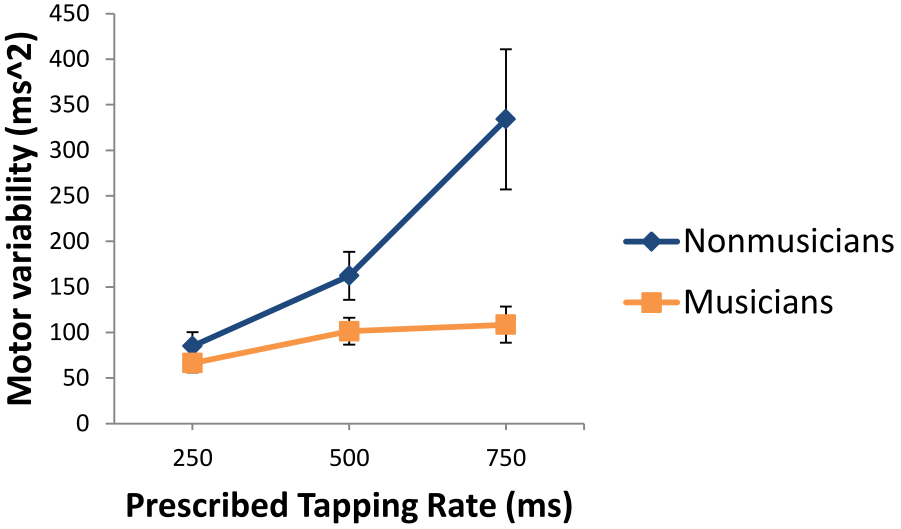

Figure 4.7. Motor variability in the unpaced phase, estimated using the Wing-Kristofferson model. Bars represent standard error.

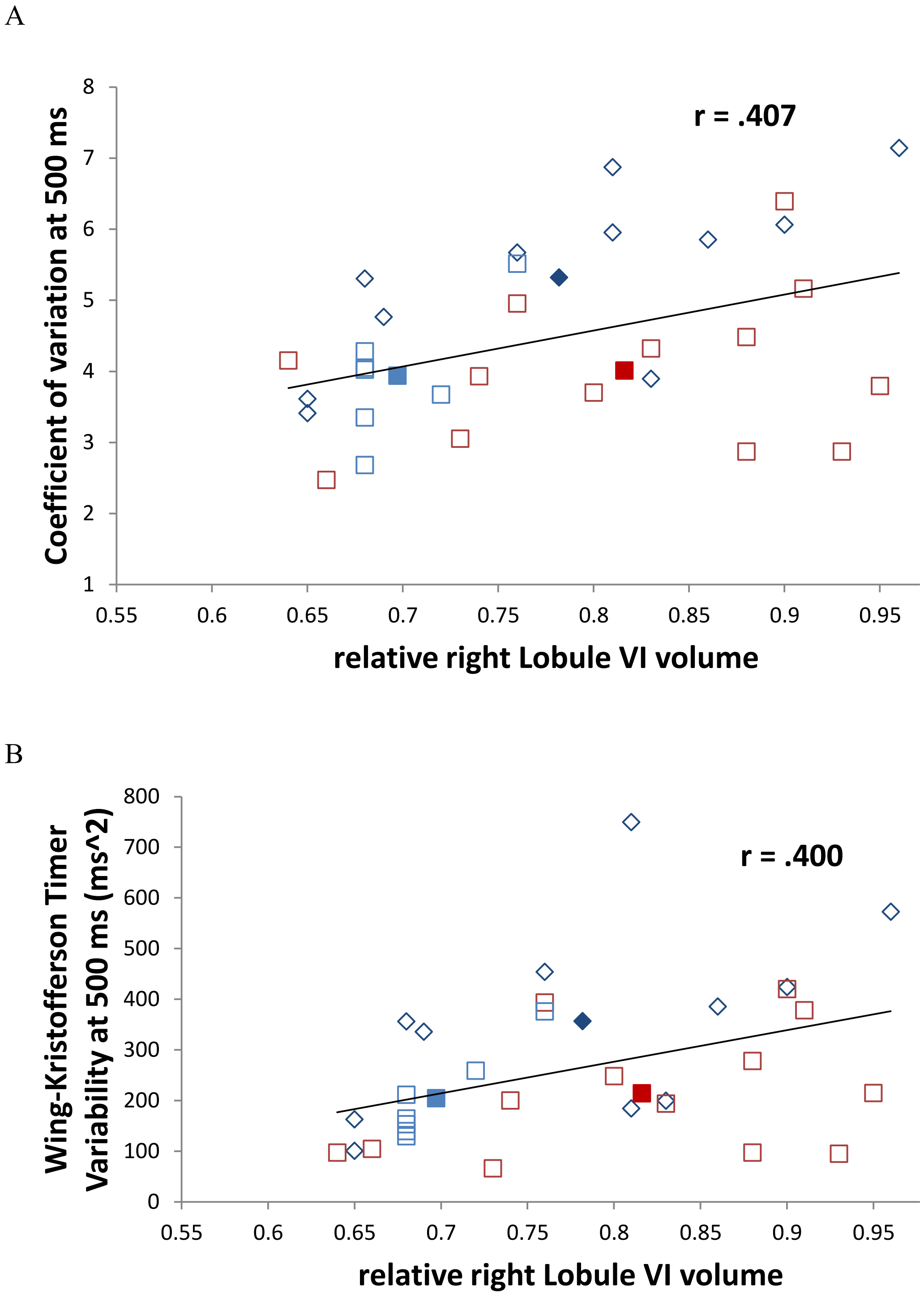

Figure 4.8. Scatter plots for 31 participants showing correlations between normalized right lobule VI volume and tapping performance at the prescribed tapping rate of 500 ms based on (A) coefficient of variation of the unpaced IRI and (B) Wing-Kristofferson timer variability. Non-musicians are shown as dark blue diamonds, ET musicians as light blue squares and LT musicians as red squares. Filled diamonds and squares represent subgroup means.

Chapter 5: General Discussion

The work presented here aimed to further our understanding of timing and sensorimotor synchronization by examining the behavioural effects of musical training on these processes. Another goal was to analyze the neural correlates of musical training and timing by focusing on the cerebellum. Further evidence for the existence of a sensitive period for musical training was also sought. All three studies used motion capture technology and custom-written software to analyze the kinematics of movement and its relation to timing. The third study also used structural MRI data and a novel segmentation of the cerebellum that permitted localized volumetric analyses within this brain region.

Overall, the pattern of behavioural results across the three studies suggests that musicians are likely using different strategies than non-musicians to maintain accurate and precise timing. Results indicate that musicians do more with less -- the superior timing performance of musicians may be achieved with the use of less sensory information compared to non-musicians. The finding that smaller volumes of cerebellar regions are associated with better timing, and with musical training in general, may reflect this same pattern of ``less is more`` and the pattern appears to be enhanced if musical training is initiated during the sensitive period before the age of seven years. I will argue below that the behavioural and brain differences between musicians and non-musicians that may be indicative of more efficient and parsimonious use of sensory information may, in turn, be a reflection of a top-down approach to sensorimotor processing that is learned from musical training.

After reviewing the results of the individual studies, I will discuss how the findings can be integrated across studies to provide a deeper understanding of timing and musical training. I will end with some suggestions for future research that could further clarify our comprehension of these areas.

5.1 Review of main findings

The first study of this dissertation examined differences in how musicians and non-musicians use tactile information and kinematics in paced tapping. A previous study of individuals with musical training found that the asymmetry of finger trajectory negatively correlated with asynchrony when tapping in the air without any tactile feedback, with the explanation that the relatively greater velocity of downward flexion, compared to upward extension, led to greater proprioceptive information that improved synchrony (Balasubramaniam, Wing, & Daffertshofer, 2004). The present study reproduced this result for musicians but not for non-musicians, although both groups were equally synchronous. This suggests that musicians and non-musicians are using different strategies to synchronize. The addition of tactile information, in the form of a blocked piano key, was associated with significant negative asynchrony-asymmetry correlations for both groups. Tapping on an unblocked piano key, which I argued yielded even more tactile information than a blocked key, was associated with a significant asynchrony-asymmetry correlation for non-musicians only. A possible explanation of these results is that the piano key yields tactile information early in the downward flexion phase of a tap but only musicians are taking advantage of this, obviating a reliance on proprioceptive information. An open question is how non-musicians, without a significant asynchrony-asymmetry correlation when tapping in the air, were able to achieve the same level of asynchrony as musicians in this condition. We know that disruption of the posterior parietal cortex (PPC) reduces asynchrony, possibly by disrupting the PPC's relay of information related to multisensory integration to premotor areas, resulting in a delay of movement initiation (Krause et al., 2012). It may be the case that the absence of tactile information when tapping in the air, had the same functional effect for non-musicians.

With regard to how tactile information affected synchronization, non-musicians' negative mean asynchrony worsened with the addition of tactile information while musicians' asynchrony was unaffected. This finding was interpreted in the context of sensory processing models of negative mean asynchrony that explain the negative asynchrony as the result of faster processing of auditory compared to somatosensory information, requiring tap responses to precede metronome tones in order for the brain to perceive synchrony (Aschersleben, Gehrke, & Prinz, 2001; Drewing & Aschersleben, 2003). The processing overhead associated with tactile information was not evident in musicians' asynchrony measures, suggesting that they process tactile information more efficiently and effectively than non-musicians. This interpretation could explain why, as suggested above, only musicians were able to take advantage of the additional tactile feedback from the piano key.

This study has two major limitations that suggest caution in interpreting its results. First, the manipulation of tactile feedback across conditions was a nonparametric one. Whether an individual acquires more tactile information from tapping on a blocked or an unblocked piano key is an arguable point. Second, the changes in kinematics that likely accompanied the changes in tactile feedback across conditions (e.g. the collision with the piano key) may confound the effects of changes in the level of tactile information. A follow-up study that would better control for kinematic differences across levels of tactile information could clarify the findings of the first study. For example, a manipulation of the area or texture of an otherwise fixed surface would affect tactile feedback without substantially changing the kinematics.

In light of these limitations, a more conservative interpretation of the results of the first study would be an examination solely of group differences within, but not across, conditions. In the air-tapping condition, we may still conclude that musicians and non-musicians are using different strategies to synchronize. In the blocked-key condition, both groups behaved similarly with regard to asynchrony and asymmetry. In the piano-key condition, musicians were less asynchronous and only non-musicians exhibited the asynchrony-asymmetry correlation. This latter finding may reflect an expertise effect in use of the piano keyboard, such that musicians may have a well refined motor program for pressing a piano key that minimizes the need for proprioceptive and tactile information.

The second study of this dissertation compared musicians and non-musicians on the prototypical event-based and emergently timed tasks of finger tapping and circle drawing respectively. As predicted, we found that expertise in event-based timing did not transfer to emergent timing, supporting the independence of these two modes. Musicians had smaller variability in their unpaced tapping compared to non-musicians but performed no better at unpaced circle drawing than non-musicians. This finding also confirmed that musical training privileges event-based timing. On the other hand, we found evidence that the most experienced musicians might have been using event-based timing for circle drawing, based on negative lag one covariances for circle drawing and a marginally significant correlation of timing variability between the two tasks. We speculated that this subset of musicians may have been primed to use event-based timing, similarly to how practice effects within an experiment may have led to the unexpected use of event-based timing (Studenka, Zelaznik, & Balasubramaniam, 2011).

An interesting difference between musicians and non-musicians had to do with how kinematics related to timing. In the case of non-musicians, we found what we expected to find:

timing variability and jerkiness of movement within a response cycle were negatively correlated for tapping and positively correlated for drawing. Surprisingly, in the case of musicians, their timing variability and movement jerk were uncorrelated for both tasks. This could be related to the greater precision of musicians' internal clocks diminishing the need for the additional information garnered from jerky movement (Balasubramaniam, Wing, & Daffertshofer, 2004) and to these more precise clocks being (sometimes) used for circle drawing as well. I discuss this particular finding in the context of the results from the other two studies in the following section.

In the third study, a comparison of early- and late-trained musicians with non-musicians, all right-handed, revealed that early-trained musicians had reduced volume in bilateral cerebellar white matter and right Lobules IV, V and VI, compared to late-trained musicians. Surprisingly, smaller, not larger, cerebellar volumes were associated with smaller timing variability on a finger-tapping task, with greater duration of musical training and with an earlier age of start of musical training. While this runs counter to the more usual association of larger brain volumes with experience and better behavioural performance, I showed that it is consistent with the findings of other studies of musicians that have associated smaller volumes, less grey matter density, and decreased activation with musical training (Granert, Peller, Jabusch, Altenmüller, & Siebner, 2011; James et al., 2013; Jäncke, Shah, & Peters, 2000; Krings et al., 2000).

Another key finding of this third study was the association between Wing-Kristofferson timer, but not motor, variability with the volume of right cerebellar lobule VI. This finding is consistent with functional imaging studies (E, Chen, Ho, & Desmond, 2012) but, again, the direction of association was unexpected, with smaller volumes of lobule VI associated with greater timing precision. The associations of smaller cerebellar volumes with better timing performance and greater musical training were interpreted as suggesting that musical training facilitated efficient and parsimonious neural implementations of timing and other music-related tasks.

5.2 Integration of findings across studies

Several pieces of evidence from the three studies suggest that musicians use less sensory information more efficiently for achieving temporally accurate and precise movement, compared to non-musicians. In the first study, adding tactile information to a synchronization task did not affect the negative mean asynchrony of musicians, while it worsened that of non-musicians. In the context of the sensory accumulator model of negative mean asynchrony (Aschersleben, 2002; Aschersleben, Gehrke, & Prinz, 2001), this could mean that musicians are able to integrate tactile information into a central representation of a tap so quickly that there is no apparent overhead in terms of greater NMA, but it could also mean that musicians are using minimal tactile information to form a percept of a tap for synchronization. In support of this latter explanation, we know that professional pianists have greater tactile discrimination in their index fingers compared to non-musicians (Ragert, Schmidt, Altenmüller, & Dinse, 2004). The ability to exhibit enhanced response to sensory stimuli appears to extend to the auditory domain, where musicians show elevated auditory brainstem response to the upper tone of a musical interval, despite its relatively lower acoustic intensity (Lee, Skoe, Kraus, & Ashley, 2009).

In the unpaced phase of a tapping task, the musicians of study II did not show the correlation between movement jerk and IRI variability that non-musicians exhibited. Additional analysis of the kinematic data of the third study reproduced this pattern (Table 5.1). The musicians tested in the second study had event-based timer variability that was about half that of the non-musicians who were tested. Given this more precise timing ability, musicians may not need the enhanced proprioceptive information gleaned from jerky movement. The smaller cerebellar volumes observed in early-trained musicians may also be related to this possibly more parsimonious and efficient use of sensory information. James et al. (2013) also suggested a diminished need for sensory feedback as the explanation for smaller grey matter density in areas related to sensorimotor processing in musicians' brains.

How could musicians learn to get by with less sensory information yet achieve superior performance? There is some evidence that musicians employ a top-down approach in sensorimotor synchronization and other music-related tasks, while non-musicians appear to follow a more bottom-up approach. A functional brain imaging study of differences in how musicians and non-musicians reproduced auditory rhythms of varying complexity showed that musicians had greater activation in cortical areas such as the dorsolateral prefrontal cortex, as metrical complexity increased and this was interpreted as an indication of top-down processing, in the form of grouping of input stimuli, compared to the bottom-up processing of the non-musicians (Chen, Penhune, & Zatorre, 2008). In a study of paced finger tapping that compared drummers, pianists and non-musicians, drummers showed stronger interactions between the PPC and the thalamus compared to the other two groups and this was associated with lower response variability (Krause, Schnitzler, & Pollok, 2010) . It is possible that, in the brains of musicians, sensory information is being filtered in an optimal fashion under the guidance of cortical areas linked to motor planning, while non-musicians may use a less efficient means of filtering and processing sensory information. Along these same lines, in a task of melodic improvisation, musicians and non-musicians performed similarly but showed different patterns of brain activity, such that musicians exhibited deactivation of the temporoparietal junction, a region thought to control bottom-up processing of sensory input (Berkowitz & Ansari, 2010). The authors interpreted this deactivation as a means for musicians to facilitate top-down processing, such as grouping of musical notes into melodies, by filtering out sensory input that is irrelevant to the expert musician. Anecdotally, in the set of studies presented here, musicians, particularly drummers, described in post-experiment interviews how they broke down even the simple isochronous rhythms employed in our tasks, into sub-rhythms, as a means of maintaining synchrony. A top-down approach by expert musicians with well-defined motor programs for finger tapping could account for their superior timing accuracy and precision and weaker reliance on sensory information such as proprioception.

5.3 Future directions

The group differences between musicians and non-musicians and the correlations between timing and musical training are not sufficient for establishing a causal link from musical training to timing ability. It may be that a child with good timing ability will find musical improvisation more pleasurable and be more motivated to play music compared to a child with less precise timing. It may also be the case that innately good timing and musical training work together to produce even better timing performance in the adult musician. Current evidence related to other musical processes and brain regions supports “nurture” over “nature”. A longitudinal study compared a group of young children receiving music lessons to a control group and found that, after 15 months of musical training, there were brain differences in auditory and motor areas and these brain changes in the musical training group correlated with performance improvements in melody and rhythm discrimination and fine motor tests, respectively (Hyde et al., 2009).

The work presented here provides some indication that the same case may hold for timing ability. In the third study, the correlations between years of musical experience, timer variability, and the volume of cerebellar right lobule VI suggest the possibility of a mediational relationship between these three variables. More years of training and smaller right VI volume were both associated with better timing, while more years of training was associated with smaller right VI volume. It may be that right VI volume is mediating the relationship between musical experience and timer variability, evidence which would further strengthen support for the role of right Lobule VI in timing and musical performance and indicate that musical-training-related plasticity in this region results in reduced timing variability. However, we did not have brain imaging and behavioural data for all 38 musicians and we could not reproduce significant correlations between these three variables for the smaller subset of 20 musicians for whom we had both MRI and behavioural data, leaving us unable to carry out a mediational analysis. Future research could investigate the possibility of mediation with a more focused study of sufficient power. Investigating this in a longitudinal context could also help to answer the nature versus nurture question for timing and musical training.

Such a longitudinal study could also track how and when the relationships between kinematics and timing change as a function of duration and intensity of training. However, it would also be of interest to verify whether these differences between musicians and non-musicians noted in this dissertation can be induced through training of musically naïve adults and whether these differences persist in adults who no longer practice music but did so as children.

Additional work is also needed for a more complete understanding of how musical training affects kinematics and timing in finger tapping and how different brain regions contribute to timing accuracy and precision. Krause and colleagues' (2012) found that repetitive transcranial magnetic stimulation (rTMS) of the PPC during paced tapping affected timing accuracy but not precision. Additionally, musicians exhibited enhanced connectivity between the thalamus and premotor areas and, for percussionists only, between the thalamus and the PPC

(Krause, Schnitzler, & Pollok, 2010). A study combining rTMS of the PPC with motion capture, and that would compare different kinds of musicians with non-musicians, could further our understanding of the functional network underlying paced tapping and allow us to further explore how top-down processing might be implemented in finger tapping.

Another area that could be clarified by further research relates to the results of study II, with regard to the likelihood that more experienced musicians were using event-based timing for circle drawing. Testing a large group of musicians with a uniform distribution of age of initiation and years of training would help to resolve this issue. Furthermore, using unpaced sequences of sufficient length to calculate a moving window of lag one autocorrelations (Delignières & Torre, 2011) would allow tracking of changes in the timing mode used, as a function of musical experience.

5.4 Conclusion

Returning to the four questions asked at the beginning of this dissertation, the studies presented here demonstrated that musical training appears to weaken the relationship between kinematics and timing, perhaps because the more precise timing of musicians, combined with top-down processing, renders kinematic feedback less important. The research represented in this dissertation also showed that musical training is associated with better event-based timing but appears to have no effect on emergent timing, strongly supporting the independence of these two modes of timing and suggesting that musical performance is largely dominated by event-based timing. An analysis of regional cerebellar volumes demonstrated differences that were linked to musical training, lent support to the hypothesis that there is a sensitive period for musical training that affects the cerebellum as well as other brain regions, and indicated that timing precision in unpaced finger tapping is linked to the volume of lobule VI.

Three sets of findings stand out as particularly striking and invite further inquiry. First, the effect of musical training on the relationship between kinematics and timing was somewhat surprising. Second, the direction of the association of cerebellar volumes with musical training and timing control was unexpected. I suggested that these two sets of findings are linked by a top-down approach to the timing of repetitive rhythmic movement that is the result of musical training. Additional study is needed to confirm this explanation. Third, the possible use by more experienced musicians of event-based timing in a circle drawing task was also unexpected and can be confirmed by further investigation.

Table 5.1. Correlations between normalized mean squared jerk (Z-coordinate of finger movement) and detrended IRI variance in the unpaced phase of Study III, *p* values in parentheses.

	Prescribed Tapping Rate		
	250 ms	500 ms	750 ms
Musicians	-.141 (.554)	-.418 (.067)	-.328 (.159)
Non-musicians	-.735 (.010) *	-.266 (.430)	-.672 (.023) *

Note. *Significant at $p < .05$.

References

Abdul-Kareem, I. A., Stancak, A., Parkes, L. M., Al-Ameen, M., Alghamdi, J., Aldhafeeri, F. M., … Sluming, V. (2011). Plasticity of the superior and middle cerebellar peduncles in musicians revealed by quantitative analysis of volume and number of streamlines based on diffusion tensor tractography. Cerebellum (London, England), 10(3), 611–623. doi:10.1007/s12311-011-0274-1

Ad-Dab'bagh Y, Einarson D, Lyttelton O, Muehlboeck J-S, Mok K, Ivanov O, Vincent RD, Lepage C, Lerch J, Fombonne E, Evans AC. The CIVET Image-Processing Environment: A Fully Automated Comprehensive Pipeline for Anatomical Neuroimaging Research. Poster presentation at the 12th Annual Meeting of the Organization for Human Brain Mapping (OHBM) in Florence, June 2006.

Aschersleben, G. & Prinz, W. (1995). Synchronizing actions with events: The role of sensory information. Perception & Psychophysics 57,305-317.

Aschersleben, G. (2002). Temporal control of movements in sensorimotor synchronization. Brain Cogn 48,66-79.

Aschersleben, G., Gehrke, J., & Prinz, W. (2001). Tapping with peripheral nerve block: A role for tactile feedback in the timing of movements. Exp Brain Res 136,331-339.

Baer, L. H., Thibodeau, J. L. N., Gralnick, T. M., Li, K. Z. H., & Penhune, V. B. (2013). The role of musical training in emergent and event-based timing. Frontiers in human neuroscience, 7, 191. doi:10.3389/fnhum.2013.00191

Baharloo, S., Johnston, P. A., Service, S. K., Gitschier, J., & Freimer, N. B. (1998). Absolute *pitch: an approach for identification of genetic and nongenetic components. American Journal of Human Genetics, 62(2), 224–231. doi:10.1086/301704

Bailey, J. A., & Penhune, V. B. (2010). Rhythm synchronization performance and auditory working memory in early- and late-trained musicians. Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale, 204(1), 91–101. doi:10.1007/s00221-010-2299-y

Bailey, J. A., Zatorre, R. J., & Penhune, V. B. (2013). Early musical training is linked to grey matter structure in the ventral pre-motor cortex and auditory-motor rhythm. synchronization performance. Journal of Cognitive Neuroscience. doi:10.1162/jocn_a_00527

Bailey, J., & Penhune, V. B. (2012). A sensitive period for musical training: contributions of age of onset and cognitive abilities. Annals of the New York Academy of Sciences, 1252, 163–170. doi:10.1111/j.1749-6632.2011.06434.x

Balasubramaniam, R. (2006) Trajectory formation in timed rhythmic movements. In M.L. Latash & F. Lestienne (eds) Mot Control and Learning (pp 47-54). Springer: New York.

Balasubramaniam, R., Wing, A. M., & Daffertshofer, A. (2004). Keeping with the beat: movement trajectories contribute to movement timing. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 159(1), 129–134. doi:10.1007/s00221-004-2066-z

Bear, M.F., Connors, B.W., & Paradiso, M.A. (2001). *Neuroscience: Exploring the Brain* (2nd ed.). Baltimore: Lippincott Williams & Wilkins.

Berkowitz, A. L., & Ansari, D. (2010). Expertise-related deactivation of the right temporoparietal junction during musical improvisation. *NeuroImage*, *49*(1), 712–719. doi:10.1016/j.neuroimage.2009.08.042

Bernard, J. A., & Seidler, R. D. (2013). Relationships Between Regional Cerebellar Volume and Sensorimotor and Cognitive Function in Young and Older Adults. Cerebellum (London, England). doi:10.1007/s12311-013-0481-z

Billon, M., Semjen, A., & Stelmach, G. E. (1996). The Timing Effects of Accent Production in Periodic Finger-Tapping Sequences. *Journal of Motor Behavior*, *28*(3), 198–210. doi:10.1080/00222895.1996.9941745

Chakravarty, M. M., Steadman, P., van Eede, M. C., Calcott, R. D., Gu, V., Shaw, P., … Lerch, J. P. (2013). Performing label-fusion-based segmentation using multiple automatically generated templates. Human brain mapping, 34(10), 2635–2654. doi:10.1002/hbm.22092

Chen, J., Penhune, V.B., & Zatorre, R. J. (2008). Moving on time: brain network for auditory-motor synchronization is modulated by rhythm complexity and musical training. J Cogn Neurosci 20,226-239.

Chen, J., Penhune, V.B., & Zatorre, R. J. (2009). The role of auditory and premotor cortex in sensorimotor transformations. Ann N Y Acad Sci 1169,15-34.

Collier, G. L., & Ogden, R. T. (2004). Adding drift to the decomposition of simple isochronous tapping: an extension of the Wing-Kristofferson model. Journal of Experimental

Psychology. Human Perception and Performance, 30(5), 853–872. doi:10.1037/0096-1523.30.5.853

Crovitz, H. F., & Zener, K. (1962). A group-test for assessing hand- and eye-dominance. Am J Psychol 75,271-276.

Delignières, D., & Torre, K. (2011). Event-based and emergent timing: dichotomy or continuum? A reply to Repp and Steinman (2010). Journal of motor behavior, 43(4), 311–318. doi:10.1080/00222895.2011.588274

Doumas, M., & Wing, A. M. (2007). Timing and trajectory in rhythm production. J Exp Psychol: Human Perception and Performance, 33, 442-455.

Drewing, K. (2013). Delayed auditory feedback in repetitive tapping: a role for the sensory goal. *Quarterly Journal of Experimental Psychology (2006)*, *66*(1), 51–68. doi:10.1080/17470218.2012.694454

Drewing, K., & Aschersleben, G. (2003). Reduced timing variability during bimanual coupling: a role for sensory information. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *56*(2), 329–350. doi:10.1080/02724980244000396

E, K.-H., Chen, S.-H. A., Ho, M.-H. R., & Desmond, J. E. (2012). A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. Human brain mapping. doi:10.1002/hbm.22194

Elliot, M.T., Welchman, A.E., & Wing, A.M. (2009). Being discrete helps keep to the beat. Exp Brain Res 192,731-737.

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. J Neurosci 5(7),1688-1703.

Fraisse, P. (1980). Les synchronisations sensori-motrices aux rythmes [The sensorimotor synchronization of rhythms]. In J. Requin (Ed.), Anticipation et comportement (pp. 233–257). Paris: Centre National.

Franěk, M., Mates, J., Radil, T., Beck, K., & Pöppel, E. (1991). Finger tapping in musicians and nonmusicians. International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology, 11(3), 277–279.

Gaser, C., & Schlaug, G. (2003). Gray matter differences between musicians and nonmusicians. Ann N Y Acad Sci 999,514-517.

Gérard, C. & Rosenfeld, M. (1995). Pratique musicale et régulations temporelles. L'Année psychologique, 95, 571-591.

Getty, D. J. (1975). Discrimination of short temporal intervals: A comparison of two models. Perception & Psychophysics, 18(1), 1–8.

Goebl, W. & Palmer, C. (2008). Tactile feedback and timing accuracy in piano performance. Exp Brain Res 186, 471-479.

Granert, O., Peller, M., Jabusch, H.-C., Altenmüller, E., & Siebner, H. R. (2011). Sensorimotor skills and focal dystonia are linked to putaminal grey-matter volume in pianists. Journal of neurology, neurosurgery, and psychiatry, 82(11), 1225–1231. doi:10.1136/jnnp.2011.245811

Hänggi, J., Koeneke, S., Bezzola, L., & Jäncke, L. (2010). Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. Human brain mapping, 31(8), 1196–1206. doi:10.1002/hbm.20928

Hutchinson, S., Lee, L. H.-L., Gaab, N., & Schlaug, G. (2003). Cerebellar volume of musicians. Cerebral cortex (New York, N.Y.: 1991), 13(9), 943–949.

Huys, R., Studenka, B. E., Rheaume, N. L., Zelaznik, H. N., & Jirsa, V. K. (2008). Distinct timing mechanisms produce discrete and continuous movements. PLoS Computational Biology, 4(4), e1000061.

Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., & Schlaug, G. (2009). The effects of musical training on structural brain development: a longitudinal study. Annals of the New York Academy of Sciences, 1169, 182–186. doi:10.1111/j.1749-6632.2009.04852.x

Ivry, R B, Keele, S. W., & Diener, H. C. (1988). Dissociation of the lateral and medial cerebellum in movement timing and movement execution. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 73(1), 167–180.

Ivry, R. B., & Hazeltine, R. E. (1995). Perception and production of temporal intervals across a range of durations: evidence for a common timing mechanism. Journal of Experimental Psychology. Human Perception and Performance, 21(1), 3–18. doi:10.1037/0096-1523.21.1.3

Ivry, R. B., Keele, S. W., & Diener, H. C. (1988). Dissociation of the lateral and medial cerebellum in movement timing and movement execution. Experimental Brain Research. 73(1), 167-180.

Ivry, Richard B, Spencer, R. M., Zelaznik, H. N., & Diedrichsen, J. (2002). The cerebellum and event timing. Annals of the New York Academy of Sciences, 978, 302–17.

James, C. E., Oechslin, M. S., Van De Ville, D., Hauert, C.-A., Descloux, C., & Lazeyras, F. (2013). Musical training intensity yields opposite effects on grey matter density in cognitive versus sensorimotor networks. Brain Structure & Function. doi:10.1007/s00429-013-0504-z

Jäncke, L., Loose, R., Lutz, K., Specht, K., & Shah, N. J. (2000). Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. *Brain Research. Cognitive Brain Research*, *10*(1-2), 51–66.

Jäncke, L., Shah, N. J., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. Brain research. Cognitive brain research, 10(1-2), 177–183.

Johnson, J. S., & Newport, E. L. (1989). Critical period effects in second language learning: the influence of maturational state on the acquisition of English as a second language. Cognitive Psychology, 21(1), 60–99.

Joy, S., Fein, D., & Kaplan, E. (2003). Decoding Digit Symbol: Speed, memory, and visual scanning. Assessment, 10(1), 56-65. doi: 10.1177/0095399702250335

Kaplan, E., Fein, D., Morris, R., & Delis, D. (1991). WAIS-R as a neuropsychological instrument. San Antonio, TX: The Psychological Corporation.

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

Kincaid, A.E., Duncan, S., & Scott, S.A. (2002). Assessment of fine motor skill in musicians and non-musicians: differences in timing versus sequence accuracy in a bimanual fingering task. Percept Mot Skills 95,245-257.

Knudsen, E. I. (2004). Sensitive periods in the development of the brain and behavior. Journal of Cognitive Neuroscience, 16(8), 1412–1425. doi:10.1162/0898929042304796

Koch, G., Oliveri, M., Torriero, S., Salerno, S., Lo Gerfo, E., & Caltagirone, C. (2007). Repetitive TMS of cerebellum interferes with millisecond time processing. Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale, 179(2), 291–299. doi:10.1007/s00221-006-0791-1

Kral, A., & Eggermont, J. J. (2007). What's to lose and what's to learn: development under auditory deprivation, cochlear implants and limits of cortical plasticity. Brain Research Reviews, 56(1), 259–269. doi:10.1016/j.brainresrev.2007.07.021

Krause, V., Bashir, S., Pollok, B., Caipa, A., Schnitzler, A., & Pascual-Leone, A. (2012). 1 Hz rTMS of the left posterior parietal cortex (PPC) modifies sensorimotor timing. *Neuropsychologia*, *50*(14), 3729–3735. doi:10.1016/j.neuropsychologia.2012.10.020

Krause, V., Pollok, B., & Schnitzler, A. (2010). Perception in action: the impact of sensory information on sensorimotor synchronization in musicians and non-musicians. Acta Psychologica, 133(1), 28–37. doi:10.1016/j.actpsy.2009.08.003

Krause, V., Schnitzler, A., & Pollok, B. (2010). Functional network interactions during sensorimotor synchronization in musicians and non-musicians. NeuroImage, 52(1), 245–251. doi:10.1016/j.neuroimage.2010.03.081

Krings, T., Töpper, R., Foltys, H., Erberich, S., Sparing, R., Willmes, K., & Thron, A. (2000). Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. Neuroscience letters, 278(3), 189–193.

Kuhl, P. K. (2010). Brain mechanisms in early language acquisition. Neuron, 67(5), 713–727. doi:10.1016/j.neuron.2010.08.038

Lee, K. M., Skoe, E., Kraus, N., & Ashley, R. (2009). Selective subcortical enhancement of musical intervals in musicians. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 29(18), 5832–5840. doi:10.1523/JNEUROSCI.6133-08.2009

Lemoine, L., & Delignières, D. (2009). Detrended windowed (lag one) autocorrelation: a new method for distinguishing between event-based and emergent timing. Quarterly Journal of Experimental Psychology (2006), 62(3), 585–604. doi:10.1080/17470210802131896

Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. Proceedings of the National Academy of Sciences of the United States of America, 97(8), 4398–4403. doi:10.1073/pnas.070039597

Manto, M., Bower, J. M., Conforto, A. B., Delgado-García, J. M., da Guarda, S. N. F., Gerwig, M., … Timmann, D. (2012). Consensus paper: roles of the cerebellum in motor control--the diversity of ideas on cerebellar involvement in movement. Cerebellum (London, England), 11(2), 457–487. doi:10.1007/s12311-011-0331-9

Matthews, C. G., & Klove, H. (1964). Instruction manual for the Adult Neuropsychology Test Battery. Madison: University of Wisconsin Medical School.

Mauk, M. D., & Buonomano, D. V. (2004). The Neural Basis of Temporal Processing. Annual Review of Neuroscience, 27, 307–340. doi:10.1146/annurev.neuro.27.070203.144247

Müller, K., Schmitz, F., Schnitzler, A., Freund, H. J., Aschersleben, G., & Prinz, W. (2000). Neuromagnetic correlates of sensorimotor synchronization. J Cogn Neurosci 12(4),546-555.

Nigmatullina, Y., Hellyer, P. J., Nachev, P., Sharp, D. J., & Seemungal, B. M. (2013). The Neuroanatomical Correlates of Training-Related Perceptuo-Reflex Uncoupling in Dancers. Cerebral Cortex, bht266. doi:10.1093/cercor/bht266

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia, 9(1), 97–113.

Paillard, J. (1949). Quelques donne´es psychophysiologiques relatives au de´clenchement de la commande motrice [Some psychophysiological data relating to the triggering of motor commands]. L’Anne´e Psychologique 48,28–47.

Park, M.T., Pipitone, J., Baer, L., Winterburn, J.L., Shah, Y., Chavez, S., Schira, M.M., Lobaugh, N.J., Lerch, J.P., Voineskos, A., & Chakravarty, M.M. (in press). Derivation of high-resolution MRI atlases of the human cerebellum at 3T and segmentation using multiple automatically generated templates. NeuroImage.

Penhune, V. B. (2011). Sensitive periods in human development: evidence from musical training. Cortex; a journal devoted to the study of the nervous system and behavior, 47(9), 1126–1137. doi:10.1016/j.cortex.2011.05.010

Peretz, I., & Zatorre, R. J. (2005). Brain organization for music processing. Annual Review of Psychology, 56, 89–114. doi:10.1146/annurev.psych.56.091103.070225

Pollok, B., Gross, J., & Schnitzler, A. (2006). How the brain controls repetitive finger movements. J Physiology 99(1),8-13.

Ragert, P., Schmidt, A., Altenmüller, E., & Dinse, H. R. (2004). Superior tactile performance and learning in professional pianists: evidence for meta-plasticity in musicians. The European Journal of Neuroscience, 19(2), 473–478.

Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. Psychonomic Bulletin & Review, 12(6), 969–992.

Repp, B. H. (2010). Sensorimotor synchronization and perception of timing: effects of music training and task experience. Hum Mov Sci 29(2),200-213.

Repp, B. H. (2010). Sensorimotor synchronization and perception of timing: effects of music training and task experience. Human Movement Science, 29(2), 200–213. doi:10.1016/j.humov.2009.08.002

Repp, B. H., & Doggett, R. (2007). Tapping to a very slow beat: A comparison of musicians and nonmusicians. Music Perception, 24(4), 367–376. doi:10.1525/mp.2007.24.4.367

Repp, B. H., & Steinman, S. R. (2010). Simultaneous event-based and emergent timing: synchronization, continuation, and phase correction. Journal of Motor Behavior, 42(2), 111–126. doi:10.1080/00222890903566418

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

Robertson, S. D., Zelaznik, H. N., Lantero, D. A., Bojczyk, K. G., Spencer, R. M., Doffin, J. G., & Schneidt, T. (1999). Correlations for timing consistency among tapping and drawing tasks: evidence against a single timing process for motor control. Journal of Experimental Psychology. Human Perception and Performance, 25(5), 1316–1330.

Roithner, R., Schwameder, H., & Müller, E. (2000). Determination of optimal filter parameters for filtering kinematic walking data using Butterworth low pass filter. ISBS - Conference Proceedings Archive, 1(1). Retrieved from https://ojs.ub.uni-konstanz.de/cpa/article/view/2197

Schlaug, G. (2001). The brain of musicians. A model for functional and structural adaptation. Ann N Y Acad Sci 930,281-299.

Schlaug, G., Jäncke, L., Huang, Y., Staiger, J. F., & Steinmetz, H. (1995). Increased corpus callosum size in musicians. Neuropsychologia, 33(8), 1047–1055.

Schmahmann, J. D., Doyon, J., McDonald, D., Holmes, C., Lavoie, K., Hurwitz, A. S., … Petrides, M. (1999). Three-dimensional MRI atlas of the human cerebellum in proportional stereotaxic space. NeuroImage, 10(3 Pt 1), 233–260. doi:10.1006/nimg.1999.0459

Semjen, A., Schulze, H. H., & Vorberg, D. (2000). Timing precision in continuation and synchronization tapping. Psychological Research, 63(2), 137–147.

Sergent, V., Hellige, J. B., & Cherry, B. (1993). Effects of responding hand and concurrent verbal processing on time-keeping and motor-implementation processes. Brain and Cognition, 23(2), 243–262. doi:10.1006/brcg.1993.1058

Shannon, R. V., Zeng, F.-G., Kamath, V., & Wygonski, J. (1995). Speech recognition with primarily temporal cues. Science, 270(5234), 303–304. doi:10.1126/science.270.5234.303

Spencer, R. M. C., & Ivry, R. B. (2005). Comparison of patients with Parkinson's disease or cerebellar lesions in the production of periodic movements involving event-based or emergent timing. Brain and Cognition, 58(1), 84–93. doi:10.1016/j.bandc.2004.09.010

Spencer, R. M. C., & Zelaznik, H. N. (2003). Weber (slope) analyses of timing variability in tapping and drawing tasks. Journal of Motor Behavior, 35(4), 371–381.

Spencer, R. M. C., Verstynen, T., Brett, M., & Ivry, R. B. (2007). Cerebellar activation during discrete and not continuous timed movements: An fMRI study, NeuroImage, 36, 378-387. doi:10.1016/j.neuroimage.2007.03.009

Spencer, R. M. C., Zelaznik, H. N., Diedrichsen, J., & Ivry, R. B. (2003). Disrupted timing of discontinuous but not continuous movements by cerebellar lesions. Science (New York, N.Y.), 300(5624), 1437–1439. doi:10.1126/science.1083661

Steele, C. J., Bailey, J. A., Zatorre, R. J., & Penhune, V. B. (2013). Early musical training and white-matter plasticity in the corpus callosum: evidence for a sensitive period. The Journal of neuroscience: the official journal of the Society for Neuroscience, 33(3), 1282–1290. doi:10.1523/JNEUROSCI.3578-12.2013

Stevens, L.T. (1886). On the time sense. Mind 11,393-404.

Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. NeuroImage, 44(2), 489–501. doi:10.1016/j.neuroimage.2008.08.039

Stoodley, C. J., Valera, E. M., & Schmahmann, J. D. (2012). Functional topography of the cerebellum for motor and cognitive tasks: an fMRI study. NeuroImage, 59(2), 1560–1570. doi:10.1016/j.neuroimage.2011.08.065

Studenka, B. E., & Zelaznik, H. N. (2008). The influence of dominant versus non-dominant hand on event and emergent motor timing. Human movement science, 27(1), 29–52. doi:10.1016/j.humov.2007.08.004

Studenka, B. E., & Zelaznik, H. N. (2011). Synchronization in repetitive smooth movement requires perceptible events. Acta Psychologica, 136(3), 432–441. doi:10.1016/j.actpsy.2011.01.011

Studenka, B. E., Zelaznik, H. N., & Balasubramaniam, R. (2012). The distinction between tapping and circle drawing with and without tactile feedback: An examination of the sources of timing variance. Quarterly Journal of Experimental Psychology. doi:10.1080/17470218.2011.640404

Teulings, H. L., Contreras-Vidal, J. L., Stelmach, G. E., & Adler, C. H. (1997). Parkinsonism reduces coordination of fingers, wrist, and arm in fine motor control. Experimental Neurology, 146(1), 159–170. doi:10.1006/exnr.1997.6507

Thaut, M. H., Stephan, K. M., Wunderlich, G., Schicks, W., Tellmann, L., Herzog, H., … Hömberg, V. (2009). Distinct cortico-cerebellar activations in rhythmic auditory motor synchronization. Cortex; a journal devoted to the study of the nervous system and behavior, 45(1), 44–53. doi:10.1016/j.cortex.2007.09.009

Théoret, H., Haque, J., & Pascual-Leone, A. (2001). Increased variability of paced finger tapping accuracy following repetitive magnetic stimulation of the cerebellum in humans. Neuroscience letters, 306(1-2), 29–32.

Tiemeier, H., Lenroot, R. K., Greenstein, D. K., Tran, L., Pierson, R., & Giedd, J. N. (2010). Cerebellum development during childhood and adolescence: a longitudinal morphometric MRI study. NeuroImage, 49(1), 63–70. doi:10.1016/j.neuroimage.2009.08.016

Torre, K., & Balasubramaniam, R. (2009). Two different processes for sensorimotor synchronization in continuous and discontinuous rhythmic movements. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 199(2), 157–166. doi:10.1007/s00221-009-1991-2

Turvey, M.T. (1977). Preliminaries to a theory of action with reference to vision. In R.E.Shaw & J. Bransford (Eds.), Perceiving acting, and knowing: Toward an ecological psychology (pp. 211-265). Hillsdale, NJ: Erlbaum.

Verstynen, T., Konkle, T., & Ivry, R. B. (2006). Two types of TMS-induced movement variability after stimulation of the primary motor cortex. *Journal of Neurophysiology*, *96*(3), 1018–1029. doi:10.1152/jn.01358.2005

Vorberg, D., & Wing, A. (1996). Modeling variability and dependence in timing. In Herbert Heuer and Steven W. Keele (Ed.), Handbook of Perception and Action (Vol. Volume 2, pp. 181–262). Academic Press. Retrieved from http://www.sciencedirect.com/science/article/pii/S1874582206800071

Watanabe, D., Savion-Lemieux, T., & Penhune, V. B. (2007). The effect of early musical training on adult motor performance: evidence for a sensitive period in motor learning. Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale, 176(2), 332–40. doi:10.1007/s00221-006-0619-z

Wechsler, D. (1997). Wechsler Adult Intelligence Scale: WAIS-III. Manual. San Antonio, TX: The Psychological Corporation, 1997

Wing, A. M. (1977). Perturbations of auditory feedback delay and the timing of movement. *Journal of Experimental Psychology. Human Perception and Performance*, *3*(2), 175–186.

Wing, A. M. (2002). Voluntary timing and brain function: an information processing approach. Brain and Cognition, 48(1), 7–30. doi:10.1006/brcg.2001.1301

Wing, A. M., & Kristofferson, A. B. (1973). Response delays and the timing of discrete motor responses. Perception & Psychophysics, 14(1), 5–12.

Winterburn, J. L., Pruessner, J. C., Chavez, S., Schira, M. M., Lobaugh, N. J., Voineskos, A. N., & Chakravarty, M. M. (2013). A novel in vivo atlas of human hippocampal subfields using high-resolution 3 T magnetic resonance imaging. NeuroImage, 74, 254–265. doi:10.1016/j.neuroimage.2013.02.003

Woollett, K., & Maguire, E. A. (2011). Acquiring “the Knowledge” of London’s layout drives structural brain changes. Current Biology: CB, 21(24), 2109–2114. doi:10.1016/j.cub.2011.11.018

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

Zelaznik, H. N., & Rosenbaum, D. A. (2010). Timing processes are correlated when tasks share a salient event. Journal of Experimental Psychology: Human Perception and Performance. doi:10.1037/a0020380

Zelaznik, H. N., Spencer, R. M. C., & Ivry, R. B. (2002). Dissociation of explicit and implicit timing in repetitive tapping and drawing movements. J Exp Psychol Hum Percept Perform 28(3),575-88.

Zelaznik, H. N., Spencer, R. M. C., Ivry, R. B., Baria, A., Bloom, M., Dolansky, L., et al. (2005). Timing Variability in Circle Drawing and Tapping: Probing the Relationship Between Event and Emergent Timing. Journal of Motor Behavior, 37(5), 395-403.