# LINKING THE SPATIAL DIMENSION TO THE TIMING CONTROL OF RHYTHMIC MOVEMENTS

By

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#### ABSTRACT

Rhythmically timed movements are integral to a wide range of human behaviors, including the production of fluent speech, music performance, dance, and sports, to name a few. Deficits in the timing of rhythmic movements have been observed in numerous neurological conditions, which can be devastating for an individual's quality of life. One common method to investigate mechanisms underpinning the timing of rhythmic actions is a finger tapping task in which individuals synchronize finger taps with a series of tones that establish a target inter-tap interval (ITI) and then continue to produce the target interval after the tones stop. The data of interest in these studies have almost exclusively consisted of the time series of tap onsets and associated sequence of ITIs. Because all movements are inherently spatiotemporal, the thesis investigated herein is that our understanding of timing processes is incomplete because previous work ignores the contributions of spatial elements of an individual's movements to their timing control. The experiments reported here fill this gap by using continuous motion tracking to measure the spatiotemporal dynamics of paced and unpaced rhythmic finger tapping and by considering the relation between spatiotemporal measures and timing accuracy and precision.

Five experiments tested a series of hypotheses about contributions of spatiotemporal factors to the timing control of rhythmic movements. Experiment 1 tested a *preferred velocity hypothesis* that integrates amplitude and tempo for unpaced tapping. Participants completed unpaced tapping tasks that separately assessed preferred movement amplitude (finger height) and tempo (Mean ITI). In support of this hypothesis, participants produced similar amplitudes and tempi regardless of instructions for either preferred amplitude or tempo. Experiments 2 and 3 tested an *amplitude control hypothesis* for paced tapping where participants matched a wide range of target ITIs. Consistent with this hypothesis, individuals decreased tap amplitude with

shorter target ITIs and variability in amplitudes predicted variability in ITIs. Further supporting this hypothesis, forcing participants to produce low and high amplitudes during paced tapping interfered with timing accuracy and precision in a manner consistent with amplitude as a parameter in timing control. The *preferred velocity hypothesis* was further supported by results showing that timing was less variable for conditions where participants tapped at target amplitudes and tempi that, in combination, were closer to their preferred velocity.

Experiment 4 extended this line of work to timing control of tapping at slow tempi (near the temporal boundary where perceived rhythm breaks down). Of primary interest was a *dwell time hypothesis*, which proposes that at slow target ITI when amplitude cannot be increased further to lengthen intervals, participants increase dwell time (how long their finger rests on the table) to produce longer ITIs. Providing initial support for this hypothesis, participants kept tap amplitude constant and increased tap dwell time to produce longer ITIs. At the slowest target ITI, a bimodal distribution in tap dwell times also was observed, reflecting individual differences in dwell time strategy where some participants kept a constant proportion of dwell time to target ITI, while others increased the proportion of dwell time at slower tempi (longer ITIs).

As a follow-up, Experiment 5 manipulated tap dwell time during paced tapping at comfortable and very slow tempi (ITIs). Participants successfully lengthened or shortened their dwell time at the slow ITI, regardless of their preferred dwell time. Timing accuracy and precision at the slow ITI were particularly poor when participants were instructed to produce short dwell times, suggesting that longer dwell times at slow tempi facilitate temporal accuracy and precision. Altogether, results provide novel evidence of contributions of spatial characteristics of rhythmic movements to their temporal control and lays the foundations for a new theory of timing and temporal control that links the dimensions of space and time. Copyright by CAROLYN KROGER 2022

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## LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
ADHD	Attention Deficit Hyperactivity Disorder
BG	Basal Ganglia
BPM	Beats Per Minute
CV	Coefficient of Variation
DT	Dwell Time
EEG	Electroencephalogram
fMRI	Functional Magnetic Resonance Imaging
HD	Huntington Disease
IOI	Inter-onset Interval
IRI	Inter-response Interval
ITI	Inter-tap Interval
MEP	Motor Evoked Potential
PD	Parkinson's Disease
SD	Standard Deviation
SE	Standard Error
SMT	Spontaneous Motor Tempo
SMA	Spontaneous Motor Amplitude
SNc	Substantia Nigra Pars Compacta
TMS	Transcranial Magnetic Stimulation
W&K	Wing and Kristofferson

#### **CHAPTER 1: OVERVIEW**

Rhythmically timed movements, characterized by some form of periodic or quasiperiodic movement pattern, are integral to a range of human behaviors. These include the production of fluent speech, music performance, dance and sports, to name a few. Deficits in the timing of rhythmic movements have been observed in a wide range of neurological conditions, including Parkinson's disease (PD), Huntington disease (HD), developmental coordination disorder, developmental stuttering, constructional apraxia, and cerebellar lesions (de Castelnau et al., 2007; Falk et al., 2015; Freeman et al., 1996; Ivry & Corcos, 1993; Ivry & Keele, 1989; Ivry et al., 1988; Kobinata et al., 2020; O'Boyle et al., 1996; Rose et al., 2020; Whitall, et al., 2008; Wing et al., 1984). Timing deficits associated with neurological disease or brain injury can have devastating repercussions for independence and quality of life. Dysfunction in the coordination of timed movements can disrupt gait and the control of fine motor movements such as speech production and eating (Caron et al., 2020; Dayalu & Albin, 2015; Jankovic, 2008; Park, 2017; Sares et al., 2019; Weintraub & Mamikonyan, 2019; Zelaznik et al., 1997).

A general theme of many studies investigating control processes in the timing of rhythmic movements has been to focus exclusively on the temporal dimension of movement as a probe of the brain's clock, while ignoring the spatial dimension. Yet, all movements are inherently spatiotemporal. One common approach has been to study the timing of a very simple rhythmic movement, namely finger tapping, in unpaced and paced task contexts. For unpaced tasks, participants are typically asked to tap at a tempo that is not too fast or too slow, but just right for them, providing an assessment of their preferred tapping tempo (Collyer, et al, 1994; McAuley et al., 2006). Most paced tasks, in contrast, specify a target inter-tap interval, which individuals attempt to match and maintain. Paced timing has often been assessed via a

synchronization-continuation (sometimes abbreviated as sync-continue) tapping task where individuals are asked to synchronize a series of finger taps with an isochronous auditory pacing signal that establishes the target inter-tap interval. They then continue tapping at the same tempo after the pacing signal stops for a fixed duration or number of taps, thus attempting to produce the target inter-tap interval in the absence of its explicit presentation.

Sync-continue tapping studies have focused almost exclusively on time series of tap onsets and associated produced inter-tap intervals to provide estimates of an individual's temporal accuracy (difference between produced and target inter-tap intervals) and precision (variability in the produced intervals). These measures are often used to make inferences about the characteristics of the underlying timing mechanism (clock) that brains use to produce the series of inter-tap intervals. Little to no consideration is given to how the spatial dimension of an individual's finger tapping movements may contribute to timing performance.

The overarching goal of this dissertation is to bridge this gap by using continuous motion tracking to investigate how the spatial characteristics of an individual's movements may contribute to their timing control for unpaced and paced rhythmic finger tapping. Five experiments were conducted to test novel hypotheses about how spatiotemporal factors ignored in most rhythmic finger tapping studies potentially affect individual's preferred tempi in unpaced tasks and their temporal accuracy and precision in paced sync-continue tapping. By bringing the dimension of space into the study of timing mechanisms, rather than treating the time series of tap onsets and associated produced inter-tap intervals as the only data of interest, this dissertation changes our views about the nature of neural mechanisms for timing events.

Chapter 2 reviews data and theories related to the temporal control of rhythmic movements with a focus primarily on unpaced and paced rhythmic finger tapping. First, temporal

characteristics of rhythmic finger tapping and related phenomena as well as neurological findings are reviewed. Next, interval-based timing theories and a prominent interval timing model for rhythmic finger tapping performance are discussed. These theories and the associated model assume a central clock-like mechanism that meters out each temporal interval, which is then produced by a separate motor mechanism. Next is a brief review of studies on spatiotemporal interactions in rhythmic timing that cannot be accounted for by interval-based timing theories, highlighting some limitations of the models. Finally, Chapter 2 develops several novel hypotheses about how the spatial characteristics of rhythmic finger tapping movements may affect their timing.

Chapter 3 provides a general overview of methods used in this dissertation. This chapter describes survey measures and the sync-continue tapping task used to test proposed hypotheses about rhythmic timing. Methods for motion-tracking data collection, processing, and analysis as well as primary dependent measures used to evaluate spatial and temporal performance are described.

Chapter 4 presents Experiment 1, which tests a preferred velocity account of the concept of preferred tempo in unpaced rhythmic tapping. The proposed *preferred velocity hypothesis* assumes that individuals' intrinsic preferences for tempo and amplitude in unpaced tapping are critically related, reflecting their preferred tap velocity according to V = 2A/ITI. In this experiment, participants first performed a spontaneous motor amplitude (SMA) task in which they repetitively tapped their finger at their preferred amplitude followed by a spontaneous motor tempo (SMT) task in which they tapped their finger at their preferred tempo. Then, participants completed a target amplitude version of the SMT task where they tapped at their preferred tempo at 3 target finger heights. Of primary interest is (1) how tightly coupled produced inter-tap

intervals and produced amplitudes are across the preferred tempo and preferred amplitude tasks, respectively, and (2) whether different target amplitudes impact individual's preferred tempi in the target amplitude version of the SMT task.

Chapter 5 presents an initial test of an *amplitude control hypothesis* for paced rhythmic tapping using the sync-continue task at a wide range of target inter-tap intervals (tempi). The *amplitude control hypothesis* proposes that rather than individuals using an internal clock to meter out the target inter-tap interval, people tap at a constant (preferred) velocity and alter the height (amplitude) of their finger movements to produce the target inter-tap interval (ITI). This hypothesis predicts that individuals will reduce tap amplitude to produce shorter target inter-tap intervals and increase tap amplitude to produce longer target inter-tap intervals. As a test of this hypothesis, participants in Experiment 2 completed sync-continue tapping at a range of target tempi from fast to slow, corresponding to target inter-tap intervals from 250 ms to 1150 ms in 150 ms steps. Here, the *amplitude control hypothesis* predicted a linear relation between tap amplitude and produced inter-tap interval, with higher amplitudes produced for longer target inter-tap intervals (slower tempi). An alternative *velocity control hypothesis* is also considered, which proposes that people keep amplitude constant across different target inter-tap intervals and instead change the average velocity of their movements to match the target inter-tap interval.

Chapter 6 presents a further test of preferred velocity and the amplitude control hypotheses initially examined in Experiments 1 and 2, respectively. The same participants from Experiment 1 returned to complete Experiment 3, where they performed sync-continue tapping at a range of target inter-tap intervals with the twist that they also had to match three different target amplitudes (a low amplitude, their preferred amplitude measured in Experiment 1, and a high amplitude). Timing accuracy and variability were evaluated for the different combinations

of target amplitude and target inter-tap intervals to assess how explicitly manipulating tap amplitude affected timing performance for different target inter-tap intervals. The *amplitude control hypothesis* predicts that timing performance will be best in conditions when combinations of target amplitude and target ITI are congruent (i.e., low amplitudes at short target inter-tap intervals and high amplitudes at long target inter-tap intervals) and worst in conditions when combinations of target amplitude and target ITI are incongruent (i.e., high amplitudes at short intervals and low amplitudes at long intervals). This experiment also tested the *preferred velocity hypothesis* by examining whether preferred velocity (measured in Experiment 1) predicted timing performance, where performance is predicted to be better in conditions that required tap velocities closer to each participant's preferred velocity.

Chapters 7 and 8 extend this new line of work to the timing control of paced tapping at slow tempi (near the temporal boundary where perceived rhythm breaks down). Of primary interest is the role of dwell time (the duration that participants keep their finger on the table between tap onsets) in timing accuracy and precision. Chapter 7 introduces a *dwell time hypothesis*, which proposes that, at slow tempi when tap amplitude cannot be increased further to lengthen inter-tap intervals, individuals use tap dwell time to match the target inter-tap interval. Experiment 4 tests this hypothesis by having participants perform sync-continue tapping at tempi ranging from comfortable to very slow (506 ms – 1709 ms target ITIs). Changes in tap dwell time across target tempi were examined to test whether participants kept dwell-time *hypothesis*. Chapter 8 reports Experiment 5, which explicitly manipulated tap dwell time during paced tapping at a comfortable tempo and very slow tempo. Participants first performed sync-continue tapping without instructions regarding dwell time and then did sync-continue tapping while

instructed to produce maximally-short or maximally-long dwell times. The *dwell time hypothesis* predicts that timing performance will be better for dwell time conditions that more closely matched participants' preferred dwell times and that, in general, performance will be worse when participants are forced to produce short dwell times to match long target inter-tap intervals (slow tempi).

Finally, Chapter 9 summarizes the results of the five experiments and their support for the proposed hypotheses. The contributions of the reported experiments are discussed in the context of previous work as well as implications for theories of rhythmic movement timing. Limitations of the experiments and future avenues for research are also discussed.

#### **CHAPTER 2: BACKGROUND**

### Introduction

Researchers have studied human rhythmic movement timing in various contexts for over a century (Stevens, 1886; Woodworth, 1899) and the topic has garnered considerable attention in the last few decades (Repp, 2005). In the context of this dissertation, "rhythmic" refers to the quality of a repeated pattern (of stimuli or actions) having strong temporal regularity or periodicity. Studies of rhythmic behaviors in the milliseconds-to-seconds time scale have often used tasks that require participants to produce simple, regularly timed repetitive motor movements (e.g., tapping a finger) and examined sequences of produced inter-tap intervals (ITIs). Research on rhythmic movement timing has broadly focused on the production of unpaced (sometimes referred to as "spontaneous") rhythmic movements (Fraisse, 1982) and those paced by a metronome or other regularly timed signal. In terms of paced movements, studies have examined synchronization with a pacing signal (Erlich, 1958; Michon, 1967) as well as the reproduction of or continuation of interval sequences after the pacing signal has stopped (Stevens, 1886; Wing & Kristofferson, 1973b). Paced and unpaced tasks have been used in a broad variety of contexts and populations to assess timing performance and make inferences about internal timekeeping mechanisms.

#### Timing of Unpaced Rhythmic Movements and the Concept of Preferred Tempo

In terms of unpaced rhythmic timing, research has focused on the tempo produced during repetitive motor actions, operationalized as the mean produced inter-response interval (IRI), and the variability of produced IRIs. In the context of finger tapping tasks, the IRI is the same as the inter-tap interval (ITI). One widely used paradigm to estimate an individual's preferred motor tempo is the spontaneous motor tempo (SMT) task, in which a participant is asked to repetitively

tap their finger at their self-selected, most natural or comfortable pace (Fraisse, 1956). In this task, participants are instructed to produce their "most comfortable" or "just right" finger tapping tempo as a measure of preferred tempo. The tempo and variability of inter-tap intervals (ITI) are thought to reflect intrinsic qualities of an internal timing mechanism (Hammerschmidt et al., 2021). Several key findings regarding preferred tapping tempo and variability have been reported across studies of SMT. I will briefly describe three here: inter- and intra-individual differences in preferred motor tempo, differences between preferred motor tempo in clinical populations and healthy controls, and the correlation between preferred motor tempo and preferred perceptual tempo.

Fraisse (1982) was one of the first researchers to note that the range of tempi produced by different individuals during SMT finger tapping centered around a mean of 600 ms inter-tap intervals (ITIs), but he observed that between individuals, SMTs ranged from ~200 ms to 1400 ms ITI. He also noted that within individuals, there was very little (3 – 5 %) variation in produced mean tempo from trial-to-trial. Since then, other studies have shown that the average SMT produced by adults tends to be around 500 – 600 ms ITI, and that each individual's SMT is not one set value but is centered within a range of frequencies known as an entrainment window (Hammerschmidt et al, 2021; McAuley et al., 2006; Moelants, 2002). When SMT is measured across trials and across days, participants tend to show less within-subject than between-subject variability (Hammerschmidt & Wollner, 2022; Moussay, et al., 2002), reflecting some stability in an individual's preferred motor tempo. Other factors such as age, time of day, and clinical diagnoses systematically affect an individual's SMT (Drake et al., 2000; Hammerschmidt et al., 2021; Kliger-Amrani & Zion-Golumbic, 2020b; Rose et al., 2020).

In terms of the impact of age on preferred tempo, a cross-sectional study by McAuley and colleagues (2006) examined SMT in 305 individuals ranging in age from 4 to 95 years and showed that SMT was faster for young children and slowed into adulthood, at which point it remained relatively stable, then slowed further in advanced age (75 and beyond). In another unpaced task, participants produced their fastest and slowest motor tempi by tapping their finger as fast as possible and as slow as possible while maintaining a regular rhythm. Adults produced a range of fastest and slowest tempi from around 170 to 2500 ms ITI, with the range being narrower for children (under 18 years) and older adults (75 + years). This range is thought to reflect an entrainment region, outside of which the perception and production of rhythm breaks down. Moreover, studies have shown that this range of tempi is ideal for performance on other rhythmic perceptual and motor tasks (Fraisse, 1963; Kliger-Amrani & Zion-Golumbic, 2020b).

In addition to the effects of aging on SMT over the lifespan, small systematic changes in preferred tempo have been observed over the course of the day. Several studies of SMT production at different times in the 24-hour cycle have found that SMT was related to arousal, where small increases in produced tempi were associated with higher arousal (Moussay et al., 2002). Hammerschmidt and Wollner (2022) had participants produce tapping SMT at four different times of day for seven days. Results showed that within-subjects, changes in arousal over the course of the day associated with different chronotypes (e.g., "morning larks" versus "night owls") and predicted changes in SMT throughout the day, where increases in arousal within an individual were predictive of increasingly fast SMT during the 24-hour cycle.

Characteristic differences in SMT production have also been shown in some clinical populations compared with healthy controls. Rose et al. (2020) had adults with Parkinson's Disease (PD) and young healthy controls as well as age-matched controls tap with their finger or

toes at their preferred tempo. For finger tapping, patients with PD had faster SMTs than young healthy controls but not age-matched controls, and patients with PD were more variable in the timing of their finger taps than age-matched but not young healthy controls. For toe tapping, patients with PD had faster SMT than both young healthy and age-matched controls. In a finger tapping study on patients with basal ganglia (BG) lesions following stroke, Schwartze and colleagues (2011) observed more variability in produced SMT in the lesion group than controls. These studies suggest a role for the BG in unpaced timing performance, as PD is known to originate from neurodegeneration in the substantia nigra pars compacta (SNc), a BG nucleus component. In a study on attention deficit hyperactivity disorder (ADHD), Kliger-Amrani and Zion-Golumbic (2020b) had adults diagnosed with ADHD and age-matched controls tap with their index finger while counting from 1 to 10 at their preferred tempo. Individuals with ADHD had faster mean SMT and greater variability across SMT trials than controls. Together, these results highlight differences in preferred motor tempo and variability of produced inter-tap intervals during unpaced rhythmic movements in neurological populations when compared to healthy individuals.

In addition to reflecting preferences for temporal production, SMT is associated with preferred perceptual tempo, that is, the preferred tempo of auditory events such as musical beats (Moelants, 2002). The notion of preferred tempo is well-established in the field of human timing research (Baruch et al., 2004; Boltz, 1994; Drake, et al., 2000; Halpern, 1988; Lapidaki & Webster, 1991). Similar to preferred motor tempo, preferred perceptual tempo has been shown to be about 100 - 120 BPM (500 - 600 ms IOI), and research has shown that SMT is highly predictive of preferences for perceptual tempo, for example when listening to sequences of auditory tones or musical pieces (McAuley et al., 2006; Michaelis et al., 2014; van Noorden &

Moelants, 1999). In their large-scale study discussed previously, McAuley et al. (2006) measured preferred perceptual tempo by having participants rate the tempo of tone sequences as "too fast," "too slow," or "just right" on a 20-point scale in addition to measuring SMT. Across a wide range of ages, SMT and preferred perceptual tempo were correlated, with faster SMT predicting preferences for faster tempi of tone sequences. The relationship between preferred perceptual and motor tempi has also been examined using motor-evoked potentials (MEPs). In a transcranial magnetic stimulation (TMS) study, Michaelis et al. (2014) measured preferred motor tempo in an SMT finger tapping task. Then they had participants passively listen to tone sequences equal to or faster/slower than their SMT and delivered single-pulse TMS to the primary motor cortex while MEPs were recorded in participants' dominant hand. Behavioral results confirmed that ratings of preferred perceptual and motor tempi were positively correlated. Furthermore, corticospinal excitability was modulated by listening to their preferred tempo, as observed in greater changes to MEPs for auditory rhythms at or near their preferred tempo, which suggests a role for auditory rhythms at preferred tempi in priming rhythmic movements.

To summarize, studies on unpaced rhythmic timing show that individuals demonstrate a range of preferred spontaneous motor tempi (SMT) that center on an average of  $\sim$ 500 – 600 ms ITI and extend  $\sim$ 300 ms ITI faster and  $\sim$ 900 ms ITI slower, reflecting an entrainment region. Outside of the bounds of these tempi, the perception and production of rhythm breaks down. An individual's preferred tempo range is dependent on individual factors such as age and clinical diagnosis, with a general slowing of SMT from childhood to adulthood and faster SMT associated with various neurological conditions that affect rhythmic timing. Within individuals, SMT tends to be relatively consistent across trials and days, with small fluctuations associated with changes in arousal. Furthermore, SMT is correlated with preferred perceptual tempo,

implicating a common internal timekeeper for rhythmic perceptual and motor tasks. The strong relationship between preferred perceptual and motor tempi raises the question whether other preferences are related to producing rhythmic movements. For example, do people have preferred movement amplitudes or velocities associated with their preferred tempo? This and related questions will be addressed later in this dissertation.

#### **Timing of Paced Rhythmic Movements**

A second category of tasks for investigating rhythmic movement timing is paced tasks. These involve coordinating motor actions in time with a rhythmic sequence of perceptual events. Sensorimotor synchronization (SMS) involves aligning movement onsets with the onsets of a periodic stimulus such as a metronome, often by tapping a finger in time with auditory events such as tones or clicks that occur at regular intervals. Synchronization performance has been examined across a wide variety of tasks and modalities (for two comprehensive reviews, see Repp, 2005 and Repp & Su, 2013), but I will focus on SMS in finger tapping tasks with an auditory stimulus. Two aspects of performance on these tasks are discussed below: first, an increase in variability of produced inter-tap intervals (ITI) with mean ITI and second, a difference in synchronization performance between musicians and non-musicians.

Although participants are able to synchronize inter-tap intervals (ITI) with an auditory pacing stimulus reasonably well between around 200 ms to 2000 ms ITI, they do so with some variability (Repp, 2006). That is to say, there are measurable asynchronies between the onset of the tone and each produced tap, and the variability of produced inter-tap intervals (ITI) has historically been used as a global measure of synchronization performance. Across tempi (mean ITIs) within the typical adult entrainment region, ITI variability during synchronization conforms to a pattern consistent with Weber's law, which specifies a ratio of ITI variability to tapping

tempo. Weber's law was first established in the context of sensation (Fechner, 1860/1966) to describe sensitivity to changes in stimulus intensity proportional with stimulus magnitude and was first applied to movement characteristics by Woodworth (1899). Since then, it has been used to characterize variability in time perception and production for intervals in the millisecond-tosecond range (Gibbon, 1977; Gibbon et al., 1984; Rakitin et al., 1998; Wearden & McShane, 1988). In its application to produced time intervals during paced tapping tasks, Weber's law describes a linear increase in standard deviation (SD) of produced inter-tap intervals (ITI) as a function of the mean ITI. This relationship is represented as a constant ratio, often referred to as a Weber fraction. Thus, in practice, the coefficient of variation (CV = SD/Mean ITI) is often used to quantify temporal variability during SMS to account for systematic changes in standard deviations (SD) of produced ITI as a function of mean ITI.

The increase in SD of produced ITI with longer synchronization intervals is wellestablished in studies on finger tapping with isochronous (equally spaced in time) sequences of sounds. Loras et al. (2012) directly tested the correspondence between produced timing variability and variability predicted by Weber's law across a range of comfortable tapping tempi. Participants synchronized to isochronous metronome clicks at inter-onset intervals (IOIs) ranging from 500 to 950 ms in 150 ms increments by tapping their finger in counterclockwise succession on 3 touchpads arranged in an equilateral triangle, examining the time series of inter-tap intervals (ITIs). They found that standard deviation (SD) of ITI increased linearly with IOI and CV remained relatively constant across all tempi, in accordance with Weber's law.

Peters (1989) examined timing variability at a range of rates extending faster and slightly slower. Participants synchronized finger tapping with isochronous sequences of tones at IOIs ranging from 180 to 1000 ms. The SD of produced ITIs generally increased with IOI duration.

However, CV sharply decreased from 180 to 300 ms IOI, then very gradually decreased as IOI slowed from 300 to 1000 ms IOI. Peters interpreted these results as evidence that tempi faster than 300 ms IOI were too fast for precise timing control during finger tapping and that SD scales with IOI duration at rates above 300 ms IOI.

Mates et al. (1994) extended these findings to tempi slower than 1000 ms IOI. They had participants perform finger tapping SMS with isochronous sequences of tones at IOIs of 300 to 4600 ms. The SD of ITI generally increased with IOI duration; however, the nature of this relationship was different for the fastest (300 ms IOI) and slowest (2400 - 4600 ms IOI)conditions. When examining CV of produced ITI, there was increased variability in the 300 ms IOI condition, reflecting limitations in synchronization performance at fast tempi. Furthermore, CV was approximately consistent between the 450 and 1800 ms IOI conditions but increased around the 2400 ms IOI condition. Participants tended to show a pattern of variability consistent with Weber's law for interval production in the range of comfortable tapping tempi (between 450 and 1800 ms ITI), that is, a constant linear increase in SD with ITI. However, for slow tapping tempi (above 1800 ms ITI), variability increased above what would be predicted. These findings are in accordance with studies showing that rhythms are best perceived and produced within an entrainment region of around 300 to 1800 ms IOI for the typical adult. However, outside the range of comfortable tapping tempi, synchronization variability increases over and above what is predicted by Weber's law. Taken together, these findings support that variability in synchronized tapping with an auditory pacing stimulus conforms to Weber's law, but only for tempi within a comfortable ITI range (for a review on tempo limits of SMS, see Repp, 2006).

A second consideration for SMS timing performance has been the role of musical training. This has historically been an area of interest because musicians have extensive practice

and experience with synchronizing rhythmic movements to auditory stimuli, for example when practicing an instrument with a metronome or playing in an ensemble. Results on effects of musical experience on synchronization performance have shown that musicians show better temporal accuracy and precision (variability) than nonmusicians. Repp and Doggett (2007) had six musicians and ten non-musicians synchronize finger tapping with isochronous tone sequences ranging from 1000 to 3500 ms IOIs. These tempi were slower than those used in most other synchronization studies and IOIs above around 1000 ms to 1500 ms (i.e., outside the typical adult entrainment region) require more effort (e.g., attentional resources) to maintain synchronization accuracy (smaller mean asynchronies) than nonmusicians. For both musicians and nonmusicians, SD increased with ITI; however, nonmusicians showed a greater increase in SD, especially at slower rates, and overall musicians were less variable in their timing compared to nonmusicians.

One study by Drake et al. (2000) examined relationships between SMT and synchronization performance in musicians and nonmusicians. They had 80 musicians and 100 nonmusicians across a wide age range perform SMT and synchronization with isochronous sequences of 150 to 1500 ms IOI, as well as synchronization with a musical piece. Results showed an interaction between musical training, synchronization accuracy, and SMT. Musicians were more successful (accurate) in synchronizing than nonmusicians and also had a tendency to produce slower SMT than nonmusicians. They also found that participants chose to synchronize with musical pieces at beat levels closer to their SMT and overall SMT was correlated with synchronization tempo.

Scheurich et al. (2018) followed up on this relationship between musical training, synchronization ability, and preferred tempo. Twenty musicians and twenty nonmusicians completed a musical finger tapping task in which they were instructed to tap the rhythm of a familiar melody ("Mary Had a Little Lamb") on a keyboard that produced each successive note of the melody with each tap. They first tapped the melody at their preferred tempo, then in synchrony with a metronome set at their preferred tempo as well as 15% and 30% faster and slower. Musicians had better synchronization accuracy than nonmusicians, especially at slower tempi. They also had more flexibility in synchronizing to tempi farther from their preferred tempo. Together, these findings show a musical training advantage for temporal performance during SMS in auditory-paced finger tapping. They also show that musicians have an extended entrainment region where musicians are more successful at synchronization with tempi farther from their preferred tempo than nonmusicians.

An extension of the sensorimotor synchronization (SMS) task is the synchronizationcontinuation (hereafter: sync-continue) task. In this task, participants first synchronize with a rhythmic pacing stimulus and then continue to produce movements at the same tempo after the pacing stimulus stops. In contrast with SMS-only tasks, the sync-continue paradigm has two task phases: a sync phase in which participants produce movement onsets in time with external perceptual events (e.g., a metronome) and a continue phase in which participants continue to produce the tempo provided during the sync phase without the presence of externally-paced event onsets (e.g., after the metronome stops). This type of task allows for the examination of movement timing performance at specific target tempi without asynchrony information from external stimuli. The sync-continue paradigm (first introduced by Stevens, 1886) has been used extensively to study how people maintain a target tempo during rhythmically timed movements,

with variations in type of rhythmic movement, pacing signal modality, and populations studied. As a simple demonstration of its wide use, a Google Scholar search of "synchronizationcontinuation" returned 784 results! For this dissertation, I will focus primarily on sync-continue finger tapping tasks with an auditory pacing stimulus (for a review, see Collyer & Church, 1998). Three key aspects of timing performance during sync-continue tapping are discussed below: first, patterns of temporal variability and accuracy (e.g., "drift") during continuation at different target tempi, second, effects of musical training on continuation timing performance, and third, findings from neuroimaging studies comparing brain activity during the sync and continue phases of sync-continue tapping.

The first aspect of sync-continue tapping considered is timing performance during the continue phase, specifically the accuracy in maintaining the sync tempo (i.e., the mean produced continuation inter-tap interval) and the variability of produced inter-tap intervals (ITIs) during continuation. Semjen et al. (2000), had participants perform sync-continue finger tapping at target ITI ranging from 200 to 640 ms. They found that, while ITIs were very close to the target ITI during the sync phase, during the continue phase mean ITIs were shorter for longer target ITIs, reflecting a tendency to speed up during continuation, especially for slower tempi. They also found that SD of produced ITIs increased with target ITI for both tapping phases. This study showed that timing variability (SD) increases with ITI for continuation tapping in accordance with Weber's law and that participants tended to speed up (drift) during continuation tapping relative to the synchronization tempo, especially at slower target tempi.

Madison (2001) examined drift during the continue phase of sync-continue tapping in two experiments. In the first experiment, participants produced sync-continue tapping at target ITIs ranging from 400 to 2200 ms. During continuation, SD generally increased with ITI, with a

sharper increase in SD at target ITI above 1000 ms, in line with findings on synchronization tapping. In a second experiment designed to locate the point at which this change in the slope of SD as a function of ITI occurs, participants produced sync-continue tapping at target ITI from 700 to 1100 ms in 100 ms increments and from 1200 ms to 1600 ms in 200 ms increments. Participants showed marked increases in continuation drift (speeding up) around 1000 ms and 1400 ms target ITI. This implies that the range of tempi for successful continuation is narrower than for synchronization.

To measure the relation between preferred tempo and drift during continue tapping, McAuley et al. (2006) examined the correlations between SMT and continuation tapping performance. Participants produced their preferred tempo in an SMT task and performed synccontinue tapping at seven target ITI from 150 to 1709 ms. Participants produced mean continuation ITIs slower than the fastest target ITI (150 ms) and faster than the slowest target ITI (1709 ms) and individual SMTs were correlated with continuation accuracy at the median target tempo (506 ms). Furthermore, relative temporal variability (CV) during continuation tapping was lowest for target tempi closer to individuals' SMTs. A more recent study by Kliger-Amrani and Zion-Golumbic (2020b) extended these findings to faster and slower tempi. Participants performed SMT tapping and sync-continue tapping at a range of target ITI from 250 to 2200 ms. Individuals' continuation accuracy was best at tempi closer to their preferred tempo and their continuation tapping tempo drifted away from the target tempi toward their SMT. In a further study of the relationship between SMT and sync-continue tapping performance, Delevoye-Turrell et al. (2014) had participants do SMT finger tapping as well as sync-continue finger tapping and cycling at their preferred tempo as well as target tempi that were 100 to 500 ms IOI faster or slower than their preferred tempo. Sync-continue variances for finger tapping and

cycling were lower for target tempi closer to their SMT, and participants reported that synccontinue tasks with target tempi at or near their SMT were "easier."

In sum, these studies show that patterns of variability in produced continuation ITI are generally consistent with Weber's law within a limited range of target tempi centered on an individual's preferred tempo; this range, however, is smaller than for synchronization. Furthermore, individuals drift during continuation tapping toward their preferred tempo. Considered together, the smaller entrainment region for continuation compared to synchronization tapping and the tendency to drift in the direction of preferred tempi during continuation suggest that people have an internal timing mechanism that can be flexibly entrained by auditory rhythms, but when the rhythm is removed, they gradually return to a tempo closer to their preferred (internal) tempo.

With respect to effects of musical training on continuation tapping performance, a number of studies have examined differences between musicians and nonmusicians in the accuracy and variability of produced continuation ITIs. Keele et al. (1985b) had nonmusicians and highly-skilled pianists perform sync-continue tapping with their finger and foot at a 400 ms target ITI. Because they observed drift in the production of continuation ITIs, they fitted a linear trend line to ITIs and calculated SD based on the detrended time series. Results showed that pianists had overall less variability in their produced ITIs compared to nonmusicians, and SDs were correlated between participants' ITIs during finger and foot tapping, suggesting a common timing mechanism across effectors. To expand this finding to a range of target tempi, Baer et al. (2013) compared sync-continue tapping performance between 22 musicians and 17 nonmusicians at four target ITI: 400, 550, 700, and 850 ms. They found that musicians had less variability in produced continuation ITI than nonmusicians. Furthermore, the slope of the

relationship between variability and target ITI was different between musicians and nonmusicians, where musicians exhibited a smaller increase in variability with ITI compared to nonmusicians. Together, these studies show that musicians perform continuation tapping more precisely than nonmusicians, especially at slower target tempi.

Finally, studies of sync-continue performance have used neuroimaging such as functional magnetic resonance imaging (fMRI) and electroencephalogram (EEG) to elucidate neurological underpinnings of synchronization and continuation timing. Results show different patterns of neurological activity associated with sync and continue phases of tapping. In an fMRI study, Rao and colleagues (1997) examined neural activity in healthy participants during sync-continue tapping, passive listening to tone sequences, and a pitch discrimination task. Participants completed sync-continue tapping at 300 and 600 ms target ITI with their right index finger, passively listened to tones presented at the same tempi, or listened to pairs of tones and responded when they heard a change in pitch (160 Hz pitch change upward or downward). The comparisons of interest in terms of brain activity were between the tapping task and the two auditory tasks (passive listening and pitch discrimination) as well as between the sync and continue phases of tapping. Brain activity was significantly higher than baseline (rest) in the left sensorimotor cortex and right cerebellum for both phases of tapping compared to the auditory tasks. Of particular interest was the observation of additional activation during the continue compared to sync phase in the medial premotor loop, consisting of the supplementary motor area, left caudal putamen, and left ventrolateral thalamus, implicating a medial premotor pathway in producing internally-paced time intervals.

In another study comparing fMRI activity during sync and continue tapping phases, Lewis and colleagues (2004) had participants do sync-continue tapping at 500 ms IOI. Results

were consistent with the findings of Rao et al. (1997), with a few additional findings attributed to a greater volume of data collected. Increased activation during the sync compared to continue phase was observed in the bilateral superior temporal gyrus and right transverse temporal gyrus, reflecting activity in auditory cortices associated with hearing the pacing signal. Increased activation during the continue compared to sync phase was observed bilaterally in the supplementary motor area, ventrolateral prefrontal cortex and putamen. These studies highlight a role for the supplementary motor area and putamen specific to continuation tapping.

In an EEG study examining functional connectivity, Serrien (2008) examined corticocortical interactions during sync-continue tapping at a 500 ms target ITI. Beta-band frequency coherences were evaluated for intra- and interhemispheric, and mesial-central groupings to compare regional functional connectivity during the sync and continue phases. Results showed an increase in degree of coherence for the continue compared to sync phase but only for mesial-central connectivity. They interpreted the findings as increased functional communication in midline regions for maintaining an internally-paced versus externally-paced rhythmic movement task. Considered together, results of neuroimaging studies implicate auditory and motor brain regions for the synchronization of finger tapping with an auditory stimulus, with additional activation in and functional connectivity across medial brain areas such as the supplementary motor area and basal ganglia (BG) during continuation tapping.

To summarize, studies of paced rhythmic timing using sensorimotor synchronization and sync-continue finger tapping tasks show four key behavioral and neurological findings. First, temporal accuracy and variability during both sync and continue tapping change as a function of target tempo and musical training. Across individuals, timing variability (SD) linearly increases with inter-tap interval (ITI), conforming to Weber's law. However, this relationship changes at

very fast and very slow tapping tempi, at which point temporal variability increases at a rate beyond that predicted by Weber's law. This breakdown in timing performance at more extreme ends of rhythmic tempi reflects the bounds of an entrainment region where synchronization and continuation timing performance are at their best. This entrainment region is smaller for continuation tapping ( $\sim 300 - 1400$  ms ITI) compared to synchronization tapping ( $\sim 300 - 1800$ ms ITI). Second, within individuals, a relationship between paced and unpaced rhythmic timing performance is demonstrated by the finding that individuals tend to be more accurate and less variable when synchronizing to tapping tempi closer to their SMT and tend to drift toward their SMT during continuation, reflecting a role of endogenous rhythmic timing mechanisms that are flexibly entrained by rhythmic stimuli then gradually revert back to preferred tempi after their removal. Third, musical training improves temporal accuracy and precision during both synchronization and continuation tapping. Finally, sync and continue tapping both show increased neural activity in auditory and motor regions of the brain, with additional activity and functional connectivity between supplementary motor areas and basal ganglia during continue tapping. In the next two sections, I will outline two competing models of rhythmic timing, interval models and entrainment models.

#### **Interval Models of Rhythmic Timing**

Most studies using the sync-continue tapping task have made inferences about underlying neural timing mechanisms that control rhythmic movements by analyzing the sequences of intertap intervals (ITIs) produced by participants during the continuation phase of tapping. A common assumption in these studies is that produced ITIs are controlled by an interval-based timing mechanism, whereby some form of internal clock in the brain measures the absolute duration of each successive to-be-produced time interval independent of the preceding produced

interval (Doumas & Wing, 2007; Ivry, 1996; Ivry & Hazeltine, 1995; Meck, 2003; Wing, 1980). Wing & Kristofferson (1973a, 1973b) formalized this view in the following open-loop model. They proposed that the sync phase establishes by an internal central clock an unbiased estimate of the to-be-produced target time interval and each produced inter-tap interval (ITI) during the continue phase is the result of two processes: a central clock process and motor implementation process, each with independent sources of variance. The central component is defined by the clock interval ( $C_i$ ) produced by the internal clock process. Two motor delays associated with the initiating ( $M_i$ ) and terminating ( $M_{i+1}$ ) finger taps then mark out each produced inter-tap interval (ITI<sub>i</sub>). Based on this formulation, the equation for successively produced inter-tap intervals is:

$$ITI_i = C_i + M_{i+1} - M_i \tag{1}$$

Thus, each produced inter-tap interval is equal to the sum of a sample of the clock interval C and the difference between the two sampled motor delays (M) that bound the produced interval. In this equation, the expected (mean) value of the clock, C, is assumed to be set by the target ITI given by the pacing signal in the sync phase and the expected (mean) value of the motor delay is an unknown constant that varies between individuals. Moreover, because the clock and motor processes are assumed to be independent random variables with normal variances, the variance of the produced ITIs or total variance ( $\sigma^2_T$ ) can be determined by the sum of the clock ( $\sigma^2_C$ ) and motor ( $\sigma^2_M$ ) variances as follows:

$$\sigma^2_T = \sigma^2_C + 2\sigma^2_M \tag{2}$$

The variance of the motor delay process can be directly estimated by the negative lag-1 autocovariance of successive intervals:

$$\sigma_M^2 = -autocov(1) \tag{3}$$

The two model terms combined then make it possible to estimate the variance of the putative clock process by subtraction:

$$\sigma^2_C = \sigma^2_T + 2autocov(1) \tag{4}$$

The ability of the Wing & Kristofferson (W&K) model to decompose the produced sequence of inter-tap intervals in sync-continue tapping into separate clock and motor sources of variance has been a useful property of this model for investigations of normal and disordered timing processes.

For example, for rhythmic timing in typical adults, the W&K model can account for the relationship between mean ITI and ITI variability during continuation tapping (i.e., Weber's law for interval production) (Collier & Ogden, 2004; Ivry & Hazeltine, 1995; Keele et al., 1985b), the observed pattern of alternating short and long ITIs during repetitive tapping (Shaffer, 1978; Wing, 1980; Wing & Kristofferson, 1973b), and the reduction of ITI variability when tapping with multiple effectors (i.e. the bimanual advantage) (Helmuth & Ivry, 1996).

The W&K model has been further useful for decomposing tapping variability in various patient populations, identifying timing deficits which the model attributes to increases in variability of the central clock component (Freeman et al., 1996; Ivry & Corcos, 1993; Ivry & Keele, 1989; Ivry et al., 1988; O'Boyle et al., 1996). Wing and colleagues examined timing deficits in a patient with Parkinson's disease (PD) using a sync-continue tapping task (Wing et al., 1984). They leveraged the fact that the patient showed a greater deficit in her right than left hand, decomposing the variance of inter-tap intervals (ITI) into the W&K model clock and motor components for each hand and comparing timing variability between the two hands. They found that the patient had greater ITI variability in her right (impaired) hand than left (unimpaired) hand, which was not attributable to the motor component, indicating a deficit in central timing

processes. In addition to research on clock deficits associated with PD, other work has applied the W&K model to sync-continue performance in patients with a variety of neurological diseases and disorders.

Ivry and Keele (1989) compared clock and motor variance during continuation tapping among patients with Parkinson's disease (PD), cerebellar lesions, cortical (posterior frontal lobe) lesions, and peripheral neuropathy in the hand or arm as well as two healthy control groups: younger (college-age) and older (50+ years) adults. Cerebellar patients had higher clock variance than all other patient or control groups, while cerebellar, cortical, and peripheral neuropathy patients had higher motor variance than other groups. For the patient groups, within-subjects comparisons between affected and unaffected limbs showed that cerebellar, cortical, and PD patients had increased clock variance in their affected limb, suggesting a deficit in central timekeeping processes. A follow-up study on patients with medial or lateral cerebellar lesions showed that lateral cerebellar patients displayed increased clock but not motor variance, while medial cerebellar patients had increased motor but not clock variance, suggesting that lateral but not medial cerebellar lesions result in central timing deficits attributed to the impaired functioning of an internal clock (Ivry et al, 1988). Central timing deficits have also been identified in patients with Huntington disease (HD), as shown in a study by Freeman and colleagues (1996). HD patients showed an increase in both clock and motor variance relative to controls during sync-continue tapping.

One limitation of the W&K model and, more generally, all interval-based models of rhythmic timing, is that inferences about internal timing processes are based solely on the time series of tap onsets extracted from continuous movements. This ignores the fact that even simple rhythmic movements such as finger tapping are continuous movements in space and time and

that spatial elements of individuals' movements may contribute in significant ways to movement timing. In the following section, I will describe a contrasting set of rhythmic timing models known as entrainment models.

#### **Entrainment Models of Rhythmic Timing**

Alternative to interval models of timing are entrainment models, which do not implicate an internal clock for measuring and producing successive time intervals. These models instead propose that self-sustaining, flexible neural oscillators are entrained by environmental stimuli and provide an internal referent temporal structure of events that can be compared to external temporal events as they unfold in real-time. Simply put, neural entrainment involves alignment of the phase and period of cyclical peaks in neural activity (i.e., oscillator amplitude) with rhythmic sensory events. These models fall within the broader framework of dynamic attending theory (DAT; Jones, 1976; Jones & Boltz, 1989; Large & Jones, 1999), which assumes that attention is not a constant process, but consists of rhythmic fluctuations in "attentional energy" across time. Peaks in neural activation guide attention to expected points in time, for example when a sensory stimulus is expected to occur.

In terms of synchronizing finger tapping with a sequence of tones, this requires producing each tap at a point in time when a tone is predicted to be heard. Thus, peaks in oscillator activity serve to align the timing of incoming sensory information from the auditory signal and sensory feedback from the goal response (tap), with some variability. Oscillators are assumed to have intrinsic periods (tempi) but are flexible in that they can be entrained by range of stimulus tempi constituting an entrainment region. By virtue of the self-sustaining nature of these oscillators, people can continue tapping at a tempo previously set by a rhythmic auditory stimulus, that is, they can continue producing responses on a time course consistent with when previous auditory
events would be expected to occur, even after their cessation. However, given enough time after the pacing stimulus is gone, the strength of the entrained period is assumed to decay with the oscillator eventually resuming its un-entrained (intrinsic) period.

Entrainment theories can account for numerous timing phenomena, perceptual and generative in nature, over and above what can be explained by interval theories of timing. One example is the influence of preceding temporal events on the perception and production of subsequent time intervals (i.e., relative timing) (Barnes & Jones, 2010; Ellis & Jones, 2000; Grahn & Brett, 2007; McAuley & Jones, 2003). In contrast, interval models assume the independent measurement of successive temporal events via the explicit encoding of durations (i.e., absolute timing). One well-established phenomenon in the time perception literature is an increased sensitivity to changes in interval duration for isochronous sequences containing more repetitions of the to-be-judged interval (Drake & Botte, 1993; Miller & McAuley, 2005). Entrainment models propose that temporal resolution (i.e., phase and period alignment) is refined as attention is entrained by repetitive stimuli as they unfold in time. In terms of time production, these models can account for tempo boundaries observed during synchronization and continuation tapping (Delevoye-Turrell et al., 2014; Mates et al., 1994; Repp, 2006), since attentional oscillators are assumed to be naturally limited in their range of possible entrainment periods (tempi). Furthermore, these theories predict the observation of drift in continuation tapping toward an individuals' SMT (Kliger-Amrani & Zion-Golumbic, 2020b; Madison, 2001; McAuley et al., 2006) by a gradual return from the oscillator period entrained by an environmental stimulus (e.g., metronome) to its intrinsic period (tempo) after stimulus removal.

Entrainment models can also account for influences of visuospatial information on spatiotemporal synchronization dynamics. Interval models assume that attention to time

competes for attentional resources shared by other modalities (Block & Zakay, 1996; Thomas & Cantor, 1975; Thomas & Weaver, 1975). These models would predict that when people synchronize with a dynamic visual stimulus, they ignore subtle differences in spatial aspects of the stimulus in order to attend to temporal ones. However, individuals have been shown to mimic spatial characteristics of a dynamic visual pacing stimulus in their produced tapping movements. For example, when visually synchronizing with another individual or on-screen images of a virtual tapping finger, individuals increase tap amplitude corresponding to observed increases in tap amplitude by the other person or images of the tapping finger (Hove & Keller, 2010, Kroger et al., 2021), in line with entrainment theories. Mimicry of to-be-ignored spatial information during synchronization implies a coupling of spatial and temporal characteristics of rhythmic movements in contexts when they are compatible or facilitative (Prinz, 1997). These findings are consistent with entrainment theories, which assume that attention has analogous spatial and temporal properties, where attention can be maximized for an object/event or location in space and time. Where interval theories require limited attentional resources to encode a specific (absolute) interval in memory, entrainment theories propose that attention is employed in real time and is entrained by external events as they unfold.

Neural evidence for entrainment models of rhythmic timing comes from a number of EEG studies showing that rhythmic neural oscillations align with regular (periodic) stimuli as well as fMRI studies showing increased activation in motor areas of the brain and functional coupling of sensory and motor areas during auditory rhythm perception and rhythm production (e.g. tapping) (Cameron & Grahn, 2014; Chen et al., 2006; Chen et al., 2008a; Crasta et al., 2018; Damm et al, 2020; Grahn & Brett, 2007; Kung et al., 2013; Nijuis et al., 2021; Nozaradan et al., 2011). An EEG study by Nozaradan et al. (2011) examined steady-state evoked potentials

(SSEPs) while participants listened to a tone with amplitude (volume) peaks that occurred at a 144 BPM tempo (corresponding to 416.7 ms IOI). There were three listening conditions: a control condition in which they listened and monitored for a short interruption in the tone, a duple-meter condition in which they were instructed to imagine a subjective beat (accent) that occurred every-other tone, and a triple-meter condition in which they were instructed to imagine a subjective beat (accent) that occurred every-other tone. The duple-meter condition induced a subjective musical beat like that of a march, and the triple-meter condition induced a subjective musical beat like that of a waltz. Results showed SSEPs with amplitude peaks that corresponded to the 416.7 ms IOI, which reflected neural entrainment to the rhythm of the volume peaks throughout the tone. Furthermore, during the duple-meter condition, SSEPs showed amplitude peaks at the level of every other interval (corresponding to 833.4 ms IOI) and during the triplemeter condition, SSEPs showed peaks at every third interval (corresponding to 1250.1 ms IOI). These results demonstrated that neural oscillations were time-locked to the stimulus and were also influenced by top-down rhythmic structure induced via instructions to imagine subjective accents at different periodicities when listening to the same stimulus at the same tempo. These results provided evidence that neural responses were dynamically modulated (entrained) by rhythmic stimuli, and that the periodic nature of this entrainment was influenced by instructions to attend to different temporal points of the same rhythms.

In an fMRI study, Grahn and Brett (2007) examined neural activity while participants listened to sequences of tones that were rhythmic (simple integer ratios separating tones) or irregular (non-integer ratios between tones) and performed a reproduction task and a rhythm discrimination task. Simple rhythmic stimuli induced the perception of a regular (periodic) musical beat, thereby affording temporal prediction, whereas irregular stimuli afforded neither.

For the reproduction task, participants heard a sequence three times and then reproduced the sequence by tapping their finger. For the discrimination task, they listened to two sequences and decided whether they were the same or different. Participants reproduced and discriminated simple rhythmic sequences more accurately than irregular sequences, suggesting that rhythmic structure facilitated temporal perception and production. When reproducing or discriminating simple rhythms compared to irregular tone sequences, increased brain activity was observed in supplementary motor areas, superior temporal gyri, caudate nucleus, and putamen. These results therefore implicate motor areas and the basal ganglia in perceiving and reproducing rhythmically structured tone sequences, suggesting that inducing a regular beat affords entrainment and recruits motor areas involved in synchronizing to rhythmic stimuli even when no motor response is required.

Together, neuroimaging studies provide evidence that oscillatory neural activity entrained by periodic (rhythmic) stimuli is influenced by attention to different hierarchical levels of tempo and motor regions of the brain are recruited during both rhythm perception and reproduction, specifically for rhythms that induce the perception of a regular musical beat. These studies support entrainment theories, which assume a closed-loop mechanism that involves the generation of an internal rhythm (oscillator) that is coupled by rhythmic events via sensory feedback.

To summarize, where interval models of rhythmic timing implicitly ignore contributions of spatial characteristics of stimuli and movements to rhythmic timing by implicating an internal clock mechanism that does not incorporate sensory feedback, entrainment models account for interactions between spatial and temporal characteristics of rhythm production via a mechanism of dynamic coupling between external and internal oscillations using multisensory feedback.

Entrainment models of rhythmic timing are supported by behavioral studies showing dynamic interactions between spatial and temporal characteristics of rhythmic movements as well as neuroimaging studies showing peaks in neuronal activity that correspond to the period (tempo) of auditory stimuli and functional coupling of sensorimotor areas during rhythm perception and production. Some evidence for the contributions of spatial characteristics of movements to rhythmic movement timing comes from several sources outside of the sync-continue tapping literature.

#### Evidence for a Role of Space in Rhythmic Movement Timing

Studies on spatiotemporal dynamics of rhythmic movements have examined a variety of cyclical movements such as circle drawing and manual oscillations, and to a lesser extent, finger tapping. In order to simultaneously examine spatial and temporal dynamics, researchers have typically used motion tracking to record movement kinematics, then extracted trajectory and temporal onset information from these data. Typically, they have examined changes in movement tempo at different target amplitudes and, conversely, changes in movement amplitude (distance) at different target inter-response intervals (IRIs). These studies have demonstrated a relationship between preferred amplitude and preferred tempo where the former increases with target tempo (IRI) and the latter increases with target amplitude.

Studies have examined the relationship between preferences for movement amplitude and tempo during paced and unpaced tasks. In unpaced tasks, longer preferred tempi are found to be associated with larger preferred amplitudes for various oscillatory movements. In an unpaced pendulum-swinging task, Yu et al (2003) had participants swing three pendulums of different lengths (36, 40, and 48 cm) at their preferred tempo using wrist movements. Participants preferred slower tempi and larger amplitudes when swinging longer pendulums, suggesting that

changes in preferred tempo and amplitude were driven by different physical characteristics of the movement. They also found a relationship between preferred amplitude and preferred tempo, where the preferred amplitude of pendulum motion increased with preferred tempo.

Studies using paced tasks have examined changes in produced amplitude at different target tempi as well as changes in produced tempo at different target amplitudes. In a paced task, Kay et al. (1987) had participants synchronize repetitive wrist flexion-extension oscillations with an auditory metronome at six tempi from 1 to 6 Hz (corresponding to 166.7 – 1000 ms IOI). During cyclical wrist movements, changes in movement tempo were associated with corresponding changes in movement amplitude, where amplitude increased with inter-onset interval. In a paced circle-drawing task, Ringenbach et al. (2003) had participants draw circles in time with a metronome at tempi between .77 and 2.5 Hz (400 – 1298.7 ms IOI), instructing them to complete one circle per metronome cycle. Circle diameter, corresponding to movement amplitude in the drawing task, increased with IOI, extending previous findings to 2-dimensional rhythmic movements. These studies showed that when synchronizing movements to an auditory metronome, participants increased their self-selected (preferred) movement amplitude at slower metronome tempi.

To further study the relation between preferred amplitude and preferred tempo, Rosenbaum and colleagues (1991) examined repetitive finger flexion-extension, akin to finger tapping without contacting a surface in between "taps," comparing an unpaced target amplitude condition and a paced, self-selected amplitude condition. First, participants produced their preferred tempo at four target amplitudes of 2, 4, 6, and 8 cm. They found that preferred tempi were slower for larger target amplitudes. Then, with no target amplitude, participants did the same finger oscillation task in synchrony with a metronome at each of their preferred tempi

produced in the target amplitude task. Results showed that preferred amplitude was larger at slower target tempi. Together, these studies suggest a bidirectional relationship between preferred movement amplitude and preferred tempo, raising the possibility that people have a preferred movement velocity underlying preferences for movement amplitude and tempo.

The covariation between amplitude and tempo when producing rhythmic movements exposes a significant potential limitation of using interval timing models to make inferences about underlying 'clock' mechanisms. That is, models assuming that each absolute time interval is metered out by an internal clock and then produced via a separate motor implementation process (with independent sources of variance) do not consider the role of space and cannot account for spatiotemporal interactions during rhythmic movement tasks. By contrast, entrainment models of rhythmic timing assume that rhythmic timing during synchronization and continuation is accomplished via the entrainment of self-sustaining, flexible neural oscillators by rhythmic stimuli and allow for the incorporation of multisensory feedback that promotes predictive processes, including spatial information.

In the next section, I propose a set of novel hypotheses regarding the control of rhythmic movement timing in sync-continue finger tapping that consider spatial aspects for the control of produced time intervals. These hypotheses will be tested in the five experiments described in subsequent chapters of this dissertation.

#### **Hypotheses**

The key observation motivating the hypotheses tested in this dissertation is that the relationship between amplitude and produced time interval (period) of rhythmic movements is best expressed in terms of average movement velocity, where the equation for velocity is given by:

$$V = S/T \tag{5}$$

In this equation, S is the total displacement of the limb and T is the total duration of the movement for one cycle. For rhythmic finger tapping, where tap amplitude is the maximum height of the finger between taps, total finger displacement (S) for a given inter-tap interval (ITI) is equal to two times the tap amplitude (A), and the equation for average tap velocity can be written as:

$$V = 2A/ITI \tag{6}$$

Solving for ITI, the inter-tap interval (ITI) is given by:

$$ITI = 2A/V \tag{7}$$

This formulation, expressing the ITI as a function of tap amplitude and velocity, leads to a number of hypotheses regarding potential interactions between spatial and temporal characteristics during unpaced and paced sync-continue tapping.

*Preferred Velocity Hypothesis for Unpaced Tapping:* The proposal that the relation between amplitude and produced inter-tap interval is best expressed by velocity leads to the possibility that previous studies finding a preferred tempo in unpaced rhythmic movements reflect a preferred velocity. The *preferred velocity hypothesis* proposes that individuals' intrinsic preferences for tap amplitude and tempo are critically related, reflecting their preferred velocity according to Equation (6). This hypothesis predicts a tight coupling between an individual's preferred tempo produced in a spontaneous motor tempo task and preferred amplitude produced in a spontaneous motor amplitude task, where the relationship between preferred amplitude and tempo can be used to estimate their preferred tap velocity, which is predicted to be constant across tasks. The *preferred velocity hypothesis* is tested in Experiment 1 (Chapter 4) and Experiment 3 (Chapter 6). *Amplitude Control Hypothesis for Paced Tapping:* If each produced inter-tap interval (ITI) in sync-continue tapping is a function of tap amplitude and velocity (Equation 7), then at least two possibilities for controlling produced ITI emerge that do not involve an internal clock. The first, an *amplitude control hypothesis*, proposes that individuals maintain a constant (preferred) velocity and use the amplitude of their movements to produce different ITIs. An alternative is that individuals keep tap amplitude constant and modulate average velocity. The *amplitude control hypothesis* predicts that people will systematically change amplitude to match different target inter-tap intervals (ITIs), where smaller amplitudes are associated with shorter ITI. This hypothesis also predicts that tap amplitude variability will be related to ITI variability and timing accuracy and precision (variability) will be better when people tap at target amplitudes and tempi that elicit tap velocities closer to their preferred velocity. Alternatively, a *velocity control hypothesis* predicts that people keep tap amplitude constant across target ITI, controlling ITI by changing tap velocity. The amplitude control and velocity control hypotheses are tested in Experiments 2 and 3.

*Dwell Time Hypothesis for Slow Tapping:* One question that emerges from the basic observation that people are limited in how high they can lift their finger between taps is: how do people control ITI at slow tapping tempi, when tap amplitude cannot increase further to produce longer ITIs? The control of rhythmic movements at slow tempi is of particular interest because research shows that individuals are less accurate and more variable when producing long ITIs (above ~1400 ms for continuation tapping) compared to comfortable tempi (i.e., those well-within their entrainment region). During continuation tapping at slower tempi (longer target ITIs), individuals are more variable in their timing and show a tendency to drift (speed up) in the direction of their preferred tempo.

Studies of rhythmic movements at slow tempi have also shown a relationship between tempo and dwell time (the duration that the movement is paused between cycles). Evidence that dwell time increases with IOI comes from studies that examined synchronization of oscillatory movements (Adam & Paas, 1996; Park et al, 2017; van der Wel et al., 2009) and synchronization of finger tapping (Billion & Semjen, 1995; Cos et al., 2015). These findings suggest that people have different spatiotemporal strategies for producing slow tempi compared to comfortable and fast tempi; however, this phenomenon has not been investigated in the context of sync-continue tapping and the relationship between dwell time and amplitude has not been thoroughly studied. Furthermore, studies on dwell time have not examined timing accuracy and variability when dwell time is explicitly manipulated. The dwell time hypothesis proposes that, when amplitude cannot be increased further to lengthen produced intervals, people increase dwell time to produce longer inter-tap intervals. This hypothesis predicts that participants keep tap amplitude constant at slow target tempi and increase tap dwell time to produce longer inter-tap intervals. This hypothesis also predicts that timing performance will be better for conditions with manipulated (shorter or longer) dwell times closer to preferred dwell times. The dwell time hypothesis is tested in Experiment 4 (Chapter 7) and Experiment 5 (Chapter 8).

The next chapter describes some general methods used in the five experiments.

#### **CHAPTER 3: GENERAL METHODS**

# Introduction

In this chapter, the materials, equipment, and other aspects of the methods used in all five experiments will be described, including the general data processing and analysis procedures for the continuous finger movement data.

#### **Survey Materials**

All participants completed a background survey that included questions about age, sex, ethnicity, handedness, music training and experience, language background, hearing ability, general health and wellbeing on the day of the experiment, and any strategies used for completing the experiment.

# **Tapping Tasks**

All participants completed tapping tasks with their self-reported dominant hand, and any participants who self-identified as ambidextrous were given the option to tap with whichever hand they felt more comfortable. For all experiments, participants either performed an unpaced task where they tapped with their index finger at their preferred tempo or amplitude (finger height) or a synchronization-continuation (sync-continue) tapping task. On each trial of the sync-continue task, participants were instructed to tap their index finger in synchrony with an isochronous sequence of tones and then to continue tapping at the same pace for some time after the tones stopped. The fixed inter-onset interval (IOI) between tone onsets defined participants' target inter-tap interval (ITI), which I will also refer to as the target tempo for the sync-continue tapping task. Continuous finger motion data were recorded for both the unpaced and paced tasks.

# Stimuli and Equipment

The synchronization (pacing) signal consisted of sixteen 50-ms 440-Hz sine tones each followed by a silent duration to create a sequence of 15 IOIs that specified the target ITI. The silent duration was manipulated to change the target inter-tap interval (ITI) in different conditions. For example, to create a synchronization sequence with a 550-ms target ITI, 500 ms of silence followed each 50-ms tone. After the continuation phase during which participants continued to produce the target ITI to the best of their ability, there was a longer, 200-ms 440-Hz sine tone that signaled participants to stop tapping. The duration of the continuation phase varied with the target ITI to allow for approximately 30 produced inter-tap intervals following synchronization. Thus, for each trial, participants produced ~45 tap intervals: 15 synchronization intervals.

Pacing tones were presented over Sennheiser HD 280 Pro headphones at a comfortable listening level. Tapping responses were collected using an Ascension trakSTAR electromagnetic motion tracking system (trakSTAR by Ascension Technology Corp, Shelburne, VT, USA) at a 200-Hz sampling rate. One sensor from this continuous motion-tracking device was attached to the distal phalanx of the index finger of the participant's tapping hand and recorded x, y, and z coordinates of finger movements (Figure 1).

#### **Data Processing and Analysis**

For each trial of unpaced or paced task performance, the time series of discrete tap onsets was extracted from the continuous motion tracking data along with additional spatiotemporal measures of interest using a customized program in MATLAB and the signal processing toolbox. Figure 2 shows a sample of raw continuous finger motion data, which labels portions of the signal that correspond to three main variables of interest: the produced inter-tap interval, tap

amplitude (maximum finger height), and dwell time (the duration that individuals kept their finger on the table after a tap onset). The customized program extracted the time series of tap onsets (the z-axis minimum position that corresponded to the location of the sensor when the index finger was in contact with the table), the time series of tap amplitudes (the maximum height of the index finger between taps), and the time series of tap dwell times (the duration within each tap cycle that participants leave their finger on the table). These measures were then used to calculate the dependent variables of interest.

In general, to assess timing performance, the DVs of interest were the mean, standard deviation (SD), coefficient of variation (CV), and the directional and absolute error of the produced inter-tap intervals (ITIs). Directional error provided a measure of the signed difference between the mean produced ITI and target ITI. Absolute error provided a measure of the absolute difference between the mean produced ITI and target ITI. With respect to tap amplitude (maximum finger height), the DVs of interest were the mean, standard deviation, and coefficient of variation of tap amplitudes. To assess dwell times, I measured mean dwell times and mean dwell-time proportions (dwell time/produced inter-tap interval). The timing analyses followed the guidelines of Helmuth and Ivry (1996) and filtered produced ITIs to remove 'double' taps (intervals < 50% of the target ITI) and 'missed' taps (intervals > 150% of the target ITI). Moreover, prior to calculating SD of produced ITIs, time series were linearly detrended to remove any systematic drift that would artificially inflate standard deviations due to a non-stationary mean. Detrending fit a linear regression line to the sequence of continuation inter-tap intervals for each trial and the SD of produced ITIs was based on the residuals.



Figure 1. Example of motion-tracking sensor attached to index finger. The sensor was fixed to the top of the participant's tapping finger with a piece of medical tape.



Figure 2. Example of raw continuous finger motion data for several finger taps showing key spatiotemporal dependent variables examined in the experiments (produced inter-tap interval, tap amplitude, and dwell time).

# **Informed Consent Procedure**

Prior to voluntary participation, all participants were informed about the nature of the study as well as potential risks and benefits of participation and signed a consent form approved by the Michigan State University Institutional Review Board.

# CHAPTER 4: TEST OF A PREFERRED VELOCITY ACCOUNT OF PREFERRED TEMPO Introduction

Many studies show that spontaneous (preferred) motor tempo (typically assessed using unpaced rhythmic finger tapping) centers around 500 - 600 ms (~100 - 120 bpm) (Fraisse, 1982; Hammerschmidt et al, 2021; McAuley et al., 2006; Moelants, 2002). There are nonetheless large individual differences in preferred tempo, with produced tempi in spontaneous motor tempo (SMT) tasks ranging from around 200 ms at the fast end to 1800 ms at the slow end (Fraisse, 1982; Hammerschmidt et al, 2021; Hammerschmidt & Wollner, 2022; Kliger-Amrani & Zion-Golumbic, 2020b). Although some factors contributing to individual differences in preferred tempo have been identified, such as age (Hammerschmidt et al, 2021; McAuley et al., 2006), individual differences in preferred tempo are still not well understood. One unanswered question of interest here is whether preferred tempo depends on movement amplitude. One possibility is that an individual's preferred tempo may not reflect a pure time preference per se, but rather a preference to produce a particular (preferred) movement velocity (V) that reflects of a combination of amplitude and produced inter-tap interval according to V = 2A/ITI (Eq. 7) where A is the maximum height of the finger movement (amplitude) and ITI is the produced inter-tap interval. If so, then changes in movement amplitude should alter preferred tempo in order to maintain a constant preferred velocity. To test this possibility, an initial experiment was conducted which had participants generate their spontaneous (preferred) tempo and their preferred movement amplitude using an unpaced finger tapping task. Participants then generated their spontaneous (preferred) tempo for different target amplitude conditions.

# **Experiment 1**

Experiment 1 tested a preferred velocity account of preferred tempo by having participants perform spontaneous motor amplitude (SMA) and spontaneous motor tempo (SMT) tasks where they tapped their finger at their preferred amplitude and preferred tempo, respectively, without any instructions about tempo for the SMA task and without any instructions about amplitude for the SMT task. Participants then completed a target amplitude version of the SMT task in which participants tapped at their preferred tempo at three target amplitudes ranging from low to high. The *preferred velocity hypothesis* predicts that participants will produce the same tempo and amplitude regardless of whether they are asked to produce their preferred tempo without any instructions about tempo (SMT task) or to produce their preferred amplitude without any instructions about tempo (SMA task). Moreover, when asked to produce their preferred tempo at different target amplitudes, they should alter their preferred tempo to maintain a constant preferred velocity.

#### Methods

*Participants and design*: Twenty undergraduates (15 female, 5 male) from Michigan State University ranging from 18 to 26 years in age (M = 19.8, SD = 2.3) completed the experiment in return for partial credit in an undergraduate psychology course. Based on selfreport; 17 were right-handed, 2 were left-handed, and 1 was ambidextrous. The 17 right-handers and 1 ambidexter completed all tasks with their right hand and the 2 left-handers completed all tasks with their left hand. A within-subjects design was used, with all participants completing four tapping tasks: a maximum tapping amplitude task, the spontaneous motor amplitude (SMA) task, the spontaneous motor tempo (SMT) task, and a target amplitude version of the spontaneous motor tempo task.

Stimuli and apparatus: Participants completed all tasks with their dominant index finger while wearing the motion-tracking sensor (see General Methods). For the target amplitude version of the SMT task, target amplitudes were presented using an amplitude guide that was on the table in front of the participant. Figure 3 shows a photograph of the amplitude guide, which was made of wooden planks with 2 digital calipers on each side set to move each adjustable arm in the vertical plane. A length of thin black elastic thread connected the moving arms of the calipers, spanning them in the horizontal plane, which allowed target amplitudes to be set by moving the arm of both calipers up or down. The calipers displayed a readout of the height of the string in mm, where the baseline of 0 mm was set at the point where the elastic thread was barely touching the top of the sensor on the participants' tapping finger when at rest on the table. This made it possible to set target amplitudes that accounted for differences in the thickness of each participant's index finger. To set each target amplitude, the experimenter manually adjusted each caliper arm from the 0 mm baseline to the target height. The elastic thread functioned as the target amplitude stimulus, which was positioned directly above the individual's tapping finger. Target amplitude was reached when the elastic was visibly disturbed (i.e., vibrated) without being displaced far enough to create a perceptible resistance (i.e., not stretched to the point that it slowed finger movement), ensuring that participants could not rely on proprioceptive feedback to match the target amplitude.

*Procedure*: All participants performed four tasks in the following order: 1) a maximum amplitude task in which participants raised their finger as high as possible off the table, 2) the spontaneous motor amplitude (SMA) task in which participants tapped their finger at a comfortable finger height (amplitude), meaning neither too high nor too low but just right for them (with no instructions about tapping tempo), 3) the spontaneous motor tempo (SMT) task in

which participants tapped at a comfortable tempo that was neither too fast nor too slow by just right for them (with no instructions about tapping amplitude), and 4) the target amplitude version of the SMT task in which participants tapped at their preferred comfortable tempo at three target amplitudes (10 mm, 30 mm, 50 mm).

For each trial of the maximum amplitude task, participants wore headphones and started with their hand relaxed and resting on the table. They followed recorded instructions to lift their index finger as high as possible off the table and hold it there (5 s), then to relax their finger back to the table, and to repeat the process one more time per trial. There were 2 trials of the maximum amplitude task lasting 40 s each. The average of maximum possible amplitudes collected across both trials was used to estimate each participant's maximum tap amplitude.

For the SMA task, participants tapped a regular beat at a comfortable finger height. They were instructed to choose a finger height between taps that was "not too high and not too low" while maintaining a regular beat (with no instructions about tapping tempo). Participants completed 4 trials of the SMA task and mean produced tap amplitude across the 4 trials was used to estimate each participant's preferred amplitude. For the related SMT task, participants tapped a regular beat at a comfortable tapping tempo. They were instructed to choose a tempo that was "not too fast and not too slow" and maintain a steady beat throughout (with no instructions for tapping amplitude). Participants completed 4 trials of SMT and the mean produced inter-tap interval across the 4 trials was used to estimate each participant's preferred to choose a tempo that was

For the target amplitude version of the SMT task, participants were instructed to tap at their most comfortable pace, "not too fast and not too slow," while also matching the height of their finger between taps to the height of the string on the amplitude guide. There were three target amplitude conditions, corresponding to 10 mm, 30 mm and 50 mm above the table.

Participants placed their hand on the amplitude guide with their tapping finger positioned directly below the target amplitude string. To match each target amplitude, they were instructed to raise their finger high enough for the motion sensor (fixed on top of their tapping finger) to barely touch the string above before lowering their finger back to the table. Their goal was to just noticeably vibrate the string between each tap while maintaining a steady tapping beat at their most comfortable tempo. Before setting each target amplitude, the experimenter moved both caliper arms into position so that the string just barely touched the sensor on top of the participant's finger while at rest on the table. This was set as the 0 position so that each target height was exactly 10, 30, or 50 mm above the neutral resting point of the participant's finger on the table. The fact that the string on the amplitude guide was made of thin elastic, combined with the fact that the motion-tracking sensor was affixed on top of the tapping finger meant that participants could not feel when they met the target amplitude and had to look at their tapping finger to match the target amplitude, meaning that amplitude matching was a visually-guided task that did not rely on tactile feedback. Participants completed 4 trials of the SMT task at each target amplitude. The mean produced inter-tap interval across the 4 trials was used to estimate each participant's preferred tempo at each of the three target amplitudes.

After completing all four of the tasks, I measured finger length, hand size, and asked for self-reported height. Finally, participants completed a background survey (see General Methods). The entire experiment lasted ~60 minutes.



Figure 3. Photos of amplitude guide apparatus. A) Amplitude guide with elastic string spanning adjustable caliper arms on each side. B) Amplitude 0 calibration. The calipers were each set to 0 mm at the location corresponding to the top of the sensor attached to the participant's tapping finger with medical tape. C) Example of 30 mm target amplitude at tap onset. D) Example of 30 mm target amplitude with finger raised to target amplitude (barely touching string).

*Data Processing and Analysis:* The time series of tap onsets and DVs of interest were extracted from continuous data using a custom MATLAB program as described in the General Methods. Because of the wide range of preferred tempi across participants in the unpaced tapping tasks, the number of tap intervals produced in the allotted 40-s trial duration ranged from 17 to 154. Because some participants produced far fewer inter-tap intervals (ITIs) than others, time series were truncated to include only the first 20 produced ITIs and trials in which fewer than 20 intervals were produced were removed, which resulted in the removal of 5 trials (1.25%). I calculated maximum tap amplitude, as well as produced tap amplitudes and inter-tap intervals for the spontaneous motor amplitude (SMA) task, spontaneous motor tempo (SMT) task, and SMT task with three target amplitudes: 10, 30, 50 mm. Mean amplitudes and produced inter-tap intervals (ITIs) were also combined to create a tap velocity measure that reflects the average velocity of vertical (up and down) finger movements for all taps (V = 2A/Mean ITI). If performance on the SMA and SMT tasks reflects a preferred velocity, then estimated velocity was predicted to be the same for the SMA and SMT tasks.

# Results

*Maximum Tap Amplitude:* There was a wide range of observed maximum possible amplitudes (*Range* = 43.8 – 86.8 mm, M = 64.5 mm, SD = 12.0 mm). Although several participants reported having difficulty raising their finger to the 50 mm target amplitude, only one participant's maximum possible tap amplitude was below the 50 mm target in the target amplitude version of the SMT task. Because individual differences in range of motion may be influenced by biomechanical factors such as finger length and connective tissue in the hands (e.g., Superficialis tendons, Extensor tendons, etc.), I calculated the Pearson correlation between finger length and maximum tap amplitude. Maximum tap amplitude was not correlated with finger length in our sample, r(18) = .28, p = .23. The maximum amplitude measure was used to set target amplitudes for each participant in Experiment 3 (participants were the same).

*SMA and SMT Tasks:* Table 1 shows means and standard deviations of produced tap amplitudes and produced inter-tap intervals (ITI) for the preferred amplitude (SMA) and preferred tempo (SMT) tasks. Recall that for the SMA task, mean tap amplitudes reflect preferred tapping amplitudes with no instructions given about tapping tempo; conversely, for the SMT task, mean produced ITIs reflect participants preferred tempo with no instructions given

about tapping amplitude. Table 1 shows that, regardless of task, participants produced similar tap amplitudes and tap tempi. Paired samples t-tests showed no significant task difference in each tap amplitude, t(19) = 1.77, p = 0.094, 95% CI = -10.0 - 117.6, or tap tempo, t(19) = 1.83, p =0.08, 95% CI = -0.4 - 5.9) across tasks. Figure 4 shows the relation between produced ITIs (Panel A) and produced tap amplitudes (Panel B) in the SMA and SMT tasks. Correlational analyses revealed that produced ITIs were strongly positively correlated across the SMA and SMT tasks (produced ITIs, r(18) = 0.81, p < 0.001; tap amplitudes: r(18) = 0.80, p < 0.001). These findings show that preferred amplitude and preferred tempo are tightly coupled, which supports the *preferred velocity hypothesis*. Estimated preferred velocities for up and down tap movements (V = 2A/ITI) for the SMA task and SMT tasks were M = 11.2 cm/s and M = 11.7cm/s, respectively.

# Table 1.

Mean produced inter-tap interval (ITI) and tap amplitude for the Spontaneous Motor Amplitude (SMA) and Spontaneous Motor Tempo (SMT) tasks in Experiment 1. Standard deviations are shown in parentheses. Column three shows estimated average velocity (V = 2A/ITI). Similar estimates of V for the SMA and SMT tasks support the view that participants' preferred amplitudes and preferred tempo reflect a preferred velocity.

Task	Produced ITI (ms)	Tap Amplitude (mm)	Estimated Average $V(\text{cm/s})$
SMA	609.9 (200.5)	32.0 (9.8)	11.2
SMT	556.2 (230.0)	29.2 (11.0)	11.7



Figure 4. A) Relation between produced inter-tap intervals (ITIs) for the spontaneous motor tempo (SMT) and spontaneous tap amplitude (SMA) tasks in Experiment 1. B) Relation between produced tap amplitudes for the SMT and SMA tasks. Participants produced similar ITIs and tap amplitudes regardless of instructions.

*SMT Task – Target Amplitude Version:* Table 2 shows mean tap amplitudes and produced ITIs for the 10 mm, 30 mm, and 50 mm target amplitude conditions. As shown in the table, participants were reasonably good at matching the target amplitudes, except for the lowest, 10 mm, target amplitude condition where they showed a tendency to overestimate the target amplitude. Paired samples t-tests on percent error of produced tap amplitude showed that participants were better at producing the 30 mm (M = 23.3%, SD = 10.1%) compared to 10 mm target amplitude (M = 80.6%, SD = 31.1%) (t(19) = 10.50, p < .001, 95% CI = 45.93 - 68.78) and better at producing the 50 mm (M = 12.7%, SD = 8.3%) compared to 30 mm target amplitude (t(19) = 6.74, p < .001, 95% CI = 7.24 - 13.77).

With respect to preferred tempo, a one-way repeated-measures ANOVA on produced ITIs showed a main effect of target amplitude (F(2,38) = 10.57, p < .001,  $\eta^2_p = .36$ ). Participants altered their preferred tempo in the different target amplitude conditions in a direction consistent with the *preferred velocity hypothesis*. Their preferred tempi were faster (produced inter-tap

intervals shorter) with lower target amplitudes than for higher target amplitudes. Follow-up paired samples t-tests showed that produced ITIs were significantly shorter for the 10 mm target amplitude compared to the 30 mm condition (t(19) = -4.00, p < .001, 95% CI = -130.24 - .40.75) and marginally significantly lower for the 30 mm compared to 50 mm target amplitude condition (t(19) = -2.10, p = .051, 95% CI = -186.43 - .66). Thus, lower and higher target amplitudes resulted in faster and slower preferred tempi, respectively.

#### Table 2.

Mean produced inter-tap interval (ITI) and tap amplitude for the three target amplitude versions of the SMT task in Experiment 1. Standard deviations are shown in parentheses. Column three shows the mean of estimated average velocities (V = 2A/ITI). Participants produced different ITIs and average velocities across target amplitudes.

Target Amplitude	Produced ITI (ms)	Tap Amplitude (mm)	Estimated V (cm/s)
10mm	625.0 (321.1)	18.1 (3.1)	7.14
30mm	710.5 (327.4)	37.0 (3.0)	12.27
50mm	803.4 (437.7)	56.3 (4.3)	17.44

To see how well the shift in preferred tempo with changes in target amplitude aligns with a constant preferred velocity, the estimated preferred velocity from the SMA and SMT tasks (combined) was used to predict mean produced ITI (preferred tempo) for the three target amplitude conditions. Figure 5 shows the observed mean produced ITI for each target amplitude compared to predicted mean ITI if participants had used a single constant preferred velocity to generate their preferred tempo at all three target amplitude conditions. Although preferred tempo shifted in the predicted direction with changes in target amplitude (based on a *preferred velocity hypothesis*), it did not change as much as predicted if participants were using a single constant preferred velocities.



Figure 5. Mean observed (solid line) vs. predicted (dotted line) ITIs for the 10 mm, 30 mm, and 50 mm target amplitude versions of the SMT task. The predicted ITIs are derived from the preferred velocity hypothesis using a preferred velocity estimate of 11.42 cm/s obtained from the SMA and SMT tasks. Participants changed ITI with target amplitude, but not as much as predicted if they kept a constant preferred velocity.

#### Discussion

Experiment 1 tested a preferred velocity account of preferred tempo. Participants first produced their maximum tap amplitude to provide an upper (high) estimate of tap amplitude for each participant. They then performed spontaneous motor amplitude (SMA) and spontaneous motor tempo (SMT) tasks where they produced their preferred amplitude and preferred tempo, respectively. Finally, they completed a target amplitude version of the SMT task for low, medium and high finger amplitudes. There were three main findings. First, participants produced similar preferred tempi and preferred amplitudes regardless of whether they performed the SMT or SMA tasks. Moreover, the estimated preferred velocity was nearly identical for both tasks and produced amplitudes and produced inter-tap intervals were highly correlated across the SMT and SMA tasks. Second, consistent with a preferred velocity account of preferred tempo, participants altered their preferred tempo for different target amplitudes in the direction predicted by the preferred velocity estimated from the SMA and SMT tasks. Finally, the amount of preferred tempo shift was less than predicted suggesting that participants may have a range of preferred velocities.

In terms of the first main finding, this experiment provided initial evidence for a strong link between mean ITI and tap amplitude when people produced their preferred tap amplitude (SMA) or their preferred tap tempo (SMT). This implies a preferred average tap velocity underlying the relationship between preferred tap tempo and amplitude, and in fact preferred velocities were very similar for both the SMT and SMA tasks, supporting a *preferred velocity hypothesis*. For both tasks, the ranges (SMA: 264.0 – 1262.5 ms; SMT: 274.8 – 1241.9 ms) and mean produced ITI (see Table 1) were in accord with those reported in previous studies (Boltz, 1994; Collyer et al., 1994; Drake et al., 2000; Fraisse, 1982; Hammerschmidt et al., 2021; McAuley et al., 2006; Moelants, 2002).

In terms of the second and third main findings, when producing SMT at different target amplitudes, target amplitude affected produced ITI (preferred tempo) in the direction predicted by the *preferred velocity hypothesis*, where produced ITI (preferred tempo) was shorter (faster) with lower target amplitudes. Although participants altered their preferred tempo in the different target amplitude conditions, they did so less than predicted if they kept average velocity constant. The tendency to change velocity as well as preferred tempo with target amplitude highlights that

individuals may have a range of preferred velocities for rhythmic tapping. This is in line with previous findings that individuals also have a range of preferred tempi in SMT tapping tasks (Kliger-Amrani & Zion-Golumbic, 2020a).

One additional finding from the target amplitude SMT task was a difference in amplitude accuracy where participants produced larger (50 mm) more accurately than smaller (10 mm) target amplitudes. Interestingly, they also tended to produce amplitudes larger than the target. This may be due to the nature of the target amplitude task, since they were required to match the target amplitude by visibly disrupting the string on the apparatus, which led participants to avoid underestimating target amplitude (i.e., not raising their finger high enough to touch the string). Although several participants reported having difficulty repetitively tapping at the 50 mm target amplitude condition, only one produced a mean tap amplitude below 50 mm in this condition.

In sum, this experiment provides initial support for the *preferred velocity hypothesis* by demonstrating that average (preferred) velocity was similar for the spontaneous motor amplitude and tempo tasks where participants produced similar preferred amplitudes and tempi regardless of instructions. The target amplitude version of the SMT task further revealed that they altered their preferred tempo when asked to tap with different target amplitudes in the direction predicted by the *preferred velocity hypothesis*. The next chapter extends these findings for unpaced rhythmic tapping to paced sync-continue tapping where participants have to match and then maintain a range of target inter-tap intervals. The experiment provides an initial test of the *amplitude control hypothesis*.

#### CHAPTER 5: TEST OF AN AMPLITUDE CONTROL HYPOTHESIS, PART I

# Introduction

Chapter 4 provided initial support for a preferred velocity account of preferred tempo – typically assessed using an unpaced spontaneous motor tempo task. In Experiment 1, participants were first asked to produce their spontaneous motor amplitude (SMA) and spontaneous motor tempo (SMT) and then completed a target amplitude version of the SMT task. The results showed a tight coupling between preferred tapping tempo and preferred tap amplitude for both SMA and SMT tasks, supporting the hypothesis that preferred tempo does not reflect a preferred time interval per se, but rather a preferred velocity of rhythmic movements. For the target amplitude version of the SMT task, preferred tempo shifted in the direction predicted by the *preferred velocity hypothesis* but not to the extent predicted, suggesting that individuals have a range of preferred velocities (rather than a single preferred velocity) guiding the timing of unpaced rhythmic movements.

The current chapter addresses a question that emerges from the preceding chapter: how does preferred velocity affect the timing control of *paced*, rather than *unpaced*, rhythmic movements where participants have to match a particular target inter-tap interval? One possibility, based on the *amplitude control hypothesis*, is that individuals keep their preferred velocity constant (or constant within a range of preferred velocities) across different target intertap intervals and vary tap amplitude to match the target interval. An alternative *velocity control hypothesis* predicts that individuals will keep tap amplitude constant across a range of target inter-tap intervals and vary movement velocity to match the target interval. The goal of Experiment 2 was to test these two hypotheses by having participants perform the sync-continue

tapping task at a range of target inter-tap intervals (tempi) and then examine the relation between tap amplitude and produced inter-tap intervals.

#### **Experiment 2**

In this experiment, participants performed sync-continue tapping at a wide range of target inter-tap intervals (ITIs) that included time intervals (tempi) that were generally longer (slower) than those tested in many previous studies. In total, there were seven target inter-tap intervals (or tempi). The shortest was 250 ms (a relatively fast tempo) and the longest was 1150 ms (a relatively slow tempo). The intermediate target ITIs were in 150 ms increments between 250 ms and 1150 ms. If participants use amplitude to match the target ITI while keeping velocity constant, then there should be a positive linear relationship between tap amplitude and target ITI. The *amplitude control hypothesis* also predicts a positive correlation between amplitude variability and produced ITI variability (if amplitude is used to control the sequence of produced time intervals, then variability in amplitude control should affect variability in the timing of the produced intervals). On the other hand, if individuals do not use amplitude to match the target ITI, and amplitude variability and the variability of produced time intervals should not be correlated.

# Methods

*Participants*: Thirty participants from Michigan State University participated in this experiment in return for partial credit in an undergraduate psychology course. Three participants were not included in the final sample. One individual did not follow task instructions (they did not tap for 8 trials of the experiment). Data from two other individuals were not recorded successfully due to equipment error. The final sample of twenty-seven individuals (17 female, 10 male) ranged from 18 to 27 years of age (M = 20.6, SD = 2.6). All participants reported normal

hearing. Based on self-reported handedness, 26 participants were right-handed, and 1 was ambidextrous. Participants varied in number of years of music training, with 21 participants reporting some music training ranging from 2 - 12 years of formal music lessons (M = 5.9, SD = 3.1). None were professional musicians.

*Design:* The experiment used a 2 (Tempo Order: Ascending vs. Descending) X 7 (Target ITI: 250, 400, 550, 700, 850, 1000, 1150 ms) mixed-factorial design, with Tempo Order as a between-subject variable and Target ITI as a within-subject variable. Participants who tapped in the ascending order completed trial blocks starting with the fastest tempo (250 ms) and ending with the slowest (1150 ms), while participants who tapped in descending order completed blocks starting with the slowest tempo (1150 ms) and ending with the fastest (250 ms). The final sample consisted of 14 participants in the ascending order condition and 13 in the descending order condition.

*Stimuli and apparatus*: The synchronization (pacing) signal consisted of sixteen 50-ms 440-Hz sine tones with inter-stimulus intervals of 200, 350, 500, 650, 800, 950, or 1100 ms to create sequences of 15 inter-onset-intervals (IOIs) of 250, 400, 550, 700, 850, 1000, and 1150 ms corresponding to the seven tested target inter-tap intervals (ITIs). Following the continuation phase, a longer, 200-ms 440-Hz sine tone signaled participants to stop tapping after 16.5, 26.4, 36.3, 46.2, 56.1, 66.0, and 75.9 seconds for the seven respective target tempi to allow for 15 synchronization and a minimum of ~30 continuation ITIs per trial. Thus, for each trial, participants produced ~45 tap intervals: 15 synchronization and ~30 continuation intervals. Headphones and motion-tracking apparatus were the same as described in General Methods.

*Procedure*: Participants first performed the sync-continue tapping task at the 7 different target ITIs while continuous finger motion data were recorded. Participants completed 4 trial

blocks at each target ITI (250, 400, 550, 700, 850, 1000, and 1150 ms) in either ascending or descending order. Approximately half of the participants (n = 14) completed the trial blocks in ascending tempo (fast-to-slow) order, and the remaining participants (n = 13) completed the trial blocks in descending tempo (slow-to-fast) order. Maximum finger heights were also measured by having participants keep their dominant (tapping) hand flat on the table and raise only their tapping (index) finger as high as possible from the table. Additionally, measurements of hand size, index finger length, and height were used to evaluate potential contributions of biomechanical factors to sync-continue tapping performance. Finally, participants completed the  $\sim$ 60 minutes.

*Data Processing and Analysis:* Continuous finger motion data processing for synccontinue tapping was the same as described in General Methods. Trials with fewer than 30 produced inter-tap intervals during the continuation phase were removed, which resulted in the removal of 10 trials (1.32%). One issue with data recording for this experiment was discovered after data collection was finished: motion tracking data were recorded at a 250 Hz rather than 200 Hz sampling rate for all but 3 participants. Because performance was not systematically different for the two sampling rates, all participants were included in the analyses. Except for an overall assessment of sync-continue tapping performance, analyses focused primarily on the continuation phase of tapping.

# Results

*Sync-Continue Tapping Performance:* Figure 6 shows an example of continuous finger motion data from one participant for one sync-continue trial of the 700 ms target ITI condition. The line shows the vertical trajectory of the finger over time where local minima (at 0 amplitude)

represent finger taps and local maxima represent tap amplitudes (maximum finger height). Figure 7 shows the mean produced ITI during sync-continue tapping for each of the seven target ITI conditions. As shown in Figure 7, participants were able to reasonably accurately match the target ITI after several taps and continue tapping at each target ITI once the pacing tones stopped. There was a slight tendency to speed up tapping during the continuation phase, especially at the slower tempi (longer ITIs); Table 3 provides a descriptive summary of mean produced inter-tap intervals during sync and continue phases for each of the target ITIs. Figure 8 shows the standard deviations (SDs) of produced ITI as a function of target ITI. With respect to variability, a 2 (Tempo Order: ascending vs. descending) X 7 (Target ITIs: 250, 400, 550, 700, 850, 1000, 1150 ms) mixed-measures ANOVA on SDs of produced ITIs during the continuation phase showed a main effect of Target ITI ( $F(6, 150) = 43.20, p < .001, \eta^2_p = .63$ ), no main effect of Order Condition ( $F(1, 25) = 2.47, p = .13, \eta^2_p = .09$ ), and an interaction between Target ITI and Order Condition ( $F(6, 150) = 5.05, p < .001, \eta_p^2 = .17$ ) where participants in the ascending order increased SD with ITI more than participants in the descending order. SDs were greater at longer target ITIs (slower tempi); and in accordance with Weber's law, the relationship between SDs and target ITI was linear ( $F(1,25) = 83.26, p < .001, \eta^2_p = .77$ ) (Repp, 2005).



Figure 6. Example of continuous finger motion data showing the first 30 s of one tapping trial for one participant in the 700 ms target ITI condition in Experiment 2. The line shows the vertical trajectory of the finger over time, where each point represents the vertical position sampled every 5 ms (200 Hz sampling rate). Local minima (at 0 amplitude) are finger taps and local maxima are single tap amplitudes (maximum finger height).



Figure 7. Series of mean produced inter-tap intervals (ITIs) during sync and continue phases for each of the 7 target ITI conditions in Experiment 2. Target ITIs are indicated by the grey horizontal lines. The vertical dotted line delineates the sync phase (left) and the continue phase (right). Participants showed a tendency to speed up during continuation more at longer target ITI conditions.

Table 3.

Mean produced inter-tap intervals (ITIs) with standard deviations in parentheses for the synchronization phase and the continuation phase of sync-continue tapping for the seven target ITIs examined in Experiment 2.

Target ITI (ms)	Sync ITI (ms)	Continue ITI (ms)	
250	238.2 (22.0)	246.2 (21.2)	
400	379.7 (40.4)	381.7 (52.9)	
550	534.3 (33.3)	522.6 (66.6)	
700	684.2 (23.1)	664.4 (63.6)	
850	828.6 (38.3)	806.9 (56.1)	
1000	975.6 (48.7)	943.0 (80.9)	
1150	1120.5 (75.6)	1103.4 (95.2)	


Figure 8. Standard deviation (SD) of produced ITIs as a function of target ITI in Experiment 1. SD scores increased linearly with the target ITI in line with Weber's Law.

Relationship between Tap Amplitude and Target ITI: Figure 9 shows mean tap amplitude (maximum finger height) as a function of target ITI. Mean tap amplitudes increased with ITI, in line with the *amplitude control hypothesis*. A 2 (Tempo Order: ascending vs. descending) X 7 (Target ITI: 250, 400, 550, 700, 850, 1000, 1150 ms) mixed-measures ANOVA on tap amplitude showed a main effect of Target ITI ( $F(6, 150) = 11.10, p < .001, \eta^2_p = .31$ ) where amplitudes were lower with shorter target ITI conditions. There was no main effect of Order Condition ( $F(1, 25) = .08, p = .78, \eta^2_p = .003$ ) and no interaction ( $F(6, 150) = 1.73, p = .12, \eta^2_p = .06$ ). Consistent with the *amplitude control hypothesis*, post-hoc trend analyses revealed a significant linear relationship between tap amplitude and target ITI ( $F(1,25) = 19.03, p < .001, \eta^2_p = .43$ ). There was also a significant quadratic component ( $F(1, 25) = 4.12, p = .05, \eta^2_p = .14$ ), reflecting larger decreases in amplitude at shorter ITIs (faster tempi) and smaller increases in amplitude at longer ITIs (slower tempi). A simple linear regression was also performed to test the extent to which produced tap amplitude predicted mean produced ITI during continuation tapping. The regression was statistically significant where tap amplitude significantly predicted produced ITI ( $\beta = .34, t = 4.92, p < .001$ ).



Figure 9. Mean tap amplitude as a function of target ITI with best-fitting regression line in Experiment 2. Mean tap amplitudes increased with ITI.

*Relationship between Tap Amplitude Variability and Produced ITI Variability:* Figure 10 shows the relationship between coefficients of variation (CVs) in tap amplitudes and produced

ITIs for each participant at each target ITI. Supporting the *amplitude control hypothesis*, there was a robust positive correlation between CVs for tap amplitudes and produced ITIs (r(187) = .86, p < .001) where greater variability in tap amplitudes was associated with greater variability in produced ITIs.



Figure 10. Relationship between coefficients of variation (CVs) of tap amplitudes and produced inter-tap intervals for each participant at each target ITI in Experiment 2. Amplitude variability positively correlated with ITI variability.

#### Individual Differences in Relationship between Tap Amplitude and Produced Inter-Tap

*Intervals:* To investigate potential individual differences in support for the *amplitude control hypothesis*, the best-fitting line for the relation between tap amplitude and produced ITI for the seven target tempo (ITI) conditions was calculated for each participant. The slope of these best-

fitting lines estimated the average rate of change in amplitude as a function of produced ITI. For this analysis, positive slopes indicated that tap amplitude increased with longer target ITI (e.g., slower tapping tempi) in line with the *amplitude control hypothesis*, while slopes of zero indicated that participants kept amplitude constant. A one-sample t-test on slopes compared to 0 revealed that, on average, mean slope (M = 11.62, SD = 13.76) was significantly positive, (t(26) = 4.39, p < .001).

It is important to note, however, there was substantial variability in slopes across participants. The distribution of participants' slopes is shown in Figure 11. Slopes ranged from -8.28 to 40.55 mm/s and the overall shape of the distribution was bimodal. So, while average slope is significantly positive, this does not take into account the fact that some individuals have highly positive slopes while others have slopes centered near zero. This suggests that some individuals are matching the target ITI by changing tap amplitude in accordance with the *amplitude control hypothesis* while others are keeping amplitude constant. This raises the possibility that individuals have different strategies for producing time intervals that match the target ITI in the sync-continue task, with some decreasing (increasing) tap amplitude to produce shorter (longer) ITIs (while keeping average tap velocity constant), while others are keeping tap amplitude constant and increasing (decreasing) average tap velocity to produce shorter (longer) ITIs.



Figure 11. Frequency distribution of all slopes showing relationship between amplitude and produced ITI for each participant (n = 27) in Experiment 2. The overall shape of the distribution appeared to be bimodal.

To further investigate individual differences in participants' use of an amplitude control or velocity control strategy, K-means clustering was performed on slopes, dividing participants into 2 groups based on their proximity to cluster centers. This resulted in Group 1 consisting of n = 12 participants clustered around a mean slope of -1.69 and Group 2 consisting of n = 15 participants clustered around a mean slope of 22.28. Figure 12 shows mean tap amplitude as a function of target ITI for each group. One-sample t-tests against 0 slope confirmed that Group 1 had a mean slope not significantly different from 0 (M = -1.69, 95% CI = -5.50 - 2.11) (t(11) = -.98, p = .35, d = -.28), while Group 2 had a significantly positive slope (M = 22.28, 95% CI = 18.36 - 26.19) (t(14) = 12.20, p < .001, d = 3.15). For Group 2, the pattern of amplitudes and produced ITIs was consistent with the *amplitude control hypothesis*; for Group 1, the pattern was consistent with maintaining a constant amplitude, supporting the view that some individuals use amplitude while others use velocity to control the produced ITI in sync-continue tapping.



Figure 12. Mean tap amplitude as a function of target ITI for the amplitude control and velocity control groups identified by K-means clustering in Experiment 2. The amplitude control group showed a linear increase in tap amplitude with ITI but the velocity control group did not.

*Biomechanical Factors and Amplitude Control:* To better understand how biomechanical factors may relate to the use of tap amplitude as a control parameter used to match the target ITI, two finger measurements were analyzed: finger length (from palmar digital crease at the

metacarpophalangeal joint to the tip of the index finger) and maximum finger amplitude (maximum possible height participants could raise their finger off the table). These measures allowed an evaluation of whether finger length (a component of limb resonance) (Rosenbaum et al., 1991; Wagenaar & Van Emmerik, 2000) or range of finger motion are related to the tendency to use tap amplitude to match the different target ITIs in the sync-continue tapping task. Correlations were calculated between both of these measures and slopes of the relationship between tap amplitude and produced continuation ITI. Finger length did not correlate with slope (r(25) = .05, p = .80). However, maximum finger amplitude positively correlated with slope of the relationship between tap amplitude and ITI (r(25) = .39, p = .04). Larger maximum amplitudes were associated with larger slopes. Participants who could lift their finger higher showed a greater tendency to systematically vary amplitude when having to produce different target ITIs in sync-continue tapping. This suggests that biomechanical constraints on the range of finger tapping amplitude contribute to individual differences in amplitude control strategies, where a larger possible range of motion is associated with a greater degree of amplitude change as a function of ITI.

*Music Training and Amplitude Control:* Finally, to explore whether music training was related to individual differences in a participant's tendency to use tap amplitude to match the target inter-tap interval, number of years of formal music lessons was correlated with the slope of the relationship between tap amplitude and mean produced ITI. The correlation was negative (r(25) = -.50, p = .008). More music training was associated with smaller slopes indicating less change in tap amplitudes across produced ITI. This suggests that more music training is related to less reliance on amplitude control to match target tempi in sync-continue tapping.

#### Discussion

Experiment 2 examined the relationship between movement amplitude and movement timing during paced sync-continue tapping at a wide range of target inter-tap intervals (ITIs). The experiment served as an initial test of the amplitude control hypothesis whereby participants are proposed to produce a given target ITI by maintaining a constant average movement velocity and then decreasing or increasing finger amplitude to produce the correct target ITI (based on V = 2A/ITI). There were four main findings. First, consistent with the *amplitude control* hypothesis, tap amplitude increased linearly with ITI. Second, providing additional support for the amplitude control hypothesis, variability in tap amplitudes predicted variability in produced ITIs. Third, there were large individual differences in the slopes of the relationship between tap amplitude and produced ITI where some participants increased amplitude with longer produced ITIs, consistent with an amplitude control strategy, while others kept amplitude constant, consistent with a velocity control strategy. Finally, strategy differences were associated with how high participants could lift their finger (as measured by their maximum tap amplitude). Individuals who could raise their finger higher (i.e., they had a greater range of tap amplitudes) were more likely to show a pattern of tap amplitudes in line with the *amplitude control* hypothesis.

While the finding that tap amplitude increased linearly with target ITI confirmed predictions of the *amplitude control hypothesis*, this relationship was mediated by produced ITI, where the rate of change in tap amplitude as a function of target ITI was larger for faster produced ITI and smaller for slower produced ITI. Participants changed amplitude as a function of target ITI at a greater rate at fast tapping tempi than at slow tempi, indicating that the use of amplitude to produce target ITI varies at fast and slow tapping tempi. It is important to note that

previous studies on rhythmic movement timing showing a linear relationship between amplitude and ITI have focused on a narrow range of tempi, typically at 1 Hz (1000 ms ITI) or faster (Kay et al., 1987; Rosenbaum et al., 1991; Vaughan et al., 1996). If the change in amplitude is smaller at slower tempi (i.e., non-linear) as suggested by the results of the current experiment, these studies may make claims about a linear change in amplitude that does not generalize to movements at slower tempi. Furthermore, previous studies averaged amplitudes across all participants, preventing the observation of individual differences in amplitude-tempo relationships. This raises the possibility that previous observations of an increase in amplitude at slower tempi are driven by a subset of participants who change amplitude with target tempo (ITI) without considering that some individuals may not. The current experiment is the first to my knowledge to demonstrate individual differences in the use of amplitude as a potential control parameter for matching different target ITIs where some people change amplitude and others keep amplitude constant across ITI, which shows the importance of examining patterns of spatiotemporal movement data within individuals to better understand the control of rhythmic movement timing.

In this experiment, participants with a greater range of possible tap amplitudes were notably more likely to adopt an amplitude control strategy. Individuals with a smaller possible range of finger motion are more restricted in the amount they can increase tap amplitude to produce longer ITIs, which may lead them to keep a more consistent amplitude across ITIs. Such a result suggests that biomechanical factors contribute to individual differences in amplitude control strategies. The results also showed that more formal music training was related to smaller slopes, indicating that more music training was associated with a tendency to keep amplitude constant, in line with a velocity control strategy. Playing a musical instrument requires precise

spatiotemporal control of finger movements to produce the correct notes at the correct time, which may have an impact on how people with musical training time their finger movements.

To summarize, results of Experiment 2 show the interdependence of spatial and temporal characteristics of paced sync-continue tapping and provide initial support for an *amplitude control hypothesis*. Previous work on sync-continue tapping has predominantly focused on only the temporal dimension of individuals' movements to make inferences about the nature of the brain's timing mechanism. This experiment also provided evidence of large individual differences not previously reported, with tapping behavior for some participants consistent with an amplitude control strategy, and for others with a velocity control strategy. These individual differences in the use of amplitude control or velocity control strategies appear to depend on both an individual's maximum finger height during tapping (suggesting there are biomechanical constraints on how effective an amplitude control strategy can be) and music training. One outstanding question from Experiments 1 and 2 concerns how having participants tap at different target amplitudes, rather than at their self-selected amplitude, affects their timing performance at different target inter-tap intervals. In Experiment 3, this question is addressed by explicitly manipulating target amplitude in paced sync-continue tapping.

# CHAPTER 6: TEST OF AN AMPLITUDE CONTROL HYPOTHESIS, PART II Introduction

Experiment 2 provided preliminary support for an *amplitude control hypothesis* in the production of time intervals in paced sync-continue tapping. In line with the *amplitude control* hypothesis, self-selected amplitude increased linearly with target ITI and amplitude variability predicted variability in the sequence of produced ITIs. These effects were most pronounced at the shortest target inter-tap intervals where self-selected tap amplitudes were lowest. Analyses of individual differences revealed that not all participants varied amplitude in a manner consistent with the *amplitude control hypothesis*. Some participants kept amplitude constant across target inter-tap intervals supporting an alternative velocity control hypothesis. Factors underlying these individuals included maximum range of possible finger motion and extent of musical training. Results from individuals with a greater range of finger tapping motion were more likely to support the amplitude control hypothesis. One limitation of Experiment 2 is that participants selfselected their tapping amplitudes; thus, the initial support reported for the *amplitude control* hypothesis was correlational in nature. Experiment 3 addresses this issue and extends Experiment 2 by explicitly manipulating target amplitude during paced sync-continue tapping at different target ITIs.

## **Experiment 3**

Participants from Experiment 1 returned to the lab and performed paced sync-continue tapping in nine conditions: three target amplitudes ranging from low to high crossed with three target ITIs ranging from short to long. Maximum tap amplitude and preferred tap amplitude (SMA) measured in Experiment 1 were used to set target amplitudes for each participant. Of

primary interest was whether, in line with the *amplitude control hypothesis*, individuals have better timing performance during sync-continue tapping for congruent target amplitude-target ITI combinations (e.g., low amplitude-short ITI, high amplitude-long ITI) than for incongruent target amplitude-target ITI combinations (e.g., high amplitude-short ITI, low amplitude-long ITI).

A secondary aim of the experiment was to test the *preferred velocity hypothesis* introduced in Experiment 1 by examining whether timing performance is better for conditions that are near an individual's preferred velocity. Each combination of target amplitude and target ITI determines a specific tap velocity according to V = 2A/T where A corresponds to target tap amplitude and T corresponds to the target ITI. The *preferred velocity hypothesis* predicts that timing performance should be better for combinations of target amplitudes and inter-tap intervals that yield an average velocity that is closer to their preferred velocity measured in Experiment 1.

#### Methods

*Participants and Design*: The same participants who completed Experiment 1 returned after 1 to 12 days to complete Experiment 3. Participants were twenty undergraduates (15 female, 5 male) between the ages of 18 and 26 years (M = 19.8, SD = 2.3) The experiment implemented a 3 (Target ITI: 250 ms, 550 ms, 1150 ms) X 3 (Target Amplitude: low, preferred, high) within-subjects design.

*Stimuli and Apparatus*: The synchronization pacing signal consisted of sixteen 50-ms 440-Hz sine tones followed by 200, 500, and 1100 ms of silence to create a sequence of 15 equal inter-onset-intervals (IOIs) corresponding to target inter-tap intervals of 250, 550, and 1150 ms. A longer, 200-ms 440-Hz sine tone signaled to participants to stop tapping after 16.5, 36.3, and 75.9 seconds for the three respective target ITIs to allow for ~45 produced ITIs per trial (15

synchronization and 30 continuation intervals). Target amplitudes were set individually for each participant based on their maximum possible amplitude and spontaneous motor amplitude (SMA) from Experiment 1, where low amplitude was 50% of SMA, preferred amplitude was equal to SMA, and high amplitude was 85% of maximum possible amplitude. The same experimental set up was used as in the previous experiments.

*Procedure*: Participants performed sync-continue tapping at the three target tempi (corresponding to target inter-tap intervals of 250 ms, 550 ms, 1150 ms) and the three target tap amplitudes (low, preferred, high). Participants were pseudo-randomly assigned to 1 of 4 possible counterbalanced orders (see Table 4). Target amplitude was presented in blocks from low-to-high or high-to-low, and target ITI was presented in ascending (fast-to-slow) or descending (slow-to-fast) order within each target amplitude block. No participants produced an SMA higher than 85% of their maximum possible amplitude. Participants performed 4 trials of sync-continue tapping for each of the 9 conditions. After tapping, they completed the same daily strategies survey as they did in Experiment 1. The entire experiment lasted ~60 minutes.

### Table 4.

			0		6	1			
Order 1	Low Amplitude			Preferred Amplitude			High Amplitude		
	250 ms	550 ms	1150 ms	250 ms	550 ms	1150 ms	250 ms	550 ms	1150 ms
Order 2	High Amplitude			Preferred Amplitude			Low Amplitude		
	250 ms	550 ms	1150 ms	250 ms	550 ms	1150 ms	250 ms	550 ms	1150 ms
Order 3	Low Amplitude			Preferred Amplitude			High Amplitude		
	1150 ms	550 ms	250 ms	1150 ms	550 ms	250 ms	1150 ms	550 ms	250 ms
Order 4	High Amplitude		Preferred Amplitude			Low Amplitude			
	1150 ms	550 ms	250 ms	1150 ms	550 ms	250 ms	1150 ms	550 ms	250 ms

Participants were assigned to 1 of 4 possible order conditions for Experiment 3. Target amplitudes were blocked together and target ITIs were presented in either ascending (fast-to-slow) or descending (slow-to-fast) order within a target amplitude block.

*Data Processing and Analysis:* All data processing and analysis procedures were the same as in Experiment 2. Trials with fewer than 30 produced inter-tap intervals in the continuation phase were removed, which resulted in the removal of 4 trials (.6%). Results reported below focus on the continuation phase of tapping.

# Results

Success Matching Target Amplitude: First, I confirmed that the manipulation of target amplitude was successful. Figure 13 shows the mean standardized tap amplitudes for the 3 target amplitudes and 3 target ITI conditions. Tap amplitudes were standardized (z-scored) for each participant to take into account the different ranges of target amplitudes used for each participant, effectively putting all participants on the same amplitude scale. A 3 (Target Amplitude: low, preferred, high) x 3 (Target ITI: 250 ms, 550 ms, 1150 ms) within-subjects ANOVA on standardized tap amplitude showed a main effect of Target Amplitude (F(2, 38) =419.52, p < .001,  $\eta^2_p = .96$ ), a main effect of Target ITI (F(2, 38) = 26.26, p < .001,  $\eta^2_p = .58$ ), and an interaction between Target ITI and Target Amplitude ( $F(4, 76) = 15.87, p < .001, \eta^2_p =$ .45). As expected, standardized tap amplitude was smallest for the low target amplitude (M = -1.1, SD = .2), largest for the high target amplitude (M = 1.2, SD = .3) and intermediate for the preferred amplitude condition (M = -.1, SD = .3). The interaction between Target ITI and Target Amplitude for produced tap amplitude reflects a greater change in produced tap amplitude at the 250 ms target ITI in the preferred and high target amplitude conditions. In the fastest tempo (short ITI) condition, tap amplitude was reduced more for the preferred and high target compared to low target amplitude.



Figure 13. Mean standardized (z-score) tap amplitude for the three target amplitude conditions at the three target tempi in Experiment 3. Perfectly straight horizontal lines would represent consistent accuracy in matching target amplitude across target tempi. Participants produced smaller amplitudes in the 250 ms ITI conditions compared to other conditions.

Effect of Target Amplitude on Tapping Performance: Figure 14 shows the time series of

produced ITI for the nine combinations of target amplitude and target ITI. In general, participants were able to reasonably match the target ITI regardless of the target amplitude. A 3 (Target ITI: 250 ms, 550 ms, 1150 ms) X 3 (Target Amplitude: low, preferred, high) ANOVA on produced ITIs during the continuation phase showed a main effect of Target ITI (F(2, 38) =1019.82, p < 001,  $\eta^2_{P} = .98$ ), but no effect of Target Amplitude or interaction (both p > .05). Mean directional error (represented as the percentage difference between produced and target ITIs) for the nine conditions is shown in Table 5. Evaluation of the effect of target amplitude on

timing accuracy was performed by a 3 (Target ITI: 250 ms, 550 ms, 1150 ms) X 3 (Target Amplitude: low, preferred, high) ANOVA on percent directional error of produced continuation ITIs. The results showed a main effect of Target Amplitude ( $F(2, 38) = 9.39, p < .001, \eta_p^2 = .33$ ) where timing accuracy was worse for higher Target Amplitudes, a main effect of Target ITI  $(F(2, 38) = 19.58, p < .001, \eta^2_p = .51)$  where accuracy was worse for faster Target ITIs, and an interaction between Target ITI and Target Amplitude ( $F(4, 76) = 17.25, p < .001, \eta^2_p = .48$ ). Participants showed a tendency to tap slower (larger positive error) than the target ITI in high target amplitude and fast (250 ms) target ITI conditions. The tendency to slow down at the 250 ms ITI was most pronounced at the high target amplitude. To unpack the interaction, pairedsamples t-tests were conducted on percent directional error in the 250 ms ITI condition. Post-hoc t-tests showed that directional error was greater in the high amplitude compared to low (t(19) =5.47, p < .001, 95% CI = 9.24 - 20.71) or preferred (t(19) = 3.88, p = .001, 95% CI = 4.09 - 100013.67) and greater for the preferred compared to low amplitude condition (t(19) = 3.43, p = .003, 95% CI = .2.38 - 9.81). At the fast target ITI, participants produced increasingly longer (slower) continuation ITIs as target amplitude increased.



Figure 14. Time series of produced ITIs for the nine target amplitude and target ITI combinations in Experiment 3. Grey horizontal lines show the target ITI. The region to the left of the vertical dotted line shows the sync phase and the region to the right shows the continue phase. Participants increased ITIs during the continue phase in the 250 ms target ITI condition, especially in the high amplitude (cyan) condition.

Table 5.

Mean percent directional error of produced continuation ITIs with standard deviations in parentheses for the nine target amplitude and target ITI conditions in Experiment 3. Participants produced longer (positive) ITIs than the target in the 250 ms target ITI condition, especially for higher target amplitudes.

Target Amplitude (mm)	Target ITI (ms)	% Directional Error
Low	250	4.1 (5.9)
	550	-2.0 (6.7)
	1150	-1.2 (11.9)
Preferred	250	10.2 (11.5)
	550	0.2 (6.3)
	1150	-2.5 (11.3)
High	250	19.0 (11.8)
	550	0.2 (4.8)
	1150	-0.7 (8.5)

Figure 15 shows the coefficient of variation (CV) of produced ITIs during the continuation phase for all conditions. A 3 (Target ITI: 250 ms, 550 ms, 1150 ms target ITI) X 3 (Target Amplitude: low, preferred, high) ANOVA on CVs showed a main effect of Target Amplitude ( $F(2, 38) = 4.94, p = .02, \eta^2_p = .20$ ), a main effect of Target ITI ( $F(2, 38) = 28.21, p < .001, \eta^2_p = .60$ ), and an interaction between Target ITI and Target Amplitude ( $F(4, 76) = 9.83, p < .001, \eta^2_p = .34$ ). In general, CVs were greater for the 250 ms target ITI compared to the 550 ms and 1150 ms conditions. There was no difference in CV between the 550 ms and 1150 ms target ITIs (p > .05). With respect to target amplitude, target amplitude had no effect on CV for the 550 ms and 1150 ms target ITIs (the two slower tempi). However, in line with the *amplitude control hypothesis*, for the 250-ms target ITI (fastest tempo), CVs were lowest (best) for the congruent (low-amplitude-short target ITI condition) and highest (worst) for the incongruent (high-

amplitude-short target ITI condition). Paired samples t-tests confirmed that in the 250 ms target ITI condition, ITI CV was higher for the high amplitude compared to low (t(19) = 4.82, p < .001, 95% CI = .01 - .03) or preferred (t(19) = 3.00, p = .007, 95% CI = .005 - .03) and higher for the preferred compared to low amplitude condition (t(19) = 2.10, p = .05, 95% CI = .00001 - .02).



Figure 15. Coefficient of variation (CV) of the produced ITIs during the continuation phase for the nine combinations of target amplitude and target ITI in Experiment 3. ITI variability was higher in the 250 ms target ITI condition, especially for higher target amplitudes.

# Preferred Velocity and Timing Variability: To further test the preferred velocity

*hypothesis* introduced in Experiment 1, I examined the relationship between preferred velocity and timing performance across target amplitudes and tempi. To investigate whether timing variability during continuation was related to preferred velocity, I calculated the absolute difference between the average of SMT and SMA velocity in Experiment 1 (preferred velocity) and produced average velocity during continuation in Experiment 3 (|preferred velocity – produced velocity|) as a measure of velocity compatibility in each Target Amplitude-Target ITI condition. I conducted a simple linear regression to see whether the difference between preferred and produced velocity predicted ITI CV during continuation tapping. The regression was statistically significant ( $R^2 = .13$ , F(1, 178) = 27.73, p < .001) where velocity compatibility predicted timing variability ( $\beta = .37$ , t = 5.27, p < .001). Temporal variability was lower when average continuation tap velocity was closer to preferred average velocity.

# Discussion

Experiment 3 extended the results of Experiment 2 by explicitly manipulating tap amplitude and then investigating the effects of tapping at the different target amplitudes on timing performance at a range of target ITIs. There were five main findings. First, timing performance in sync-continue tapping was less precise (more variable) overall at the 250-ms target ITI than the two longer ITIs (i.e., the two slower tempi). Second, participants successfully modulated tapping amplitude to match the three target amplitudes. Third, tapping at the different target amplitudes did not affect timing accuracy during sync-continue tapping (i.e., how closely the mean produced ITIs matched the target ITIs). Fourth, tapping at the different target amplitudes did however affect timing precision (variability); at the shortest (250 ms) ITI, tapping was less precise (more variable) when the target amplitude was congruent with the target ITI (low amplitude – short ITI) than when the target amplitude was incongruent with the target ITI (high amplitude – short ITI). Finally, consistent with the *preferred velocity hypothesis*, timing precision (measured by the coefficient of variation of produced inter-tap intervals) was better (less variable) when participants tapped at a velocity that was closer to their preferred velocity.

The finding of greater timing variability at the shortest 250 ms ITI is consistent with the results of previous studies showing that Weber's law for time interval discrimination and production breaks down at fast tapping tempi corresponding to around a 250 ms ITI (Repp, 2003, 2006). Also, at the 250 ms target ITI, participants showed the least temporal variability (greatest temporal precision) in the congruent high target amplitude condition and the greatest temporal variability (least temporal precision) in the incongruent low target amplitude condition, providing support for the *amplitude control hypothesis*. Moreover, participants favored lower tapping amplitudes in service of producing the faster (250 ms) target ITI. This finding is consistent with the results of Experiment 2, which showed that participants reduced tap amplitude to produce faster ITIs, providing additional support for the *amplitude control hypothesis*.

The results of this experiment are also similar in some respects to other work. Dione and Delevoye-Turrell (2015) found that when participants synchronized finger tapping along 6 points around a circle at target tempi that corresponded to 300 ms to 1100 ms tapping intervals, participants showed more temporal variability and tended to underestimate target distance, producing circles of smaller radii when tapping faster (with tapping intervals < 500 ms). However, to my knowledge, this is the first study to show a similar pattern of results for synccontinue tapping with a spatial and temporal goal. Worse spatial and temporal performance when tapping at targets that entail moving farther faster implies that tapping performance is constrained by the individual's maximum movement speed.

The finding that temporal variability was lower when people were tapping closer to their preferred velocity provides additional support for the *preferred velocity hypothesis* initially examined in Experiment 1. Experiment 3 extended the findings of Experiment 1 to conditions

where people were required to produce various combinations of tap amplitude and tempo. In the target amplitude version of the SMT task in Experiment 1, participants were free to change their average velocity at each target amplitude by changing their produced ITI. Although there was some change in preferred tempo with different target amplitudes in Experiment 1, participants also changed average velocity at different target amplitudes, providing evidence for a range of preferred velocities. Experiment 2 showed that when tap velocity is constrained by explicitly manipulating both target amplitude and target ITI (tempo), timing performance is better when the required tap velocity is closer to the preferred velocities produced by the same participants in Experiment 1.

As an interim summary, results of Experiments 1 - 3 provide evidence for a systematic relationship between tap amplitude and tempo during unpaced and paced sync-continue tapping; this relationship also appears to be different at fast tempi compared to slow tapping tempi. The suggestion here is that when tapping at fast tempi that require movement speeds at or near maximum, people can match the short target ITI only by decreasing tap amplitude (ITI = 2A/V; Eq. 7). In this equation, V is at an upper limit and thus the only way to reduce (shorten) ITI is to decrease A (tap amplitude). However, when tapping at a slow enough tempo, people encounter the opposite problem; they reach their maximum tap amplitude (finger height) and thus can no longer change (in this case, increase) tap amplitude to match the target ITI. In this case in the equation ITI = 2A/V, the tap amplitude is constant (i.e., at maximum) and then presumably, velocity, V, must change to match longer target ITIs. It is conceivable that velocity, V, also has a slow limit. This raises the question: how do individuals produce slow tempi (match long target ITIs) when they have reached the upper limit of movement amplitude and velocity is no longer an effective control parameter? In the next chapter, Experiment 4 addresses the possibility that

individuals increase tap dwell time (the amount of time that they rest their finger on the table between tap onsets).

#### CHAPTER 7: TEST OF A DWELL TIME HYPOTHESIS, PART I

### Introduction

This chapter extends the work presented in previous chapters by focusing on paced tapping to very slow rhythms, which are near the temporal boundary where perceived rhythm breaks down. Of primary interest is the consideration of dwell time (the duration that individuals keep their finger in contact with the table in between taps) as an additional factor that potentially influences sync-continue tapping performance. Previous research on paced rhythmic movements has shown that when tapping slow rhythms, timing variability increases in violation of Weber's law and people tend to increase tap dwell times with ITI and there is some initial evidence that people may tend to increase dwell times with longer target ITIs (Billion & Semjen, 1995; Cos et al., 2015; Hove & Keller, 2010; Inui et al, 1998; Repp, 2006; Repp & Saltzman, 2002; Repp & Su, 2013). This suggests that tap dwell time may be an important factor to consider in the production of slow rhythms, which necessitate matching long target inter-tap intervals), finger amplitude in sync-continue finger tapping is predicted to be at a maximum (and thus can no longer be increased to lengthen produced intervals).

As initial support for the proposed *dwell time hypothesis* in the production of slow rhythms, Cos et al. (2015) found that overall dwell time during synchronization tapping increased with longer target inter-tap intervals (ITIs). However, the relationship between target ITI and the proportion of time spent dwelling between tap onsets suggested large individual differences in dwell-time proportions. Some people maintained a constant proportion of dwell time to movement time ("move time") across tapping tempi, while others increased dwell-time proportions at slower tapping tempi (longer target inter-tap intervals). The aim of Experiment 4

was to test a *dwell time hypothesis* by (1) investigating dwell time and tap amplitudes as a function of target ITI and (2) consider the relation between dwell time and timing performance for target ITIs that extended into the very slow range. The *dwell time hypothesis* proposes that at very slow tempi (long target ITIs), participants will keep tap amplitude constant and increase dwell time to match the target ITI. Unlike at short ITIs and the *amplitude control hypothesis*, the *dwell time hypothesis* predicts that dwell time, but not amplitude, will increase with longer target ITIs.

# **Experiment 4**

Experiment 4 extends the work of Cos et al. (2015) by considering changes in dwell time across a range of fast to slow target tempi and by investigating the relationship between dwell-time proportions, tap amplitude, and timing performance. Participants performed sync-continue tapping for target ITIs of 506 ms, 759 ms, 1139 ms, and 1709 ms target ITIs, spanning tapping tempi that ranged from comfortable to very slow. The selected tempi (ITIs) matched four of the sync-continue tempi examined in McAuley et al. (2006), the slowest of which is around the slow temporal boundary of the typical adult entrainment region where perceived rhythm breaks down.

#### Methods

*Participants and Design*: Forty-six individuals (39 female, 7 male) between the ages of 19 and 27 years (M = 19.4, SD = 1.6) from Michigan State University participated in return for credit in an undergraduate psychology course. The experiment used a within-subjects design where all participants completed sync-continue tapping at 4 target tempi corresponding to target inter-tap intervals (ITIs) of 506 ms, 759 ms, 1139 ms, and 1709 ms. All participants reported normal hearing. Thirty-eight participants were right-handed, 7 were left-handed, and 1 reported

being ambidextrous. The 38 right-handers and 1 ambidexter completed all tasks with their right hand and the 7 left-handers used their left hand.

*Stimuli and Apparatus*: The synchronization (pacing) signal consisted of sixteen 50-ms 440-Hz sine tones followed by 456, 709, 1089, or 1659 ms of silence to create a sequence of 15 inter-onset-intervals (IOIs) of 506, 759, 1139, and 1709 ms corresponding to the four target inter-tap intervals (ITIs). The end of the continuation phase was signaled by a longer, 200 ms 440 Hz sine tone, which occurred 30, 45, 65, or 95 seconds for the four target ITIs to allow for 15 synchronization and a minimum of ~30 continuation ITIs per trial. The same experimental set up was used as in the previous experiments.

*Procedure:* Participants performed the sync-continue tapping task at the 4 different target ITIs while continuous finger motion data were recorded. Participants completed 5 trials of the sync-continue tapping task with their dominant hand at each of the four target inter-tap intervals (506 ms, 759 ms, 1139 ms, and 1709 ms) for a total of 20 trials. Each target ITI was presented within a block of trials and the order of blocks was counterbalanced across participants (Table 6). Participants completed the same background survey as previous experiments. The entire experiment lasted ~60 minutes.

Table 6.

Order	Block 1	Block 2	Block 3	Block 4	
1	506 ms	759 ms	1139 ms	1709 ms	
2	1709 ms	1139 ms	759 ms	506 ms	
3	759 ms	506 ms	1709 ms	1139 ms	
4	1139 ms	1709 ms	506 ms	759 ms	

Latin-square counterbalancing for Experiment 4. Participants were pseudo-randomly assigned to 1 of 4 possible blocked target ITI order conditions.

*Data Processing and Analysis:* All sync-continue data analysis procedures were the same as in previous experiments. Trials with fewer than 30 continuation tap intervals produced were removed, which resulted in a total of 15 trials (1.6%) removed from the final data set. Dwell time (the length of time that finger was on the table) using a < 3mm threshold. Dwell-time proportion was calculated by dividing mean tap dwell time by mean produced ITI. Because move time represents the remaining tap time after subtracting dwell time from produced ITI (mean move time = mean ITI – mean dwell time), results are discussed only in terms of tap dwell time. As in the previous experiments, results reported below focus primarily on the continuation phase of tapping.

# Results

Sync-Continue Tapping Performance: Figure 16 shows the mean produced ITI during sync-continue tapping for each of the 4 target ITI conditions. On average, participants were able to accurately match the target ITI for both the synchronization and continuation phases of the tapping task; as can be seen in Table 7, produced ITIs for both the synchronization phase and continuation phase closely matched the target ITIs. Figure 17 shows mean coefficient of variation (CV) of the produced inter-tap intervals (ITIs) for the continuation phase for the 4 target tempi. A one-way repeated-measures ANOVA on CV showed a main effect of Target ITI ( $F(3, 135) = 10.16, p < .001, \eta^2_p = .18$ ), where participants showed worse timing precision (greater variability) at longer ITIs (slower tempi) than at shorter ITIs (faster tempi). These results are in line with results of previous studies on sensorimotor synchronization that reveal deviations from Weber's Law at slow tapping tempi; see Repp (2006) for a review. Follow-up paired-samples t-tests showed that CV was higher for the 1139 ms compared to 739 ms target ITI (t(45) = 2.42, p = .02, 95% CI = .001 - .01) and higher for the 1709 ms compared to the 1139 ms

Target ITI (t(45) = 2.42, p = .02, 95% CI = .002 - .02), but CVs for the 506 ms and 759 ms Target ITIs were not significantly different (p = .75).



Figure 16. Series of mean produced inter-tap intervals (ITIs) during sync-continue tapping for each of the 4 target ITI conditions in Experiment 4. The region to the left of the vertical dotted line shows the synchronization phase, and the region to the right of the dotted line shows the continuation phase. Participants were reasonably accurate at producing all target ITIs.

Table 7.

Mean produced inter-tap intervals (ITIs) for Sync and Continue phases for Experiment 4; standard deviations are in parentheses.

Target ITI (ms)	Produced Sync ITI (ms)	Produced Continue ITI (ms)
506	501.8 (19.2)	514.9 (105.6)
759	759.2 (18.6)	760.5 (42.6)
1139	1130.1 (54.5)	1138.0 (114.8)
1709	1699.9 (65.5)	1714.6 (133.7)



Figure 17. Mean ITI CVs for the four target ITI conditions in Experiment 4. ITI variability increased for the three slower target ITIs.

*Tap Amplitudes:* Figure 18 shows mean tap amplitude as a function of target ITI. A oneway repeated-measures ANOVA on tap amplitude revealed no effect of target ITI (F(3, 135) =1.21, p = .31,  $\eta^2_p = .03$ ). In general, participants maintained a constant tap amplitude across the four target ITIs. Furthermore, mean tap amplitude was not correlated with mean produced ITI, mean tap dwell time, or coefficient of variation in the produced ITIs (all p > .11).



Figure 18. Mean tap amplitude as a function of target ITI in Experiment 4. Tap amplitude was constant across all target ITIs.

*Tap Dwell Times:* Figure 19 shows mean tap dwell times as a function of target ITI. Dwell time increased with ITI. A one-way repeated-measures ANOVA on dwell times showed a main effect of target ITI (F(3, 135) = 65.73, p < .001,  $\eta^2_p = .59$ ) where participants increased dwell times at longer target ITIs. A linear trend analysis revealed both a significant linear trend (F(1, 45) = 85.43, p < .001,  $\eta^2_p = .65$ ), and a quadratic trend (F(1, 45) = 19.05, p < .001,  $\eta^2_p = .30$ ), suggesting larger than linear increases in dwell times at the slowest tempo (longest ITI). To evaluate whether participants changed dwell-time proportions as a function of target ITI, a repeated-measures ANOVA on dwell-time proportion was conducted. Results showed a main effect of target ITI (F(3, 135) = 3.77, p = .01,  $\eta^2_p = .08$ ). A linear trend analysis revealed a significant linear trend in proportion of dwell times across target ITIs (F(1, 45) = 5.68, p = .02,  $\eta^2_{P} = .11$ ) indicating that dwell-time proportions increased as a function of target ITI. There were no higher order trends.



Figure 19. Mean tap dwell time (ms) for the four target ITI conditions in Experiment 4. Tap dwell time increased with target ITI.

Relationship between Dwell Time Variability and Produced ITI Variability: To evaluate the relationship between dwell time variability and ITI variability during continuation tapping at the slow tempo, Pearson correlations were performed. They showed that dwell time CV was positively correlated with ITI CV (r(44) = .67, p < .001). Greater dwell time variability was associated with greater ITI variability at the slowest tempo.

*Individual Differences in Dwell-Time Proportions:* Next, I considered individual differences in changes in dwell-time proportions as a function of target ITI. Figure 20 shows frequency distributions of participants' dwell-time proportions for 9 equal-size bins for the 4

target ITI. Visual inspection revealed a wide range in dwell-time proportions with some participants showing low dwell-time proportions and others showing high dwell-time proportions. Frequency distributions of dwell-time proportions appeared to become increasingly bimodal as target ITI increased, where two peaks, one toward the left representing low dwelltime proportions and one toward the right representing high dwell-time proportions, appeared most pronounced at the longest 1709 ms target ITI (slowest tempo). This trend was confirmed by Kolmogorov-Smirnov and Shapiro-Wilk tests, which showed that the distribution of dwell-time proportions was significantly different from normal for the 1709 ms target ITI (D(46) = .15, p =.007; W(46) = .92, p = .004) but not for 506 ms, 759 ms, and 1139 ms target ITIs (all p > .11). In sum, at the slowest tapping tempo, which was on the temporal boundary where rhythm breaks down, some people show a tendency toward low dwell-time proportions, while others show a tendency toward high dwell-time proportions.



Proportion of Tap Dwell Time (DT/Mean ITI)

Figure 20. Frequency distributions of dwell-time proportions for all participants (n = 46) in Experiment 4. A) 506 ms target ITI, B) 759 ms target ITI, C) 1139 ms target ITI, D) 1709 ms target ITI. The overall shape of dwell-time proportion distributions became more non-normal as ITI increased, appearing bimodal in the 1709 ms condition.

To further investigate the individual differences in what appear to be differences in a dwell time strategy that emerges at the slowest tapping tempo (the 1709 ms target ITI), I performed K-means clustering on dwell-time proportions at the 1709 ms target ITI, dividing participants into 2 groups based on their proximity to cluster centers. This resulted in Group 1 consisting of 24 people clustered around a dwell-time proportion of .19 and Group 2 consisting of 22 people clustered around a dwell-time proportion of .60 for the 1709 ms target ITI condition. I will call Group 1 the Low Dwell group and Group 2 the High Dwell group. Figure

21 shows a representative example of raw motion tracking data for one trial at the slowest tempo for one participant in the Low Dwell group (Panel A) and one participant in the High Dwell group (Panel B). The graph shows that participants in the Low Dwell group tend to keep their finger off the table between taps, while those in the High Dwell group tend to keep their finger on the table between taps.



Figure 21. Representative examples of raw motion tracks showing the first 30 seconds in one trial from two participants in the 1709 ms target ITI condition in Experiment 4. A) One participant in the Low Dwell group. B) One participant in the High Dwell group. The participant in the Low Dwell group kept their finger on the table (zero amplitude) for short durations and the participant in the High Dwell group kept their finger on the table for long durations when producing long ITIs.

Figure 22 shows the mean dwell-time proportions across all target ITIs for each group. A 2 (Dwell Time Group: Low Dwell vs. High Dwell) X 4 (Target ITI: 506 ms, 739 ms, 1139 ms,

1709 ms) mixed-measures ANOVA on dwell-time proportions showed a main effect of Target ITI ( $F(3, 132) = 6.74, p < .001, \eta^2_p = .13$ ), where dwell-time proportion was greater at slower tempi (longer ITIs) than at faster tempi (shorter ITIs), a main effect of Dwell Time Group (F(1,44) = 69.24, p < .001,  $\eta^2_p = .94$ ), confirming that the High Dwell group had a higher mean proportion of dwell time than the Low Dwell group, and an interaction between Target ITI and Dwell Time Group (F(3, 132) = 25.47, p < .001,  $\eta^2_p = .37$ ). Post-hoc tests unpacking the interaction showed that dwell-time proportions for the High Dwell group increased linearly as a function of target ITI ( $F(1, 21) = 445.66, p < .001, \eta^2_p = .95$ ), while those for the Low Dwell group tended to remain constant or even decrease as a function of target ITI. For the Low Dwell group, dwell-time proportions were not significantly different between the 506 ms, 759 ms and 1139 ms Target ITI (all p > .16) but dwell-time proportion was lower for the 1709 ms compared to the 1139 ms Target ITI (t(23) = -2.65, p = .014, 95% CI = -.08 - -.01). In sum, the High Dwell group had a tendency to increase dwell-time proportions as target tempo got slower, but the Low Dwell group kept the proportions constant until the 1709 ms ITI (slowest tempo) condition at which point they decreased.


Figure 22. Mean dwell-time proportions for the Low Dwell and High Dwell groups as a function of target ITI in Experiment 4. The High Dwell group increased dwell-time proportions at longer target ITIs whereas the Low Dwell group tended to keep dwell-time proportion more consistent across target ITI, with a slight decrease (rather than increase) dwell-time proportion that was most pronounced at the slowest tempo (longest target ITI).

### Relationship between Dwell-Time Proportions and Tapping Performance: To evaluate

whether dwell-time proportion was related to ITI matching or variability at the slowest target ITI, I performed Pearson correlations between dwell-time proportion and percent directional error as well as coefficient of variation (CV) of produced ITI for the 1709 ms target ITI. Dwell-time proportion was not correlated with either percent directional error (r(44) = .11, p = .45) or CV of ITI (r(44) = .11, p = .45). At the slowest target ITI, greater increases in dwell-time proportion were not associated with better ITI matching or precision (variability) during continuation.

To evaluate whether dwell-time proportions influenced timing performance, I examined whether timing accuracy and timing variability differed between the Low Dwell and High Dwell groups; see Table 8 for a summary of the accuracy and variability measures for each group. With respect to accuracy, a 2 (Dwell Time Group: Low Dwell vs. High Dwell) X 4 (Target ITI: 506 ms, 739 ms, 1139 ms, 1709 ms) mixed-measures ANOVA on absolute error (produced ITI – target ITI) during continuation tapping showed a main effect of Target ITI (F(3, 132) = 9.52, p < 100.001,  $\eta_p^2 = .18$ ) where absolute error was greater for slower tempi, but no main effect of Dwell Time Group ( $F(3, 132) = .78, p = .78, \eta^2_p = .002$ ) or interaction between Dwell Time Group and Target ITI (F(3, 132) = 2.14, p = .10,  $\eta^2_p = .05$ ). With respect to variability, a 2 (Dwell Time Group: Low Dwell vs. High Dwell) X 4 (Target ITI: 506 ms, 739 ms, 1139 ms, 1709 ms ITI) mixed-measures ANOVA on CVs showed a main effect of Target ITI (F(3, 132) = 9.86, p < .001,  $\eta^2_p = .18$ ) where CV was higher (timing more variable) for slower target tempi, but no main effect of Dwell Time Group ( $F(3, 132) = .03, p = .86, \eta^2_p = .001$ ) or interaction between Dwell Time Group and Target ITI ( $F(3, 132) = .82, p = .48, \eta^2_p = .02$ ). In sum, individuals in the Low Dwell and High Dwell groups did not differ in either timing accuracy or timing variability. Next, I examined whether individual differences in dwell-time proportion were related to differences in changing tap amplitude with ITI.

#### Individual Differences in Dwell-Time Proportions and Relationship between Tap

*Amplitude and ITI:* To evaluate whether the two Dwell Time Groups differed in their tendency to keep amplitude constant (or change tap amplitude) across ITI, an independent-samples t-test was performed on the slopes of the relationship between tap amplitude and produced ITI. There was no difference in slopes between the groups (Low Dwell: M = .23, SD = .94; High Dwell: M = .17, SD = .85) (t(44) = .23, p = .82, 95% CI = -.47 - .59, d = .07). Both groups had similarly

small slopes in the relationship between tap amplitude and produced ITI, indicating that,

regardless of strategy for increasing dwell time with ITI, neither group increased tap amplitude

to produce longer target ITIs.

#### Table 8.

Mean absolute timing error (absolute value of difference between produced ITI and target ITI) and coefficient of variation (CV) of produced ITIs for the continuation phase of tapping for Experiment 4; standard deviations are shown in parentheses. Absolute ITI errors and ITI CVs increased with ITI in both groups.

Dwell Group	Target ITI (ms)	Absolute Error (ms)	CV
	506	17.8 (17.7)	0.06 (.02)
Low Dwell	759	30.9 (29.3)	0.06 (.02)
	1139	73.2 (71.7)	0.07 (.03)
	1709	120.5 (83.2)	0.08 (.03)
High Dwell	506	57.1 (141.2)	0.07 (.02)
	759	30.5 (29.8)	0.06 (.03)
	1139	86.9 (92.7)	0.07 (.03)
	1709	82.5 (83.9)	0.08 (.04)

# Discussion

The aim of Experiment 4 was to test a *dwell time hypothesis* by (1) investigating dwell times and tap amplitudes as a function of target ITI and (2) consider the relation between dwell time and timing performance for target ITIs that extended into the very slow range. The *dwell time hypothesis* proposed that at very slow tempi (long target ITIs), participants keep tap amplitude constant and increase dwell time to match the target ITI. Unlike at short ITIs and the *amplitude control hypothesis*, the *dwell time hypothesis* predicted that dwell time, but not amplitude measures, should be related to timing performance. Of additional interest were potential individual differences in the use of dwell time during sync-continue tapping, similar to

what was observed in the context of tap amplitudes in the assessment of the *amplitude control hypothesis*. There were four main findings. First, coefficient of variation (CV) of produced ITIs was not constant across target ITIs but increased at the slowest tempo (ITI) representing a deviation from Weber's Law. Second, unlike for short ITIs, tap amplitude was constant for very long (slow) ITIs. Third, dwell time increased with target ITI. Fourth, individual differences in dwell time strategy emerged at the slowest target ITI where some participants linearly increased dwell-time proportions with ITI and others kept them constant until the 1709 ms ITI at which point they decreased (rather than increased). Fifth, dwell-time proportions were not related to timing accuracy or timing precision.

The results of Experiment 4 extended findings of previous studies showing that temporal precision during sensorimotor synchronization is worse at slower ITI (Repp, 2006) and revealed a similar pattern of results in the context of continuation tapping. While these studies generally showed that increases in timing variability during rhythmic movements arose at tempi greater than ~1800 ms, in Experiment 4, timing variability was worse for tapping tempi as fast as 1139 ms ITI during the continuation phase of tapping. This may reflect the increased difficulty in maintaining slow tapping tempi after the synchronization signal has stopped.

In support of a *dwell time hypothesis*, participants did not change tap amplitude across produced ITI and instead kept tap amplitude constant across all target ITIs. This provided initial evidence that when tapping at very slow tempi, participants cannot increase tap amplitude further and therefore keep tap amplitude constant, instead increasing dwell time. Furthermore, dwell time variability was related to ITI variability, supporting the use of dwell time to produce ITI. However, increases in dwell time with slower target ITI were not uniform across individuals. Results were in accordance with those of Cos et al. (2015), providing further evidence for two

distinct strategies for increasing dwell time to produce slow tapping intervals: increasing the proportion of dwell time or maintaining an approximately constant proportion of tap dwell time and move time at slower tempi. Results extended the findings of Cos et al. (2015) by demonstrating that both groups kept a constant tap amplitude across ITI, suggesting that the different strategies for increasing dwell time with ITI (keeping a relatively constant proportion of dwell time or increasing dwell-time proportion with ITI) were not associated with different uses of tap amplitude for producing ITI.

At the slowest tempo, the group that increased dwell-time proportion kept their finger in contact with the table for around 60% of the produced ITI on average, opting for a slightly higher proportion of dwell time to move time, whereas the group that kept dwell-time proportion more consistent kept their finger in contact with the table for around 20-25% across all produced ITI. Cos et al. (2015) proposed that at slow tempi, individuals opt for a higher or lower proportion of dwell time to optimize the variability of their total produced ITI. This is in line with the finding in Experiment 4 that the two groups did not differ in timing accuracy or variability, suggesting that individuals may self-select dwell-time proportions that allow for accurate and precise synccontinue timing.

In conclusion, Experiment 4 supports the *dwell time hypothesis* by showing that when participants keep amplitude constant at slower tapping tempi, they also increase dwell time. Furthermore, dwell time variability and produced ITI variability were positively correlated, suggesting that dwell time was used as a control parameter for producing ITI. Individual differences in the degree to which participants increased dwell time with ITI at slow rates suggests a difference in dwell time strategy. One limitation of Experiment 4 is that participants were able to self-select their dwell time during continuation tapping, which might explain the

lack of difference in timing performance between high and low dwell proportion groups. In the next chapter, Experiment 5 extends the correlational findings from Experiment 4 to an experimental manipulation of dwell time. It examines whether individuals' preference for a higher or lower proportion of dwell time at a slow tapping tempo predicts timing performance when explicitly instructed to increase or decrease dwell time.

#### CHAPTER 8: TEST OF A DWELL TIME HYPOTHESIS, PART II

## Introduction

The preceding chapter examined changes in amplitude and dwell time for target tempi (inter-tap intervals) that ranged from tapping at a comfortable tempo (a 506 ms target ITI) to tapping at a very slow tempo (a 1709 ms target ITI). The dwell time hypothesis predicts that as target ITIs extend to slow tempi, participants can no longer increase tap amplitude to match the target ITI (as they approach their maximum amplitude) and, instead, increase dwell time as previously observed by Cos et al. (2015). Consistent with the dwell time hypothesis, tap amplitudes were approximately constant across comfortable to very slow tempi and dwell time increased as a function of the target ITI. In line with findings from Cos et al. (2015), participants showed a bimodal distribution of dwell-time proportions that emerged at the slowest tempo, suggesting two distinct dwell time strategies in the production of slow rhythms (one strategy where participants increased dwell-time proportion at slow tempi, and another where participants kept a constant dwell-time proportion across tempi). Experiment 5 further considered the relationship between dwell time and timing accuracy and variability by explicitly manipulating dwell time in three conditions: asking participants to 1) tap as they normally would (with their preferred dwell time), 2) tap so as to maximize their dwell time, and 3) tap so as to minimize their dwell time.

## **Experiment 5**

Experiment 5 extended Experiment 4 by directly manipulating dwell time during synccontinue tapping using an instructional manipulation. Participants performed sync-continue tapping for target ITIs of 506 ms (a comfortable tempo) and 1709 ms (a very slow tempo) with

their spontaneous (preferred) dwell time (no instructions provided regarding dwell time other than to tap normally) and with specific instructions to maximize or minimize dwell time.

## Methods

*Participants and Design*: Thirty participants (23 female, 6 male, 1 non-binary) from Michigan State University who ranged from 18 to 24 years in age (M = 19.4, SD = 1.4) completed this experiment in return for partial credit in an undergraduate psychology course. According to self-reported handedness, 28 participants were right-handed and 2 were ambidextrous. All participants completed the experiment with their right hand. The experiment implemented a 2 (Target ITI: 506 ms vs. 1709 ms) X 3 (Dwell Time Condition: preferred dwell time, long dwell time, short dwell time) within-subjects factorial design.

*Stimuli and Apparatus*: The synchronization (pacing) signal consisted of sixteen 50-ms 440-Hz sine tones followed by 456 ms or 1659 ms of silence to create a sequence of 15 interonset-intervals (IOIs) of 506, and 1709 ms corresponding to the two target inter-tap intervals (ITIs). A longer, 200-ms 440-Hz sine tone signaled participants to stop tapping after a period of 30 or 95 seconds for the two respective target ITI to allow for 15 synchronization and a minimum of ~30 continuation ITIs per trial. Headphones and motion-tracking equipment were the same as in the preceding experiments.

*Procedure*: Participants performed sync-continue tapping in three instruction conditions (tapping with their preferred dwell time, tapping with their maximally-long dwell time and tapping with their maximally-short dwell time) at two target ITIs (506 and 1709 ms) while continuous finger motion data were recorded. For the preferred dwell time condition, participants completed conventional sync-continue tapping with no instructions related to dwell time. For the maximally-long dwell time condition, participants were instructed to keep their tapping finger on

the table as long as possible between taps, only lifting it off the table briefly to produce each tap. For the maximally-short dwell time condition, participants were instructed to keep their tapping finger off the table between taps, touching the table as briefly as possible to produce each tap.

Participants completed six blocks of trials. Table 9 shows the four orders of the tapping conditions. The first two blocks of tapping were always with their preferred dwell time at each target ITI. The next two blocks were either the maximally-long dwell time or maximally-short dwell time condition at each target ITI, and the final two blocks were tapping with the opposite target dwell time instruction at each target ITI. Participants completed 4 trials of sync-continue tapping in each dwell time and target ITI condition. The order of the tapping conditions was counterbalanced between subjects. After tapping, participants completed the same background and strategies survey as in previous experiments. The entire experiment lasted ~60 minutes.

Table 9.

	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
Order 1	Preferred	Preferred	Short Dwell	Short Dwell	Long Dwell	Long Dwell
	506	1709	506	1709	506	1709
Order 2	Preferred	Preferred	Short Dwell	Short Dwell	Long Dwell	Long Dwell
	1709	506	1709	506	1709	506
Order 3	Preferred	Preferred	Long Dwell	Long Dwell	Short Dwell	Short Dwell
	506	1709	506	1709	506	1709
Order 4	Preferred	Preferred	Long Dwell	Long Dwell	Short Dwell	Short Dwell
	1709	506	1709	506	1709	506

*Four tested orders of conditions for dwell time (preferred, short, and long) and target ITI (506 ms, 1709 ms) in Experiment 5.* 

*Data Processing and Analysis:* All data analysis procedures were the same as in the preceding experiments. Trials with fewer than 30 tap intervals produced were removed, which resulted in a total of 10 trials (1.25%) removed from the final data set. Results below generally focus on the continuation phase of tapping.

### Results

Dwell Time Matching Performance: Figure 23 shows the dwell-time proportions for the two target ITI and three dwell time conditions. To test whether the instructional manipulation affected produced dwell time, A 2 (Target ITI: 506 ms vs. 1709 ms ITI) X 3 (Dwell Time Condition: preferred dwell time, long dwell time, short dwell time) repeated-measures ANOVA on dwell-time proportion during continuation tapping was conducted. Results showed a main effect of Target ITI (F(1, 29) = 17.57, p < .001,  $\eta^2_p = .38$ ) where dwell-time proportion was higher for 1709 ms compared to 506 ms target ITI, a main effect of Dwell Time Condition (F(2,58) = 88.71, p < .001,  $\eta^2_p = .75$ ) where dwell-time proportion was higher for the long compared to short Target Dwell Time conditions, and an interaction between Target ITI and Dwell Time Condition (F(2, 58) = 57.65, p < .001,  $\eta^2_p = .66$ ) where the effect of Target ITI on tap dwell-time proportion was different for the 3 Target Dwell Time conditions. Participants increased dwelltime proportion with target ITI for the long dwell time condition and decreased it for the short dwell time condition. At the slow tempo (long ITI), tapping with long dwell times led to an increase in dwell-time proportion relative to the preferred proportion (t(29) = 7.52, p < .001, 95%CI = .23 - .40) and tapping with short dwell times led to a decrease in dwell-time proportion relative to the preferred proportion (t(29) = -5.50, p < .001, 95% CI = -.32 - -.15). Thus, preferred dwell times were in-between maximally-short and maximally-long dwell times, confirming that people increased or decreased dwell time according to instructions. Next, I examined the effect of Dwell Time Condition on timing accuracy and variability.



Figure 23. Mean proportion of tap dwell time for the three dwell time conditions at the two Target Tempi in Experiment 5. Participants produced smaller dwell-time proportions in the short dwell condition and longer dwell-time proportions in the long dwell condition relative to the preferred dwell condition. Dwell-time proportions decreased with ITI in the short dwell condition and increased with ITI in the long dwell condition.

*Effect of Dwell Time on Tapping Performance:* Figure 24 shows the time series of mean produced ITIs during sync-continue tapping for each tapping condition. Participants were reasonably accurate in matching the target ITIs in both the sync and continue phases of the task in all conditions (see Table 10 for a descriptive summary). One exception is that participants had a tendency to underestimate the 1709 ms target ITI to a greater degree in the short dwell time condition. A 2 (Target ITI: 506 ms vs. 1709 ms ITI) X 3 (Dwell Time Condition: preferred dwell time, long dwell time, short dwell time) repeated-measures ANOVA on mean produced continuation ITI showed a main effect of Target ITI (F(1, 29) = 2290.64, p < .001,  $\eta^2_p = .99$ )

where participants successfully produced different target ITIs, a main effect of Dwell Time Condition (F(2, 58) = 12.04, p < .001,  $\eta^2_p = .29$ ) where participants sped up more in the short compared to preferred or long target dwell time conditions, and a significant interaction between Target ITI and Dwell Time Condition (F(2, 58) = 3.33, p = .04,  $\eta^2_p = .10$ ) where the effect of dwell time condition was different for different target ITIs. T-tests unpacking the interaction confirmed that, at the slow tempo, continuation ITIs were significantly smaller in the short compared to preferred (t(29) = 4.66, p < .001, 95% CI = 77.61 - 198.86) or long (t(29) = 3.91, p< .001, 95% CI = 66.36 - 211.88) dwell time conditions but not different between any other conditions (all p > .23). In the 1709 ms target ITI condition, participants had a tendency to speed up during continuation more when tapping with short compared to preferred or long dwell times.

Table 11 shows a summary of the accuracy and variability measures for all target ITI and dwell time conditions. With respect to timing accuracy, A 2 (Target ITI: 506 ms vs. 1709 ms ITI) X 3 (Dwell Time Condition: preferred dwell time, long dwell time, short dwell time) repeatedmeasures ANOVA on absolute error (|produced ITI – target ITI|) during continuation tapping revealed a main effect of Target ITI ( $F(1, 29) = 111.29, p < .001, \eta^2_p = .79$ ) where accuracy was better for the 506 ms compared to 1709 ms target ITI, a marginally significant effect of Dwell Time Condition ( $F(2, 58) = 3.04, p = .056, \eta^2_p = .09$ ) where accuracy was worse for the short target dwell time compared to preferred or long target dwell time conditions, and a significant interaction between Target ITI and Dwell Time Condition ( $F(2, 58) = 3.33, p = .04, \eta^2_p = .10$ ) where poorer accuracy at the 1709 ms target ITI condition was especially apparent in the short dwell time condition, as can be seen in Figure 24. Participants were more accurate at producing the comfortable tempo and less accurate when tapping with short compared to preferred or long dwell times. Timing accuracy during continuation was the worst when participants tapped at the slow tempo with short dwell times.



Figure 24. Time series of mean produced inter-tap intervals (ITIs) during sync-continue tapping for each combination target ITI and dwell time condition in Experiment 5. The region to the left of the vertical dotted line is the sync phase, and the region to the right of the dotted line is the continue phase. Participants produced shorter ITIs (sped up) during continuation in the short dwell condition compared to preferred and long dwell conditions at the 1709 ms target ITI.

Table 10.

Dwell Time Condition	Target ITI (ms)	Sync ITI (ms)	Continue ITI (ms)
Preferred Dwell	506	507.7 (7.0)	508.9 (17.2)
	1709	1695.5 (33.3)	1704.2 (160.0)
Short Dwell	506	502.7 (21.1)	505.0 (20.5)
	1709	1650.7 (161.3)	1566.0 (190.2)
Long Dwell	506	506.9 (7.7)	509.3 (24.1)
	1709	1708.4 (157.5)	1703.8 (145.0)

Mean produced inter-tap interval (ITI) for Sync and Continue phases for the six combinations of target ITI and dwell time condition in Experiment 5; standard deviations are in parentheses.

Figure 25 shows the coefficient of variation (CV) of the produced ITI during the continuation phase as a function of Target ITI and Dwell Time Condition. With respect to timing variability, a 2 (Target ITI: 506 ms vs. 1709 ms) X 3 (Dwell Time Condition: preferred dwell time, long dwell time, short dwell time) repeated-measures ANOVA on continuation ITI CV revealed a main effect of Target ITI ( $F(1, 29) = 2.92, p < .001, \eta^2_p = .57$ ) where CV was higher for 1709 ms compared to 506 ms Target ITI, a marginal effect of Dwell Time Condition (F(2,58) = 2.92, p = .06,  $\eta^2_p = .09$ ), where CV was higher for the short dwell time than preferred or long dwell time, and an interaction between Target ITI and Dwell Time Condition (F(2, 58) =3.55, p = .03,  $\eta^2_p = .11$ ) where the increase in timing variability at the 1709 ms ITI was greater for the short Dwell Time Condition. Post-hoc paired-samples t-tests unpacking the interaction showed that, for the 1709 ms target ITI, CV was higher for short compared to preferred dwell times (t(29) = 2.79, p = .009, 95% CI = .005. – .04) but was not different between other Dwell Time Conditions (all p > .18), confirming that temporal precision was worse for the short Dwell Time Condition at the slow tempo. In sum, participants showed more timing variability during continuation tapping at the slow (1709 ms ITI) compared to the comfortable (506 ms ITI) target

ITI, especially when tapping with a short target dwell time. Thus, timing variability increased more at the slow target tempo when participants were instructed to tap with short dwell times. Next, I examined relationships between tap amplitudes and dwell times.

### Table 11.

Mean absolute timing error (absolute value of difference between target ITI and produced ITI) and variability (ITI CV) for continue tapping phase for Experiment 5 with standard deviations in parentheses.

Dwell Time Condition	Target ITI (ms)	Absolute Error (ms)	CV
Due forme d Drevell	506	13.1 (11.3)	.06 (.01)
Preferred Dwell	1709	133.8 (84.3)	.07 (.02)
Short Dwall	506	41.3 (16.0)	.06 (.02)
Short Dwell	1709	182.5 (151.3)	.09 (.05)
Long Dwall	506	18.3 (15.7)	.06 (.02)
	1709	110.6 (91.0)	.08 (.03)

Relationship between Tap Amplitude and Dwell Time: To examine whether producing longer or shorter dwell times as a result of the instructional manipulation predicted produced tap amplitudes, a simple linear regression was performed. The regression was statistically significant where dwell-time proportion significantly predicted produced tap amplitude ( $\beta = -.45$ , t = -5.52, p < .001). Producing shorter dwell times was associated with producing larger amplitudes, demonstrating a tradeoff between dwell time and tap amplitude as a result of instructing people to produce longer or shorter dwell times. These results suggest that when participants were required to tap with short dwell times, they increased tap amplitude to produce longer tap intervals. Next, I examined relationships between preferred dwell-time proportion and timing accuracy and variability.



Figure 25. Mean CV of produced ITIs during the continuation phase for the two target ITI and three dwell time conditions in Experiment 5. ITI variability increased at the 1709 ms target ITI condition, especially in the short dwell condition.

#### *Relationship between Preferred Dwell-Time Proportion and Tapping Performance:*

Figure 26 shows the frequency distributions of tap dwell-time proportions for the 506 ms and 1709 ms Target ITI conditions split into 9 equal-size bins. Similar to Experiment 4, participants displayed a qualitatively broader range of preferred dwell-time proportions at the 1709 ms ITI compared to the 506 ms ITI condition. However, the frequency distribution in the 1709 ms target ITI condition did not replicate the bimodal distribution found in Experiment 4. To assess whether participants had better timing accuracy or variability when tapping at a target dwell time closer to their preferred dwell time, Pearson correlations were performed between preferred dwell-time

proportion and absolute ITI error and ITI CV at the slow tempo in all Dwell Time Conditions. No correlations were significant (all p > .15). Finally, I examined relationships between dwell time variability and ITI variability at the slow tempo.



Proportion of Tap Dwell Time (DT/Mean ITI)

Figure 26. Frequency distribution of preferred tap dwell-time proportions for all participants (n = 30) in Experiment 5. A) 506 ms target ITI, B) 1709 ms target ITI. The distribution of dwell times at the 1709 ms target ITI appeared more uniform than the 506 ms target ITI, and there was no evidence of a bimodal distribution of dwell times in the 1709 ms target ITI condition.

#### Relationship between Dwell Time Variability and Timing Variability: Pearson

correlations were performed to evaluate the relation between dwell time variability and ITI variability during continuation tapping at the slow target ITI. Results showed that dwell time CV was positively correlated with ITI CV (r(88) = .67, p < .001). Similar to Experiment 4, when participants were more variable in their produced dwell time, they were also more variable in the overall timing of their continuation tapping.

## Discussion

Experiment 5 served as a further test of the *dwell time hypothesis* and extended previous findings on preferred tap dwell time during sync-continue tapping by explicitly manipulating

target dwell times at comfortable and slow target ITIs (tempi). There were five main findings. First, participants successfully produced longer or shorter dwell times at both target ITIs when instructed to do so. Second, dwell time instructions influenced timing accuracy and variability at the slow target ITI (1709 ms) where timing performance was overall worse when participants tapped with short dwell times compared to preferred or long dwell times, in support of the *dwell time hypothesis*. Third, results did not replicate the findings of Experiment 4 showing a bimodal distribution in preferred dwell-time proportion at the slow target ITI. Fourth, there was no relationship between preferred dwell-time proportion and timing accuracy or variability during continuation tapping. Finally, there was a relationship between dwell time variability and total ITI variability during continuation tapping.

When explicitly instructed to tap with maximally-short or maximally-long dwell times, participants decreased or increased dwell-time proportions at the 1709 ms ITI respectively, which shows that individuals can flexibly alter the proportion of time they keep their finger dwelling on the table when tapping at a slow tempo. However, at the slow tempo, dwell time instructions affected timing accuracy and variability, where instructions to minimize dwell time caused people to speed up more during continuation and led to more timing variability compared to when participants were instructed to maximize dwell time or tapped with their preferred dwell time (no instructions regarding dwell time). This finding supported the *dwell time hypothesis* by showing that preventing individuals from increasing dwell time with ITI at slow tempi (by means of a goal to minimize dwell time) resulted in worse timing performance, indicating that increasing dwell time at slow target ITI facilitates continuation timing performance. The role for dwell time in producing slow target ITI was also supported by the finding that dwell time variability was correlated with continuation ITI variability. Additionally, producing shorter

dwell-time proportions as a result of the instructional manipulation was related to producing larger tap amplitudes, suggesting a tradeoff in tap dwell time and amplitude where participants increased amplitude when instructed to minimize dwell time. To my knowledge, this study is the first to examine continuation tapping under explicit instructions to minimize or maximize dwell time.

The lack of bimodal distribution observed in Experiment 5 was surprising and did not replicate the findings of Experiment 4 or Cos et al. (2015). Rather, the distribution of preferred dwell-time proportions in the 1709 ms ITI condition appeared more platykurtic than at 506 ms ITI in this experiment or the 1709 ms ITI in Experiment 4, indicating a relatively uniform distribution of preferred dwell-time proportions across a wide range from .08 to .74 at the slow tempo (ITI). These results are not likely due to the instructional manipulation because all participants performed the preferred dwell time condition first (conventional sync-continue tapping with no instructions related to dwell time). Furthermore, correlational analyses did not show a relationship between preferred dwell time and timing accuracy or variability. In general, preferences for shorter or longer dwell times did not predict better performance when instructed to tap with minimally-short or maximally-long dwell times.

To summarize, the findings of Experiment 5, when considered with the previous experiments, implicates dwell time as a strategy for controlling ITI at slow tempi, when amplitude cannot increase to produce longer ITI. Regardless of preferred dwell time, timing accuracy and variability were worse when participants were required to produce long ITIs with short dwell times compared to long dwell times. Thus, if amplitude is no longer a viable control parameter for increasing ITIs, individuals may switch to controlling dwell time to produce longer ITI. However, if increasing dwell time is not an option for producing longer ITIs (i.e., when

participants are asked to minimize dwell time), they produce shorter (less accurate) ITIs with more variability. The next chapter summarizes the findings of all five experiments and discusses their implications in the broader context of previous and future work on rhythmic movement timing.

#### CHAPTER 9: SUMMARY, IMPLICATIONS, AND FUTURE WORK

In this chapter, I will summarize the experiments reported and their degree of support for the hypotheses proposed in this dissertation. I will then discuss results in the context of previous research and the implications of these findings in terms of existing theories of rhythmic movement timing and applications to clinical populations. Finally, I will discuss some limitations of the present experiments and future avenues of research that follow from this work.

## Summary

The overarching goal of this dissertation has been to fill a gap in our understanding of how individuals control the timing of their movements, specifically, how spatiotemporal dynamics influence the timing of paced and unpaced rhythmic movements. Five experiments used continuous motion tracking to test novel hypotheses about how spatiotemporal factors ignored in most rhythmic finger tapping studies affect individuals' preferred tempi in unpaced finger tapping and their temporal accuracy and precision in paced sync-continue tapping. Four hypotheses were proposed and tested. The *preferred velocity hypothesis* proposes that individuals have a preferred tap velocity that underlies the relationship between preferences for tapping tempo and amplitude. The *amplitude control hypothesis* proposes that people keep tap velocity constant and change their tap amplitude to produce longer target inter-tap intervals (ITIs) and an alternative *velocity control hypothesis* proposes that people keep tap amplitude constant, changing tap velocity to produce different target ITIs. The dwell time hypothesis proposes that, at slow target tempi when amplitude cannot be increased to produce longer ITIs, people increase their dwell time (the duration that their finger rests on the table between taps) to produce longer ITIs.

Experiment 1 tested the preferred velocity hypothesis by having participants complete a series of unpaced tapping tasks to separately assess their preferred movement amplitude and tempo. First, participants performed a spontaneous motor amplitude (SMA) task and a spontaneous motor tempo (SMT) task where they tapped with their preferred amplitude and tempo, respectively. They then performed a target amplitude version of SMT tapping where they tapped at their preferred tempo at a range of target amplitudes. Experiment 2 tested the *amplitude control hypothesis* for tapping interval production by having participants perform sync-continue tapping at target ITI that ranged from fast to slow (250 to 1150 ms) and examining relationships between tap amplitude and ITI. Experiment 3 served as an additional test of this hypothesis by using a novel sync-continue tapping task that had participants tap at a range of target amplitudes from low to high at different target ITI from fast to slow (250 - 1150 ms) and examined the accuracy and variability of produced tap amplitude and ITI. Secondarily, as a further test of the preferred velocity hypothesis relationships were examined between preferred tap velocity (measured in Experiment 1) and timing variability in target amplitude/ITI conditions that elicited tap velocities nearer to or farther from their preferred velocity.

Experiment 4 served as an initial test of the *dwell time hypothesis* by having participants perform sync-continue tapping at a range of target ITIs from comfortable to very slow (506 – 1709 ms) and examined produced dwell time and timing accuracy and variability. Experiment 5 further tested this hypothesis by manipulating tap dwell time while people produced sync-continue tapping at comfortable and very slow target ITIs (506 and 1709 ms) and examining timing accuracy and variability under different dwell time instructions. Participants completed sync-continue tapping at each tempo in three dwell time conditions: no instructions about dwell time, instructions to maximize dwell time, and instructions to minimize dwell time.

*Support for the Preferred Velocity Hypothesis:* Initial support for the *preferred velocity hypothesis* came from the results of Experiment 1, which showed that participants produced tap amplitudes and inter-tap intervals that were tightly linked (highly similar) across the unpaced spontaneous motor tempo (SMT) and spontaneous tap amplitude (SMA) tasks. In further support of the hypothesis, the target amplitude version of the SMT task revealed that participants altered their preferred tempo in the direction predicted by the preferred velocity estimated from the SMT and SMA tasks. The range of preferred tempi produced at different target amplitudes, however, was smaller than predicted if participants used a single (constant) preferred velocity, suggesting that individuals have a range of preferred velocities.

Additional support for the *preferred velocity hypothesis* came from Experiment 3, which had participants produce paced sync-continue tapping at a range of target amplitudes and target ITIs. Each combination of target amplitude and ITI corresponded to a different required tap velocity, allowing for the examination of relationships between preferred tap velocity (measured in Experiment 1) and timing variability in target amplitude/ITI conditions that elicited tap velocities nearer to or farther from their preferred velocity. Supporting the *preferred velocity hypothesis*, timing variability was lower when participants were tapping with an average velocity closer to their estimated preferred velocity.

Support for the Amplitude Control Hypothesis: Experiment 2 provided some initial support for the amplitude control hypothesis. First, consistent with this hypothesis, tap amplitude increased linearly with the target ITIs and amplitude variability predicted variability in the produced ITIs. However, large individual differences were observed. Analyses revealed that although some participants increased tap amplitude with longer ITIs, other participants kept amplitude constant across target ITIs, consistent with the alternative velocity control hypothesis.

These individual differences suggest that some individuals may use an amplitude control strategy while others may use a velocity control strategy to match target ITIs in sync-continue tapping. Of additional interest was the finding that individual differences in tapping 'strategy' were associated with participants' range of maximum tap amplitude, where participants with a greater possible range of tap amplitudes (larger maximum amplitudes) were more likely to show a pattern of tap amplitudes consistent with an amplitude control strategy. A relationship was also found between more formal music training, measured in years of lessons, and a tendency to keep tap amplitude constant, in line with a velocity control strategy. Together, these results suggest that some individuals change amplitude to match the target ITI in sync-continue tapping, while others keep amplitude constant across target ITIs suggesting that they use a velocity control strategy.

Experiment 3 provided additional support for the *amplitude control hypothesis*. Participants performed sync-continue tapping at a range of target amplitudes and target ITIs, where some conditions were congruent with an amplitude control strategy (e.g., low amplitudes at fast target ITI and high amplitudes at slow target ITI) and others were incongruent (e.g., high amplitudes at fast target ITI and low amplitudes at slow target ITI). Timing accuracy and variability were worse in one of the incongruent tapping conditions in particular, the high amplitude-fast ITI condition. In this condition, participants reduced tap amplitude, undershooting the target amplitude, to match the shorter target ITIs. Participants also showed more timing variability at the fast tempo when tapping with a high amplitude compared to preferred and low amplitudes, in line with the hypothesis. Together, Experiments 2 and 3 provide multiple sources of support for the *amplitude control hypothesis*. They also reveal large individual differences in

tapping strategy and associated biomechanical constraints on whether individuals use tap amplitude as a control parameter to match target ITIs in sync-continue tapping.

Support for the Dwell Time Hypothesis: Initial support for the dwell time hypothesis came from Experiment 4, which had participants perform sync-continue tapping a range of target ITIs from comfortable to very slow tempi. Participants kept tap amplitude constant at slow target ITIs and increased dwell time to produce longer ITIs, in line with the hypothesis. Furthermore, at the slowest target ITI, a bimodal distribution of tap dwell times emerged, where some participants kept dwell time as a proportion of ITI relatively constant across target ITI and others increased dwell-time proportion with ITI, results that reveal individual variation in the use of dwell time to produce longer ITIs. Despite these individual differences in how participants increased dwell time with ITI, they were not related to timing accuracy or variability.

To further probe how tap dwell time is used to control produced ITI at slow target tempi (ITIs), Experiment 5 followed up on the findings of Experiment 4 by explicitly manipulating tap dwell time while people produced sync-continue tapping at a comfortable and very slow target ITI using an instructional manipulation. Participants were successful in flexibly altering their dwell time to be longer or shorter when tapping at slow tempi, indicating that people can produce longer ITIs without increasing dwell time, however dwell time instructions affected timing performance. Regardless of preferred dwell time, timing accuracy and variability were worse at the slow target ITI (tempo) when tapping with short compared to preferred or long dwell times. In both experiments, dwell time variability was correlated with total ITI variability at the slow target ITI. In line with the *dwell time hypothesis*, these findings suggest that longer dwell times at slow tapping tempi facilitate the production of longer ITIs. Together, results of these experiments provided general support for the *dwell time hypothesis*. They showed that

individuals self-selected longer dwell times at slower ITIs, keeping tap amplitude constant, and minimizing dwell time led to less accurate and precise production of the slow target ITI when compared to maximizing or tapping with preferred dwell times.

*Contributions of the Present Work:* This work makes four primary contributions to the timing literature. First, Experiment 1 provided initial evidence for a preferred velocity that links movement amplitude and tempo, and Experiment 3 provided evidence that preferred movement velocity facilitates successful matching of target tempi.

Second, the experiments show evidence for individual differences in the use of amplitude and velocity as control parameters for producing target time intervals where, in Experiment 2, some individuals use an amplitude control strategy and others use a velocity control strategy. Individual differences in the use of an amplitude control strategy are related to biomechanical and musical training factors, where individuals with a greater range of possible tap amplitudes are more likely to use an amplitude control strategy, but individuals with more musical training are more likely to use a velocity control strategy. The use of amplitude control also appears to be tempo-dependent, where amplitude does not change at slower tapping tempi, as shown in Experiment 4.

Third, individuals can flexibly control dwell time at comfortable and slow target tempi, where participants are able to increase or decrease produced dwell time when instructed to do so, but at a cost to timing performance in some cases, as shown in Experiment 5.

Finally, Experiment 5 shows that reducing dwell time at a slow tapping tempo leads to worse timing control, further implicating the use of longer dwell times as a strategy for controlling the production of long intervals.

## Implications

*Implications for Understanding Preferred Motor Tempo:* The phenomenon of preferred tempo has been studied in many contexts, including the production of unpaced rhythmic finger tapping. Results of Experiment 1 build on studies of preferred tempo and preferred amplitude for tapping by showing evidence for an underlying preferred average tap velocity that integrates tap amplitude and tempo. Previous studies have focused on the relationship between produced amplitude and tempo when participants are matching either a target tempo or amplitude (Kay et al., 1987; Rosenbaum et al., 1991). Experiment 1 extended these findings by showing a strong link between preferred amplitude and tempo during rhythmic tapping in spontaneous motor tempo and spontaneous motor amplitude tasks. It also provided evidence that people have a range of preferred velocities, in line with previous research showing that people have a range of preferred tempi (Hammerschmidt et al, 2021; Hammerschmidt & Wollner, 2022; Kliger-Amrani & Zion-Golumbic, 2020a; Moelants, 2002).

Rosenbaum et al. (1991) found that when performing finger oscillations (akin to tapping without making contact with a surface) at different target amplitudes, participants scaled their produced (self-selected) tempo with amplitude, and when performing a similar task at different target tempi, they scaled their produced amplitude with tempo. The slope of the relationship between amplitude and tempo for each participant was slightly different for target amplitude and target tempo tasks. Rosenbaum and colleagues proposed that the intersection between these two lines represents an individual's amplitude-tempo combination for optimal motor performance (i.e., a preferred velocity). These studies, however, are correlational. Experiment 3 extended these findings by having participants produce a range of target amplitudes at a range of target ITIs, requiring different amplitude-tempo combinations that elicited different tap velocities. The

results support the idea that tapping at one's preferred velocity is optimal for accurately and precisely matching ITIs. They do this by showing that timing error and variability were lower when participants tapped at target amplitudes and tempi that, in combination, were closer to their preferred velocity in a context when both target amplitude and tempo were fixed.

Implications for Understanding the Production of Fast and Slow Target Tapping Tempi: Previous research has provided evidence for fast and slow tempo limits of entrainment, where rhythmic auditory sequences presented outside this range are not perceived as rhythms. Beyond the fast limit, successive auditory events are perceived as a single unified event or stimulus. The lower (fast) limit of inter-onset intervals (IOIs) for auditory sequences to be perceived as successive events is around 100 ms, where smaller IOIs are heard as a continuous sound or pitch (London, 2002). Beyond the slow limit, rhythms break down and auditory events are perceived as isolated or disconnected in time (Bolton, 1894; Fraisse, 1984; Poppel, 1997). Successive events separated by greater than around 3000 ms are perceived as separate events and no higher levels of hierarchical rhythmic structure can be determined. The window of time bounded by this upper limit has often been referred to as the "subjective" or "psychological present," with conceptual origins dating back over a century (James, 1890). These studies on the fast and slow tempo limits of perceptual rhythms reflect cognitive limits on the perception of auditory events as being independent or part of a rhythmic structure.

In terms of rhythm production, various studies have shown upper and lower limits similar to what has been found in perceptual studies. The entrainment window, however, is slightly narrower for production than perception (for a review of tempo limits in rhythm production, see Repp, 2006). McAuley et al. (2006) found that in an unpaced rhythmic tapping task, adults' fastest and slowest possible tapping tempi were around 170 ms and 2500 ms ITI, respectively.

There are also constraints on timing performance during fast and slow paced tapping, where accuracy and precision (variability) of synchronization and continuation tapping at ITIs shorter than around 300 ms and longer than around 1400 ms are worse than within a comfortable range of tempi closer to one's preferred tempo (Kliger-Amrani & Zion-Golumbic, 2020b; Mates et al., 1994; McAuley et al., 2006; Peters, 1989; Repp, 2006). It goes without saying that people can only move so fast. That is, there is an upper limit of speed for controlling oscillatory (cyclical) movements. There is also a lower limit, at which point smooth, oscillatory movements are broken down into smaller component movement phases via the introduction of pauses in motion (i.e., a dwell phase) (Adam & Paas, 1996; van der Wel et al., 2009; Park et al., 2017). In addition to a limited entrainment region, these tempo limits reflect biomechanical constraints on rhythm production.

The experiments reported here have implications for how people produce rhythmic movements at a range of tempi that span the entrainment region for sync-continue tapping. First is the observation in Experiment 2 of a greater rate of change in tap amplitude with ITI at fast tempi compared to slow tempi. This finding suggests that when tapping at a fast enough tempo such that velocity (V) reaches an upper limit, tap amplitude (A) must decrease to produce shorter ITI based on ITI = 2A/V (Eq. 7). This was supported by the finding in Experiment 3 that when required to produce short target ITIs at a high target amplitude, amplitude decreased below the target. Second is the observation from Experiment 4 that, at slow tempi, tap amplitude does not change and dwell time increases with ITI. When tapping at slower tempi, tap amplitude reaches an upper limit and cannot be increased further to produce longer tap intervals. Additionally, movement velocity is presumed to reach a lower limit at slow tapping tempi (Park et al., 2017). Thus, at slower tapping tempi, individuals take increasingly longer pauses (dwell times) to

increase ITI. Thus, the equation above (Eq. 7) can be modified to include the parameter of dwell time (DT) for producing ITI:

$$ITI = 2A/V + DT \tag{8}$$

Where the 2A/V term represents the duration of movement time ("move time") and the DT term represents the portion of each ITI when A and V are equal to zero (i.e., when the finger is at rest on the table). At very fast tapping tempi (short ITI), the DT term is assumed to be negligible (near zero), and dwell time is not a control parameter for ITI production (Dione & Delevoye-Turrell, 2014). Support for dwell time as a control parameter for producing long ITI comes from Experiment 5, which showed that timing accuracy and precision were worse when tapping at a slow tempo with short dwell times. One surprising finding from Experiments 4 and 5 was that longer or shorter self-selected (preferred) dwell-time proportions at slow tapping tempi were not related to accuracy or variability of produced ITIs. One possibility is that some people control ITIs at slow tempi by keeping a constant ratio of dwell time and move time across slow tempi while others increase the proportion of dwell time to keep move time approximately constant. Additional studies to address this limitation of the present experiments are discussed below in Future Work.

*Implications for Entrainment and Interval Models of Rhythmic Timing*: The observation of spatiotemporal interactions during sync-continue tapping cannot be accounted for by interval models of rhythmic timing. From an interval theory perspective, differences in rhythmic tapping performance across tempi (ITIs) can be explained by an open-loop internal clock mechanism that functions independently of sensory feedback. For example, increases in timing variability at slower tapping tempi are assumed to reflect time-dependent limitations on cognitive resources such as attention and memory processes (Block & Zakay, 1996; Semjen et al., 2000; Thomas &

Cantor, 1975; Thomas & Weaver, 1975). These theories do not consider a role for spatial dynamics in rhythmic movement timing. Entrainment theories of timing, however, assume a role for sensory feedback that allows for dynamic multisensory coupling during sync-continue tapping.

Results from the five experiments are consistent with entrainment models, which allow for multimodal coordination of perception-action goals as they unfold in time, for example between auditory events and tactile and proprioceptive feedback from the effector (tapping finger) during synchronization (Lagarde & Kelso, 2006). Entrainment models propose that internal rhythms are entrained by rhythms in the environment; in the case of synchronization with an isochronous stimulus, the tempo of the regular rhythm (i.e., metronome) provides an internal template for optimizing temporally accurate and precise movement planning and execution (Thaut, 2013). Because velocity is a mathematical time derivative of changes in finger position during tapping, the fixed intervals in an isochronous auditory sequence provide a temporal anchor for the motor system to plan and execute the tapping motion. When entrained by a rhythm, the nervous system is provided upcoming tap intervals, and thus has the information necessary to predict the time and space left to produce each tap at any point in the movement. At a given tempo, fixing other spatiotemporal parameters such as amplitude or velocity would serve to further simplify and strengthen the coupling between internal and external rhythmic events (oscillations). Entrainment provides a signal for coordinating timed movements and modulates patterns of muscle activation for controlling spatial movement dynamics (Michaelis et al., 2014; Stupacher et al., 2016).

Evidence from the current experiments that people scale spatiotemporal aspects of their movements to produce different target tap intervals supports the idea that anchoring movement

goals (taps) to fixed (expected) time points via entrainment during synchronization reduces uncertainty in ITI in the ITI = 2A/V equation (eq. 7). This allows the brain to map and scale amplitude and velocity parameters in order to produce each ITI. According to Thaut (2013), the brain optimizes movements by matching them to an internal spatiotemporal template. Synchronizing with isochronous intervals involves a stable timing template that affords tempo matching via fixed spatiotemporal relations. When producing a target ITI, individuals do not drastically alter their amplitude or average velocity within or across trials, as shown in the current experiments. This supports the idea that people fix spatiotemporal relations when synchronizing with a fixed ITI, then maintain these during continuation. Changing the spatiotemporal template by increasing or decreasing ITI causes a change in the ratio of 2A/V with ITI.

The current findings have implications for how, from an entrainment perspective, people use the control parameters of amplitude (A) and velocity (V) to produce rhythmic movements. Results from Experiment 2 suggest that individuals scale up or down different target (fixed) ITIs based on equation (7) by altering either the numerator, using an amplitude control strategy, or the denominator, using a velocity control strategy. For example, to decrease ITI, those who use an amplitude control strategy keep V constant and decrease A with shorter ITI, whereas those who use a velocity control strategy keep A constant and increase V with shorter ITI. To produce very long tapping intervals, individuals may fix both A and V and increase ITI by increasing dwell time (DT) according to ITI = 2A/V + DT (Eq. 8). This is supported by the results of Experiment 4 showing that amplitude is held constant and DT increases with longer ITIs at slow tapping tempi. Experiment 5 showed that when DT cannot be increased to produce longer ITIs (due to instructions to minimize DT), timing accuracy and precision (variability) are worse. As discussed above, the results of the experiments also support the existence of cognitive, neurological, and biomechanical constraints on these control parameters that cannot be accommodated by interval theories of rhythmic timing.

Implications for Understanding the Role of Music Training in Rhythmic Timing: Playing a musical instrument involves rhythmic timing with fine motor demands such as precise finger control when depressing keys, valves, or strings. Formal music training has previously been associated with differences in finger tapping performance, where amateur or professional musicians tend to produce slower spontaneous motor tempi and show more accurate and precise synchronization than nonmusicians (Baer et al., 2013; Drake et al., 2000; Keele et al, 1985b; Repp, 2005; Repp & Doggett, 2007; Repp & Su, 2013; Scheurich et al., 2018). The finding in Experiment 2 that more formal musical training was associated with a tendency to keep amplitude constant across target ITIs expands on previous studies by showing that musical background is related to differences in spatial dynamics of sync-continue finger tapping. These results suggest that music training may be associated with adopting particular modes of spatiotemporal control, for example keeping amplitude constant and controlling velocity to produce target tap intervals. Because of the small sample sizes and lack of professional musicians in these experiments, further research is needed to better understand how music training affects spatial and temporal control of rhythmic movements.

*Implications for Understanding Timing Behavior in Clinical Populations:* The results of the five reported experiments have implications for theories of rhythmic timing and related models and their application to clinical populations. One interval timing model commonly used to assess timing in clinical populations is the Wing and Kristofferson (W&K) model (1973a, 1973b). This model decomposes total continuation tapping variance into separate central (clock)

and peripheral (motor) components, where motor variance is a constant estimated by the autocovariance of successive intervals and clock variance accounts for the remainder. The W&K model has been used to diagnose impaired central timing processes in a variety of neurological conditions such as cerebellar lesions, Parkinson's disease, and Huntington disease (Freeman et al., 1996; Ivry & Corcos, 1993; Ivry & Keele, 1989; Ivry et al., 1988; O'Boyle et al., 1996; Wing et al., 1984). However, spatial influences on timing performance cannot be explained by differences in central clock functioning. Interval models do not take into account spatial characteristics of tapping movements that affect the timing of rhythmic movements, as shown in this dissertation. This poses a problem for the diagnostic application of these models to time series data for assessing timing deficits in motor disorders that affect spatial control of movements.

From an entrainment perspective, clinical populations with purported timing deficits are proposed to have impaired auditory-motor coupling reflecting reduced neural entrainment by rhythmic stimuli. Studies on clinical populations such as children with developmental coordination disorder and developmental stuttering have shown that timing deficits during synchronization or continuation tasks are tempo-dependent. For example, timing accuracy or precision are worse for slow compared to fast tapping tempi (de Castelnau et al., 2007; Falk et al., 2015; Whitall, et al., 2008). However, results of experiments reported in this dissertation reveal tempo-dependent differences in spatial control parameters for producing rhythmic movements. Thus, studies on rhythmic timing in individuals with neurodevelopmental disorders that ignore spatial movement dynamics may erroneously conclude that timing processes are disrupted, overlooking potential effects on the control of different spatiotemporal parameters for producing fast and slow rhythmic movements.

In sum, based on the results of the current experiments, disrupted spatial control of movements due to neurological disease or injury may affect timing accuracy and variability during rhythmic tapping in the absence of a specific timing deficit. Thus, we must be cautious when evaluating neurological timing deficits. The time series of produced rhythmic movements should not be analyzed in isolation without considering the potential impacts of disruptions in spatial control on timing (cf. Dalla Bella et al., 2017). In the next section, I will propose ways to address some limitations of the current experiments.

#### **Future Work**

Future research on spatiotemporal characteristics of rhythmic movement timing should extend the current findings to address some of the limitations of the experiments. First, I plan to further test the hypotheses proposed in this dissertation by examining other aspects of kinematic data such as velocity profiles during sync-continue tapping. Second, equations proposed to describe the relationship between spatial and temporal aspects of rhythmic tapping movements (e.g., Eq. 8) will be developed into a formal behavioral model with subsequent validation and testing of the model fit to behavioral data. Finally, I plan to examine the role of spatial characteristics of sync-continue tapping on movement timing in clinical populations.

One aspect of data collection in the current experiments that proved to be a source of both strengths and limitations was the quantity and richness of kinematic (motion tracking) data collected. Three-dimensional continuous motion tracking was invaluable for testing the proposed hypotheses; however, these data could be subjected to many analyses that were not within the scope of this dissertation. For example, a measure that I will consider in future work is the velocity profile of tapping movements, which represents point estimates of velocity magnitude over movement position. This will allow for a closer examination of produced velocities on a

more fine-grained scale, such as how movement velocities unfold over the course of each tap. Future experiments will test predictions of the preferred velocity and amplitude control hypotheses using velocity profiles to estimate mean (point) velocity as well as the range of produced velocities across taps. For example, the *amplitude control hypothesis* predicts that during fast tempo finger tapping when movement velocity reaches a maximum, amplitude decreases. This prediction will be directly tested by measuring maximum tap velocity and then comparing it to movement velocities of fast tapping tempi at the point when tap amplitude begins to decrease.

The examination of velocity profiles may address another limitation of these experiments, namely, the estimation of dwell time via a position measure (duration of finger contact with the table). Estimating dwell time based on the amount of time that tap amplitudes were near zero (< 3 mm above the table) ignores the possibility that rest phases (where velocity is near zero) may be introduced at other positions of the tap cycle, for example between finger extension and finger flexion. This point in the tap cycle, when the direction of motion reverses, always corresponds to a moment of zero velocity. The current experiments treated this brief pause in motion as negligible, however, results of Experiment 4 suggest that some individuals may maintain a near-zero velocity for an extended duration following finger extension and preceding finger flexion, corresponding to a "hold phase" during which they hold their finger relatively motionless in the air before returning it to the table for the next tap (Figure 21, Panel A). One possibility is that participants who produced relatively shorter dwell times increased the duration of the hold phase. This is also relevant for the surprising finding in Experiment 5 that people were able to produce longer intervals without increasing dwell time in the short dwell time condition. In future work, I
will examine changes in velocity, dwell time, and hold time across tapping tempi to better understand how movement dynamics change during fast and slow tapping.

In terms of behavioral modelling, I plan to modify equations underlying proposed hypotheses in this dissertation (e.g., Eq. 8) to develop a formal model of sync-continue tapping that can account for tapping behaviors across a wide range of tempi. This model will consider the control parameters of tap amplitude, velocity, and dwell time (as well as hold time) for producing ITIs and additionally take into consideration the timing of separate subphases of finger motion that tap "move time" comprises (e.g., duration of finger extension and finger flexion). Previous research on rhythmic finger tapping has demonstrated differential changes in durations of finger extension (lifting the finger following contact with the table) and finger flexion (moving the finger to contact the table following a reversal in movement direction) across target ITI (Balasubranamiam et al., 2004; Hove & Keller, 2010). These studies show that while finger flexion duration is held relatively constant across ITI, finger extension duration increases with ITI. These studies highlight the importance of modelling spatial and temporal characteristics of component subphases of finger tapping motion to understand control parameters for producing different target ITI. Future behavioral models will take into consideration all of the spatial and temporal parameters of sync-continue tapping discussed here to better predict performance on this task for the purpose of elucidating underlying neural timing mechanisms.

Finally, to better understand and disentangle different timing and motor deficits in clinical populations, I plan to examine both spatial and temporal aspects of rhythmic movements in individuals with neurological disorders that are proposed to affect timing. Studies of timing deficits in patients with movement disorders have focused on timing accuracy and precision of

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tapping, typically without considering how deficits in spatial control may influence timing results (Falk et al., 2015; de Castelnau et al., 2007; Freeman et al., 1996; Ivry & Keele, 1989; Rose et al., 2020; Whitall, et al., 2008; Wing et al., 1984). However, experiments reported in this dissertation demonstrated a role for tap amplitude and velocity in producing rhythmic tapping, suggesting that individuals with movement disorders affecting spatial aspects of motor control may appear to have timing deficits where none are present. One prediction from the amplitude control and velocity control hypotheses is that when amplitude and velocity control are disrupted by disease or injury, patients will produce rhythmic movements with more timing variability than healthy controls. Thus, an apparent timing deficit that is the result of a non-temporal dysfunction of motor control could be misconstrued in its etiology and subsequent treatment. In future work, I plan to examine timing accuracy and precision as well as spatial dynamics of rhythmic movements such as sync-continue tapping in individuals with neurological disorders such as PD and chronic stuttering (Falk et al., 2015; Freeman et al., 1996; Ivry & Keele, 1989; Rose et al., 2020; Wing et al., 1984; Zelaznik et al., 1997).

In conclusion, this dissertation critically links spatial dynamics to the timing of rhythmic movements at different tempi, providing initial support for a new set of hypotheses for the control of paced and unpaced rhythmic finger tapping. Experimental findings support a role for tap amplitude, velocity, and dwell time in producing time intervals during rhythmic tapping. The experiments also revealed individual differences in spatiotemporal movement dynamics, highlighting the importance of examining how movement dynamics and timing vary both within and across individuals to better understand neural timing mechanisms. Results of the five experiments have implications for existing timing models and their application to the evaluation of timing deficits in clinical populations.

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