SENSORIMOTOR INTERACTIONS IN PREDICTIVE TIMING

SENSORIMOTOR INTERACTIONS IN PREDICTIVE TIMING:
THE BENEFITS OF MOVING TO THE BEAT

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Abstract

The interplay between movement and sound shapes numerous behaviours, such as foot tapping to the beat of a song or playing a musical instrument. Sensorimotor integration is critical for these tasks, allowing us to make predictions about upcoming events in time and synchronize movements in time with those predicted events. The processing of predictable timing information is tightly linked with movement where listening to rhythmic information alone is sufficient to activate regions of the brain important for the planning and execution of movement. My Ph.D. research has focused on motor timing and temporal prediction, particularly how audiomotor interactions are involved in listening to rhythmic information. My research demonstrates how movement interacts with the perceived timing of external auditory events and improves objective timing abilities. I have also documented ways in which sensory feedback, musical expertise and types of motor synchronization mediate this interaction. Overall, my findings are the first to document that synchronizing movements with predictable auditory information can serve to improve the internal representation of timing, illustrating movement's role in temporal prediction and suggesting one reason we may move to the beat in musical settings.

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List of Abbreviations

ANOVA	Analysis of variance
bpm	Beats per minute
CI	Confidence interval
CV	Coefficient of variation
d	Cohen's d
df	Degrees of freedom
η^2	Eta-squared
F	F ratio
IOI	Inter-onset interval
ITI	Inter-tap interval
M	Mean
n	Number of participants
p	p-value, probability
SD	Standard deviation
SEM	standard error of the mean
t	t-statistic
χ^2	Chi squared statistic

Declaration of Academic Achievement

This thesis is comprised of four empirical manuscripts that each examine the perceptual benefits that arise due to movement synchronized with external auditory information. The studies examine different sensory feedback conditions, participant groups and synchronizing motor effectors. Chapters 2, 3 and 4 are articles that have been published in peer-reviewed journals. Chapter 5 consists of a manuscript that is currently in preparation for publication. Each empirical chapter represents a single manuscript for which I am the primary author.

The remainder of this preface is designed to clarify my contributions to the manuscripts that comprise the chapters of this thesis.

Chapter 1: Introduction

Author: Fiona C. Manning

Chapter 2: "Moving to the beat" improves timing perception

Authors: Fiona C. Manning & Michael Schutz
Publication: Psychonomic Bulletin & Review, 2013, volume 20, issue 6, pages 1133-1139.
Comments:
My role in this manuscript included experimental design, data collection (with human participants), data analysis and interpretation of the results. I was also the primary author of this manuscript. The second author is my thesis supervisor. A number of undergraduate students assisted with data collection.

Chapter 3: Movement enhances perceived timing in the absence of auditory feedback
Authors: Fiona C. Manning & Michael Schutz
Publication: Timing & Time Perception, 2015, volume 3, issue 1, pages 3-12.
Comments:
My role in this manuscript included experimental design, data collection (with human participants), data analysis and interpretation of the results. I was also the primary author of this manuscript. The second author is my thesis supervisor. A number of undergraduate students assisted with data collection.

Chapter 4: Trained to keep a beat: Movement-related enhancements to timing perception in percussionists and non-percussionists
Authors: Fiona C. Manning & Michael Schutz
Publication: Psychological Research, 2016, volume 80, issue 4, pages 532-542.
Comments:
My role in this manuscript included experimental design, data collection (with human participants), data analysis and interpretation of the results. I was also the primary author of this manuscript. The other author is my thesis supervisor. A number of undergraduate students assisted with data collection.

Chapter 5: Motor effector choice affects movement's impact on temporal prediction abilities
Authors: Fiona C. Manning, Jennifer Harris & Michael Schutz
Publication: Under review
Comments:
My role in this manuscript included experimental design, data collection (with human participants), data analysis and interpretation of the results. I was also the primary author of this manuscript. The second author, Jennifer Harris, assisted with data collection, analysis and interpretation and part of this project comprised her undergraduate thesis. The third author is my thesis supervisor. A number of undergraduate students assisted with data collection.

Chapter 6: Discussion

Author: Fiona Manning

As a final note to the reader, each of Chapters 2 through 5 represents a manuscript that is intended to stand alone as a published article. As a result, there is a fair amount of redundancy present within the introductory sections to each of these chapters that the reader should be aware of. That being said, the experiments presented within each manuscript are distinct works that are intended to address separate, yet complimentary, objectives.

Chapter 1: Introduction

Prediction is a critical component of perceptual processing, which occurs across sensory modalities and exists on a number of timescales. Predictions are influenced by prior knowledge, where top-down information can inform the timing of events and the expectations associated with these events. This thesis will discuss prediction abilities on a sub-second scale, where auditory events that are presented on the order of milliseconds are quickly processed, allowing us to create predictions rapidly and often without conscious effort. Notably, I will discuss how multisensory cues are used to facilitate prediction of regularly occurring temporal events, in particular how synchronized movements inform the perceived timing of auditory information. Prior to the study reported in Chapter 2 of this thesis, research on sensorimotor interactions suggested that motor information could be used to subjectively disambiguate auditory sequences (Phillips-Silver & Trainor, 2007; Su & Pöppel, 2012). However, the initial experiments reported in this thesis are, to my knowledge, the first studies to document objective improvements to prediction abilities following synchronized movements. These findings help clarify movement's role in perception, suggesting that despite the auditory system's refined ability to process temporal information, movement information is combined with auditory inputs to allow us to more accurately predict the onset of upcoming temporal events.

1.1 Predictive Timing

In order to successfully complete daily tasks, we continuously update predictive information and correct for errors using sensory feedback. For example, when reaching for an object in space, it is critical to evaluate the movements of the arm and hand, and predict the time at which it is appropriate to close the hand around the object. Visual and proprioceptive feedback guides the spatial movements of the arm while tactile feedback allows one to decide on the amount of pressure required to grasp and raise the object. Information from multiple senses is combined to complete these seemingly simple tasks.

Not only are we able to accurately predict the onset of temporal events, we are also able to easily synchronize movements to external temporal events that are rapidly perceived and processed. The capacity to synchronize movements with predicted auditory information involves a complex series of processes. While listening to sequences of events, we must extract regularities from complex streams of information, make predictions about future events in time, and coordinate movements with the expected onset of these events. We do this rapidly and often automatically using temporal information, where seemingly little effort is required.

1.1.1 Prediction in the temporal domain

Although information containing temporal regularities is acquired by many sensory modalities, in multimodal stimuli we rely most heavily on auditory processing for accurate timing perception. In general, we have greater temporal resolution in audition compared to vision (Holcombe, 2009). Temporal discrimination is also generally better in the auditory domain compared to the visual or tactile domains: thresholds for timing detection are much lower for auditory information compared to visual or tactile information (Bresciani, Dammeier, & Ernst, 2008; Rammsayer, 2014). Additionally, we do not tend to synchronize movements spontaneously with visual information, as we do with auditory information.

Pattern identification and reproduction are also more accurate in the auditory domain (Glenberg & Jona, 1991; Glenberg, Mann, Altman, Forman, & Procise, 1989). We excel at synchronizing movements with auditory information compared to visual information (Repp & Penel, 2004). There is also a greater asynchrony and limits on synchronization observed when participants tap with isochronous visual light flashes compared to sounds (Aschersleben & Bertelson, 2003; Y. Chen, Repp, & Patel, 2002; Kolers & Brewster, 1985; Repp & Penel, 2002; Repp, 2003). This difference is mitigated when visual stimuli contain spatiotemporal information, such an image of a moving bar or a bouncing ball (Grahn, 2012; Hove, Fairhurst, Kotz, & Keller, 2013; Hove, Iversen, Zhang, & Repp, 2013); however, motor synchronization is still most accurate with auditory stimuli. Some researchers even suggest that auditory rhythms induce an internal reference that guides movements whereas visual rhythms do not (Jäncke, Loose, Lutz, Specht, & Shah, 2000). Additionally, cortical regions involved in motor response, such as the putamen, are more active during auditory sequences compared to visual sequences, which may reflect more precise timing (Hove, Fairhurst, et al., 2013; Witt, Laird, & Meyerand, 2008). Furthermore, when information in auditory and visual domains contain conflicting temporal information, judgments are more strongly influenced by auditory than by visual information (Fendrich & Corballis, 2001; Morein-Zamir, Soto-Faraco, & Kingstone, 2003; Recanzone, 2003; Shams, Kamitani, & Shimojo, 2000; Walker & Scott, 1981).

Temporal regularity is important to auditory perception, leading to rapid recognition and processing of auditory sequences (Kiebel, von Kriegstein, Daunizeau, & Friston, 2009), and optimized levels of attentional resources allocated to event processing (Correa, Lupiáñez, & Tudela, 2005). Prediction is of great importance auditory processing because events need to be rapidly decoded on the order of milliseconds to quickly establish expectations for subsequent events. Incoming sensory information is full of regularities and we rely on prior knowledge of past events to prepare for future perceptions. For example, sequences of tones that contain regularities set up predictions about the timing of upcoming tones based on the information processed from the timing of previous tones. In the last few decades, numerous studies offered evidence of predictive processing for temporal information, and this research has led to various theories regarding predictive timing. The multiple timer model describes the processing of time intervals relative to an internal oscillator or pacemaker (Ivry, 1996; Ivry & Richardson, 2002). The phase of the “internal clock” is compared against perceived regularities, and the rate of this internal clock is constantly updated based on phase differences in external information (Wing &

Kristofferson, 1973; Vorberg & Wing, 1996). Similarly, a prominent theory in the timing literature that is highly relevant to the studies presented in this thesis is dynamic attending theory, which considers how oscillating attention impact timing perception.

1.2 Dynamic Attending

In rhythmic auditory stimuli such as music, periodicities can be easily identified in rhythmic patterns. Dynamic attending theory postulates that temporal regularities that are extracted from streams of sound events drive oscillating levels of attentional energy peaking at the onset of an upcoming event (Jones & Boltz, 1989; Large & Jones, 1999). The regularity perceived in external temporal events generates predictions about subsequent events (Jones & Boltz, 1989). This causes attention to modulate dynamically over time, peaking at the points where an event is expected to occur (Jones & Boltz, 1989; Jones, 1976; Large & Jones, 1999; Large & Kolen, 1994). Many behavioural studies offer support for the attentional component of dynamic attending theory, where processing benefits exist for events occurring on salient accented, or highly anticipated, positions (Jones et al., 1982; Jones et al., 2002). This entrainment model speculates that the timekeeper consists of oscillators that, in the presence of regular external stimulation, synchronize and adapt their internal rhythms to align with the timing of external information (Barnes & Jones, 2000; Large, 2008). The timekeeper then acts as an internal reference for comparison with future external temporal events.

1.2.1 Behavioural evidence

Dynamic attending theory explains timing abilities by suggesting that an internal timekeeper is established that causes events to be anticipated at certain points in time. When violations to these anticipated events occur in otherwise periodic stimuli they are readily identified. Dynamic attention leads to processing benefits for expected events, since detection is facilitated when timing and pitch deviants occur in simple rhythms at expected points in time, where attention is at its peak (Jones, Moynihan, MacKenzie, & Puente, 2002; Jones, Boltz, & Kidd, 1982; Jones & Yee, 1997; Klein & Jones, 1996). In timing deviation tasks, participants identify deviations occurring in regularly timed sequences. The most accurate detection occurs for events presented at the expected time, compared to late or early events for which detection is less accurate (Barnes & Jones, 2000; McAuley & Jones, 2003). These detection abilities for early, on-time, and late events creates a timing profile that has an inverted-U shape. This inverted U-shaped timing profile supports attentional models of timing since the peaks of attention often coincide with external events. A greater degree of attention is allocated towards an anticipated event compared to a non-anticipated (early or late) event, leading to superior perceptual performance in these conditions (Jones & Boltz, 1989; Jones, 1976; Large & Jones, 1999). In other studies that examine target detection abilities in early vs. late mid-sequence timing deviations, authors find a perceptual asymmetry in expectancy profiles where late deviations are easier to detect than early deviations (Large & Jones, 1999; McAuley, 1995). Since attention increases prior to the expected onset of an event, attention may be greater for late deviants than for early deviants (McAuley & Kidd, 1998) leading to this asymmetry, assuming that expectation continues to build following the delay of an anticipated event.

1.2.2 Neural evidence

Support for the oscillatory component of dynamic attending theory comes from neurophysiological studies that demonstrate how the intrinsic oscillatory activity of neurons in various frequency bands reflects the dynamic modulation of attention in the presence of temporal regularities in external stimuli (Herrmann & Henry, 2014). In rhythmic listening tasks, auditory regions show periodic modulations of beta activity, where beta power increases prior to an anticipated temporal event, and decreases after the anticipated event is processed (Fujioka, Trainor, Large, & Ross, 2009, 2012; Iversen, Repp, & Patel, 2009). Auditory activity co-modulates with activity in motor regions, suggesting that beta activity is involved in predictive timing and communication between auditory and motor areas (Fujioka et al., 2012). This research demonstrates that the observed correlation between neural activity in these different cortical regions reflects a preparatory function for movement initiation, as beta band activity is thought to be associated with the sensorimotor network (Murthy & Fetz, 1992). These studies also present evidence for beta activity as an endogenous (internally-generated) rhythmic process, given that the increase in beta power prior to anticipated events occurs independent of stimulus rate (Fujioka et al., 2009, 2012) and increases in power when the presence of accents are simply imagined (Iversen et al., 2009). Oscillatory activity in the gamma band also appears to be involved in temporal prediction, where an increase in gamma activity is observed prior to the onset of predicted events and is more reflective of exogenous stimulus features (Iversen et al., 2009; Snyder & Large, 2005). Together these findings illustrate that the processing of anticipatory mechanisms involves interactions between external stimulus information and an internal representation of anticipated events.

Building on this support for dynamic expectancy modulations over time, the resonance theory of beat and meter (Large & Snyder, 2009; Large, 2008) proposes that beat and meter percepts arise from neuronal populations resonating at the frequency and subharmonics of the beat, leading to neuronal entrainment. The brain coordinates oscillatory activity that arises in different frequency bands, which allow for efficient communication between different cortical regions (Large, 2008). Low frequency oscillatory activity that responds to periodic stimuli provides empirical support for resonance theory. Steady-state evoked potentials in low frequencies reflect neural firing that occurs at the rate of the stimulus and peak at the beat frequency and subharmonics corresponding to frequencies that reflect metrical processing (Nozaradan, Peretz, Missal, & Mouraux, 2011). These steady-state evoked potentials are also observed for rhythmic patterns, even at positions that do not align with acoustic energy but instead at the position of perceived metrical accents (Nozaradan, Peretz, & Mouraux, 2012). These studies offer support for the resonance theory of beat and meter by demonstrating the neuronal responses that map onto the beat frequency and subharmonics (meter), suggesting that this neuronal entrainment may lead to the corresponding *perception* of beat and meter (Large & Snyder, 2009; Large, 2008). This perception and organization of temporal information might be the first step in embodying the beat, and form the basis of beat-based movements (Large, 2000).

1.3 Perceptual Timing Processes

As described in section 1.2.1, timing abilities are highly contingent on attention. Various factors influence perceptual timing abilities and attention, including stimulus rate, contextual cues, and top-down information. Lower-level timing information, such as timing sensitivity in individual events, is used to update higher-level constructs such as beat and meter, where temporal information is extracted on an event-to-event basis and fit into the overall timing scheme (Vorberg & Wing, 1996).

1.3.1 Higher-level timing processes

Our ability to track events in time is restricted to a range of tempi for event sequences, and the ideal rate of event sequences changes across the lifespan (McAuley, Jones, Holub, Johnston, & Miller, 2006). The inter-onset interval (IOI) defines the time that elapses between auditory event onsets and can describe the rate or tempo of an isochronous event sequence. Events are considered part of a continuous stream of sounds, rather than individual events if events occur predictably and are spaced by an IOI of between 150 and 2000 ms isochronously in time (Fraisse, 1967). Perceptually, the most optimal event tracking occurs for events that are spaced by an IOI of between approximately 300 ms and 800 ms (Drake & Botte, 1993), reaching a maximal sensitivity at approximately 600 ms (Fraisse, 1967).

The context and higher-level structure of sequences impact sequence tracking abilities. In tasks where event sequences are tracked across time, participants show greater accuracy in responding to rhythmically simple compared to complex event sequences (Jones & Pfordresher, 1997; Large, Fink, & Kelso, 2002; Large & Palmer, 2002; Pfordresher, 2003). Additionally, the temporal context that precedes timing changes (i.e., isochronous and expressive music and clicks) influences perceptual salience for these changes (Repp, 2002). Greater degrees of isochrony across events in a sequence also leads to higher sensitivity for temporal deviants (Friberg & Sundberg, 1995).

One common musical context that facilitates listening is the presence or perception of a metrical structure. The perception of meter arises from accents that are spaced regularly in a sequence with at least two levels of periodicity (Lerdahl & Jackendoff, 1983; London, 2004; Parncutt, 1994; Povel & Essens, 1985). Metrical accents that exist on certain beats of a sequence are thought to increase the degree of attention allocated towards those beats (Jones et al., 1982), allowing deviants to be more easily detected.

Subjective metrical accents can be perceived in isochronous nonmetric sequences (Parncutt, 1994; Povel & Okkerman, 1981), which also leads to processing differences in subjectively accented and unaccented events (Abecasis, Brochard, Granot, & Drake, 2005; Brochard, Abecasis, Potter, Ragot, & Drake, 2003; Potter, Fenwick, Abecasis, & Brochard, 2009). Additionally, a metrical context imposed on an event sequence may enhance attention overall. For example, changes to interval durations in simple patterns are easier to detect for patterns presented in a metrical context (Yee, Holleran, & Jones, 1994). Change detection thresholds are also lower for sequences that contain a stronger meter compared to weaker meter (Grube & Griffiths, 2009). In general, the presence of metrical accents in auditory sequences may allow for more efficient processing of temporal events.

1.3.2 Lower-level timing processes

Lower-level timing cues influence perceived timing of higher-level features. As events are perceived, the internal representation of an external sequence of sounds is continuously updated (Ivry & Richardson, 2002; Schulze, 1978; Vorberg & Schulze, 2002; Vorberg & Wing, 1996). In discrimination tasks, the ability to distinguish between intervals is thought to be related to variability in the interval timer (Drake & Botte, 1993; Ivry & Hazeltine, 1995; Ivry & Keele, 1989; Keele, Pokorny, Corcos, & Ivry, 1985). To complete these discrimination tasks participants rely on local timing cues, such as local stimulus rate, to inform the timing of overall sequences even when instructed to ignore it (Barnes & Jones, 2000; Jones & McAuley, 2005; McAuley & Jones, 2003; McAuley & Kidd, 1998). Small temporal deviants are often introduced to predictable sequences to identify participants' timing thresholds (Ehrlé & Samson, 2005; Jones & Yee, 1997; Keele, Nicoletti, Ivry, & Pokorny, 1989; Madison & Merker, 2002).

Section 1.2.1 described a perceptual asymmetry that exists in expectancy profiles for event timing. This asymmetry might exist due to fluctuations in attention (Large & Jones, 1999; McAuley & Kidd, 1998; McAuley, 1995), but also might be influenced by top-down knowledge of phrase-final lengthening tendencies in musical sequences (Palmer & Krumhansl, 1990; Repp, 1998) for deviants that occur at the end of event sequences. In tasks where participants must discriminate the tempo of isochronous sequences, comparison patterns separated from standard patterns by a temporal interval are presented early, late, or on-time, relative to the onset of the first event in the standard pattern. Early onset conditions showed higher detection thresholds than for on-time or late comparison patterns (McAuley & Kidd, 1998). This is best explained using an oscillator-based account where listeners can compensate for interruptions in temporal patterns by discounting the first interval of the comparison sequence (Large & Jones, 1999).

1.3.1 Expertise in perceptual timing

In musical situations, rhythmic abilities are highly practiced and performed. Overall, musicians tend to demonstrate superior timing abilities compared to nonmusicians. In higher-level timing contexts, musicians demonstrate lower thresholds for detecting sequence isochrony (Jones & Yee, 1997; Madison & Merker, 2002; Yee et al., 1994), tempo changes (Drake & Botte, 1993), and beat detection (Cameron & Grahn, 2014; Matthews, Thibodeau, Gunther, & Penhune, 2016). In lower-level timing contexts for single events, musicians also outperform nonmusicians. This is the case for both duration-based timing tasks comparing two intervals (Rammsayer & Altenmüller, 2006) and detecting temporal deviants within or at the end of rhythmic sequences (Jones, Jagacinski, Yee, Floyd, & Klapp, 1995; Jones & Yee, 1997; Lim, Bradshaw, Nicholls, & Altenmüller, 2003; Rammsayer & Altenmüller, 2006; van Vugt & Tillmann, 2014; Yee et al., 1994). There are reports documenting that percussionists have the highest sensitivity of all musician groups (Cameron & Grahn, 2014; Ehrlé & Samson, 2005; Krause, Pollok, & Schnitzler, 2010), however other accounts show general benefits to high- and low-level timing abilities in musicians but no differences between musician groups (Matthews et al., 2016). Although there is a clear relation between musical training and refined timing abilities overall, it is not clear whether musicians acquire superior timing abilities from training or if individuals who originally possess better timing abilities are more successful musicians who seek out or continue their training due to these abilities.

1.4 Motor Synchronization

Audio-motor synchronization requires the integration of sensory information from various modalities in order to optimally produce action based on perceptual information (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Wing, Doumas, & Welchman, 2010). The majority of studies in the sensorimotor synchronization literature examine discrete timed finger tapping movements (reviewed in Repp & Su, 2013; Repp, 2005). Movement quality is measured in two ways: tap asynchrony, the degree to which taps align with an external sound; and tapping variability, the consistency of the inter-tap interval (ITI).

1.4.1 Tap asynchrony

Tap asynchronies are observed in both musicians and nonmusicians when they synchronize movements with an external beat and tap on average 20-80 ms in advance of the beat (Aschersleben, 2002). This tapping behaviour is referred to as a negative mean asynchrony (NMA) and might reflect anticipation of corresponding auditory information. The NMA increases when auditory feedback from the taps are delayed, demonstrating that sensory information directly impacts movements (Aschersleben & Prinz, 1997; Mates & Aschersleben, 2000), a relationship further discussed in section 1.5. The NMA differs across motor effectors, with foot tapping displaying a larger NMA than finger tapping (Billon, Bard, Fleury, Blouin, & Teasdale, 1996). The reason for the NMA remains unclear; however, the ubiquity of this asynchrony has lead to two primary hypotheses to explain its course. The nerve conduction hypothesis describes the origin of the NMA in the periphery, caused by the difference in conduction time from the tap (which differs based on the synchronizing effector) to the central representation (see Figure 1.1). Due to this difference in conduction time, the tap must be executed in advance of the sound in order for these events to be centrally perceived as synchronous (Aschersleben & Prinz, 1995, 1997; Fraisse, 1980; Paillard, 1949).

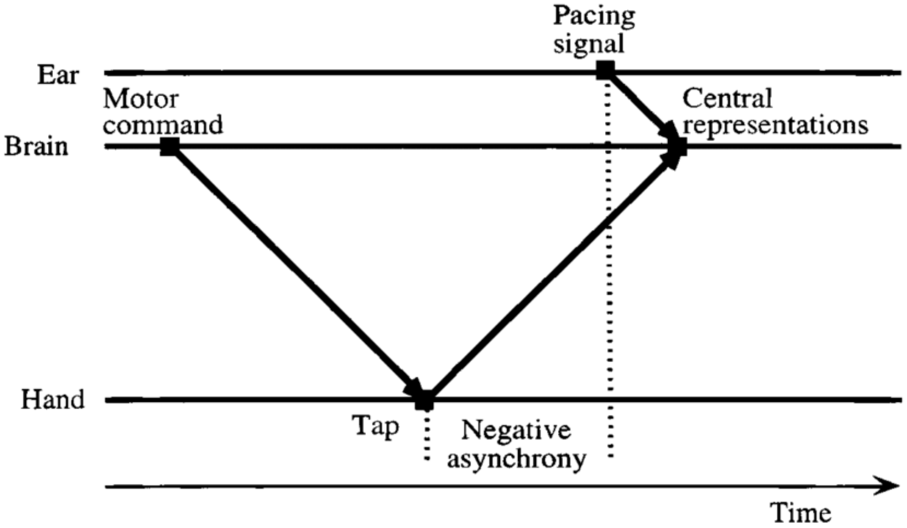

Figure 1.1 The nerve conduction hypothesis (Aschersleben, 2002).

The sensory accumulator model also posits that synchrony must be established centrally, however it describes a threshold-dependent account of sensory processing where the steepness of an accumulation function (see Figure 1.2) determines the amount of time that exists between the tap and the external sound. This time discrepancy varies between motor effectors because the threshold for central detection (and therefore the steepness of the curve) differs across effectors (Aschersleben, Gehrke, & Prinz, 2004). The steepness of this curve may also differ across participants showing various magnitudes of tap asynchronies; participants displaying larger tap asynchronies would have higher thresholds, and steeper curves than would participants who display smaller tap asynchronies.

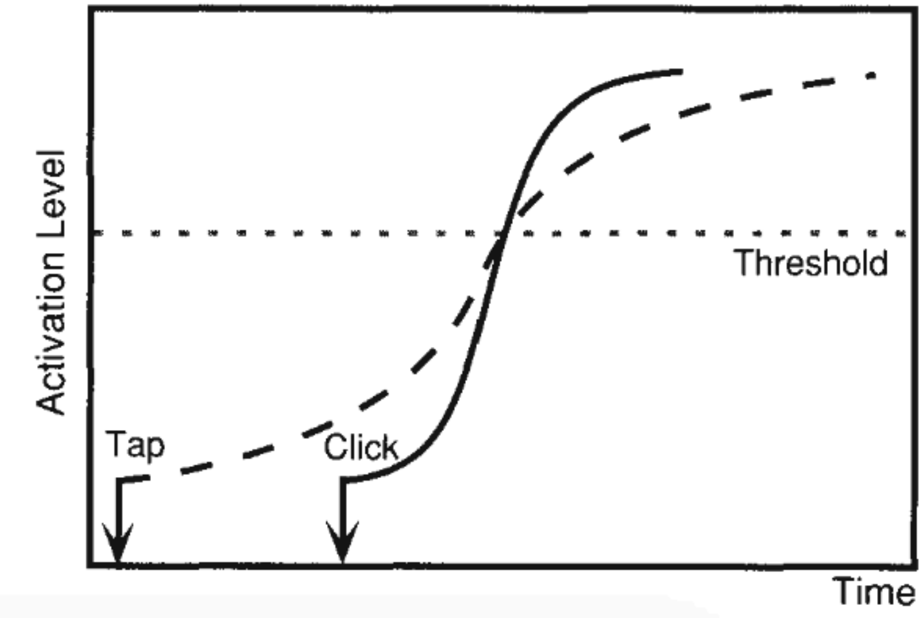

Figure 1.2 The sensory accumulator model (Aschersleben, 2002).

1.4.2 Tap variability

The variability of motor output is another important aspect of synchronization abilities. Synchronization variability decreases throughout childhood and remains relatively constant throughout adulthood (Drewing, Aschersleben, & Li, 2006). The variability in movement timing is thought to reflect inaccuracies in the central timekeeper (Vorberg & Wing, 1996), suggesting that motor abilities might be related to perceptual timing abilities. Models that describe timing control specify that tapping variability can be explained by central and peripheral sources of variability; the internal clock and motor response variance, respectively (Wing & Kristofferson, 1973). Tapping variability increases with interval length (Ivry & Hazeltine, 1995; Wing, 1980), reflecting Weber's law in motor synchronization.

1.4.3 Comparisons across motor effectors

Sensorimotor synchronization abilities are largely assessed through finger tapping tasks due to its simplicity. Motor synchronization is also thought to originate from a common motor source (Doumas & Wing, 2007; Wing & Kristofferson, 1973). Support for this notion comes from studies that compare outputs across motor effectors, where a relationship is observed between tap asynchronies (Billon et al., 1996) and variability (Fujii et al., 2011; Keele et al., 1985) of different motor effectors within subjects.

However, clear differences exist across different motor effectors when synchronizing with external auditory events. For example, foot tapping is more asynchronous than stick tapping (Fujii et al., 2011). Interestingly, while variability decreases with practice across both finger and stick tapping (Madison, Karampela, Ullén, & Holm, 2013), finger tapping is significantly more variable (Collier & Ogden, 2004; Madison, 2001) than tapping using a drumstick (Fujii & Oda, 2009; Madison & Delignières, 2009). The motor control literature describes differences in the degrees of freedom in motor kinematics that may be manipulated in various effectors (Latash, 2014; Todorov & Jordan, 2002). A greater number of degrees of freedom in a motor effector can allow for more error correction and manipulation, and thus greater consistency, in movements (Winold, Thelen, & Ulrich, 1994). This is an important consideration when describing movement abilities across different effectors.

1.4.4 Expertise in motor synchronization

Musicians and nonmusicians are well able to synchronize movements with external auditory information. Musicians, however, show a clear advantage in motor timing abilities (Aschersleben, 2002; Matthews et al., 2016; Repp & Doggett, 2007; Repp, London, & Keller, 2013; Repp, 1999a, 2010). This advantage differs based on musical background, where some groups gain greater timing advantages compared to others. For example, percussionists appear to outperform other musicians in motor timing tasks (Cameron & Grahn, 2014; Krause et al., 2010). Even short-term synchronization training in different motor effectors leads to an improvement in movement consistency (Madison et al., 2013), demonstrating the immediate benefits of training on synchronization abilities.

When musicians synchronize movements with external auditory information, they perform better when the auditory information most closely aligns with musical scenarios. For example, musicians coordinate movements more accurately with a changing sequence when the tempo decreases later in the sequence rather than increases (Loehr, Large, & Palmer, 2011), as this more accurately reflects phrase final lengthening that occurs in musical pieces (Palmer & Krumhansl, 1990; Repp, 1998). Musicians readily adapt movements to changing tempi (Repp & Keller, 2004), perhaps due to refined auditory imagery abilities (Pecenka & Keller, 2009). Musicians also tap more regularly with musical excerpts than do nonmusicians (Drake, Penel, & Bigand, 2000). Movement synchronization in musicians yields low variability particularly when synchronizing using movements most similar to their instrument of training (Keele, Pokorny, Corcos, & Ivry, 1985; Krause et al., 2010; Stoklasa et al., 2012). Long- and short-term training clearly benefits sensorimotor synchronization and experience with musical scenarios and motor effectors appears to have a clear impact on synchronization abilities.

1.5 Sensory Integration of Temporal Information

For accurate perception, we encounter many sources of sensory information and integrate a wealth of information in an efficient and optimal manner. In the spatial domain, the combination of sensory cues reduces the variance of the internal representation of an external stimulus. This is made evident by findings demonstrating how cues are combined and weighted according to their reliability (Ernst & Banks, 2002; Ernst & Bülthoff, 2004). Typically we rely most heavily on the visual domain for spatial information and the auditory domain for temporal information, due to a greater degree of precision in processing for the respective sensory modalities (Morein-Zamir et al., 2003; Soto-Faraco, Spence, & Kingstone, 2004). However, the weighing of information can shift away from this tendency if the signal in the more prominent sensory modality (for example spatial processing in the visual domain) is considerably degraded (Alais & Burr, 2004). Similarly, although audition dominates the temporal domain in perceptual and motor timing tasks containing multimodal information (Grahn, 2012; Repp & Penel, 2002, 2004; Repp, 2003), the presence of more reliable temporal information in modalities other than audition can lead to a reduction in typically-observed auditory dominance (Bresciani et al., 2008; Hove, Iversen, et al., 2013). Structurally, timing networks (e.g., the putamen) are similarly active during beat perception and synchronization with auditory and visual stimuli that offer temporal information, such as a bouncing ball (Grahn, 2012; Hove, Fairhurst, et al., 2013). This might suggest that timing networks are amodal and act as a general network for synchronization and temporal processing (Grahn & Rowe, 2009; Teki, Grube, Kumar, & Griffiths, 2011).

1.5.1 Multisensory integration for motor synchronization

Despite the pronounced capacity for the auditory system to process temporal information in isolation, the combination of multiple sensory cues further promotes processing. Timing consistency in motor synchronization arises from variability that comes from perceiving events and synchronizing movements by relying on multiple sensory inputs (Wing & Kristofferson, 1973; Wing, 2002). Specifically, motor timing relies on information from the auditory and tactile domains, where tapping shows the smallest asynchrony from a pacing signal when both auditory and tactile feedback are readily available (Wing et al., 2010). Timing cues that are available from multiple modalities are integrated in an optimal manner and lead to the most accurate synchronization (Elliott, Wing, &

Welchman, 2010); however participants rely most heavily on feedback from auditory signals (Elliott, Wing, & Welchman, 2011; Kolers & Brewster, 1985). In the case of a temporal discrepancy between sensory inputs, the modalities are treated independently and movements are timed to the cue that offers the greatest sensory reliability (Elliott et al., 2010). Additionally, the amount and integration of auditory and tactile feedback produced by each movement impact synchronization quality (Finney, 1997; Maduell & Wing, 2007; Wing, 1977).

Since auditory feedback has the greatest impact on motor synchronization abilities, a great deal of research has manipulated the amount and type of feedback that is available. The absence of auditory feedback increases tap asynchronies (Aschersleben & Prinz, 1995, 1997; Mates, Radil, & Pöppel, 1992), as does the absence of tactile feedback (Aschersleben, Gehrke, & Prinz, 2001). Delayed feedback adversely affects motor timing in musical performance (Finney, 1997; Furuya & Soechting, 2010a; Gates, Bradshaw, & Nettleton, 1974), where the tap that occurs immediately after the delay is shortened and tapping becomes more variable overall (Pfordresher & Palmer, 2002). This might reflect compensatory mechanisms in subsequent movements (via the auditory feedback loop) to update predictive timing behaviours and adapt to these new predictions (Furuya & Soechting, 2010a; Wing, 1977).

1.6 The Role of Movement in Predictive Timing

1.6.1 Movement impacts perception

A great deal of research in the last few decades seeks to understand the integration of auditory and movement information in predictive timing situations. This integration is frequently examined through multisensory tasks such as musical performance and considers the perspective of both the musician and the listener. It is clear that movement can generate sounds, for which movements need to be precisely timed and executed. However sensory feedback that occurs as a consequence of moving impacts subsequent movements, creating an auditory-motor feedback loop (see Zatorre, Chen, & Penhune, 2007). The ways in which movements affect the perception of auditory events is less clearly understood.

Recent neuroimaging studies report that the audiomotor relationship is critical for the perception of beat-based information presented in the auditory domain. In these studies, the authors report evidence for overlapping regions of processing rhythmic auditory and motor information. Specifically, motor areas, including the cerebellum, prefrontal cortex, supplementary motor areas and the basal ganglia are required not only for motor synchronization to rhythmic information (Bangert et al., 2006; Bengtsson et al., 2009; J. L. Chen, Penhune, & Zatorre, 2008a; Grahn & Brett, 2007) but also for the *perception* of rhythms, even when no overt movement is executed. These motor regions that are involved in both motor planning and execution are involved not only in initiating and executing the movements necessary for synchronizing movements to auditory information, but also for the processing of beat information. Additionally, studies that examine the time-locked response of cortical activity in prediction also report audio-motor communication, which might suggest a coordination of auditory and motor responses in listening tasks (Fujioka et al., 2009, 2012; Iversen et al., 2009). This might suggest that the auditory cortex relays information to motor regions in order to process and initiate movement.

Behaviourally, this interaction is evident through several studies that demonstrate ways in which movement can change the perception of auditory information in ambiguous listening situations. Movement modifies duration perception, where auditory, tactile or visual events that are paired with a button press are perceived as longer than those that are not (Press, Berlot, Bird, Ivry, & Cook, 2014). Free movement synchronized with isochronous event sequences (i.e., head nodding, foot tapping) allows participants, particularly nonmusicians, to more easily extract and identify the pulse in ambiguous rhythmic sequences (Su & Pöppel, 2012). In musical imagery tasks, finger tapping with imagined music allows for more accurate timing (Jakubowski, Farrugia, & Stewart, 2016; Schaefer, Vlek, & Desain, 2011).

In ambiguous metrical scenarios, movement shapes the interpretation of accenting structure in ambiguous rhythms. One such set of studies presented ambiguous 6-note sequence with possible interpretations for accents on every second or third beat (Phillips-Silver & Trainor, 2007). In a training phase, participants bounced on every second or third beat of the 6-note sequence, reflecting a duple or triple meter respectively. In the test phase participants later more often reported *hearing* duple or triple accents corresponding to the movement in the training phase. This pattern is also observed in infants. When they are passively bounced by an experimenter in either a duple or triple fashion they later listen longer (through looking behaviour) at the test version congruent with the way in which they were previously bounced (Phillips-Silver & Trainor, 2005). It appears that movement of the head is the most important part (Phillips-Silver & Trainor, 2007, 2008) and that metrical interpretation is at least in part attributed to vestibular input from this movement (Trainor, Gao, Lei, Lehtovaara, & Harris, 2009). These studies are corroborated by neural evidence showing changes to neural entrainment in low frequencies that reflects movement patterns in otherwise ambiguous rhythms (Chemin, Mouraux, & Nozaradan, 2014).

1.6.2 Measuring perceptual and motor timing interactions

Interestingly, accuracy in motor synchronization is correlated with perceptual abilities, suggesting a common timing mechanism for internal representations and externalized execution of movements (Buonomano & Karmarkar, 2002; Guttman, Gilroy, & Blake, 2005; Ivry & Schlerf, 2008; Keele et al., 1985; Schubotz, Friederici, & von Cramon, 2000). Some studies that examine synchronization and perceptual abilities within the same individuals, report correlational evidence for a single timing source for multiple separate measures of the internal timing representation. More accurate tappers performed better on detection tasks overall, in studies that examine a relationship between movement timing and timing perception (Pashler, 2001; Repp, 1999b). Linear relationships that are observed between variability in perception and production of temporal intervals are thought to suggest a common timing mechanism for both timing processes (Ivry & Hazeltine, 1995), where less perceptual weight may be allotted to less consistent (i.e., less reliable) movements.

These studies clearly demonstrate ways in which movement can shape the perception of rhythmic information in musical settings. They supports theories that describe a common coding mechanism for event timing in perception and action (Hommel et al., 2001; Prinz, 1997). These theories are often described as embodied cognitive approaches, where executing an action engages the same sensorimotor brain regions as does perceiving the outcome of that action. Additionally, recent internals models describe the flow of information between sensorimotor systems, inverse models describe information transfer from perception to action and forward models describe information transfer from action to perception (Wolpert, Ghahramani, & Jordan, 1995). These models seek to explain the role of action in music listening and perception, with many studies supporting each side of the sensorimotor feedback loop (see Maes, Leman, Palmer, & Wanderley, 2014 for a review).

1.7 Thesis Overview

This thesis seeks to further examine interactions between auditory and motor systems. Specifically, throughout these chapters I aim to demonstrate how movement not only influences the perception of external auditory information, but also how movement can lead to objective improvements in timing abilities. This thesis will discuss how tapping can enhance the ability to identify timing deviations at the end of an auditory sequence (Chapter 2), and how sensory feedback facilitates this enhancement (Chapter 3). This thesis will also discuss how rhythmic expertise interacts with sensorimotor synchronization abilities (Chapter 4) and how motor effector experience might be specific to this enhancement (Chapter 5). Finally, I will discuss how these studies have advanced the field of sensorimotor integration, highlighting specific recent literature supporting these findings and suggesting some future directions for this research (Chapter 6).

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Chapter 2: "Moving to the beat" improves timing perception.

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2.1 Preface

Although it is clear that auditory information is important for timed movements, since movements are easily synchronized with predictable auditory events, the reason for this behaviour remains unclear. The processing of auditory and motor information are intricately linked, where listening to predictable auditory events is sufficient to activate motor regions of the brain (Bangert et al., 2006; Bengtsson et al., 2009; J. L. Chen, Penhune, & Zatorre, 2008a; Grahn & Brett, 2007). This suggests that these regions are not only important for executing synchronized movements with external auditory information, but also for the processing of predictable temporal events.

Prior to the study presented in this chapter, sensorimotor integration research had reported correlations between motor synchronization and rhythmic listening abilities in separate tasks (Buonomano & Karmarkar, 2002; Guttman, Gilroy, & Blake, 2005; Ivry & Schlerf, 2008; Keele et al., 1985; Pashler, 2001; Schubotz, Friederici, & von Cramon, 2000). These studies suggest a common internal representation for auditory and motor timing tasks (Hommel et al., 2001;

Ivry & Hazeltine, 1995; Prinz, 1997). Furthermore previous reports of auditory-motor interactions in behavioural tasks describe subjective changes to interpreting different aspects of auditory rhythms following movements (Phillips-Silver & Trainor, 2007, 2008; Su & Pöppel, 2012). These studies demonstrate clear ways in which movement information can shape the perception of otherwise ambiguous temporal information.

In the current study, we explicitly tested whether synchronizing movement to predictable auditory events could serve to objectively improve timing abilities, particularly when auditory information is absent. To examine this question we carried out a timing detection experiment to compare performance when participants tap along with an auditory sequence or when listening only. Two subsequent experiments in this chapter aim to clarify which segment of the tone sequence is important for movement to improve timing detection abilities.

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2.2 Abstract

Here we demonstrate that "moving to the beat" can improve the perception of timing, providing an intriguing explanation as to why we often move when listening to music. In the first experiment participants heard a series of isochronous beats and identified whether the timing of a final tone after a short silence was consistent with the timing of the preceding sequence. On half of the trials participants tapped along with the beat, and on half of the trials they listened without moving. When the final tone occurred later than expected, performance in the movement condition was significantly better than performance in the no-movement condition. Two additional experiments illustrate that this improved performance is due to improved timekeeping rather than a shift in strategy. This work contributes to a growing literature on sensorimotor integration by demonstrating body movement's objective improvement in timekeeping, complementing previous explorations involving subjective tasks.

Keywords: timing perception, sensorimotor integration, perception and action, music

2.3 Introduction

Although we often bob our heads and tap our feet when listening to music, the reason for this behavior remains elusive. One possible explanation is that this movement might improve our perception of the music via interactions between the sensory and motor systems. This proposed explanation is consistent with observations that event perception and action planning capitalize on the same internal mechanism (Prinz, 1997). It is similarly consistent with the unified theories of event processing that describe perception and action planning within a single framework (Hommel, Müsseler, Aschersleben, & Prinz, 2001); a framework crucial for the production and perception of complex auditory information such as music.

Neurological research provides evidence for interactions between the auditory and motor systems (Fujioka, Trainor, Large, & Ross, 2012; Grahn & McAuley, 2009) as well as sensory and motor regions (D'Ausilio, Altenmüller, Olivetti Belardinelli, Lotze, & Belardinelli, 2006; Grahn & Brett, 2007; Grahn & Rowe, 2009). These findings support the idea of a "cross-talk" between perceptual systems (Goodale & Westwood, 2004). Sensorimotor integration research offers insight into the complex relationship between perception and action, and music represents a rich window for this exploration (Zatorre et al., 2007).

Not only is movement central to music production, it occurs naturally and automatically during music listening amongst both musicians and nonmusicians. Although the ability to synchronize movements to an auditory beat does not require training or practice, musical experience is helpful in perceiving (Ehrlé & Samson, 2005; Jones & Yee, 1997; Madison & Merker, 2002; Yee et al., 1994) and producing (Repp & Doggett, 2007; Repp, 2010) isochronous sequences. Despite our tolerance for timing irregularities in musical sequences (Madison & Merker, 2002), changes in isochronous sequences are quite salient. Here we complement previous work examining the perceptual effects of music listening on body movement by exploring movement's effect on our ability to detect timing changes in isochronous sequences.

2.3.1 Subjective measures of movement and auditory perception

Movement's effect on listeners' perception of music raises questions about its effects on those performing it. Studies investigating whether movement alters one's own perception have typically used subjective tasks. For example, body movement can affect the perception of metric structure: a subjective "grouping" of beats. Participants moving on every second or third beat while listening to an ambiguous auditory rhythm later report that the motion-consistent meter sounds more familiar (Phillips-Silver & Trainor, 2007; 2008). Extensive musical exposure is not a requirement, as infants bounced in this manner exhibit similar effects (Phillips-Silver & Trainor, 2005). Vestibular stimulation is crucial, as artificial vestibular input independent of physical head movement is sufficient to trigger the phenomenon (Trainor, Gao, Lei, Lehtovaara, & Harris, 2009).

Moving to an auditory sequence also facilitates subjective pulse extraction (i.e., identifying "the beat"), particularly for tempi within comfortable movement frequencies. Movement while listening also influences the amount of synchrony between this extracted pulse and the auditory sequence (Su and Pöppel, 2012). Although this indicates that movement can facilitate pulse extraction, its effect on perceived *timing* remains an open question. This relationship can (and frequently has) been explored through tapping; a paradigm useful for studying synchronization as well as timing acuity (see Repp, 2005 for an extensive review).

In contrast to tapping itself, tapping's effect on perception is less well researched. Nonetheless, Repp (2002) explored the role of musical context in sensorimotor synchronization and in timing perception. After hearing a piano solo either with either consistent timing or small perturbations, trained musicians listened to a separate rhythmic sequence in one of three conditions: *perception-only*, where they identified perturbations; *synchronization-only*, where they tapped along to the sequence; and *perception-and-synchronization*, where they both tapped along and identified perturbations. Detection of perturbations in the *perception-only* and the *perception-and-synchronization* conditions was significantly impaired by timing perturbations, yet performance in the *synchronization-only* condition was not affected. Here, perception was more sensitive to preceding context than was movement (tapping). As it was beyond the study's scope, Repp did not explicitly address whether synchronization influenced the ability to detect deviations within the rhythm.

2.3.2 Present study

Here, we build upon previous work by introducing an objective task that does not require musical training to explore whether "moving to the beat" affects timing perception. While complementary explorations of action's effect on perception use *subjective* ratings of pitch direction (Repp & Goehrke, 2011; Repp & Knoblich, 2007; 2009), metric structure (Phillips-Silver & Trainor, 2005; 2007; 2008) and beat extraction (Su & Pöppel, 2012), here we use an *objective* task focused on timing. In order to obtain results that generalize to the general population, we did not select participants based on musical abilities (as done in related research; Krause et al., 2010; Repp, 2002; Repp & Knoblich, 2007; 2009).

We hypothesized that participants would more accurately discriminate timing deviations when moving (i.e., tapping) along to a sequence compared to when listening alone. This is based on the assumption that tapping initiates an additional timing mechanism activated by motor networks. A consistency between motor and auditory timing loops may create a stronger reference signal with which to compare the target sounds. This finding would provide insight useful for musicians by demonstrating that body movement can improve their perception of timing. In addition, it may shed light on the reasons listeners often move automatically to the beat: that it aids in our ability to "understand" music's temporal structure, thereby contributing to our knowledge of links between perception and action.

2.4 Experiment 1

2.4.1 Method

Materials and apparatus. We conducted the experiment using customized software developed by the MAPLE Lab playing MIDI "woodblock" sounds (gmBank = 115) through Sennheiser HDA200 headphones. An Alesis Trigger i/O - Trigger-to-MIDI USB Interface converted signals from an electronic drum pad (Roland PDX-8) into MIDI messages sent to an iMac computer[1]. Each trial consisted of sixteen tones divided into groups of four (i.e., four measures with four beats each) followed by a probe tone (see Figure 2.1). The first of each group used a higher relative pitch (C5; 523-Hz) than the others (G4; 392-Hz) to induce a sense of meter. In the last group, the second, third and fourth "tones" were silent. In half of the trials the probe tone was consistent with the pattern, and in the other half it was inconsistent. We used two different inter-onset intervals (IOIs): 400 ms (150 beats-per-minute) and 600 ms (100 bpm), both falling within an ideal range for perception and production (Drake & Botte, 1993).

Design and procedure. Participants performed 64 trials grouped into eight blocks. We asked participants to tap along to half of the blocks (movement condition) and to remain still during the other blocks (no-movement condition). Four of the eight trials within each block included an "on-time" (i.e., at an offset of 0 ms) probe tone, with the others at one of four offsets; either 30% or 15% of the IOI (both early and late). Participants experienced each of the four IOI (400

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[1] The temporal variability of this system ranges from 3.4-8.3 ms (M = 5.4 ms) between events, which falls below the threshold of detection (Drake & Botte, 1993; Hibi, 1983).

ms; 600 ms) x Movement-Condition (movement; no-movement) combinations twice after completing five warm-up trials. We randomized both the order of the experimental blocks and the order of the trials within each block for each participant.

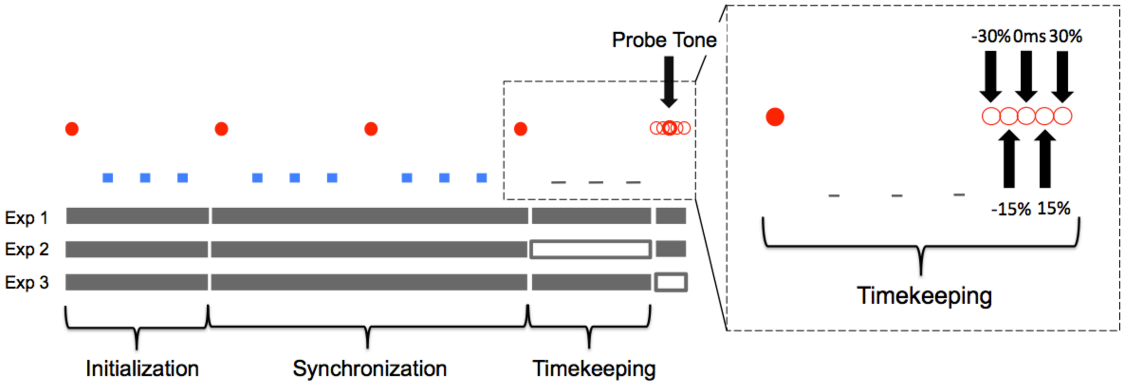

Figure 2.1 Trial structure with initialization, synchronization and timekeeping segments labeled. Filled circles represent the accented tones, squares unaccented tones, lines silent beats and empty circles possible probe tone locations. The grey boxes beneath the segment labels summarize the movement trial tapping instructions for each experiment, with filled boxes indicating tapping and empty boxes indicating beats without motion.

During movement blocks, participants tapped on each beat of the stimulus (all three segments, including the probe tone) on a drum pad using an Innovative Percussion (IP-1) drumstick. We asked participants to remain as still as possible during the no-movement blocks (i.e., no foot-tapping, head-bobbing, etc.). Using a 2 alternative forced choice task, participants judged whether the final probe tone in each trial sounded "on-time" (i.e., consistent with the repeated sequence), and indicated their confidence on a scale from 1 (not at all confident) through 5 (very confident). To help retain attention, participants received feedback on the correctness of these judgments.

Participants. Forty-eight undergraduates from the McMaster University Psychology participant pool participated in exchange for course credit. We excluded eight participants who failed to follow instructions (and therefore did not accomplish the task). This group included those who either tapped during more than 25% of the no-movement trials (n = 2), failed to tap during more than 25% of the movement trials (n = 2), or failed to tap on at least 50% of the beats within the timekeeping segment (n = 4). The remaining 40 participants (28 females, 12 males) ranged in age from 17 to 35 years (*M* = 18.4, *SD* = 2.8) and reported normal hearing and normal or corrected-to-normal vision. Participants had 0-12 years of music lessons (*M* = 4.4, *SD* = 3.5) and tapped with their dominant hand. The experiment met ethics standards according to the McMaster University Research Ethics Board.

2.4.2 Results and discussion

We assessed the percentage of "on-time" responses in all conditions using a 2(IOI) x 5(Offset) x 2(Movement-Condition) repeated-measures ANOVA. The most important finding was the main effect of movement ($F(1,39) = 33.80$, $p <$

.0001), reflecting a difference in task performance between the movement and no-movement conditions (shown in Figure 2.2a). We also observed a main effect of offset ($F(4,156) = 43.35$, $p < .0001$), reflecting a distinction in performance based on the probe-tone offset. Additionally, we observed a two-way interaction between movement condition and offset ($F(4,156) = 12.65$, $p < .0001$), indicating that the effect of movement was not uniform across all of the 5 probe-tone offsets. We found a large difference in task performance (proportion of *correct* identification of the probe tone position derived from the "on-time" judgments) between the movement ($M = 0.747$, $SD = 0.207$) and no-movement ($M = 0.425$, $SD = 0.235$) conditions for the late offsets (15% and 30%) combined ($t(78) = 7.43$, $p < .0001$, $d = 1.46$), indicating better performance when tapping (see Figure 2A). In the movement conditions, late probe tones were easier to detect than early ($t(317) = 4.09$, $p < .0001$). This is consistent with similar research demonstrating that late deviations are slightly easier to detect than early deviations (Large & Jones, 1999; McAuley, 1995) as well as previously noted asymmetries in timekeeping with a changing tempo (Loehr et al., 2011). We observed a two-way interaction between IOI and offset ($F(4,156) = 9.05$, $p < .0001$) indicating that performance differed across the probe-tone offsets differently between the two IOIs. However there was no main effect of IOI or two-way interaction between IOI and movement condition, so we collapsed across IOI in Figure 2.2 for the sake of clarity.

We recorded the timing of each tap and analyzed tapping variability (i.e., a measure of synchronization ability) and its relationship to task performance. We calculated the standard deviation of the timing of taps within each movement trial during the synchronization and timekeeping segments to obtain a measure of tapping variability and compared the log of this variability to performance during these movement trials (squared to normalize the distribution). We found a negative correlation between tapping variability and the proportion of correct responses (r = -.355, p = .025), indicating that "better" tappers performed better on the detection task overall, consistent with studies reporting this type of relationship between movement timing and timing perception (Pashler, 2001; Repp, 1999b). Our design did not lend itself well to more sophisticated analyses of this relationship, as the large number of IOI x Offset x Movement-Condition allowed for only 2 repetitions of each trial. In the future we will further explore this issue using variations on this design with greater numbers of trial repetitions (permitting analyses treating performance as a continuous variable).

Additionally, we found a negative correlation between years of musical training and tapping variability (r = -.366, p = .020), indicating that participants with more musical training tapped more consistently. This parallels research demonstrating a relationship between synchronizing accuracy and musical abilities (Krause et al., 2010; Repp, 2010). Interestingly, there was no correlation between years of musical training and performance on the task (r = -.048, p = .769), contrary to other work reporting effects of musical training on the detection of timing (Ehrlé & Samson, 2005) and sequence regularity (Madison & Merker, 2002). However, future studies can investigate this relationship further by selecting musicians and nonmusicians for explicit comparison.

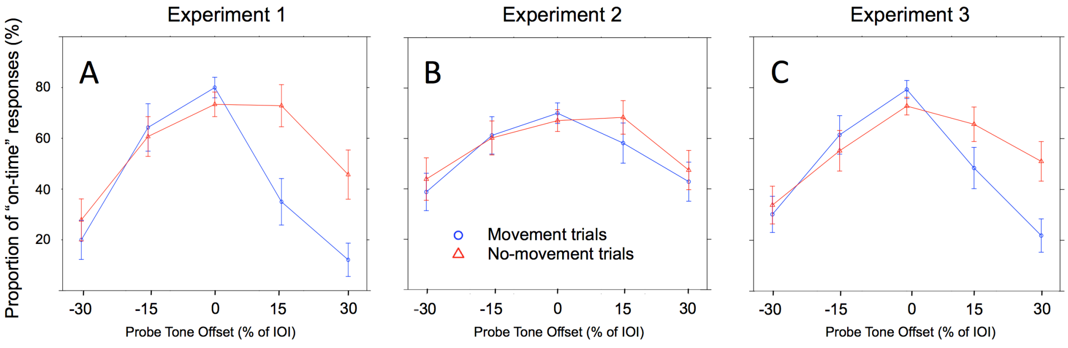

Figure 2.2 Proportion of "on-time" responses for five offset conditions. Participants perform significantly better in the movement trials for the "late" (15% and 30% offset) conditions when moving during the timekeeping segment (Experiments 1 and 3). However, movement had no effect in Experiment 2, when there was no movement throughout the timekeeping segment. Error bars represent the 95% confidence intervals.

We assessed confidence ratings using a 2(IOI) x 5(Offset) x 2(Movement-Condition) repeated-measures ANOVA. This revealed a main effect of movement ($F(1,39) = 63.54$, $p < .0001$), demonstrating greater confidence in the movement ($M = 4.17$; $SD = 0.50$) vs. the no-movement ($M = 3.90$; $SD = 0.54$) condition. This increased confidence (which did not correspond to performance improvements at all offsets) may offer additional evidence as to why listeners often move to the beat while listening.

The difference between movement and no-movement trials in Experiment 1 raises an important question: is the effect attributable to (a) movement itself, or (b) an alternative strategy afforded by movement (comparing the timing of the final tap with that of the probe tone)? To distinguish between these possibilities we conducted two additional experiments.

2.5 Experiment 2

Experiment 2 explored the importance of moving while timekeeping by eliminating movement during the three silent beats of the timekeeping segment (but retaining it for the final beat). If the effect of movement in the first experiment stemmed from calculating the difference in timing between the final tap and the probe tone (rather than from improvements in timekeeping during the silent segment), then we would expect to once again see superior performance in the movement vs. no-movement condition.

2.5.1 Method

This experiment was identical to the first, except here we asked participants to tap only on the *sounded* beats (i.e., the initialization and synchronization segments as well as the probe tone), excluding the three silent "beats" in the timekeeping segment (see Figure 2.1). Participants included 49 undergraduate students, and we excluded 2 participants who tapped during more than 50% of beats within the timekeeping segment. The remaining 47 (34 females, 13 males), ranging in age from 18 to 24 years (*M* = 18.8, *SD* = 1.2), reported normal hearing and normal or corrected-to-normal vision, and tapped with their dominant hand. Musical training ranged from 0-17 years of lessons (*M* = 5.5, *SD* = 4.7).

2.5.2 Results and discussion

The most important finding was that in contrast to Experiment 1, we did not observe a main effect of movement ($F(1,46) = 1.22$, $p = .275$) indicating that tapping had no effect on performance when participants did not move during the timekeeping segment (see Figure 2.2b). As in Experiment 1 we found a main effect of offset ($F(1,46) = 16.32$, $p < .0001$) and a two-way interaction between IOI and offset ($F(4,184) = 17.19$, $p < .0001$), reflecting a difference in performance based on IOI as a function of the probe-tone offset. We did not find a main effect of movement on confidence ratings ($F(1,46) = 0.18$, $p = .678$), indicating that participants were no more confident in their responses when moving (*M* = 3.93, *SD* = 0.58) compared to listening only (*M* = 3.90, *SD* = 0.58). These results are inconsistent with the explanation that movement's effect in Experiment 1 originated from participants comparing the timing of their final tap with the position of the probe tone. Instead, it suggests the effect of movement is the result of improved timekeeping during the silent measure, an idea we tested explicitly in the final experiment.

2.6 Experiment 3

2.6.1 Method

We tested the role of movement during timekeeping in a different manner by asking participants to tap on all beats (including those during the timekeeping segment) with the exception of the probe tone. Here, it was not possible to compare the position of the probe tone with that of the final tap, and therefore any effect of movement can be attributed to movement during the timekeeping segment. Using the same criteria as in Experiment 1, we excluded 8 participants. The remaining 40 (29 females, 10 males, 1 transgender), ranged in age from 17-24 years (*M* = 19.4, *SD* = 1.6), reported normal hearing and normal or corrected-to-normal vision. Participants had 0-15 years of musical training (*M* = 5.7, *SD* = 4.3) and tapped with their dominant hand.

2.6.2 Results and discussion

Similar to the first experiment, the most important finding was a main effect of movement on task performance ($F(1,39) = 11.03$, $p = .002$), indicating a difference in performance during the movement and no-movement trials. Again, we also observed a main effect of offset ($F(4,156) = 39.27$, $p < .0001$) and a two-way interaction between movement and offset ($F(4,156) = 10.92$, $p < .0001$). As in Experiment 1, performance in the movement trials (*M* = 0.66, *SD* = 0.22) was significantly better than performance in the no-movement trials (*M* = 0.41, *SD* = 0.21) when the probe tone occurred later than expected ($t(78) = 5.20$, $p < .0001$, $d = 1.16$), even without movement on the final beat. This complements Experiment

2 by suggesting the benefits of movement cannot be explained solely through a strategy of comparing the timing of the probe tone with the timing of participants' final taps. Nonetheless, the effect of movement was slightly less than in Experiment 1 (see Figure 2.2c), perhaps stemming from less movement overall during the final beats of these trials (previously participants continued timekeeping-through-movement until the final beat, whereas here this was not required beyond the penultimate beat). Here we also found a main effect of IOI ($F(1,39) = 9.44$, $p = 0.004$) not previously observed, as well as an interaction between IOI and offset ($F(4,156) = 10.04$, $p < .0001$). We found a main effect of movement overall on confidence ratings ($F(1,39) = 8.35$, $p = 0.006$), indicating that participants were more confident in their responses when moving ($M = 4.12$, $SD = 0.48$) than when listening alone ($M = 3.98$, $SD = 0.48$). Overall these findings further support the notion that moving to the beat both improves (and increases confidence in) our timekeeping abilities.

2.7 General Discussion

The effect of movement in Experiments 1 and 3 demonstrates that moving to the beat can objectively improve a listener's timing acuity, while Experiments 2 and 3 illustrate the importance of movement for timekeeping. Together, these results complement previous work demonstrating that body movement can influence the perception of subjective properties of temporal information such as metric structure (Phillips-Silver & Trainor, 2005; 2007; 2008) and pulse/tempo (Su & Pöppel, 2012). We note that although vestibular information is known to play a role in sensorimotor meter perception (Trainor et al., 2009), it does not appear to be a driving force in this timing paradigm. Additionally, we extend this literature by documenting that movement can objectively *improve* timing perception, facilitating more accurate detection of timing deviations.

Consistent with previous work demonstrating better accuracy in detecting late vs. early events/changes in timing (Large & Jones, 1999; McAuley, 1995), we observed an asymmetry in performance for late vs. early probe tone offsets. Detection of late offsets was better than early in the movement trials ($t(317) = 4.09$, $p < .0001$), however it was worse in the no-movement trials ($t(317)= 2.55$, $p = .011$). Curiously, our results in the movement trials parallel results from earlier studies in tasks that do not involve movement. One explanation for this puzzling outcome is that our deviations always occurred on the final tone after a silence, whereas many previous studies use deviations embedded within a sequence (Ehrlé & Samson, 2005; Mari Riess Jones & Yee, 1997; Keele et al., 1989; Madison & Merker, 2002). Mid-sequence deviations change the width of two adjacent beats (shortening one and lengthening the other), whereas our manipulation of the final tone affects only one. Although further research is needed to explore whether this accounts for our different results, previous work illustrates that the context in which timing deviations occur can influence their salience (Repp, 2002).

We observe that movement during silence was critical within our paradigm, and suspect that it may help maintain timing when auditory information is absent. This interpretation may account for why the asymmetry in our movement condition mirrors previous findings (which did not involve movement by participants)—those paradigms did not contain a silent segment requiring timekeeping. We note two possible explanations for this superior performance on late vs. early probe tones in the movement condition. First, a narrowing of focus around anticipated events (Large & Jones, 1999) may increase attention as time progresses because the to-be-expected event has not yet occurred (McAuley & Kidd, 1998). Alternatively, the perceptual asymmetry may stem from our familiarity with phrases slowing near completion to convey expression (Repp, 1998). While musicians readily adapt synchronized movements to a changing tempo (Repp & Keller, 2004), they are better at coordinating with decreasing rather than increasing tempi (Loehr et al., 2011).

This asymmetry differs slightly from expectancy profiles reported in relative timing tasks (i.e., comparing the durations of two intervals), where correct detection of timing changes at the end of a sequence follows an inverted-U shaped pattern (i.e., more accurate detection of "on-time" compared to early or late offsets) (Barnes & Jones, 2000; McAuley & Jones, 2003). Our findings suggest a different pattern of responses when judging the timing of a single beat with respect to a context sequence (as opposed to an interval), where moving enhances detection of late offsets but listening alone enhances detection of early offsets at the end of a sequence. Conveniently, the asymmetry is useful in clarifying that the benefits of movement are not solely attributable to increased attention/arousal in the movement vs. no-movement condition. Because we randomized the order of trials within each block, there is no reason to believe attention systematically varied as a function of offset direction.

Together our three experiments demonstrate that movement can objectively improve the perception of timing, a finding contributing to the rapidly growing literature on perception-action links (Hommel et al., 2001; Prinz, 1997) and sensorimotor integration (Zatorre et al., 2007). Although our participants' level of musical experience correlated with tapping variability, it did not correlate with the magnitude of movement's effect. This suggests a generalized influence of action on timing perception; further evidence in support of cross-talk between the two systems (Goodale & Westwood, 2004). These data also suggest that rhythmic movement may act as a mechanism for timekeeping, particularly during musical silences. Given the explosion of recent interest in rhythm and timing—fueled in part by the finding that nonhuman animals can also "move to the beat" (Patel, Iversen, Bregman, & Schulz, 2009)—we believe these findings on the perception of timing are relevant to a wide community.

As a result of these experiments, we conclude that movement can objectively improve our sensitivity to timing, suggesting that one reason we "move to the beat" while listening to music is to help us understand its structure. We suspect that more consistent movement enables a greater improvement in performance: a question we plan to address in future studies. Together, these data contribute to our knowledge of action influencing (and improving) our perception of auditory information in addition to informing our understanding of the perceptual abilities of music performers and listeners alike.

2.8 Acknowledgements

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Chapter 3: Movement enhances perceived timing in the absence of auditory feedback

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3.1 Preface

Sensorimotor synchronization uses information from various sensory inputs to inform motor timing. In particular inputs from auditory and tactile domains provide the most useful feedback (Elliott, Wing, & Welchman, 2010; Wing et al., 2010) however participants rely most on auditory feedback to inform motor timing (Elliott, Wing, & Welchman, 2011; Kolers & Brewster, 1985). Masking or delaying auditory feedback has substantial adverse effects on both tap asynchronies and variability of tapping (Aschersleben & Prinz, 1995, 1997; Finney, 1997; Furuya & Soechting, 2010; Mates, Radil, & Pöppel, 1992; Pfordresher & Palmer, 2002). Due to its effects on motor timing, it is clear that auditory feedback is instantaneously integrated with motor information to correct for errors in movement timing and update the timing of future movements based on the timing of past events (Furuya & Soechting, 2010; Wing, 1977).

The findings presented in Chapter 2 showed that movement serves to improve timing abilities, and that this improvement was specific to the silent segment of the trial. However this poses a potential ambiguity in the interpretation of this finding. Since the movement in the timekeeping (silent) portion of the trial sequence was key for observing this improvement in prediction abilities, we needed to test whether the auditory feedback generated by movement was effectively "filling in" missing auditory information during this segment of the trial. This important question was addressed in the study I present here in Chapter 3.

The aim of the current study seeks to clarify how the auditory consequences of movement are integrated with movement in the paradigm developed in the previous chapter. This study consisted of two groups of participants; one group who heard auditory consequences of tapping movements and the other group who did not. Expanding on our initial findings that demonstrate movement's impact on timing abilities, we further examined how auditory feedback affected this improvement and the precision of motor timing.

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3.2 Abstract

Moving (tapping) to a beat can objectively improve the perception of timing. Here we examine whether auditory feedback from tapping is a requirement for this improvement. In this experiment, two groups of participants heard a series of isochronous beats, and identified whether a probe tone after a short silence was consistent with the timing of the preceding sequence. On half of the trials, participants tapped along on an electronic drum pad up to and including the probe tone, and on half of the trials they listened without tapping. In the auditory feedback (AF) group sounds from tapping were available to participants and in the no auditory feedback (NAF) group these sounds were masked using white noise. In both groups, movement improved timing judgments of the probe tone, however this improvement was more pronounced when auditory feedback was present. Additionally, tapping was more accurate when auditory feedback was available. While previously we demonstrated an effect of movement on perceived timing, here we clarify that movement alone is sufficient to trigger this improvement (independent of the movement's auditory consequences). We identify the importance of auditory feedback as a cue for movement timing, which subsequently affects perceived timing of an external stimulus. Additionally we have demonstrated that movement alone can improve timing perception, independent of the auditory feedback caused by this movement.

Keywords: *Timing perception, auditory feedback, motor timing, tapping, perception and action*

3.3 Introduction

The interplay between movement and sound shapes everyday tasks such as tapping along with a song on the radio or playing a musical instrument. Auditory information can influence ways in which we move; for example we can readily tap along to metronome or dance along with the beat in music. Conversely movement can modify the perception of temporal information (Phillips-Silver & Trainor, 2007; Su & Pöppel, 2012), in some cases leading to improvements in timing sensitivity (Iordanescu, Grabowecky, & Suzuki, 2013; Manning & Schutz, 2013). While these auditory-motor connections are not yet fully understood, we can explore these interactions by examining simple movement synchronization with predictable auditory stimuli.

Tapping is frequently used to study simple motor synchronization with an auditory pacing signal (reviewed in Repp, 2005), and typically involves integrating temporal information from a variety of sensory inputs. While audition is generally the most reliable modality for timing (Y. Chen et al., 2002), particularly for movement synchronization (Kolers & Brewster, 1985), the addition of other modalities can improve accuracy (Maduell & Wing, 2007; Stenneken, Prinz, Cole, Paillard, & Aschersleben, 2006; Wing et al., 2010). For example, synchronization with a pacing signal is more precise when both auditory and tactile feedback are presented together, rather than individually (Wing et al., 2010).

Manipulating the temporal relationship between movement and its corresponding sound illustrates the complex cross-talk between the auditory and motor systems (Aschersleben & Prinz, 1995, 1997; Finney & Warren, 2002; Mates & Aschersleben, 2000; Mates et al., 1992; Pollok, Müller, Aschersleben, Schnitzler, & Prinz, 2004). Delaying auditory feedback impairs musical timing (Finney, 1997; Gates et al., 1974), and delaying a single note causes musicians to shorten the subsequent interval to maintain a steady tempo (Furuya & Soechting, 2010b). Additionally there is a systematic relationship between amount of delay and note-to-note variability in performance, where in general a larger delay in feedback leads to more variability (Pfordresher & Palmer, 2002). It is clear that delayed auditory feedback affects the timing of subsequent movements, presumably to compensate for the timing change (Furuya & Soechting, 2010b; Wing, 1977). These studies illustrate how modifying auditory event timing affects concurrent movement. Here we extend this work by demonstrating how movement affects the perception of concurrent auditory events.

Measurements of the asynchrony between an isochronous stimulus and participant taps are useful in indexing tapping ability (smaller asynchronies indicate more accurate synchronization), with typical asynchronies preceding tones by tens of milliseconds (see Aschersleben, 2002). In research that manipulates auditory feedback, tap asynchronies are examined to determine how feedback affects synchronization abilities. Delayed auditory feedback has detrimental effects on tapping, increasing tap asynchrony (Aschersleben & Prinz, 1995, 1997; Mates et al., 1992), while auditory feedback occurring prior to movement has little effect on tapping (Mates & Aschersleben, 2000). The detrimental effects of delaying auditory feedback highlight its importance in movement timing.

While tap asynchronies exist even when auditory feedback is present and unaltered (Fraisse, Oléron, & Paillard, 1958; Franěk, Radil, Indra, & Lánský, 1987; Hary & Moore, 1987; Mates et al., 1992), the absence of auditory feedback further increases tap asynchronies (Aschersleben & Prinz, 1995; Mates et al., 1992; Pollok et al., 2004). Similar findings are present when tactile feedback is disrupted using a local anaesthetic; removing tactile feedback increases tap asynchrony (Aschersleben et al., 2001). When both auditory and tactile cues are available, tap asynchrony is significantly lower than when one or neither timing cue is available, emphasizing the role of multiple sensory inputs in motor timing (Wing et al., 2010).

The present study examines the role of auditory feedback in the integration of auditory and motor information in a timing deviation task. Previously we observed that when participants judged the timing of a probe tone at the end of an isochronous sequence, performance improved when moving (tapping) prior to this judgment compared to when listening alone, specifically when the probe tone occurred later than expected (Manning & Schutz, 2013). Additionally we reported a relationship between tapping quality and timing judgments, where more consistent tapping correlated with better task performance. Here, our primary goal is to identify whether it is the presence of movement or the *auditory consequences* of movement that improve timing perception by comparing performance when the sound of tapping is present vs. masked. If movement improves performance even when tap sounds are masked this would suggest that movement itself is sufficient to elicit the improvement. This would be consistent with previous results showing that movement influences temporal encoding in subjective tasks, even when these movements produce no acoustic consequences (Phillips-Silver & Trainor, 2007; Su & Pöppel, 2012). However, finding that movement no longer improves performance in the absence of auditory feedback would indicate that that previously documented effects of movement in this paradigm might in fact be effects of the auditory consequences of movement. This work will inform research on the integration of auditory feedback and motor timing, as well as ways in which movement and other sensory information affects perceived timing of predictable temporal events.

3.4 Method

Two groups of participants completed this experiment. Both groups judged the timing of a probe tone at the end of an isochronous sequence while either tapping along with the sequence or listening without moving. The paradigm was adapted from Manning and Schutz (2013), using fewer conditions and more trials to allow for more fine-grained comparisons between accuracy scores and tapping data. The availability of auditory feedback differed between participant groups. In the auditory feedback (AF) group, the sound of tapping was available to participants throughout the sequence. In the no auditory feedback

(NAF) group, we removed the availability of auditory feedback by masking the sound produced by tapping (see sections 2.2 and 2.3 for details).

Participants. The AF group consisted of thirty-seven undergraduate students (27 females, 10 males) ranging in age from 18-26 years (*M* = 20.24, *SD* = 2.17). They had between 0 and 12 years (M = 3.35, SD = 3.24) of musical training. The NAF group consisted of thirty-eight different undergraduate participants (30 females, 8 males) ranging in age from 17-24 years (*M* = 19.61, *SD* = 1.71). These participants had between 0 and 16 years (*M* = 5.18, *SD* = 4.34) of musical training. Both groups participated in exchange for course credit and all participants tapped using their dominant hand.

Stimuli and Materials. In each trial, an iMac computer (OSX 10.6.8) presented a sequence of isochronous "woodblock" tones (gmBank = 115) at an inter-onset interval (IOI) of 500ms over Sennheiser HDA200 headphones (81 dB[A]). These tones were grouped together in patterns of four, where the first tone of each pattern was higher in pitch (C5; 523 Hz) than the following three (G4; 392 Hz) implying a 4/4 metric structure (see Figure 3.1). In the fourth repetition of this pattern the lower pitch tones were replaced with silence. Following this silence a probe tone either occurred on time (50% of trials) with the sequence or 15% of the IOI (75ms) late (50% of trials). Trials were presented in blocks, which varied between instructions to listen alone (no-movement condition) or to tap while listening (movement condition) with the entire sequence using a drumstick (IP-1) on an electronic drum pad (Roland PDX-8) connected to an Alesis Trigger i/O Trigger-to-MIDI Interface. White noise (74 dB[A]) masked external sounds, including the sound of the drumstick hitting the drum pad for the NAF group (while the AF group heard their taps).

Procedure. In each trial, participants reported whether the probe tone was consistent with the preceding sequence, receiving feedback on the correctness of their responses. In the movement condition participants tapped along with the sequence (using their dominant hand) through the silence up to and including the probe tone. In the no-movement condition, participants listened to the sequence and remained still. After five warm-up trials, participants completed 12 blocks (eight trials/block) for a total of 96 trials. We randomized the order of movement/no-movement blocks in addition to the order of trials within each block for each participant. In an exit survey all participants in the AF group reported being able to hear tap feedback, and no participants in NAF group reported being able to hear their tapping for the duration of the experiment.

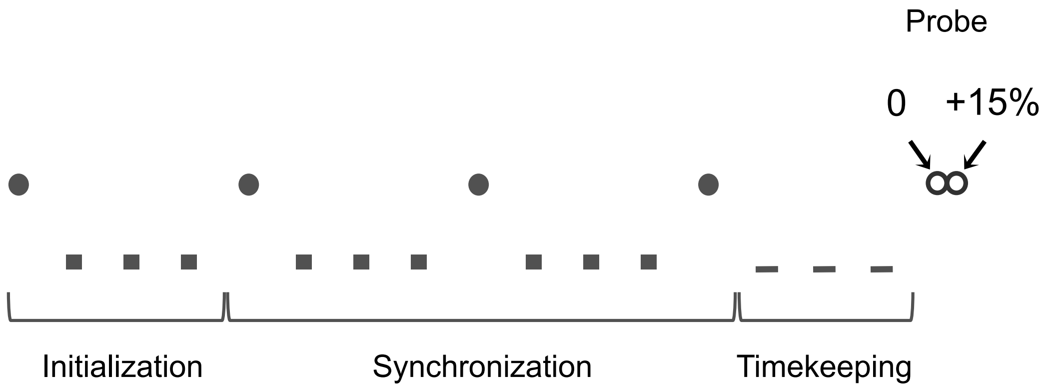

Figure 3.1 Circles represent accented tones while squares represent unaccented tones. The lines represent silent "beats" and the unfilled circles depict possible probe tone positions. Trial segments are labelled.

3.5 Results

3.5.1 Timing judgments

We collected responses (Figure 3.2) and calculated the difference in the "score" (i.e., the percentage of correct responses) in the movement vs. no-movement condition to quantify the "effect of movement" on timing judgments for each participant and probe tone offset, with positive scores indicating better performance when moving (see Figure 3.3). We conducted a 2 × 2 mixed-model ANOVA on the effect of movement using auditory feedback (group) as a between-subjects factor and offset as a within-subjects factor. We found a main effect of auditory feedback ($F(1,73) = 7.26$, $p = .009$), indicating a difference between the AF group and NAF group on task performance. There was no main effect of offset ($F(1,73) = 1.98$, $p = .164$), and no interaction between group (AF/NAF) and offset ($F(1,73) = 0.49$, $p = .487$). Movement affected both the NAF ($t(37) = 4.48$, $p < .0001$) and AF ($t(36) = 6.40$, $p < .0001$) groups, however, movement's effect was lower in the NAF group ($t(73) = 2.27$, $p < .05$). These results demonstrate that while auditory feedback may be used as a cue for timing (Kolers & Brewster, 1985; Maduell & Wing, 2007; Wing et al., 2010), movement alone can significantly improve timing perception. We conducted a correlation between performance in the movement condition and years of musical experience for each group and found a significant relationship in the NAF group ($r(37) = .41$, $p = .011$), but not in the AF group ($r(36) = .24$, $p = .146$). This suggests that participants with more musical experience performed better in the movement condition than do participants with little or no musical experience when auditory feedback is lacking, however explicit examination of this idea is needed for further discussion.

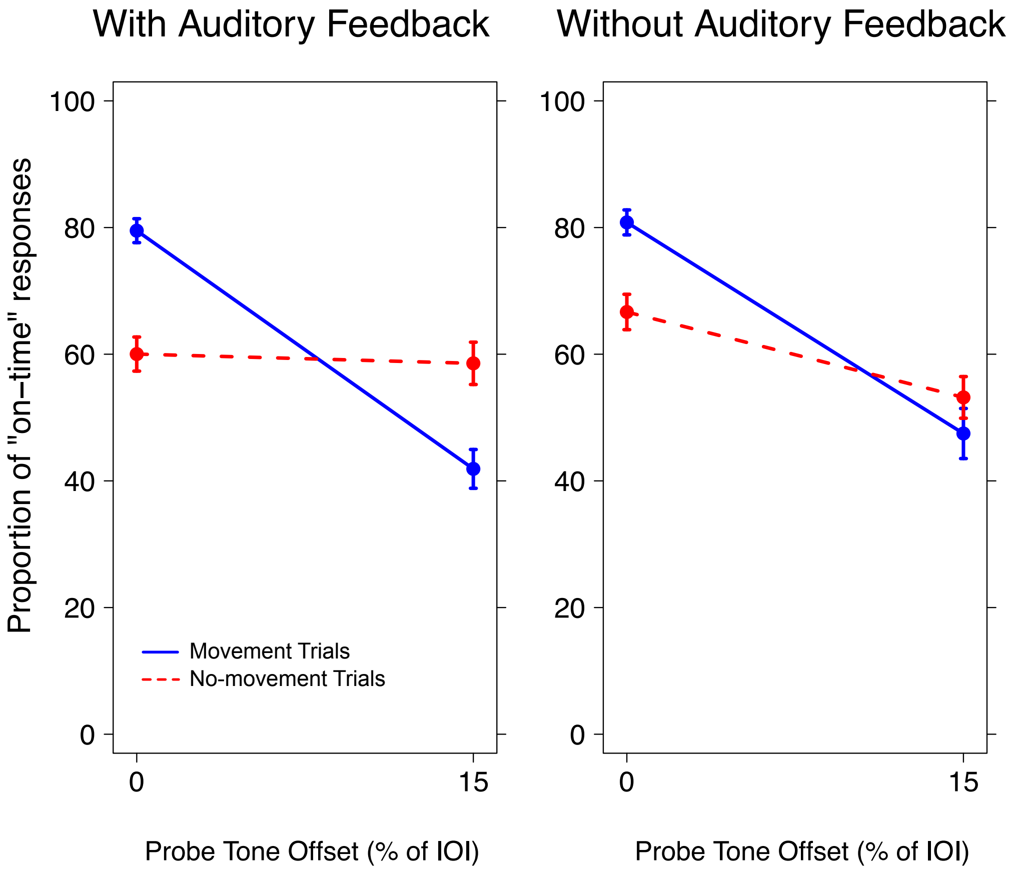

Figure 3.2. Proportion of “on-time” responses for the two offset conditions. Participants perform significantly better on the movement trials both with and without auditory feedback. Error bars represent SEM.

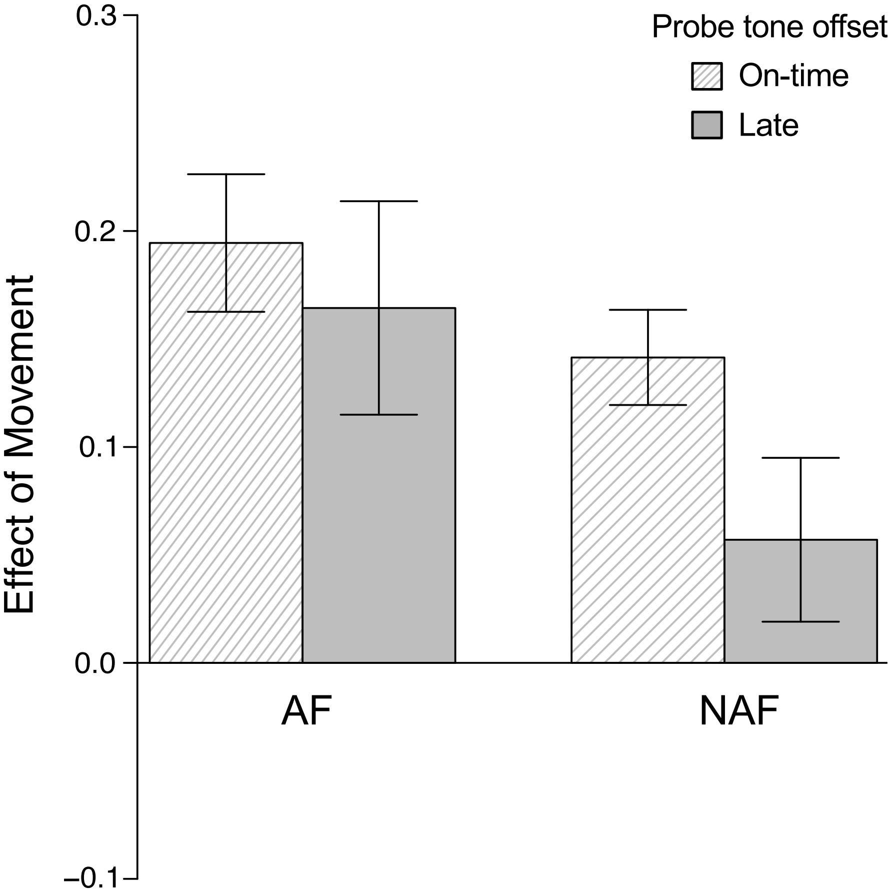

Figure 3.3 The effect of movement (movement – no-movement task score) on probe tone timing judgments for auditory feedback (AF) and no auditory feedback (NAF) groups. Error bars represent the standard error of the mean.

3.5.2 Tapping

The first four taps in each trial were disregarded, allowing participants to stabilize tapping. We computed a coefficient of variation (standard deviation of IOI/mean IOI) as a measure of variability for taps in the synchronization segment.

We also calculated the signed asynchrony between the onset of each tone and each remaining tap[2] in the synchronization and probe tone segments of the trials (Figure 3.1). The coefficient of variation was no different between groups (*t*(73) = 0.21, *p* = .833), indicating auditory feedback did not affect tapping consistency (Figure 3.4a). However, the presence of auditory feedback lowered measures of synchronization variability, where the SD of tap asynchronies in the synchronization segment were lower in the AF group compared to the NAF group (*t*(73) = 3.20, *p* = .002), a trend that approached significance for the SD of tap asynchronies at the expected probe tone (*t*(73) = 1.89, *p* = .063). The presence of auditory feedback lowered mean asynchronies (Figure 3.4b) both for taps in the synchronization segment (*t*(73) = 3.22, *p* < .005) and those concurrent with the expected probe tone (*t*(73) = 3.07, *p* < .005). We found a significant correlation between probe tone tap asynchrony and movement condition score for the AF group (*r*(35) = -.32, *p* = .050), and a trend that did not reach significance for the NAF group (*r*(36) = -.27, *p* = .099), suggesting participants with smaller probe tone tap asynchronies performed better on the timing detection task. This illustrates an interaction between tapping accuracy and timing judgments. Additional correlations between task performance and other measures of tapping are presented in Table 3.1.

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[2] Reported measures of tapping are corrected for a constant latency in the experimental setup.

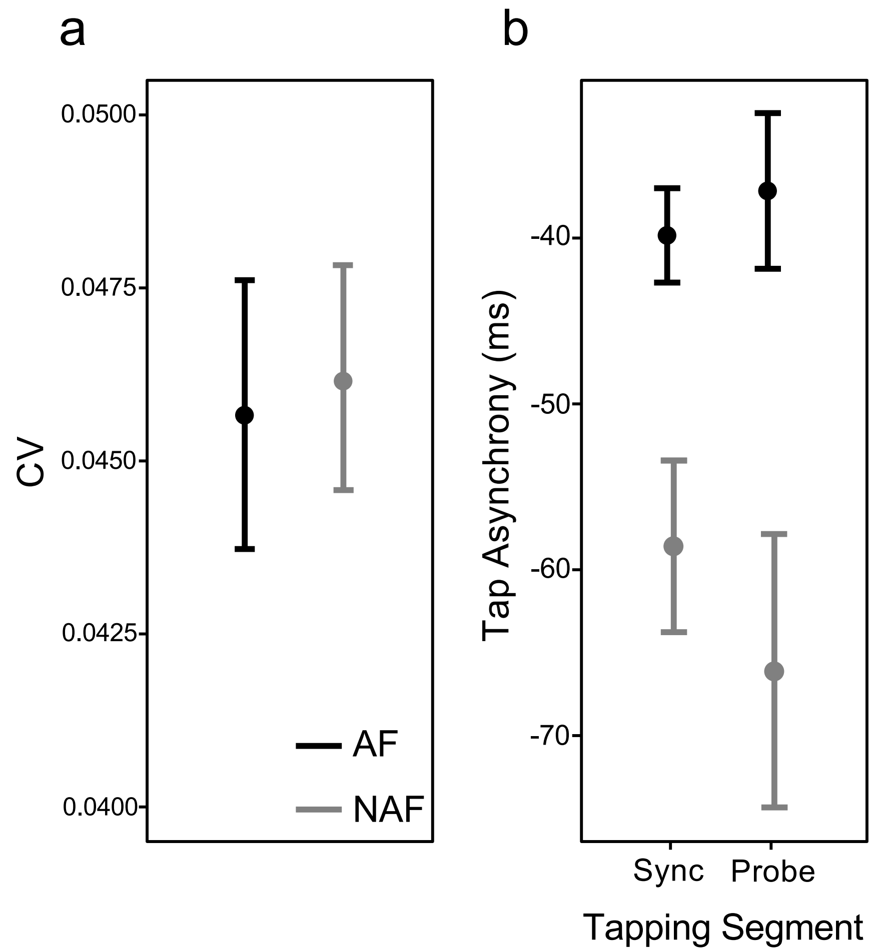

Figure 3.4. The coefficient of variation (a) and tap asynchronies (b) plotted for AF and NAF groups. Error bars represent the standard error of the mean.

	Auditory Feedback (AF) Group	No Auditory Feedback (NAF) Group
Measures of tap asynchrony		
Signed tap asynchrony		
(A) Synchronization segment	*r* = .169	*r* = .067
(B) At estimated probe tone position	*r* = -.324	*r* = -.271
Absolute tap asynchrony		
(A) Synchronization segment	*r* = -.201	*r* = -.082
(B) At estimated probe tone position	*r* = .082	*r* = .163
Measures of tap variability		
CV of synchronization segment	*r* = -.175	*r* = -.380*
SD of signed tap asynchrony		
(A) Synchronization segment	*r* = -.483**	*r* = -.252
(B) At estimated probe tone position	*r* = -.534***	*r* = -.478**
SD of absolute tap asynchrony		
(A) Synchronization segment	*r* = -.452**	*r* = -.215
(B) At estimated probe tone position	*r* = -.273	*r* = -.271
$*p < .05$ $**p < .01$ $***p < .001$		

Table 3.1. Pearson's correlations between score in movement conditions and measures of interest for the AF and NAF groups.

3.6 Discussion

This experiment investigated how auditory feedback as a consequence of movement influences the perceived timing of an external stimulus. We found that movement improved timing perception, even in the absence of auditory feedback from those movements. This extends our previous findings (Manning & Schutz, 2013) by showing that *movement itself* (independent of movement's acoustic consequences) is capable of improving timing perception. Moreover, the fact that auditory feedback further enhances movement's effect on perception complements previous research demonstrating that inputs from multiple sensory modalities enhance timing perception (Maduell & Wing, 2007; Stenneken et al., 2006; Wing et al., 2010).

The tap asynchrony data in this study illustrate that tapping is more accurate with auditory feedback, consistent with previous findings examining motor timing with and without sensory feedback (Aschersleben et al., 2001; Aschersleben & Prinz, 1995; Mates et al., 1992). In contrast, the absence of auditory feedback does not adversely affect tapping variability (see Figure 3.4a). This suggests auditory feedback may not help with the mere production of periodic movement, but is important for aligning that movement with an external stimulus. These data complement previous findings showing that temporally congruent auditory feedback leads to more accurate movement timing (Keller, Dalla Bella, & Koch, 2010) and can affect motor planning (Hatfield, Wyatt, & Shea, 2010). This may be particularly true in the timekeeping segment of trials in the present study, where movement planning is especially critical as the pacing signal is absent.

The correlation between the tap asynchrony (at the probe tone) and judgment correctness further reflects auditory-motor coupling. Since tapping occurs prior to the timing judgment, it is possible that participants are relying to some extent on the timing of their final movement to make a judgment about the timing of the probe tone. For example, smaller tap asynchronies lead to better performance on timing judgment task. Less accurate movement (denoted by a larger tap asynchrony), negatively impacts timing judgments, suggesting that any feedback from movement (either auditory or tactile) may improve perceived timing.

Taken together, these results show that despite the auditory system's capacity for precise temporal processing, movement can further improve judgments about auditory event timing. While auditory feedback from tapping provides a helpful cue, these data suggest it is not essential for improving timing perception. In showing that movement shapes timing perception and now further demonstrating how the auditory information from that movement improves movement quality, we emphasize the bidirectional interactions between auditory and motor systems. Overall the current study sheds light on the interplay between perceived and produced timing, and complements the literature on links between perception and action (Hommel et al., 2001; Prinz, 1997). This study emphasizes the role of movement and specifically motor timing in perception and clearly demonstrates that while auditory feedback may be a useful cue for timing, movement alone can improve timing perception.

3.7 Acknowledgements

We wish to thank Jennifer Harris and Amy Wang for assistance with data collection as well as Simeon Fitch and Ben Guseman of Elder Research for their software development efforts. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC RGPIN/386603-2010), Ontario Early Researcher Award (ER10-07-195), and Canadian Foundation for Innovation (CFI-LOF 30101) to Michael Schutz, PI.

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Chapter 4: Trained to keep a beat: Movement-related enhancements to timing perception in percussionists and non-percussionists.

Manning, F. C., & Schutz, M. (2016). Trained to keep a beat: Movement-related enhancements to timing perception in percussionists and non-percussionists. *Psychological Research*, *80*, 532-542. doi: 10.1007/s00426-015-0678-5.

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4.1 Preface

Musicians exhibit more sophisticated timing abilities compared to nonmusicians. Temporal discrimination abilities are more refined in musicians compared to nonmusicians (Drake & Botte, 1993; Jones & Yee, 1997; Madison & Merker, 2002; Matthews, Thibodeau, Gunther, & Penhune, 2016; Yee, Holleran, & Jones, 1994). Tapping abilities are more both most accurate and consistent in musicians, where musicians show lower tap asynchronies (Aschersleben, 2002; Repp & Doggett, 2007; Repp, London, & Keller, 2013; Repp, 1999a, 2010) and less variable tapping (Keele, Pokorny, Corcos, & Ivry, 1985; Krause et al., 2010; Matthews et al., 2016) compared to nonmusicians. There are even differences in tapping abilities after short-term training (Madison et al., 2013). Furthermore, musicians are most consistent with movements that are most similar to those used when playing their primary instrument of training (Stoklasa et al., 2012). Percussionists in particular exhibit more accurate timing abilities and synchronization abilities than other musicians, when producing tapping-like movements (Cameron & Grahn, 2014; Ehrlé & Samson, 2005; Krause, Pollok, & Schnitzler, 2010).

The studies overviewed in Chapters 2 and 3 demonstrated enhancements to predictive timing abilities following synchronized movement. These experiments included participants that had varying levels of musical training, suggesting that this improvement exists in both musicians and nonmusicians. However, this calls to question whether musical ability may impact sensorimotor interactions in this task. We explicitly examined this question in the next study by comparing percussionists (musicians with extensive experience practicing tapping movements and maintaining a beat) to non-percussionists.

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4.2 Abstract

Many studies demonstrate that musicians exhibit superior timing abilities compared to nonmusicians. Here we investigated how specific musical expertise can mediate the relationship between movement and timing perception. In the present study, a group of highly trained percussionists (n=33) and a group of non-percussionists (n=33) were tested on their ability to detect temporal deviations of a tone presented after an isochronous sequence. Participants either tapped along with the sequence using a drumstick (movement condition) or listened without tapping (no-movement condition). Although both groups performed significantly better when moving than when listening alone, percussionists gained a greater benefit from tapping when detecting the smallest probe tone delays compared to non-percussionists. This complements both the musical expertise and timing perception literatures by demonstrating that percussionists with high levels of training may further capitalize on the benefits of sensorimotor interactions. Surprisingly, percussionists and non-percussionists performed no differently when listening alone, in contrast to other studies examining the role of training in timing abilities. This raises interesting questions about the degree to which percussionists' known expertise in timing may interact with their use of motion when judging rhythmic precision.

4.3 Introduction

Sensorimotor integration constitutes an intricate series of processes involving a combination of perception and action. These processes are crucial for achieving specific goals and making predictions about upcoming events, such as hitting a ball with a racket or stepping off a street curb. For complex activities such as playing a musical instrument or dancing, auditory-motor interactions rely on precise timing mechanisms to effectively integrate large quantities of information (Zatorre et al., 2007). Such musical activities require listeners to predict the timing of upcoming auditory events based on previous information and to subsequently execute movements at a particular time for movement to be synchronized with an upcoming temporal event and/or the movements of another individual. The bidirectional interplay between auditory and movement information is evident in simple tapping studies where auditory information encourages and guides motor timing (Aschersleben & Prinz, 1995, 1997; Mates et al., 1992). Similarly, recent studies show that movement can influence subjective percepts of temporal information (Phillips-Silver & Trainor, 2007; Su & Pöppel, 2012) and even improve timing judgments (Iordanescu et al., 2013; Manning & Schutz, 2013). Typically studies investigating sensorimotor integration implement tasks that measure timing change detection and/or simple movement synchronization (frequently finger tapping) with an external stimulus (reviewed in Repp, 2005). Studies that implement simple tapping paradigms offer a useful way to examine how movements are synchronized with a predictable auditory stimulus and can help expand our understanding of complex synchronized movements.

Although both musicians and nonmusicians can readily synchronize movements to sequences containing regularly spaced auditory events, musicians are particularly adept at timing movements with these external stimuli (J. L. Chen, Penhune, & Zatorre, 2008b; Repp, 1999a). As such, musicians provide a useful view into expert temporal processing and motor timing, as well as their integration. By exploring musical training's impact on these tasks, we can gain insight into the degree that specialized training affects crosstalk between movement and timing perception. Therefore, in the present study we investigate how musical expertise modulates the integration of timing information from multiple modalities.

4.3.1 Musical experience and timing abilities

Musicians generally show superior timing detection abilities across a broad range of tasks. For example, in duration-based timing tasks where participants compare the duration of two subsequent intervals, musicians outperform nonmusicians (Rammsayer & Altenmüller, 2006). Musicians also show lower detection thresholds (higher sensitivity) than nonmusicians for timing changes at the end of as well as within isochronous sequences (Jones, Jagacinski, Yee, Floyd, & Klapp, 1995; Jones & Yee, 1997; Lim, Bradshaw, Nicholls, & Altenmüller, 2003; Rammsayer & Altenmüller, 2006; Yee, Holleran, & Jones, 1994). This is particularly true in percussionists, who exhibit the lowest detection thresholds of all musician groups (Ehrlé & Samson, 2005). Musicians also show a greater sensitivity to structural components of a temporal stimulus, including the degree of sequence isochrony (Mari Riess Jones & Yee, 1997; Madison & Merker, 2002; Yee et al., 1994) and changes in tempo (Drake & Botte, 1993). Musicians' enhanced sensitivity to timing may reflect their extensive experience attending to music's temporal structure. Alternatively, this may reflect a tendency for those who are adept at timing tasks to study music more extensively or successfully. Regardless, finely tuned timing abilities are crucial in coordinating movements with other musicians. However, little research on temporal discrimination in musicians explicitly explores how musicians' body movements, an integral component of musical timing, might influence their temporal discrimination abilities.

Musicians also exhibit superior motor timing abilities compared to nonmusicians. The negative mean asynchrony (NMA) prominently observed when tapping with an isochronous sequence (Aschersleben & Prinz, 1995; Aschersleben, 2002; Repp, 2000) is markedly smaller in amateur musicians compared to nonmusicians (often 10-30 ms vs. 20-80 ms, respectively; Aschersleben, 2002; Repp & Doggett, 2007), suggesting an expertise-driven improvement in perceived tap-tone synchrony. In professional musicians, the NMA is even smaller (sometimes approaching exact synchrony), even in sequences containing subthreshold deviations that resemble expressive timing in music (Repp, 1999a). This may suggest graded improvements in synchronization abilities that arise with musical experience.

In addition to a lower reported NMA, musicians exhibit lower variability in tapping tasks than do nonmusicians (Krause et al., 2010; Repp & Doggett, 2007; Repp et al., 2013; Repp, 2010). Since variability in movement timing is thought to reflect inaccuracies in the central timekeeper (Vorberg & Wing, 1996), this contrast in synchronization ability may represent perceptual as well as motor differences. Although it is difficult to identify whether these differences arise due to training or from selection effects, literature that examines musicians with varying types of training is consistent with the idea that musical experience does in fact drive these improvements. Movement synchronization in musicians appears to yield particularly low variability when musicians perform timing tasks using movements similar to those necessary to produce sound on their primary instrument (Keele, Pokorny, Corcos, & Ivry, 1985; Krause et al., 2010; Stoklasa, Liebermann, & Fischinger, 2012). For example, when string or wind players synchronize with a metronome they are more accurate when using their instrument of training compared to when synchronizing through finger tapping (Stoklasa, Liebermann, & Fischinger, 2012). Therefore, synchronization involving the movement effectors used on one’s primary instrument of training may rely on complex, experience-driven sensorimotor representations (Krause et al., 2010).

Although a subset of research has focused on the relationship between enhanced movement timing and temporal processing in musically trained groups, the ways in which movement directly impacts perceived timing remain unclear.

Participants (typically musicians) demonstrating low variability in motor timing generally exhibit high sensitivity in timing discrimination tasks (Keele et al., 1985). Additionally, participants with high levels of rhythm-based musical expertise (in particular, percussionists) demonstrate superior synchronization abilities (small NMAs and low variability in tapping tasks) as well as finer temporal acuity compared to other musicians and nonmusicians (Cameron & Grahn, 2014; Krause et al., 2010). These comparisons between groups with varying levels of musical expertise indicate a relationship between perceptual and motor timing abilities, where musical expertise may act as a covariate. These behavioral studies, in additional to many neuroimaging studies (Bengtsson et al., 2009; J. L. Chen et al., 2008a; Grahn & Brett, 2007; Grahn & Rowe, 2009), offer evidence for a common timing mechanism that might exist for separately measured perception and movement abilities. However further examinations of auditory-motor interactions in the same task by demonstrating the ways in which movement can modify auditory perception provide compelling support for a common source for timing abilities.

4.3.2 Assessing the effects of training on sensorimotor interactions

Exploring the relationship between musical expertise and timing abilities (both perceptual and motor) sheds light on broader links between perception and action. For example, if musical expertise in a specific domain (i.e., percussion) leads to improvements in associated motor abilities (i.e., tapping) and perceptual abilities (i.e., detecting the timing of rhythmic stimuli), this suggests that improvements may be specific to the focus of the musical training. Therefore, the ideal way to pursue this movement-timing relationship in a musical population is by studying participants who are not only musically trained, but trained to implement specific types of movements for synchronizing. Given previous research demonstrating short-term improvements in motor timing specific to the particular movement effector (i.e., finger, drumstick, etc.) used throughout training (Madison et al., 2013), this is also an important issue for motor learning more generally.

In order to explore the role of musical expertise and associated trained movement, here we explicitly investigate how movement impacts timing perception in percussionists, a subset of musicians specializing in the use of tapping-like movements. Percussionists are ideal for this type of exploration as they exhibit the greatest timing acuity (Ehrlé & Samson, 2005), as well as the most consistent movement synchronization (Cameron & Grahn, 2014; Krause et al., 2010) of all musicians. In the present study, a group of trained percussionists and a group of non-percussionists (with varying levels of musical experience) listened to an isochronous sequence while either tapping along with a drumstick or listening without movement, and identified temporal deviations at the end of this sequence in a two-alternative forced choice (2AFC) task. Similar studies that examine the relationship between perceived timing and movement typically use subjective tasks that report movement-related changes in pulse extraction (Su & Pöppel, 2012) and beat grouping (Phillips-Silver & Trainor, 2007). This study uses an objective measure to explore not just *changes* but movement-related *improvements* to timing abilities.

Here we assessed the effect of musical expertise on sensorimotor integration by asking participants to make judgments about a rhythmic sequence while either tapping along or listening without moving. We found previously that participants (with or without musical training) were better able to detect timing changes at the end of a sequence when tapping with the sequence, particularly when the probe tone occurred later than expected (Manning & Schutz, 2013). Additionally, in a follow-up study where we masked the sound of taps using white noise, we found that this improvement in perceived timing was not due to auditory feedback from the synchronized movement, but instead due to the movement itself (Manning & Schutz, 2015). Due to musicians' superior sensitivity in timing perception tasks (Madison & Merker, 2002; Rammsayer & Altenmüller, 2006), in particular percussionists (Ehrlé & Samson, 2005), here we expected percussionists to perform better than non-percussionists. Because musicians tend to exhibit more accurate motor timing (Krause et al., 2010; Repp et al., 2013; Repp, 2010) particularly when implementing movements pertaining to their instrument of training (Keele, et al., 1985; Stoklasa et al., 2012), we predicted that percussionists would also exhibit lower tapping variability and smaller NMAs than nonpercussionists. Due to the amount of movement inherently required for playing percussion instruments (i.e., striking a drum) we expected that percussionists would more accurately detect temporal deviations than non-percussionists when tapping along with the sequence. If more accurate movement timing in musicians leads to more accurate timing discrimination in this task due to a common timing mechanism for movement and perception (as proposed in correlational studies by Keele et al., 1985 and Krause, et al., 2010), we expected that percussionists would benefit more from movement than non-percussionists (i.e., observe a greater perceptual timing advantage). By directly comparing performance in a timing detection task that involves either moving along or listening without movement, these findings contribute to our understanding of the overlap in perceptual timing enhancements and accuracy of motor timing reported in musicians, specifically in percussionists. These findings will also shed light on the degree to which percussionists rely on movement as a cue for timing in musical performance.

4.4 Method

Participants. Two groups of participants completed this experiment. The first group (hereafter "percussionists") consisted of 33 (24 male, 9 female) participants, ranging in age from 17-42 years (M = 24.33, SD = 7.19). All members of this group currently played in a percussion ensemble, had between 1 and 24 years of formal percussion training (M = 9.18, SD = 5.62), and had been playing percussion instruments for 5-33 years (M = 13.36, SD = 8.07). These participants either played in percussion ensembles at McMaster University, University of Toronto, or Western University, were members of a professional percussion quartet or were percussionists attending the Percussive Arts Society

International Convention (PASIC) in November 2013 and volunteered to participate. All but two percussionists had some musical training in other instruments (0-18 years; *M* = 6.48, *SD* = 4.66).

The second group consisted of 33 participants (18 female, 15 male) ranging in age from 17-25 years (*M* = 18.73, *SD* = 1.51) who were recruited from the McMaster University psychology participant pool in exchange for course credit. These participants (hereafter "non-percussionists") had varying degrees of musical training (0-15 years; *M* = 6.79, *SD* = 4.39); all but four non-percussionists had some musical training and none had percussion training. Percussionist and non-percussionist groups did not differ in years of training on instruments other than percussion (*t*(64) = 0.27, *p* = .788), however the percussionist group included more males than in the non-percussionist group, due to a gender imbalance in instrument choice in the population. Both groups reported normal hearing and normal or corrected-to-normal vision and tapped with their dominant hand. We excluded four of the original 37 participants from the percussionist group and three of the original 36 participants from the non-percussionist group based on our exclusion criteria described below in the Design and Procedure section. This experiment met ethics standards according to the McMaster University Research Ethics Board.

Stimuli and Apparatus. We conducted the experiment using a software package developed specifically for this paradigm (Manning & Schutz, 2013).

Each trial began with a MIDI sequence consisting of 13 woodblock sounds (gmBank = 115) presented at an inter-onset interval (IOI) of 500ms (120 beats-per-minute). Since imposing meter on a sequence of beats affords enhancements in temporal encoding and attention (Essens & Povel, 1985; Grube & Griffiths, 2009; Mari Riess Jones et al., 1995), we divided the tones into four groups (see Figure 4.1), with the first tone of each group higher in pitch (C5; 523-Hz) than the remaining three (G4; 392-Hz) to evoke a 4/4 meter. In the last group of tones (the "timekeeping" segment), the second, third and fourth "beats" were silent. A single additional woodblock sound (hereafter, "probe tone") followed this timekeeping segment; on half of the trials the probe tone followed consistent timing with the sequence, and in the other half of the trials the probe tone occurred slightly late. Participants listened to the sequences through Sennheiser HDA200 headphones. An Alesis Trigger i/O Trigger-to-MIDI USB Interface converted signals from an electronic drum pad (Roland PDX-85 or PDX-100) into MIDI messages sent to an iMac computer[3].

Design and Procedure. Participants completed 64 trials grouped into eight blocks. Participants tapped along with the sequence on half of the blocks (*movement condition*) and listened without moving during the other blocks (*no-movement condition*). For half of the trials in each block, the probe tone occurred "on-time" (i.e., at an offset of 0 ms), while for the other half of the trials the probe

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[3] Accuracy of tap recording was verified in the experimental setup and tapping measurements were corrected for a constant latency in recording.

tone occurred late at an offset of 15% (75 ms) or 30% (150 ms) of the IOI and participants were aware of these potential probe tone alternatives. In a previous series of experiments we used a similar paradigm, where the probe tone fell on-time, early (15% and 30% of the IOI) or late (15% and 30% of the IOI) in movement and no-movement conditions (Manning & Schutz, 2013). These participants more accurately detected probe tone changes in the movement (relative to no-movement) condition only when the probe tone occurred *late*. Here we include only on-time and late offsets in each movement condition as we did in a follow-up study (Manning & Schutz, 2015) to examine these differences with more granularity. Participants performed five warm-up trials and then completed the full experiment (four blocks of the movement condition and four blocks of the no-movement condition). We randomized the order of the experimental blocks and the order of the trials within each block for each participant.

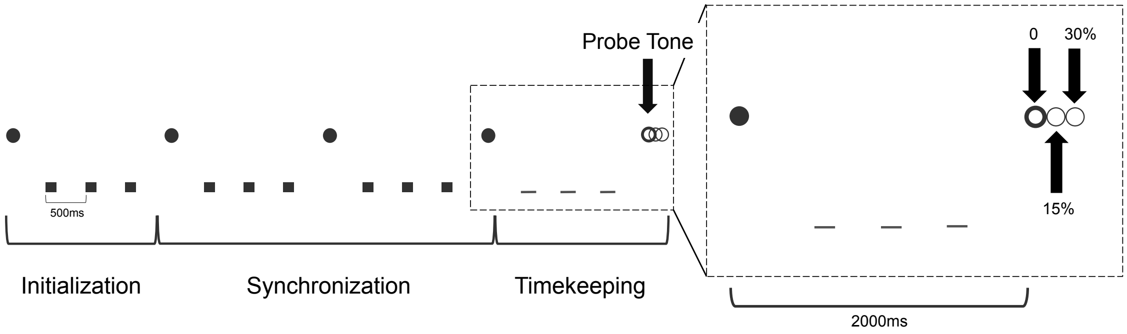

Figure 4.1. Trial structure depicting the number of stimuli with initialization, synchronization and timekeeping segments labeled. Filled circles represent the accented tones and squares represent unaccented tones in the initialization and synchronization segments. Lines indicate silent "beats" and empty circles are possible probe tone positions. The timekeeping segment is enlarged on the right to highlight probe tone offsets, and beats are spaced in 500 ms inter-onset intervals (IOIs).

Throughout the movement blocks participants tapped on each beat of the stimulus in all three segments (through the silence and including the probe tone; see Figure 4.1) using an Innovative Percussion (IP-1) drumstick or equivalent on the electronic drum pad that recorded the timing of each tap. Throughout the no-movement blocks we asked participants to remain as still as possible (i.e., refrain from foot-tapping, head-bobbing, etc.). In a 2AFC task, participants identified whether the probe tone in each trial was "on-time" (consistent with the repeated sequence of beats) or not, and indicated their confidence on a scale from 1 (not at all confident) through 5 (very confident). Participants were aware that the probe tone would occur either on-time or late (but never early). To help retain attention, participants received feedback on the correctness of these judgments.

Some participants were excluded from the original sample based on criteria set prior to the experiment. Consistent our previous criteria (Manning & Schutz, 2013), we excluded participants for tapping in more than 25% of no-movement trials, failing to tap as instructed in more than 25% of movement trials, or failing to tap on the probe tone for more than 25% of trials. This led us to exclude four percussionists; one moved excessively during the no-movement condition (finger tapped on their leg), two tapped not only on each beat, but also between these beats (i.e., every 250ms) in the movement condition, and one failed to tap in more than 25% of beats in the movement trials. In the non-percussionist group we excluded three participants; two for tapping throughout the no-movement condition on more than 25% of trials and one for failing to tap on the probe tone for more than 25% of trials.

4.5 Results

4.5.1 Perception

We examined the percentage of "on-time" responses for each movement condition and probe tone offset in both participant groups (see Figure 2b) to visualize responses. Next, we computed a score (% of correct responses) in each of the movement (movement/no-movement) and offset (on-time, 15% late, 30% late) conditions for each participant. Group performance (task score) differed in the movement trials ($t(64) = 4.06, p < .001$; two-tailed, independent samples t-test; d = 1.00), however there was no difference between group performance in the no-movement trials ($t(64) = 0.95, p = .344$). Pairwise comparisons with Bonferroni correction showed no difference in performance between groups in the different offsets of no-movement condition ($\alpha = .0167$), however the difference between groups in the 30% late probe tone offset condition approached significance ($t(64) = 2.11, p = .039$). We calculated the difference score (movement – no-movement score) to obtain a measure of the effect of movement on task performance (see Figure 4.2a). Higher values for the effect of movement indicate a greater benefit for the movement condition than for the no-movement condition. We assessed the effect of movement using a mixed-model ANOVA with "group" as a between-subjects factor (2 levels: percussionist, non-percussionist) and "offset" as a within-subjects factor (3 levels: 0%, 15% late, 30% late). We found a significant interaction between group and offset (*F*(2,128) = 17.87, $p < .001$, $\eta^2 = 0.13$), indicating that the effect of movement for each group differed at one or more levels of the offset (see Figure 4.2a). There was also a main effect of offset (*F*(2,128) = 32.79, $p < .001$, $\eta^2 = 0.21$), but the main effect of group did not reach significance (*F*(1,64) = 3.05, $p = .086$, $\eta^2 = 0.02$). Post-hoc comparisons (Tukey HSD, $\alpha = .05$) showed significant differences between percussionists and non-percussionists in the effect of movement at the 15% probe tone offset ($p < .001$; see Figure 2b), where the timing judgment task was more difficult. Group differences between the effect of movement at the 30% probe tone offset may be obscured due to a ceiling effect for the movement trials (see Figure 4.2b), since accuracy is above 90% for both groups in the movement trials only. Additionally, heteroscedasticity is violated for both percussionists (Levene's test; *F*(1,64) = 52.34, $p < .001$) and non-percussionists (*F*(1,64) = 14.55, $p < .001$) in these movement trials compared to the no-movement trials when the probe tone is 30% late, further suggesting a ceiling effect for both groups for these conditions.

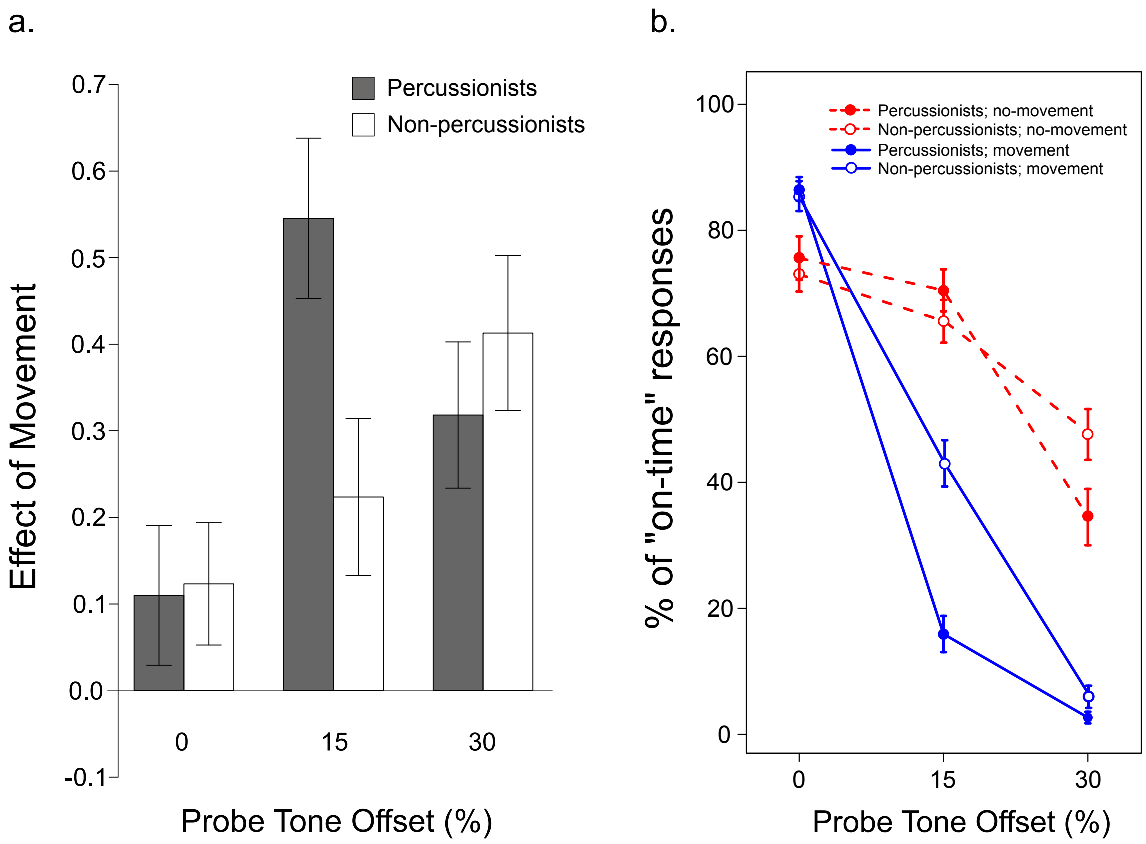

Figure 4.2. Timing detection performance for percussionists and non-percussionists. Panel a shows the effect of movement (movement score – no-movement task score) on timing judgments at each probe tone offset. Panel b displays the proportion of "on-time" responses at each offset for each movement condition and group. Error bars indicate the standard error of the mean.

4.5.2 Production

To quantify motor synchronization ability we measured the signed tap asynchrony and the coefficient of variation (CV) of tapping for the synchronization segment of each movement trial (see Figure 4.1). We also measured the signed tap asynchrony at the probe tone. Tap asynchronies for the synchronization segment were calculated by subtracting the tone onset time from the tap recorded by the electronic drum pad. The tap asynchrony for the probe tone was calculated by subtracting the *expected* probe tone onset from the recorded tap. Positive asynchronies indicate that taps fall after the sounded or expected tone, whereas negative asynchronies indicate that taps precede the tone. Asynchronies differed between percussionists and non-percussionists in both the synchronization ($t(64) = 6.03$, $p < .001$; two-tailed independent samples t-test) and at the probe tone segments ($t(64) = 4.43$, $p < .001$) where percussionists showed smaller mean tap asynchronies compared to non-percussionists (see Figure 4.3). We calculated the CV as a measure of tap variability by dividing the standard deviation of the inter-tap interval (ITI) by the mean ITI in each movement trial throughout the synchronization segment (see Figure 4.4). Percussionists tapped significantly less variably than did non-percussionists in the synchronization segment ($t(64) = 8.16$, $p < .001$).

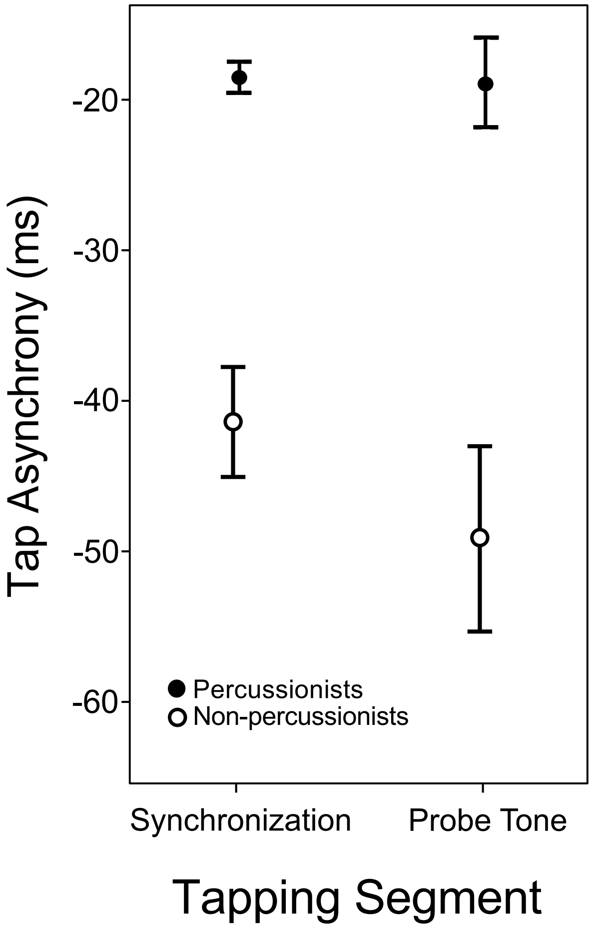

Figure 4.3. The mean signed tap asynchrony in the synchronization and probe tone segments of trials plotted for percussionists and non-percussionists. Error bars represent the standard error of the mean.

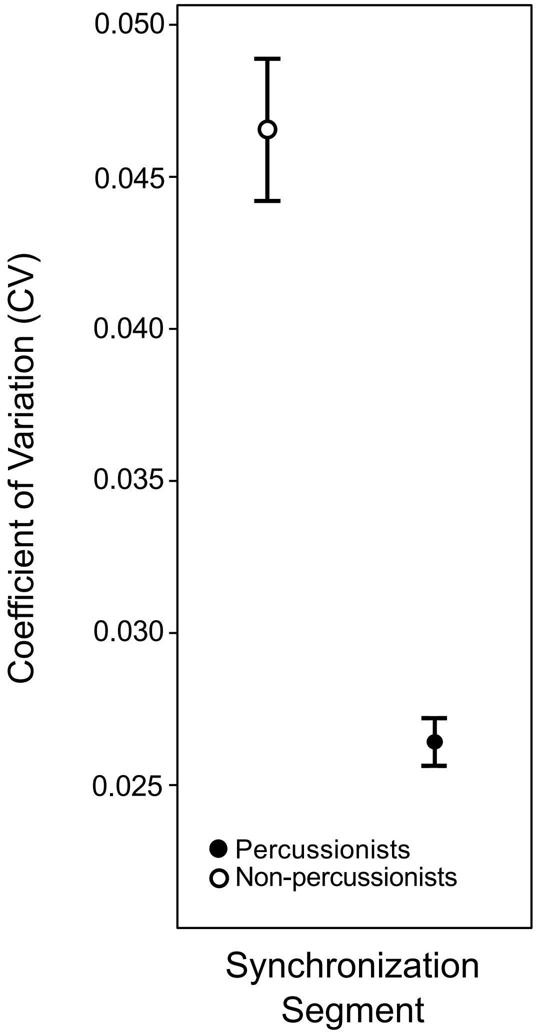

Figure 4.4. The coefficient of variation (CV) during the synchronization segment of the trials for percussionists and non-percussionists. Error bars represent the standard error of the mean.

4.5.3 Perception and production interactions

Since we observed more accurate and consistent tapping and a greater effect of movement for percussionists compared to non-percussionists when the probe tone occurs slightly (15%) late, we examined whether the differences varied systematically using Pearson's correlations between task performance and measures of tapping ability. Percussionists exhibited a significant correlation between task performance in the movement condition and mean tap asynchrony at the probe tone ($r(31) = -.40$, $p = .020$), indicating percussionists with lower tap asynchronies at the probe tone performed better on the movement trials. However non-percussionists did not show this pattern ($r(31) = .01$, $p = .958$). We also examined the relationship between the CV of tapping through the synchronization segment and performance in the movement trials and found a significant negative correlation for non-percussionists ($r(31) = -.36$, $p = .038$), but no correlation for percussionists ($r(31) = -.25$, $p = .162$). This indicates that non-percussionists who showed lower tapping variability (i.e., tapped more consistently) throughout the movement trials performed better on the probe tone discrimination task. Additional correlations are displayed in Table 4.1.

	Percussionists	Non-percussionists
Measures of tap asynchrony		
Signed tap asynchrony		
(A) Synchronization segment	r = -.044, p = .810	r = .022, p = .905
(B) At estimated probe tone position	**r = -.402, p =.020**	r = .010, p = .958
Measures of tap variability		
CV of synchronization segment	r = -.249, p = .162	**r = -.363, p = .038**
Musical Experience		
(A) Years of musical training (other than percussion)	r = .201, p = .261	r = -.092, p = .612
(B) Years of percussion training	r = 210, p = 241	
(C) Years of percussion playing	**r = .356, p = .042**	

Table 4.1. Pearson's correlations between score in movement condition and measures of interest for the percussionist and non-percussionist groups. Significant correlations (*p* < .05) are bolded.

We also conducted a binary logistic regression analysis to determine whether timing of the final tap (adjacent to the probe tone) predicts the response outcome for each trial (either correct or incorrect). In the percussionist group, as tap asynchrony increased by 1 ms, the odds of correctly identifying the timing of the probe tone decreased by 1.64% ($\chi^2 = 28.54$, $p < .001$; odds ratio (OR) = 0.984). A similar pattern emerged for non-percussionists, where the odds of correctly identifying the timing of the probe tone decreased by 0.62% ($\chi^2 = 42.60$, $p < .001$; odds ratio (OR) = 0.994) for every 1 ms increase of the tap asynchrony at the probe tone. This relationship suggests that the timing of the tap at the probe tone might be used to predict the response outcome of the trial, where more accurate tapping increases the probability of a correct timing judgment, particularly for percussionists.

4.5.4 Musical experience and task performance

We were also interested in exploring the relationship between task performance and measures of musical experience. Percussionists exhibited a significant correlation between years of experience playing percussion instruments and performance in the movement condition ($r(31) = .36$, $p = .042$). This relationship may indicate that those who are more experienced in playing percussion instruments perform better than those with less playing experience when tapping with the sequence, possibly due to experience synchronizing this type of movement with an external stimulus. However, there was no significant correlation between performance in the *no-movement* condition and years of formal percussion training (*r*(31) = .01, *p* = .950). In the non-percussionist group, we did not find a correlation between years of formal musical training and performance in the movement trials (*r*(31) = -.09, *p* = .610) and the correlation between years of formal musical training and performance in the no-movement trials approached but did not reach significance (*r*(31) = .32, *p* = .071), showing little relationship between musical experience and task performance, perhaps due to a significant proportion of these non-percussionists having little or no formal musical training.

4.6 Discussion

In this study we examined how movement facilitates timing perception in percussionists and non-percussionists. Both groups listened to a sequence of beats and identified the timing of an additional beat after a short period of silence having either tapped along using a drumstick or listened without moving. Consistent with our previous findings (Manning & Schutz, 2013, 2015) both groups performed better when tapping with the sequence compared to listening alone. However, here we extend our previous work in two important ways. First, our data demonstrate that percussionists benefit more from tapping than do non-percussionists, particularly when the task is more difficult (i.e., the 15% offset condition, see Figure 4.2). We suspect they would also have benefited more at the 30% offset condition were it not for the ceiling effect (however to preserve consistency with previous work we retained the same offset values). Future testing of intermediate offsets would help clarify the temporal window within which movement-related perceptual benefits differ between the groups. Our second and more surprising finding is that although percussionists demonstrated superior performance in the movement conditions, they did not outperform non-percussionists in the no-movement conditions, raising interesting questions regarding the degree to which percussionists depend on movement for timing. Our findings therefore complement previous perception-only experiments in which percussionists typically show greater sensitivity to timing changes (Ehrlé & Samson, 2005; Krause et al., 2010), but we observe this pattern only when percussionists are moving with the stimulus.

4.6.1 Additional interpretations

There are a few additional explanations for the greater movement-related improvements to temporal processing in percussionists compared to non-percussionists. First, we find that moving with an external beat facilitates perceived timing of subsequent temporal events. This may be due to movement enabling beat maintenance throughout the silent portion of the trial, where the pacing signal is not available, clearly demonstrating the supportive role movement plays in temporal processing (Iordanescu et al., 2013; Manning & Schutz, 2013; Su & Pöppel, 2012). However, here we find that percussionists receive a greater benefit from movement compared to non-percussionists. This may suggest that percussionists rely on movement information for timing more than do non-percussionists, perhaps due to the reliability of their movement demonstrated through more consistent and accurate tapping that is thought to arise with training (see Figures 4.3 and 4.4; Aschersleben, 2002; Krause et al., 2010; Madison et al., 2013; Repp & Doggett, 2007). Anecdotally, percussionists reported difficulty in inhibiting movement slightly more than did non-percussionists, an observation that supports this notion. Surprisingly, we did not observe a difference between percussionists and non-percussionists in the no-movement conditions, in contrast to studies reporting that percussionists perform significantly better than non-percussionists in listening-only timing tasks (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Ehrlé & Samson, 2005; Krause et al., 2010). This may be in part due to percussionists actively inhibiting movement in the no-movement trials, perhaps allocating more cognitive resources to avoid movement. We recognize that this could lead to worsened performance in no-movement conditions for the percussionists, however it might also be the case for the non-percussionists who similarly reported some trouble with remaining still. Interestingly, this highlights the close relationship between movement and auditory timing abilities and future studies should aim to identify the importance of allocating attentional resources to movement inhibition through a similar task.

Another possible explanation for these findings is that the reported improvement in perceived timing with movement may be a product of effector-specific training (i.e., stick tapping in percussionists). Non-percussionists show higher consistency when tapping with a stick compared to a finger (Madison et al., 2013), and in our previous work benefited from stick-tapping movements even without prior training (Manning & Schutz, 2013, 2015). However it is possible that percussionists' extensive training with stick tapping might have led to a greater advantage in terms of both tapping accuracy and the magnitude of the perceptual benefit. We plan to further explore the use of effectors and relative amounts of motor training in future experiments.

Additionally, the amount of movement-related sensory feedback present in each group might differ and this may contribute to performance differences. Our technical setup allowed only limited capture of participants' tapping force to the degree of sensory feedback given that participants tapped quite forcefully, but percussionists did appear to tap with more force in general, perhaps due to experience playing instruments requiring a fair amount of movement to produce sound. This might lead to differences in sensory feedback, particularly in auditory and tactile feedback. Although we know that auditory feedback is helpful in guiding movement timing, its presence is not essential for movement to benefit perceived timing (Manning & Schutz, in press). However, with more forceful tapping participants would also receive more tactile feedback, which facilitates motor timing (Wing et al., 2010) and this additional sensory information may enhance subsequent perceptual abilities.

We note finally that percussionists in our study volunteered their time to participate in the experiment whereas non-percussionists received course credit. Although this might lead to differences in motivation between the groups, it is important to note that we did not find differences between group performance in the no-movement trials. Moreover, as we were primarily interested in the effect of movement, a within-subjects variable, a difference in motivation would not undermine our primary question of interest (i.e., the effect of movement on task performance in percussionists vs. non-percussionists).

4.6.2 Production and perception interactions

Consistent with research on tapping and musical training, the present data demonstrate that percussionists exhibit tapping that is more accurate (denoted by smaller tap asynchronies) and less variable (lower CVs) compared to non-percussionists. This finding complements literature showing smaller NMAs produced by musicians compared to non-musicians (Aschersleben & Prinz, 1995; Repp, 1999a) and less variable tapping for musicians compared to nonmusicians (Krause et al., 2010; Repp & Doggett, 2007; Repp et al., 2013), particularly for percussionists (Krause et al., 2010). Interestingly, this is especially true when musicians implement movements pertaining to their instrument of training (Keele et al., 1985; Stoklasa, Liebermann, & Fischinger, 2012). Here we measure motor timing using a tapping task, which is most like movements executed by percussionists. Although these tapping movements improve timing perception for both groups, they provide greater benefit to the group for whom they are consistent with their extensive training.

In percussionists and non-percussionists, tap asynchrony at the probe tone predicted response accuracy, suggesting a dependence on the timing of movement proximal to the probe tone (response target) for timing judgments. Previously we demonstrated that movement improves timing abilities (Manning & Schutz, 2013, in press), here we build on this by showing that movement *timing* further improves timing detection, where more accurate motor timing prior to the response (such as that observed in percussionists) leads to greater accuracy in the timing detection task. We also found a correlation between performance in the movement condition and tapping variability in non-percussionists, where less variable tapping may have led to better task performance. Contrary to non-percussionists, there was no correlation between task performance in the movement conditions and tapping variability in percussionists, a correlation that was observed between tapping measures and performance in a timing perception task with musicians and nonmusicians (Keele et al., 1985; Krause et al., 2010). This may be due to percussionists' very low measures of tapping variability (Figure 4.4) or exceptional performance on the probe tone task in the movement condition, but further investigation is necessary to determine if these measures of tapping quality and perceptual abilities are related in percussionists.

4.6.3 Interactions with musical experience

We examined musical experience both as a function of years of formal lessons and years of playing a given instrument to index the amount of practice participants have not only with musical practice but also with executing movements in musical situations. The analyses between musical experience and task performance yielded a correlation between performance in the movement condition and years of percussion playing in percussionists, but no correlation between score in the no-movement condition and years of playing. This lends further support to the notion that percussionists gain a greater timing benefit when moving and their capacity for precise timing may to some extent require movement. This finding complements literature that reports musicians' superior timing detection abilities compared to nonmusicians (Ehrlé & Samson, 2005; Madison & Merker, 2002; Rammsayer & Altenmüller, 2006) and suggests a complex interaction between musical training, movement, and timing abilities. It is possible that these differences are due to explicit training, however it is important to note that pre-existing differences between movement abilities and musical proficiency or instrument choice can also play a role in these assessments. Here we contribute to this literature by demonstrating that improved task performance may be specific to conditions that employ movement for keeping time, particularly practiced movement.

4.6.4 Contributions to theories of perception and action

More broadly, our study contributes to common coding theories of perception and action (Hommel et al., 2001; Prinz, 1997; Repp, London, & Keller, 2011) as well as neural accounts describing overlapping cortical regions for motor planning and execution and beat perception (Grahn & Brett, 2007) in addition to more pronounced auditory-motor neural coupling in musically trained participants (Baumann et al., 2007; J. L. Chen et al., 2008a; Grahn & Rowe, 2009; Haueisen & Knösche, 2001). Additionally, these findings are in line with the embodied account of a forward internal model of action describing how action influences perception (Maes et al., 2014). Here we also provide further evidence for the notion that when movements synchronize periodically with an external beat this may set up expectations for upcoming temporal events through auditory-motor interactions (Iversen et al., 2009; Patel & Iversen, 2014). In conjunction with these accounts of action influencing perception, we argue that movement sharpens the perception of periodic auditory events, and extensive training with task-consistent movements enhances this interaction.

4.7 Conclusion

As a whole, this study shows that movement improves timing detection abilities and this improvement is mediated by musical expertise. Additionally, it presents the possibility that percussionists' superior timing abilities might to some degree be dependent upon movement, as they outperformed non-percussionists when moving with the stimulus but did not perform any better than non-percussionists when completing the detection task without movement. Although it is possible that actively inhibiting movement plays a role in this finding, future studies should address the degree to which this might divert attention from the timing task. Percussionists tapped more accurately and consistently, which likely both reflects and enhances their internal representation of timing. Superior motor timing and improvements in timing judgments in percussionists while tapping with a drumstick may be a product of effector-specific training, and future research should address whether musicians with expertise using different types of motor synchronization experience similar movement-related improvements in perception. This finding extends literature on links between perception and action in addition to training-specific movements by showing that high levels of training might lead percussionists to acquire greater timing benefits from auditory-motor interactions.

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Chapter 5: Temporal prediction abilities are mediated by motor effector and rhythmic expertise

Manning, F. C., Harris, J., & Schutz, M. (*submitted*). Temporal prediction abilities are mediated by motor effector and rhythmic expertise.

5.1 Preface

Finger tapping is the most common way to examine sensorimotor synchronization (reviewed in Repp & Su, 2013; Repp, 2005). However, many motor effectors are able to synchronize with external auditory events. Studies that compare synchronization abilities between different motor effectors in the same participants (e.g., finger tapping vs. foot tapping) report a relation between the tapping asynchronies and variability (Billon et al., 1996, Fujii et al., 2011; Keele et al., 1985). Due to these findings, movement synchronization is thought to be generated from a common internal source.

However, clear differences are observed between synchronization across motor effectors. For example, finger tapping movements are more variable than stick tapping movements (Collier & Ogden, 2004; Fujii & Oda, 2009; Madison, 2001; Madison & Delignières, 2009). These differences are thought to arise from inherent differences in motor control abilities across effectors. One particular dimension that differs between finger and stick tapping movements are the degrees of freedom that are available for manipulation. Effectors with more degrees of freedom tend to be more accurately timed (Latash, 2014; Todorov & Jordan, 2002; Winold, Thelen, & Ulrich, 1994). Finger tapping involves movement of the metacarpophalangeal joint, which contains only one degree of freedom, whereas stick tapping involves multiple degrees of freedom including the elbow, wrist and fingers.

Furthermore, motor synchronization is responsive to training, which differs across effectors. Short-term training in stick tapping leads to more consistently timed movements, whereas these benefits are less pronounced in finger tapping (Madison et al., 2013). Musicians who are trained using certain movements on their particular instrument show more consistent timing with training-specific movements compared to tapping (Stoklasa, Liebermann, & Fischinger, 2012), suggesting that motor training may not generalize entirely to other effectors.

In this chapter I examined how finger tapping in percussionists and non-percussionists and impacts temporal prediction abilities. Chapter 4 reported superior temporal discrimination abilities in percussionists compared to non-percussionists only when synchronizing movements with external auditory information, but not when listening only. However, participants synchronized stick tapping movements with the auditory signal, which are movements consistent with percussionists' training. Since perceptual benefits arise from synchronized movement more for percussionists compared to non-percussionists (Butler & Trainor, 2015; Manning & Schutz, 2016), in the next study I examined how motor training in one effector is generalized to other effectors, and whether this subsequently impacts perceptual timing abilities. Due to recent evidence reporting no difference between tapping and perceptual timing abilities between musician groups (Matthews et al., 2016) and less consistent finger tapping compared to stick tapping (Collier & Ogden, 2004; Fujii & Oda, 2009; Madison, 2001; Madison & Delignières, 2009; Madison et al., 2013), we did not expect to find the same enhancement in detection abilities in percussionists while finger tapping compared to non-percussionists.

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5.2 Abstract

Motor synchronization is a critical part of musical performance and listening. Synchronization is optimal with increased degrees of freedom where movements that can manipulate more degrees of freedom are more accurately timed. Previously, we demonstrated that stick tapping improves perception in a timing detection task, where percussionists greatly outperformed non-percussionists only when tapping along. Since most synchronization studies implement finger tapping to examine simple motor synchronization, here we completed a similar task where percussionists and non-percussionists finger tapped, movements with fewer degrees of freedom than stick tapping. Percussionists and non-percussionists listened to an isochronous beat sequence and identified the timing of a probe tone. On half of the trials they tapped along with their index finger and on half of the trials they listened without moving prior to making timing judgments. We found that both groups benefited from tapping overall. Interestingly, percussionists performed only marginally better than did non-percussionists when finger tapping and no different when listening alone, differing from past studies reporting highly superior timing abilities in percussionists. Additionally, we found that percussionists' finger tapping was less variable and less asynchronous than was non-percussionists' tapping. Moreover, in both groups finger tapping was more variable and more asynchronous than stick tapping in our previous study. This study demonstrates that the motor effector implemented in tapping studies affects not only synchronization abilities, but also subsequent prediction abilities. We discuss these findings in light of effector-specific training and degrees of freedom in motor timing, both of which impact timing abilities to different extents.

Keywords: finger tapping, sensorimotor integration, movement timing, motor effector, musical training

5.3 Introduction

Extracting regularities from auditory sequences, predicting events in time, and synchronizing movements to those events involves a complex series of multisensory processes. This seemingly simple behavior is an automatic and often unconscious response to regularities in musical sequences. Motor synchronization requires the integration of sensory information from various modalities in order to optimally produce action-based effects on perceptual information (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Wing, Doumas, & Welchman, 2010). Since sensorimotor synchronization is multisensory in nature and includes both perception and production, many studies suggest a common timing process involved in perception and production for separately measured temporal acuity and motor timing in behavioral tasks (Cameron & Grahn, 2014; Keele, Pokorny, Corcos, & Ivry, 1985; Krause, Pollok, & Schnitzler, 2010) and in neuroimaging studies (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009). This is further supported by studies that explicitly examine changes to perception that arise from movement (Chemin, Mouraux, & Nozaradan, 2014; Phillips-Silver & Trainor, 2007; Su & Pöppel, 2012) and improvements to perceived timing due to synchronized movement (Butler & Trainor, 2015; Iordanescu, Grabowecky, & Suzuki, 2013; Manning & Schutz, 2013, 2015).

Since motor timing has substantial effects on temporal prediction, it is important to examine various types of motor synchronization used by populations that implement different amounts and types of synchronization experience.

Although a subset of studies report differences between motor timing abilities in different musician groups (Cameron & Grahn, 2014; Krause et al., 2010), other recent evidence documents no difference between musicians trained on different instruments while finger tapping (Matthews, Thibodeau, Gunther, & Penhune, 2016). Furthermore, musicians time their movements most accurately when synchronizing movements consistent with their instrument of training (Fujii et al., 2011; Stoklasa, Liebermann & Fischinger, 2012). Recently we reported substantial improvements in timing detection abilities in percussionists following stick tapping movements (Manning & Schutz, 2016). The present study aims to extend these findings by explicitly examining how the timing of finger tapping impacts auditory prediction abilities in percussionists and non-percussionists. We completed the present study comparing experienced percussionists with non-percussionists to address the role of movement experience in sensorimotor integration. Percussionists typically have extensive training with drumstick tapping but not necessarily with finger tapping – the type of movement typically used in motor synchronization studies. Consequently, this study will clarify whether different motor effectors are mediated by shared timing processes in populations with and without effector-specific training, and whether this information is similarly used to inform temporal prediction.

5.3.1 Temporal prediction and musical experience

Temporal prediction and motor production abilities are both affected by musical experience. Musicians demonstrate superior temporal acuity compared to nonmusicians (Rammsayer & Altenmüller, 2006) both in identifying global elements of musical structure (Drake & Botte, 1993; Ehrlé & Samson, 2005; Madison & Merker, 2002; Yee, Holleran, & Jones, 1994) and in discriminating the timing of single events in a sequence (Jones, Jagacinski, Yee, Floyd, & Klapp, 1995; Jones & Yee, 1997; Lim, Bradshaw, Nicholls, & Altenmüller, 2003; Yee et al., 1994). Although any musical experience seems to play a role in refined temporal acuity (Matthews, et al., 2016), percussionists show the most sophisticated timing acuity of all musicians (Ehrlé & Samson, 2005; Krause et al., 2010), which may reflect specialized training in situations that involve sensorimotor synchronization.

5.3.2 Motor synchronization and musical experience

Synchronization studies that address motor timing questions typically employ simple finger tapping paradigms due to its ubiquity and simplicity in recording (see Repp, 2005 for a review). Those with or without musical training can readily tap at many tempi (Madison, 2001; Repp & Keller, 2004; Repp, 2003) and with various types of complex stimuli (Hove, Fairhurst, Kotz, & Keller, 2013; Repp, London, & Keller, 2008, 2011; Snyder, Hannon, Large, & Christiansen, 2006; Ullal-Gupta, Hannon, & Snyder, 2014). While synchronizing finger movements with isochronous auditory events, participants tend to show a negative mean asynchrony (NMA), tapping slightly in advance of the anticipated events, which is thought to reflect temporal prediction (Aschersleben & Prinz, 1995; Aschersleben, 2002; Mates, Radil, & Pöppel, 1992; Repp, 2000). Differences in the NMA appear to vary as a function of musical experience, where participants with greater levels of musical training show smaller tap asynchronies compared to those with little or no musical experience (Aschersleben, 2002; Repp & Doggett, 2007; Repp, 1999). Musicians also tap with lower variability than do nonmusicians (Repp & Doggett, 2007; Repp, London, & Keller, 2013; Repp, 2010), reflecting greater consistency in motor production. This is especially true for percussionists who show extremely low variability in tapping (Cameron & Grahn, 2014; Fujii et al., 2011; Krause et al., 2010; Manning & Schutz, 2016) and for musicians who synchronize using movements most similar to those used while playing their instrument of training (Stoklasa, et al., 2012; Manning & Schutz, 2016). While it is difficult to distinguish whether explicit training is causing these improvements, or if a propensity for well-timed movements leads individuals to pursue musical training, it is clear that short-term practice leads to considerable improvements in tapping variability (Madison, Karampela, Ullén, & Holm, 2013), which offers further support for the idea that training is a possible source of these abilities.

5.3.3 Motor effector comparisons in sensorimotor synchronization research

Although finger tapping is most commonly used to examine motor timing, some studies have compared timing in various motor effectors—parts of the body that execute movement. Movements reflect patterns in auditory structure, where larger effectors tend to synchronize with higher levels of a metrical hierarchy (i.e., at a slower rate) than do smaller effectors (Toiviainen, Luck, & Thompson, 2010).

There is some evidence that synchronization ability is correlated across effectors (Fujii et al., 2011; Keele et al., 1985), suggesting a common mechanism for timed movements. However, different effectors synchronize with varying degrees of success, where, for example, foot tapping shows greater asynchronies than hand tapping (Aschersleben & Prinz, 1995; Fraisse, 1982; Fujii et al., 2011). Interestingly, while variability decreases with practice across both effectors (Madison et al., 2013), finger tapping is significantly more variable (Collier & Ogden, 2004; Madison, 2001) than tapping using a drumstick (Fujii & Oda, 2009; Madison & Delignières, 2009). There are many differences between finger and stick tapping that could explain these differences in timing including the weight of the object in stick tapping, the amount of experience executing each type of movement and the trajectory of the movements. Additionally, the amount and integration of auditory and tactile feedback produced by each movement impacts synchronization (Finney, 1997; Maduell & Wing, 2007; Wing, 1977), where the timing of movements is more precise when multiple sources of sensory information are integrated (Wing et al., 2010). Furthermore, experience with a specific effector leads to more accurate motor timing using that effector, but this may not generalize to other effectors (Stoklasa et al., 2012).

Recently, the kinematics of timed movements have been described in terms of the motor effector's degrees of freedom (Latash, 2014; Todorov & Jordan, 2002), where movements that can manipulate more degrees of freedom are more accurately timed than movements that manipulate fewer degrees of freedom (Winold, Thelen, & Ulrich, 1994). This is an important consideration for comparing synchronization in different motor effectors and examining how their timing leads to perceptual differences. In the current study we consider this view by examining the timing of finger tapping using the metacarpophalangeal joint (i.e., the knuckle), which depends on only one degree of freedom. This synchronization study is conducted with percussionists, who are trained extensively with stick tapping motions, and non-percussionists.

5.3.4 Current study

The present study explicitly examines the extent to which motor timing abilities are generalized from one effector to another and similarly integrated with auditory information. Previously we found that participants are better at identifying timing changes after tapping along with the sequence using a drumstick compared to when listening alone, regardless of their level of musical training (Manning & Schutz, 2013). When we examined percussionists, musicians that are familiar with drumstick tapping, we found that percussionists received a greater perceptual benefit from movement, but perform no different to non-percussionists when completing the same task without movement (Manning & Schutz, 2016). This suggests that percussionists may rely on movement for their superior abilities in temporal prediction. However, this calls into question whether percussionists' improvements are restricted to the movements used while playing and practicing, reflecting task-specific motor abilities. Alternatively, these improvements may extend to all timed movements, demonstrating a general refinement in motor proficiency.

Since finger tapping is widely used in sensorimotor synchronization research to index motor timing (Repp, 2005), here we examine whether documented improvement to perception following movements also exists for finger tapping. If percussionists gain larger movement-related enhancements to perception compared to non-percussionists while *finger tapping*, this might suggest a common motor representation for multiple effectors (consistent with Fujii et al., 2011; Keele et al., 1985) that leads to these motor and perceptual benefits. However, if percussionists do not receive the same perceptual benefit while finger tapping as previously observed when stick tapping (Manning & Schutz, 2016), this would suggest that these benefits arise at least in part from experience with a specific motor effector and may not generalize to movements of all effectors. We expect that finger tapping will lead to perceptual improvements for both percussionists and non-percussionists. In light of recent evidence reporting no differences between musician groups for finger tapping performance or perceptual abilities (Matthews et al., 2016), we do not expect to observe large differences between percussionists and non-percussionists perceptual timing judgments as observed following stick tapping (Manning & Schutz, 2016). We predict that this will arise from more variable (and perhaps less reliable) motor timing information, since timed finger tapping movements are less consistent than stick tapping movements (Madison et al., 2013). This would demonstrate how strongly the quality of motor timing directly influences temporal prediction abilities. Additionally, this would suggest that rhythmic motor training does not directly affect listening abilities, but instead may depend on a learned motor training in one motor effector does not directly transfer to other effectors, perhaps due to their inherent differences in motor control.

5.4 Method

5.4.1 Participants

Participants consisted of two groups. The first group included 28 trained percussionist volunteers, hereafter "percussionists", (21 males and 7 females; 17-65 years of age, *M* = 30.50, *SD* = 12.31) with varying degrees of percussion training (2-20 years, *M* = 10.46, *SD* = 5.54), who attended the Percussion Arts Society International Convention (PASIC) in November 2013. The second group included 29 undergraduate "non-percussionists" (6 males and 23 females; 17-24 years of age, *M* = 19.00, *SD* =1.32), who were students from the McMaster University psychology participant pool who received course credit for participating in this experiment. Non-percussionists had varying degrees of formal musical training (0-13 years, *M* = 5.24, *SD* = 4.10) but none were expert musicians nor did any play percussion instruments. Participant groups did not differ in years of musical training on instruments other than percussion ($t(55) = 0.541$, $p = .591$). All participants reported normal hearing and tapped with their dominant hand. Participants gave written informed consent prior to the study in accordance with the McMaster University Research Ethics Board.

5.4.2 Stimuli and apparatus

Stimuli were identical to those used in a previous study (Manning & Schutz, 2016) and presented with customized software that played MIDI "woodblock" sounds (gmBank = 115) through Sennheiser HDA200 headphones. The stimuli consisted of a sequence of beats presented at an inter-onset interval (IOI) of 500 ms (120 bpm). The beats were grouped together with 4 beats per grouping and each grouping repeated four times within one trial (see Figure 5.1). The first beat of each grouping was of higher relative pitch (C5; 523 Hz) than the three subsequent beats (G4; 392 Hz) to induce a sense of meter and to orient attention through the trial. In the fourth repetition of the grouping, the unaccented beats were silent. After the silent segment of the trial one final probe tone occurred. On half of the trials this probe tone occurred on-time with the previous sequence (at an offset of 0 ms) and on the other half of the trials the probe tone occurred later than anticipated at one of two offsets; 15 percent of the IOI late (+75 ms) or 30 percent of the IOI late (+150 ms). An electronic hand percussion pad (Roland Handsonic 10) connected to an Alesis Trigger i/O Trigger-to-MIDI USB Interface converted finger tapping into MIDI messages sent to a MacBook Pro[4].

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[4] The accuracy of tap recording was verified in the experimental setup and tap onset recordings were corrected for using a consistent latency value through the recording.

5.4.3 Design and procedure

Participants completed 64 trials separated into eight blocks. On half of the trials (movement condition) participants tapped along with the sequence using the index finger (metacarpophalangeal joint movement) of their dominant hand throughout all segments up to and including the probe tone (see Figure 5.1). On the other half of the trials (no-movement condition) participants were instructed to remain completely still (e.g., no foot tapping or head bobbing). Blocks randomly alternated between movement/no-movement conditions and within each block four trials contained a probe tone that was on-time and four trials contained a late probe tone at one of two offsets. Participants listened to each trial and in a two-alternative forced choice (2AFC) task identified whether the probe tone was consistent with the timing of the sequence ("on-time") or not and indicated their confidence on a scale from 1 (not at all confident) to 5 (very confident). Participants received feedback on the correctness of their responses to retain attention and motivation. Participants completed 5 warm-up trails to ensure task understanding before proceeding with the rest of the experiment. The order of trials within each block was randomized for each participant.

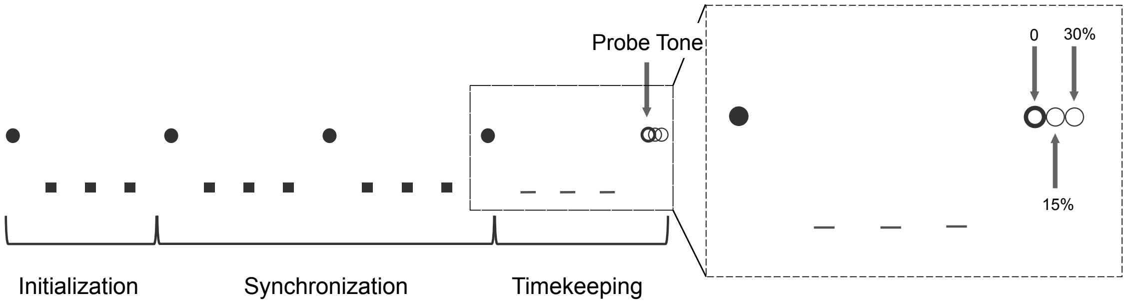

*Figure 5.1***.** A single trial depicted with labeled segments. The circles represent accented beats while the squares represent unaccented beats. The final grouping is enlarged to highlight silent "beats" (black lines) and possible probe tone offsets (unfilled circles).

5.5 Results

5.5.1 Timing judgments

First we computed a task score for each participant in the movement and no-movement conditions by calculating the proportion of correct identifications of the probe tone timing for each trial in the task. Across all movement trials the difference between percussionist and non-percussionist task score was marginally significant ($t(55) = 1.824$, $p = .073$). Interestingly we also did not find a difference between percussionists and non-percussionists in the no-movement trials ($t(55) = 1.107$, $p = .273$). Pairwise comparisons between group performance with Bonferroni correction ($\alpha = .0167$) in the movement condition showed a significant difference between groups at the 15 percent late probe tone ($t(55) = 2.801$, $p = .007$) and the 30 percent offset ($t(55) = 2.607$, $p = .012$), but showed no difference between groups in the different offsets of the no-movement condition.

Next we subtracted the no-movement score from the movement score for each participant at each probe tone offset to assess an effect of movement on task performance, which represents the degree to which finger tapping improved timing detection abilities (Figure 5.2a). The effect of movement on task performance was significantly greater than 0 in non-percussionists ($F(2,54) = 3.54$, $p = .036$, $\eta^2 = 0.079$) and approached significance in percussionists ($F(2,54) = 2.82$, $p = .068$, $\eta^2 = 0.055$)[5], indicating that finger tapping facilitated task performance in both groups. We conducted a 2 (group) x 3 (offset) mixed-model

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[5] Figure 2a visually appears to contradict this statement, however the variance for percussionists is greater than that of non-percussionists, which might explain the marginally significant effect observed for non-percussionists only.

ANOVA on the effect of movement difference scores as the dependent measure to index the degree to which the benefit of tapping changed as a function of group and probe tone offset. We did not find a main effect of group (*F*(1,55) = 0.470, *p* = .496), nor did we find an interaction between group and offset (*F*(2,110) = 0.385, *p* = .681), showing no difference between the percussionist and non-percussionist effect of movement difference scores when finger tapping. We did find a main effect of probe tone offset (*F*(2,110) = 6.843, *p* = .002, η^2 = .069), demonstrating movement affected performance differently for different offsets. We also identified the proportion of "on-time" responses to visualize responses (see Figure 5.2b).

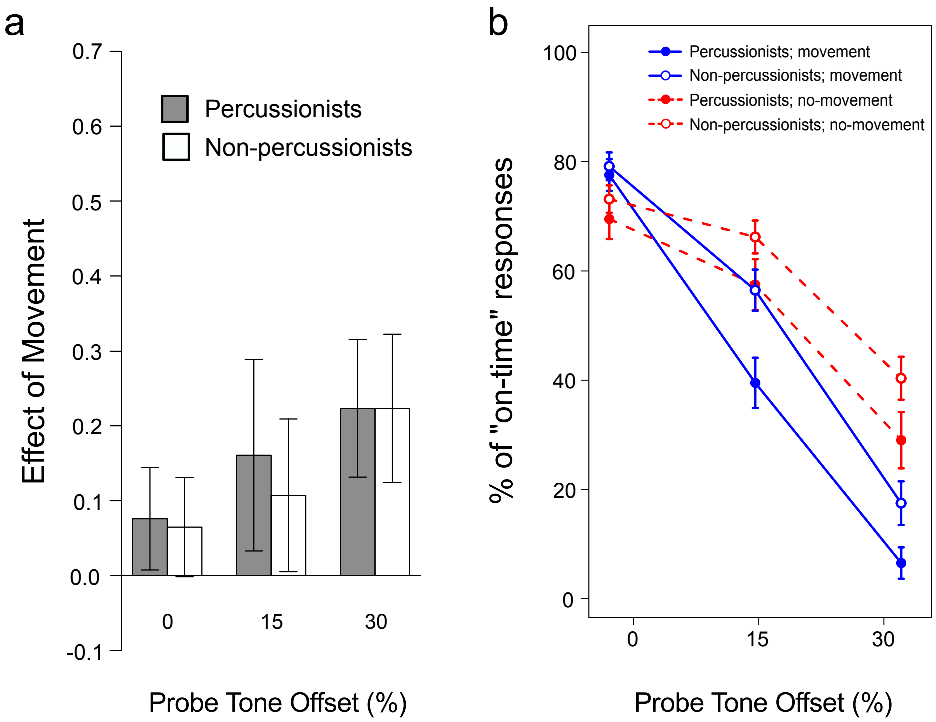

Figure 5.2 Panel a depicts the effect of movement (movement task score - no-movement task score) on timing judgments at each probe tone offset for each group. Panel b displays the percentage of "on-time" responses at each offset for each movement condition and group. Error bars indicate the standard error of the mean.

5.5.2 Tapping

We examined finger tapping in two ways. First we quantified the variance associated with taps by computing the coefficient of variation (CV) of tapping in the synchronization segment of the trials for each group (see Figure 5.1). Non-percussionists tapped with slightly more variability than did percussionists (*t*(55)

= 1.908, *p* = .062) in the synchronization segment (see Figure 5.3a). We also assessed the signed tap asynchrony by subtracting the timing of the onset of each beat to the onset of the corresponding tap. A negative asynchrony indicates that taps preceded tone onset, while a positive asynchrony indicates that taps followed tone onset. We measured the tap asynchrony both throughout the synchronization segment of the trials and at the expected probe tone position. While both groups showed a negative mean asynchrony (see Figure 5.3b), the asynchrony was significantly smaller for percussionists compared to non-percussionists both through the synchronization segment (*t*(55) = 4.511, *p* < .0001) and at the expected probe tone position (*t*(55) = 3.470, *p* = .001). This indicated that finger tapping was more aligned with the beat sequence for percussionists compare to non-percussionists.

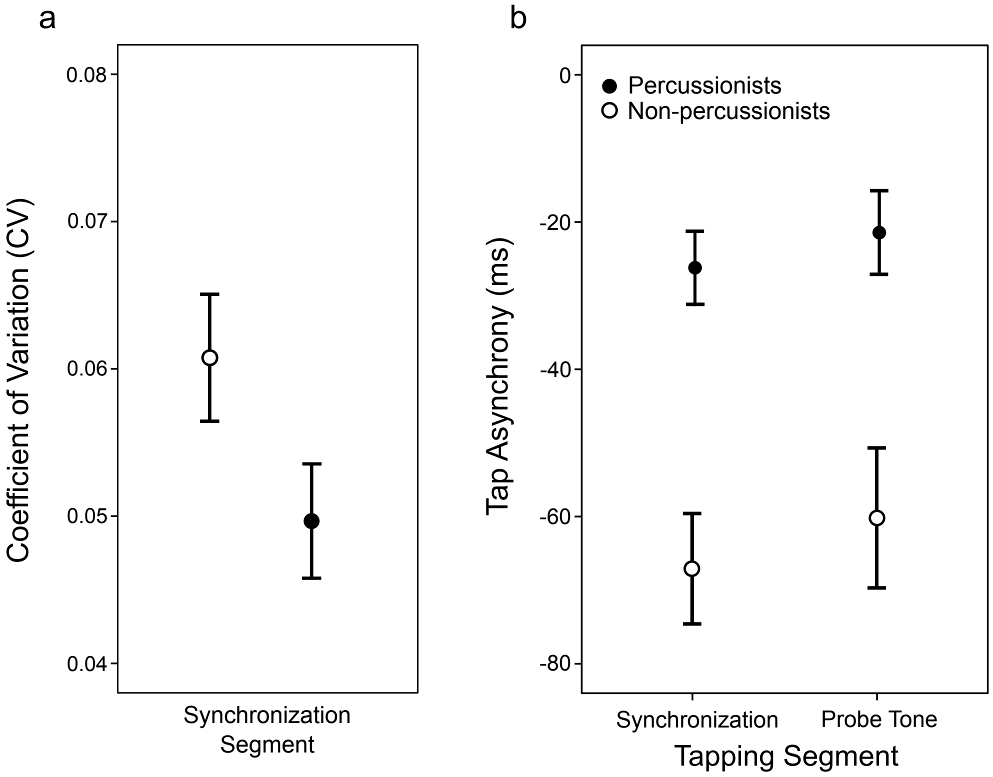

Figure 5.3. The coefficient of variation for in the synchronization segment of the beat sequence (a) and mean finger tap asynchronies in the synchronization and probe tone segments of the sequence (b) for percussionists and non-percussionists. Error bars indicate the standard error of the mean.

5.5.3 Comparison between stick and finger tapping

In a previous study we examined perceptual and motor timing abilities in percussionists and non-percussionists with stick tapping in a similar task (Manning & Schutz, 2016). There we found that percussionists outperformed non-percussionists in the movement trials, but performed no differently from non-percussionists in the no-movement trials. This raised questions surrounding whether it was percussionists' experience using a drumstick led to superior movement timing and therefore improvements in task performance while stick tapping. Here we compare task performance while finger tapping to our previous study with stick tapping. Percussionists performed no differently in the absence of movement in the present finger tapping study compared percussionists in the previous stick tapping study ($t(68) = 0.135$, $p = .865$). Non-percussionists also performed no differently in the absence of movement between studies ($t(68) = 0.340$, $p = .703$). However we do find significant differences in the movement trials between studies in both percussionists ($t(68) = 2.977$, $p < .001$) and non-percussionists ($t(68) = 1.919$, $p = .004$), where both groups show less pronounced perceptual benefits when finger tapping rather than tapping using a stick.

When we examined the quality of tapping between studies, there was significantly greater variability in finger tapping compared to stick tapping for percussionists ($t(68) = 3.27$, $p < .001$) and non-percussionists ($t(68) = 4.17$, $p < .001$) (Manning & Schutz, 2016). We also found significantly greater tap asynchronies for finger tapping compared to stick tapping in percussionists ($t(68) = 2.91$, $p = .009$) and non-percussionists ($t(68) = 2.51$, $p = .014$). This shows that finger tapping is more variable and less accurate in both percussionists and non-percussionists compared to stick tapping.

5.5.4 Interactions between perception and tapping

Since the effect of movement in both groups indicated that movement significantly improved timing judgments, we conducted Pearson's correlations between finger tapping measures and detection abilities in each group. Similar to previous findings showing a relationship between different measures of stick tapping in percussionists and non-percussionists (Manning & Schutz, 2016), we found a small relationship between finger tapping CV in the synchronization segment and task performance in non-percussionists ($r(27) = -.342$, $p = .069$), indicating those with lower variability of tapping performed better on the task, but we did not observe the same pattern for percussionists ($r(26) = -.144$, $p = .463$). We also observed a relationship between tap asynchronies measured in the synchronization segment of the trial and task score for non-percussionists ($r(27) = .397$, $p = .033$), but this was not the case for percussionists ($r(26) = .228$, $p = .243$). Next we conducted a binary logistic regression to determine the degree to which the timing of the final tap adjacent to the probe tone predicted the correctness of responses in the perceptual task. In the percussionist group as tap asynchrony increased by 1 ms, the odds of correctly identifying the timing of the probe tone decreased by 1.12% ($\chi^2 = 15.74$, $p < .001$; odds ratio (OR) = 0.943). Similarly, the timing of the final tap in non-percussionists significantly predicted the correctness of responses, where as tap asynchrony increased by 1 ms, the odds of correctly identifying the timing of the probe tone decreased by 1.08% (χ^2 = 16.51, $p < .001$; odds ratio (*OR*) = 0.954). This relationship suggests that the timing of taps adjacent to the probe tone can be used to predict the response outcome of the trial, where more accurate tapping increases the probability of a correct timing judgment, particularly for percussionists.

5.6 Discussion

The present study examined the perceptual consequences of finger tapping with auditory sequences in groups of percussionists and non-percussionists. We found that percussionists and non-percussionists perform no differently in the no-movement trials of the task, similar to our previous findings using this paradigm (Manning & Schutz, 2016). In the present study percussionists showed only a slight perceptual advantage in the movement trials compared to non-percussionists when finger tapping with the sequence. This important finding corroborates our previous stick tapping study that showed perceptual benefits of movement in both percussionists and non-percussionists, where percussionists showed a much greater benefit from this movement. However, percussionists receive a much greater perceptual benefit than non-percussionists from stick tapping compared to finger tapping. This suggests that although percussionists might rely on movement more for timing judgments, movement consistent with their training yields an even greater benefit. This perceptual difference is based on the type of movement used to synchronize with external auditory stimuli and comments on the role of effector-specific training in percussionists, complementary to other studies that report superior synchronization using explicitly trained movement (Stoklasa et al., 2012). The small difference observed here might clarify conflicting evidence for musician differences in timing abilities (Butler & Trainor, 2015; Cameron & Grahn, 2014; Krause et al., 2010; Matthews et al., 2016).

The finger tapping data in this study showed lower tapping variability and smaller tapping asynchronies in percussionists compared to non-percussionists. This is consistent with studies demonstrating that musicians exhibit highly accurate tapping compared to nonmusicians (Aschersleben, 2002; Repp & Doggett, 2007; Repp, 1999) as well as very low tapping variability (Repp & Doggett, 2007; Repp, London & Keller, 2013; Repp, 2010), particularly percussionists (Cameron & Grahn, 2014; Fujii et al., 2011; Krause et al., 2010; Manning & Schutz, 2016). Previous studies show a relationship between the quality of motor output between various effectors suggesting a common mechanism for timed movements (Fujii et al., 2011; Keele et al., 1985). Here we note that superior synchronization abilities observed in percussionists while stick tapping do not necessarily manifest in finger tapping.

Both percussionists and non-percussionists in this study relied on the timing of their final tap to make perceptual judgments about the probe tone, suggested by our regression analysis comparing perceptual and tapping data. Since we observed differences in synchronization abilities between stick and finger tapping for both percussionists and non-percussionists, as well as differences in perceptual data, this might indicate that percussionists may use finger tapping information less than stick tapping information in their perceptual timing decisions due to the lower quality of this information. This supports the notion that tapping offers an additional cue for temporal detection and the quality of synchronization allows this information to be weighted accordingly, where more consistent stick tapping (Fujii & Oda, 2009; Madison & Delignières, 2009; Madison et al., 2013) is a better cue for identifying timing of external information compared to finger tapping, which is less reliable (Collier & Ogden, 2004; Madison, 2001).

There are several differences between finger tapping and stick tapping movements that may lead to synchronization differences, and therefore to perceptual differences. In the present study finger tapping involved the movement of the index finger of the dominant hand, which allows only movement of the metacarpophalangeal joint similar to studies examining finger tapping trajectories (Balasubramaniam, Wing, & Daffertshofer, 2004; Doumas & Wing, 2007; Hove & Keller, 2010). Stick tapping, however, consists of larger movements than finger tapping, involving the wrist and perhaps forearm, depending on how a participant chooses to manipulate the stick. Research in motor control discusses how the number of degrees of freedom in goal-oriented movement might contribute to optimal control of movement (Latash, 2014; Todorov & Jordan, 2002). The kinematics involved in timed movements might explain differences in synchronization ability, where, for example in skilled musicians, movements that allow a performer to manipulate more than one degree of freedom show more tightly controlled timing (Winold et al., 1994). For the present study this may suggest that using a stick allows for more control over the movement trajectory than does finger tapping and this might lead to more precise synchronization, since the finger tapping allows only one joint to be manipulated while stick tapping may allow many joints to be manipulated. We observe differences in the tapping that support this notion, where stick tapping is more consistent than is finger tapping (see also Madison et al., 2013), which also has perceptual consequences. Additionally, those with more experience manipulating an object to execute movements, namely percussionists with a drumstick, might have even more control and therefore time motions more accurately. This improvement in synchronization due to experience may not extend fully to finger tapping since only one joint is used, compared to two or more joints involved in stick wielding using the wrist and/or forearm.

Recently a dual-route model for rhythm processing has emerged that describes two separate cognitive approaches for tracking and synchronizing with rhythm (Fischinger, 2011). In this model, two synchronization approaches may be used; one for the automatic processing of temporal events and the other for explicit monitoring (Miyake, Onishi, & Poppel, 2004). We can determine the approach that is used by diverting attention and examining subsequent synchronization performance. Percussionists are thought to typically depend on precise monitoring processes for highly accurate synchronizing and error correction (Fischinger, 2011). Since percussionists are largely trained in stick tapping and therefore exhibit larger synchronization (Cameron & Grahn, 2014) and perceptual benefits to tapping (Manning & Schutz, 2016), the motor effector involved in synchronization might require different amounts of attention. In the present study when percussionists synchronize using finger tapping they might return to an automatic approach to timing, similar to the non-percussionists, since this movement is not specific to their method of training. This may explain differences between stick and finger tapping in percussionists and non-percussionists and suggest that percussionists' extensive training in synchronization might be somewhat experience-dependent and not generalize to the synchronization ability of other motor effectors.

5.7 Conclusion

Overall this study shows that finger tapping leads to perceptual improvements for both percussionists and non-percussionists. This improvement is significantly smaller than in our previous study with stick tapping (Manning & Schutz, 2016), suggesting that less reliable finger tapping information provides a less reliable cue for perceived timing. This finding further supports interactions between motor information and timing abilities (Chemin et al., 2014; Manning & Schutz, 2013, 2015; Su & Pöppel, 2012), since differences in tapping information are reflected in perceptual judgments. More generally this support recent hypotheses describing auditory-motor interactions in beat perception (Patel &

Iversen, 2014) and a forward model of embodied action and its effects on perception (Maes, Leman, Palmer, & Wanderley, 2014). Although motor synchronization leads to improvements in perception, this interaction in mediated by musical abilities and experience with specific movements.

5.8 Acknowledgements

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Chapter 6: Discussion

6.1 Thesis Findings and Theoretical Contributions

6.1.1 Perceptual timing

The perception of predictable timing information is tightly linked with movement, and is an essential part of sensorimotor synchronization. In this thesis I demonstrated the impact of synchronized movement on perceived timing. My research showed that movement not only interacts with perceived timing of external auditory events, but also can objectively improve timing abilities. To my knowledge, the initial studies reported in this thesis were the first to document these improvements to temporal prediction following synchronized movements.

In Chapter 2, I reported improvements to temporal discrimination abilities of a final probe tone when participants tapped with an initial beat sequence compared to listening only. Two additional experiments built upon this finding by demonstrating that movement through the silent portion of the sequence is crucial for this improvement. These findings suggested that in the absence of an external auditory input to support temporal prediction, movement input allowed for effective beat tracking. Since motor regions in the brain are involved in timing processes (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Fujioka, Trainor, Large, & Ross, 2012; Grahn & Brett, 2007), this timing benefit may arise due to the involvement of additional timing networks for prediction, which would in turn generate a more reliable reference signal to compare with external targets.

Chapter 3 clarified that movement-related enhancements to perception documented in Chapter 2 were due to the synchronized movement itself throughout the silent segment of the trial instead of solely the auditory consequences that arise from that movement. This study manipulated participants' access to auditory information, where the sounds generated by tapping were either present or masked. These experiments showed that despite the auditory system's refined capacity for temporal processing in perceptual and motor timing tasks (Grahn, 2012; Repp & Penel, 2002, 2004; Repp, 2003), movement itself serves as an important cue for timing abilities, in some cases serving to improve temporal detection abilities. The findings in these experiments are consistent with studies that demonstrate how information available through other sensory modalities may be used to inform timing perception, despite auditory dominance (Bresciani, Dammeier, & Ernst, 2008; Hove, Iversen, Zhang, & Repp, 2013).

Chapter 4 addressed the extent to which highly trained rhythmic experts rely on movement information for temporal prediction. To examine this question I tested percussionists and non-percussionists on the deviation detection task with and without tapping. This study showed that percussionists greatly outperformed non-percussionists in the temporal discrimination task when tapping with the beat sequence. However, percussionists failed to outperform non-percussionists in the absence of movement information. This important finding demonstrated percussionists only outperform non-percussionists in situations that involve movement, suggesting that superior timing abilities in percussionists *depends* to some extent on movement. Moreover, this study offers insight into learned timing abilities used in perception and action, indicating that extensive practice acquiring rhythmic listening expertise depends on movement training. These movement-related dependencies reported in Chapter 4 are consistent with studies using a similar task to examine timing sensitivity with and without movements comparing percussionists to DJs (Butler & Trainor, 2015), which showed similar timing detection abilities in both groups. Percussionists and DJs may embody the temporal structure of rhythmic information and conceptualize the timing of external auditory information in terms of corresponding movements (Cameron & Grahn, 2014; Krause, Pollok, & Schnitzler, 2010).

The data presented in Chapter 5 provided new insight into how perceptual timing benefits are contingent on movement quality. Finger tapping is the most common way to assess movement abilities in the sensorimotor synchronization literature (Repp, 2005). However, finger tapping offers less reliable (i.e., less consistent) timing information compared to stick tapping (Madison, Karampela, Ullén, & Holm, 2013). This discrepancy likely explains differences between perceptual benefits that arise due to finger tapping and stick tapping (see Chapter 4) in percussionists and non-percussionists. This is consistent with recent findings demonstrating no differences between musician groups in perceptual and motor timing tasks that implement finger tapping (Matthews, Thibodeau, Gunther, & Penhune, 2016). Finger tapping uses fewer joints and less movement than does stick tapping, which allows for less control over movements overall (Latash, 2014; Todorov & Jordan, 2002; Winold, Thelen, & Ulrich, 1994). Additionally, since very slight perceptual or motor differences were observed between participant groups in the finger tapping experiment, extensive training in stick tapping movements does not appear to generalize to finger tapping abilities or to listening-only situations. This might call to question the generalizability of motor training in musician groups.

Since the initial study presented in Chapter 2 was reported, many other studies complement these findings in numerous ways. More recent studies now demonstrate that movement can serve to improve perception of beat-based information (Butler & Trainor, 2015; Iordanescu, Grabowecky, & Suzuki, 2013), musical timing imagery (Jakubowski, Farrugia, & Stewart, 2016) and perception of interval durations (Press, Berlot, Bird, Ivry, & Cook, 2014). Recently these findings were further extended to describe how synchronized finger movements facilitate target detection and suppress distractors, and that this scales with the predictability of the stimulus (Morillon, Schroeder, & Wyart, 2014). Chapters 3 through 5 further clarify that the precision of tapping directly impacts timing judgments, and that the combination of different sensory cues for timing depends on both the motor effector used for synchronizing and the training associated with a given effector. These findings serve to further demonstrate how movement and auditory inputs are integrated to facilitate timing processes.

Together these studies inform prominent theories of temporal prediction and action, by uniquely demonstrating improvements to prediction as a consequence of tapping. Dynamic attending theory postulates that temporal regularities in repetitive streams of sound events drive fluctuating levels of attentional energy (Jones & Boltz, 1989; Large & Jones, 1999; Large, 2008). In the current paradigm, since attention peaks at the expected onset of a tone (Barnes & Jones, 2000; Jones & Boltz, 1989; Jones, 1976; Large & Kolen, 1994; McAuley & Jones, 2003), attention should reach a maximum at the probe tone onset, as opposed to before or after the probe tone. As such, participants more accurately identify the probe tones that occur at the expected point in time compared to those that occur early or late.

The attentional window surrounding anticipated temporal events will differ between movement and no-movement trials. In the no-movement trials, the attentional window surrounding each beat in the sequence likely becomes wider through the silent portion of the trial, leading to a less precise internal representation of the beat. These trials lack an external reference for timing through this segment of the trial, with growing uncertainty with regards to event onsets and therefore less accurate detection of the probe tone. Conversely, in the movement trials, this attentional window will be narrower with a greater amount of attentional focus due to the presence an additional movement cue for timing when auditory information is lacking. This in turn will lead to a more refined internal representation of the stimulus with more attention allocated to the onset of the probe tone (see Figure 6.1). Additionally, when an auditory event, the participant's tap, and the peak of attention occur closer together in time, beat tracking should be more accurate (Morillon et al., 2014). In order to test more directly for this interpretation, a future study should examine neural oscillatory activity in movement trials, where participants synchronize taps with the sequence and through the silence but not at the probe tone, which leads to enhancements to timing abilities (as described in section 2.6 of this thesis). This study would test whether spectral beta power at the probe tone is greater when movement occurred prior to the timing judgment compared to power at the probe tone in the no-movement trials. This would support findings showing that spectral power can be used to predict listening accuracy in a temporal deviation task (Arnal, Doelling, & Poeppel, 2014) by suggesting that movement prior to deviants improvements detection perhaps due to greater connectivity between auditory and motor regions (Fujioka et al., 2012).

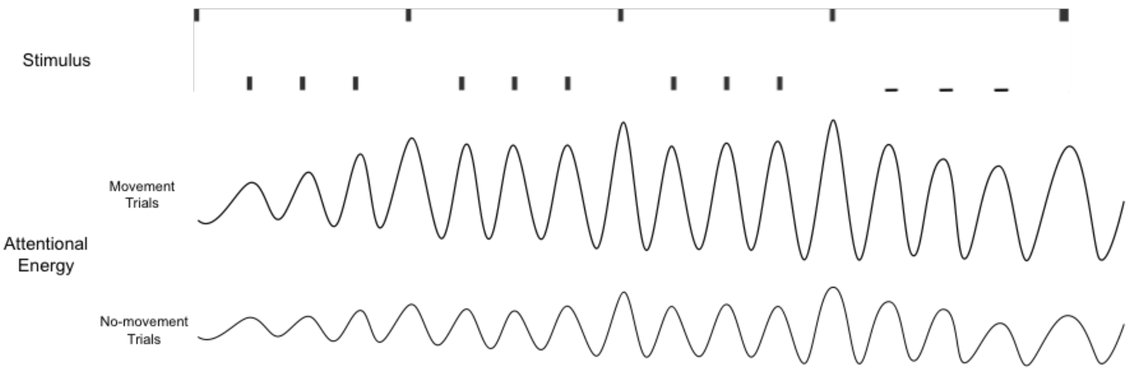

Figure 6.1. This schematic represents predicted attentional fluctuations in the paradigm implemented in this thesis for the movement and no-movement conditions based on oscillating attentional energy described and depicted in Large and Jones (1999). Attention is greater and more focused around auditory events in the movement vs. no-movement condition due to multisensory cues for timing. Additionally, there is a wider temporal window of attention surrounding events in the no-movement trials due to a less reliable internal representation.

The findings presented in this thesis also support current theories of perception and action coding that comprise an embodied cognition framework, suggesting that these processes rely on a common internal mechanism (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997). Specifically, these theories describe how actions and the sensory outcomes of those actions are processed in a similar fashion, and therefore involve similar cortical areas. As such, the integration of sensory and motor information allows for internal representations of external information, which contains bidirectional connections between the systems (Wolpert, Ghahramani, & Jordan, 1995). This work aligns specifically with the components of the model describing an embodied account of forward action processing, where action impacts the auditory perception of predicted temporal events (reviewed in Maes, Leman, Palmer, & Wanderley, 2014). Overall the findings reported in this thesis increase our understanding of bidirectional interactions between the processing of auditory and motor information, particularly forward action processing.

6.1.2 Motor timing

Of further relevance are the motor synchronization data that were collected throughout the experiments described in this thesis. Sensorimotor synchronization studies typically address questions related to human timing by examining finger tapping (see Repp, 2005 for a review). In order to accurately finger tap with external auditory information, we combine and weigh information from multiple sensory modalities, which leads to more consistent movement

(Hommel, Müsseler, Aschersleben, & Prinz, 2001; Wing, Doumas, & Welchman, 2010). Despite a perceived alignment between finger taps and sound events, tapping does not objectively align with these auditory events, often preceding these events by 20-80 ms (Aschersleben, 2002; Aschersleben & Prinz, 1995, 1997; Fraisse, 1980). The time difference between taps and sound events is thought to transpire from a discrepancy in the central timekeeper, described by the nerve conduction hypothesis (Figure 1.1) and the sensory accumulator model (Figure 1.2).

Chapter 2 reported a correlation between tap variability and the correctness of perceptual responses, indicating that participants with more consistent tapping performed better on the detection task, possibly due to a more accurate internalized representation of timing (Vorberg & Wing, 1996). The relation between tapping abilities and perception was further examined in Chapter 3, where tap asynchronies at the probe tone could directly predict perceptual responses. Additionally, taps were more temporally aligned with the auditory events when the auditory consequences of tapping were available as a reference compared to when it was masked. This finding extends previous reports of sensory integration to inform synchronization (Aschersleben et al., 2001; Mates et al., 1992) by demonstrating lower tap asynchronies when auditory feedback accompanies tapping, and how this extends to perceptual timing.

In Chapter 4 I examined how rhythmic expertise impacted sensorimotor interactions by assessing percussionists and non-percussionists in the deviation detection task with and without movement. Percussionists demonstrated significantly lower tap asynchronies than did non-percussionists when synchronizing stick tapping movements with external auditory stimuli. This corroborates findings that show a synchronization advantage for musicians (Aschersleben, 2002; Matthews et al., 2016; Repp & Doggett, 2007; Repp, London, & Keller, 2013; Repp 1999a, 2010), particularly percussionists (Cameron & Grahn, 2014; Krause et al., 2010). This also suggested that percussionists' superior movement synchronization led to more accurate perception, likely due to a more refined representation for external auditory information due to movement. Chapter 5 extended this idea further to include experience with a particular means of synchronizing. Although motor synchronization is thought to originate from a common motor source (Doumas & Wing, 2007; Wing & Kristofferson, 1973), different motor effectors synchronize movements with varying degrees of success. Finger tapping is more variable than stick tapping (Collier & Ogden, 2004; Fujii et al., 2011; Fujii & Oda, 2009; Madison et al., 2013) and it leads to smaller differences in timing abilities between movement and no-movement trials. This may be due to greater noise in the system for finger tapping due to fewer degrees of freedom available for manipulation (Latash, 2014; Todorov & Jordan, 2002). Additionally, benefits that arise due to training are only specific to movements that are highly practiced (see percussionist data in Chapters 4 vs. 5), consistent with reports of more accurate synchronization when movements are consistent one's training (Krause et al., 2010; Stoklasa, et al., 2012).

With respect to the synchronization data discussed in the preceding chapters, we may reconsider the sensory accumulator model discussed in Chapter 1 (see Figure 1.2). The sensory accumulator model (Aschersleben, 2002) posits that the disparity between taps and external auditory events is due to a central detection threshold. The tap occurs in advance of the auditory event but is perceived as synchronous because the signals arrive to the brain simultaneously following different processing times (Aschersleben et al., 2004). Since other factors influence the magnitude of tap asynchronies, this means that the thresholds for detection are likely altered based on elements such as sensory feedback, rhythmic expertise and motor effector synchronization. For this reason, I have illustrated an additional component to the sensory accumulator model that considers a modified tap onset depending on the synchronization conditions (see Figure 6.2). ‘Tap+’ in the figure indicates factors that benefit motor timing (lower tap asynchronies), such as auditory feedback from movements, rhythmic expertise and the motor effector used for synchronization. The data presented in Chapters 3 through 5 support the modification to the original figure depicting altered synchronization timing. Therefore, Tap+ can represent taps that are accompanied by auditory feedback compared to taps without this additional cue (Chapter 3), percussionist tapping compared to non-percussionist tapping (Chapter 4) or stick tapping compared to finger tapping (Chapters 4 and 5). The threshold for central detection and steepness of the function in the model varies between motor effectors (Aschersleben et al., 2004) and would also be altered by sensory cues and rhythmic expertise.

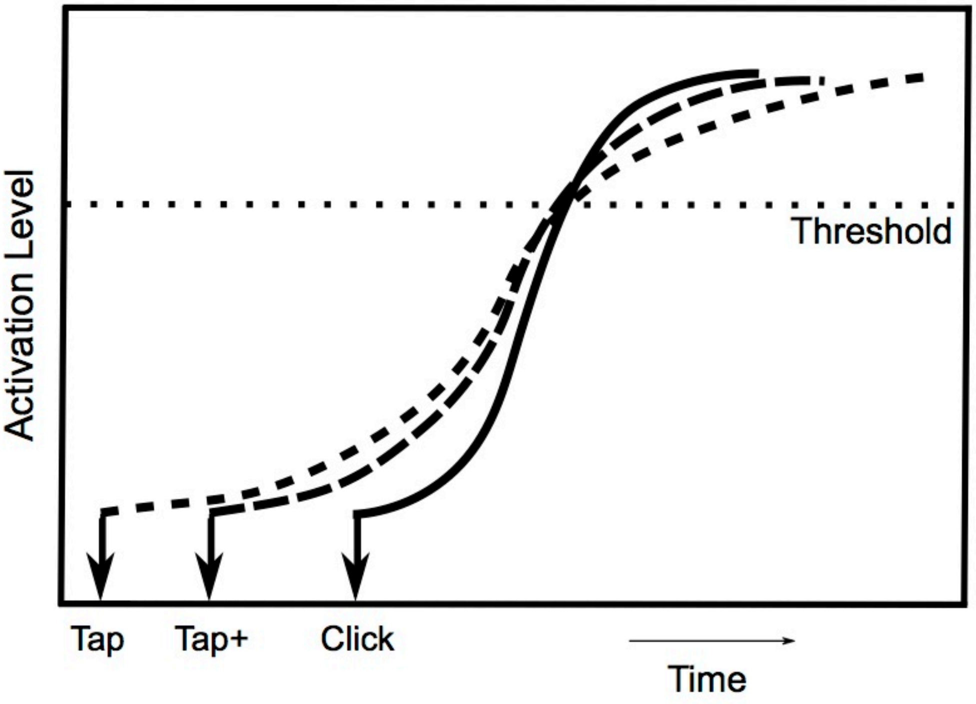

Figure 6.2. The sensory accumulator model considering additional factors (based on Aschersleben, 2002). ‘Click’ represents the auditory event with which taps are synchronized. ‘Tap’ indicates the original tap described by the model, which is based primarily on finger tapping data. ‘Tap+’ illustrates additional factors that serve to steepen the accumulation function, reducing the tap asynchrony between the tap and the click.

In Chapters 3 through 5 I made explicit comparisons between the tap asynchronies at the probe tone of the detection paradigm and the perceptual timing judgment associated with each trial. Each of these studies showed that the participants' tap asynchronies significantly predicted response accuracy, where trials in which final taps closely aligned with the expected onset of probe tones (demonstrating more accurate prediction) were more often accompanied by correct perceptual timing judgments compared to taps that were distant from the expected onset of probe tones. By considering how additional factors can influence motor timing in the sensory accumulator model, we can make predictions about how these factors impact both motor and perceptual timing abilities in synchronization tasks.

Comparisons between the perceptual judgments and tapping data in these studies also inform models describing internal event timers. The multiple timer model (Ivry, 1996; Ivry & Richardson, 2002) characterizes the internalization of timed events as a pacemaker or as oscillations used to compare with external information (similar to attentional modulations described by dynamic attending theory; see Large & Jones, 1999). Phase discrepancies between this "internal clock" and external events, such as a deviated probe tone in the detection task that fails to align with the phase of the internal clock, allows for rapid detection and phase correction (Vorberg & Wing, 1996; Wing, 2002). Synchronized tapping is also oscillatory in nature and can serve as an externalized reference (similar to the internal clock) for comparisons with the timing of probe tones in the paradigm used in this thesis. Taps that fail to align with probe tones may indicate phase discrepancies between the internal clock and the probe tone, allowing for more accurate perception. By considering the multiple timer model to describe motor synchronization data we can combine discussions of the internal clock and embodied cognition framework (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997) to further characterize shared processing between perception and action.

6.2 Limitations and Future Directions

6.2.1 Limitations and future directions of thesis work

This thesis is the first to report enhancements to perceptual timing as a consequence of movement and define specific factors that influence these enhancements. However, there are limitations to the experiments described throughout this thesis that leave unanswered questions and stimulate many future avenues for this research. In Chapter 2 the benefit to timing detection following movement was specific to the probe tone offsets that occurred later than expected. As such, late offsets were used to examine the effect of movement on perception that was observed in Chapter 2 for the studies in the remaining chapters. This was done to allow for a more rigorous assessment of the relationship between tapping and perception using more trials of each type (and thus obtaining more power in this assessment). However, it is still unclear whether the detection of early offsets is impacted by auditory feedback from tapping or rhythmic expertise. Future experiments should include both early and late offsets to determine whether a difference emerges between movement and no-movement trials in early offsets when participants are highly-trained percussionists.

The data presented in Chapter 3 outlined the impact of auditory feedback from tapping on detection abilities. The literature on sensorimotor synchronization describes the ways in which many sensory cues are combined to affect motor timing (Elliott, Wing, & Welchman, 2010; Elliott, Wing, & Welchman, 2011; Kolers & Brewster, 1985; Maduell & Wing, 2007). Tactile feedback likely plays an important role in this task, due to its importance in motor timing (Aschersleben, Gehrke, & Prinz, 2001; Balasubramaniam, Wing, & Daffertshofer, 2004; Drewing, Hennings, & Aschersleben, 2001). Vestibular information also informs timing information (Phillips-Silver & Trainor, 2008; Trainor, Gao, Lei, Lehtovaara, & Harris, 2009) and would provide additional sensory cues if participants bob their heads through the trials. Additionally, highly accurate temporal information in the visual domain containing moving stimuli may also facilitate timing abilities (Hove, Fairhurst, Kotz, & Keller, 2013; Hove, Iversen, et al., 2013). Future studies that deconstruct the relative roles of sensory feedback in this task will determine how these cues are integrated and handled in an optimal manner.

The finding in Chapter 4 that suggested percussionists perform no differently to non-percussionists in the listening-only task was surprising considering the literature describing percussionists displaying the most accurate timing abilities of all musician groups (Cameron & Grahn, 2014; Ehrlé & Samson, 2005; Krause et al., 2010). Since other research that report superior listening abilities in highly trained musicians (Drake & Botte, 1993; Jones, Jagacinski, Yee, Floyd, & Klapp, 1995; Jones & Yee, 1997; Lim, Bradshaw, Nicholls, & Altenmüller, 2003; Madison & Merker, 2002; Rammsayer & Altenmüller, 2006) and percussionists (Cameron & Grahn, 2014; Ehrlé & Samson, 2005; Krause et al., 2010) do not explicitly state that participants were instructed to remain entirely still during the task, it is difficult to compare with these studies directly without this information. With this in mind, one distinct limitation to this finding reported in Chapter 4 is that it is unclear whether percussionists' detection abilities were due to the lack of movement involved in the no-movement condition or if detection abilities were adversely affected by an active inhibition of movement in the no-movement condition (perhaps leading to divided attention). Although this speaks to the tight link between listening and movement in highly trained percussionists, it is impossible to differentiate these interpretations using the method presented in this thesis. Future studies aiming to differentiate these interpretations can implement a task where attention is divided in the movement condition (for example using a simultaneous *n*-back visual task; Pecenka, Engel, & Keller, 2013). Alternatively, the current paradigm may be implemented while participants undergo EEG recording to examine alpha power activity in the no-movement trials, a potential marker of inhibitory function

(Kayser, Wilson, Safaai, Sakata, & Panzeri, 2015; Paul, Sederberg, & Feth, 2015; Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011).

In Chapter 5, I reported differences in finger tapping between percussionists and non-percussionists, and how this movement influenced timing judgments. I found a small difference between groups in finger tapping variability and detection abilities following movement. Given the findings reported in Chapter 4, where stick tapping movements used by percussionists led to large differences in timing abilities compared to non-percussionists, this suggests that high degrees of training with a certain type of movement (stick tapping in percussionists) leads to effector-specific benefits in both movement and perception. However, with the current data, it is impossible to completely differentiate whether this is due to limitations of motor control that exist with finger tapping (Madison et al., 2013) or if training on a motor effector is domain-specific and does not easily transfer to other effectors. Finger tapping contains fewer degrees of freedom for manipulating movement variability than do larger stick tapping movements (Latash, 2014; Todorov & Jordan, 2002). I am currently running an additional study to examine the use of training-specific movements (i.e., piano keystrokes in pianists) in this paradigm to further examine the relative contributions of highly trained movements and limits to movement manipulation in different motor effectors. This will help distinguish relative contributions of movement training and motor constraints in the control of effector synchronization. While the data presented in this thesis lay the groundwork for examining forward effects of movement on perception of temporal prediction, many questions remain unanswered.

6.2.2 Future work for developing clinical applications

Although the findings presented in this thesis do not directly lend themselves to clinical applications, recent studies that include clinical populations have reported benefits to motor abilities when presented with rhythmic auditory information. Complex connections exist between auditory and motor regions of the brain (Rossignol & Melvill, 1976; Tecchio, Salustri, Thaut, Pasqualetti, & Rossini, 2000; Zatorre, Chen, & Penhune, 2007), which may play a critical role in these benefits. Recent clinical research has documented evidence for rhythmic auditory stimulation therapy as an effective option for treating disorders that affect movement abilities (see Thaut & Abiru, 2010 for a review). For example, individuals with Parkinson's disease that are presented with an auditory beat demonstrate improvements to stride length and gait (Ashoori, Eagleman, & Jankovic, 2015; McIntosh, Brown, Rice, & Thaut, 1997; Spaulding, Barber, Colby, Cormack, Mick, & Jenkins, 2013). This therapy also shows some benefit for other movement disorders including gait deficits in patients who suffer from the motor deficits that have arisen due to traumatic brain injury (Hurt, Rice, McIntosh, & Thaut, 1998) and stroke (Thaut, McIntosh, & Rice, 1997). The mechanisms underlying the positive effects of rhythmic auditory stimulation therapy are still somewhat unclear and future studies should further examine the processes underlying these benefits and the ways in which auditory prediction can facilitate motor processes. Future research should also assess whether improvements to motor responses executed with predictable auditory information observed in individuals suffering from sensorimotor disorders also lead to refinements in temporal discrimination abilities similar to those described in this thesis.

6.3 Implications and Conclusions

This thesis offers three important contributions to existing research on sensorimotor interactions in predictive timing: (1) Evidence for objective improvements to temporal prediction following synchronized movements; (2) The independent contributions of movement and auditory consequences of movement on this improvement, and (3) Interactions between rhythmic expertise and motor control limitations, and how this impacts perception.

Bi-directional interactions between auditory and motor systems are well-documented in sensorimotor integration research (Zatorre, Chen, & Penhune, 2007). The primary goal of this thesis was to determine how movement information could serve to improve perceptual timing abilities. Taken together, the chapters that comprise this thesis demonstrate explicit objective improvements to prediction following motor synchronization, which strongly support the embodied forward model of action processing (Maes et al., 2014). The forward model of action processing describes information flow from action to perception, where sensory information, including motor input, serves to facilitate or disambiguate auditory inputs from the external environment. Although much research has examined cross-talk between auditory and motor regions of the brain, including ways in which movement can modify perceptual information of auditory input, here I documented how movement can serve to improve representations of timing. To the best of my knowledge, the study presented in Chapter 2 was the first to document objective improvements to temporal prediction abilities as a result of movement synchronization. Since then, additional research has reported various improvements to timing detection in beat-based and interval timing tasks, corroborating evidence that motor synchronization serves to facilitate temporal abilities (Butler & Trainor, 2015; Iordanescu, et al., 2013, Press, et al., 2014)

Despite the high temporal precision of the auditory system, motor information can facilitate temporal abilities, perhaps by further refining the internal representation of external auditory cues. Movement may also increase attention allocation towards predictable auditory information, particularly if it aligns closely with the auditory event (Morillon et al., 2014). The finding that movement in the absence of auditory feedback can lead to this improvement, suggests that movement drives this improvement but that sensory feedback enhances the signal. Furthermore, due to extensive rhythmic training, percussionists gain an enhanced benefit to temporal prediction abilities when stick tapping with the sequence compared to non-percussionists, however this does not generalize to finger tapping benefits as a product of motor training. Current studies aim to disentangle the interpretation of these findings by examining synchronized finger movements in highly trained pianists.

Collectively this work extends previous work in the sensorimotor integration literature addressing how movement can serve to improve temporal prediction abilities, how auditory feedback might impact this interaction and in what manner extensive rhythmic movement training and select motor effectors affect this improvement. This paradigm is useful in examining movement and detection abilities in the same task, a critical step forward in understanding the impact of motor synchronization on auditory processing and temporal prediction abilities.

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