

**THE EFFECTS OF MUSICAL EXPERTISE ON
SENSORY PROCESSING**

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A THESIS SUBMITTED TO THE FACULTY OF
GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF ARTS

GRADUATE PROGRAM IN PSYCHOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO

November 2015

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ABSTRACT

The goal of this thesis was to assess sensorimotor musical experience and its impact on the way that individuals perceive and interact with real-world musical stimuli. Experiment #1 investigated multisensory integration in 14 musicians and 10 non-musicians using a two alternative forced-choice (2AFC) discrimination task, and was designed to examine whether musical expertise augmented multisensory enhancement. Musical experience did not alter the outcomes of multisensory integration, but there may be asymmetries between musicians and non-musicians in their use of auditory cues. Experiment #2 was a neuroimaging case study investigating the influence of musical familiarity on the kinesthetic motor imagery of dance accompanied by music in expert dancers. Familiarity resulted in increased hemodynamic responses in the supplementary motor area (SMA) and decreased responses in Heschl's gyrus (HG). These findings provide new evidence regarding the influence of musical expertise on sensory processing using real-world complex stimuli. This thesis suggests that expert practice shapes the way experts perceive and interact with their environments, and emphasizes the need for, and challenges of using naturalistic stimuli.

ACKNOWLEDGMENTS

I would like to sincerely thank my advisor Dr. Joseph F.X. DeSouza for providing me with the opportunity to learn, to create and to succeed. From my first day in your lab, you have provided me with so many opportunities to challenge myself and to grow as an academic. Throughout the demanding and sometimes unclear progression of my degree, you have always provided me with optimism and solutions. Thank you for your belief in me.

My lab-mates and colleagues have been an invaluable support for me throughout the past few years. Thank you to Paula, Gaby, Nevena, Charles, Paul, and all of the wonderful people I have had the opportunity to work with. You have all helped me overcome obstacles and become a better researcher. Paula, you are the rock in the lab; thank you for teaching, listening and sharing.

I would like to thank my committee member Dr. Richard Murray. Your insight and feedback have been instrumental in helping me complete my project. Dr. Laurence Harris, I owe you considerable thanks for spending the time to help me express ideas and design my project. I also want to thank all the participants whose time and involvement made all my research possible.

I have to thank my family and friends for supporting me throughout my degree. You may not have always known what I was talking about. You might have wondered how I was so busy with just a bit of school work. But believe me, your support and understanding has helped me adjust to academia and persevere over the years. Thank you so much to my parents for their support and unwavering belief. Your confidence in me has helped me overcome so much. Thank you to my future in-laws for their heartfelt guidance and support. Finally, thank you Hilary. Thank you so much for being my role model, my rock, my biggest supporter and for being my closest friend.

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LIST OF ABBREVIATIONS

A	–	Auditory Discrimination Task
A1	–	Primary Auditory Cortex
ANOVA	–	Analysis of Variance
AV	–	Audiovisual Discrimination Task
BOLD	–	Blood-Oxygen-Level Dependent
ERP	–	Event-Related Potentials
fMRI	–	Functional Magnetic Resonance Imaging
GGe	–	Greenhouse-Geisser Epsilon
GRAPPA	–	Generalized Autocalibrating Partially Parallel Acquisitions
HG	–	Heschl's Gyrus
k	–	Kernel Width
KMI	–	Kinesthetic Motor Imagery
M	–	Musician Group
MLE	–	Maximum Likelihood Estimate
NM	–	Non-Musician Control Group
PM	–	Pre-Motor
PPC	–	Posterior Parietal Cortex
PT	–	Planum Temporale
ROI	–	Region of Interest
SEM	–	Standard Error of the Mean
SMA	–	Supplementary Motor Area
STG	–	Superior Temporal Gyrus
STS	–	Superior Temporal Sulcus
TMS	–	Transcranial Magnetic Stimulation
V	–	Visual Discrimination Task
V1	–	Primary Visual Cortex
YOU	–	Youth, Outreach and Understanding Dance
α	–	Auditory Threshold

1. General Introduction

1.1 Sensorimotor Musical Expertise

Music is one of the most universal sensory stimuli to all humans (Clarke, Dibben & Pitts, 2010; Hagen & Bryant, 2003; Trainor & Corrigall, 2010). Across societies, virtually all individuals interact with music, whether alone or in larger social contexts (Burney, 2010). However, certain individuals have significantly greater exposure to music and engage in greater sensorimotor interactions with music than the average person. These individuals routinely interact with music in a way that the average individual does not. Several different lifestyles, professions, and behaviours produce such musical expertise, but the largest categories of experts are musicians and dancers. It is important here to distinguish *active* musical expertise from *passive* exposure to music. Enough passive exposure to music could create a type of expertise, whether this experience is of music in general, a specific genre, or of a favorite performer. In this thesis, musical expertise is defined as the result of significant interactions performing sensorimotor transformation, generating highly coordinated and structured movements as a function of some musical stimulus. This thesis is aimed at elucidating the role of musical expertise on aspects of sensory processing.

Experiment #1 is a cross-sectional psychophysics experiment investigating multisensory integration, and is designed to examine whether multisensory integration is modulated by musical experience. This experiment compares the multisensory integration of a naturalistic musical stimulus between experienced musicians and non-musician controls.

Experiment #2 is a neuroimaging case study investigating neural activity as measured through functional magnetic resonance imaging (fMRI) of the kinesthetic motor imagery of dance accompanied by music in dancers. This experiment is aimed at understanding the role of sensorimotor expertise and familiarity on neural activity during sensorimotor transformations of naturalistic musical stimuli.

1.2 Musicians

Musicians are a particularly interesting case of expertise. Whereas many experts in other domains have plenty of exposure to situations and stimuli that most people do

not, virtually every person has substantial exposure with music, whether intentionally or incidentally in their every-day environments (Clarke, Dibben & Pitts, 2010; Nettl, 2005). Therefore, what makes experienced musicians unique from other individuals is their participation in structured training and rehearsal. This provides researchers with the ability to qualitatively and quantitatively assess each musician's degree of expertise (i.e., years of experience, level of training, and hours of practice per week), and this information is essential when investigating the influence of expertise on perception and behaviour. For these reasons, musicians represent a unique model for studies of learning and neuroplasticity (Münste, Altenmüller & Jäncke, 2002; Peretz & Zatorre, 2005).

Musicians gain their unique exposure to music via two streams: through critical listening and through music production. While learning their art, musicians must analyze both their instructors' musical examples, as well as critically evaluate exemplar music (such as live performances and other audio media). These abilities to actively process musical stimuli are particularly crucial when musicians develop their unique sound while learning to correctly play their instrument. Aesthetics are important in music, and to master their art, musicians must develop a pleasing and appropriate sound, regardless of the genre. One's sound does not only include the notes that they play, or the rhythms that they choose, but it also includes their speed, timbre, intonation, dynamics and phrasing (Clendinning & Marvin, 2013). Timbre and phrasing are particularly difficult to communicate verbally, but are best understood via example. Thus, it is important that musicians develop the ability to evaluate these elements in order to reproduce them.

Musicians' significant sensorimotor expertise comes from their production of music, through years of learning, practice and performances. A less popularly discussed characteristic of musicians and musical performance is their mastery of highly coordinated movements. Musicians coordinate various parts of their bodies to manipulate their instruments in a highly synchronized and coordinated fashion. All musicians, regardless of the instrument they play or the genre of music they perform, require a high degree of coordinated movements. Yet, the exact nature of these movements and the extent of their scope vary widely depending on the instrument and genre of choice. A simpler instrument, such as one's voice, still requires some motor coordination to move and shape air, generating specific sounds and tones. A pianist

requires the coordination of many body parts, including their legs, torso, and upper limbs. Percussionists possibly have the most complex movements in music performance, including the coordination of intricate movement patterns involving all limbs. High levels of coordination that produce aesthetically pleasing and appropriate sounds are a prime example of sensorimotor expertise, as they must conform to strict spatial and temporal requirements. Musicians' movements need not only be highly articulate, but also well timed. Therefore, the command of such challenging movements requires substantial repetition and training.

Extensive exposure to music and training has been shown to modulate and enhance numerous cognitive abilities, including verbal (Anvari, Trainor, Woodside & Levy, 2002; Kolinsky, Cuvelier, Goetry, Peretz & Morais, 2009; Moreno & Besson, 2006), spatial-temporal abilities (Hetland, 2000; Rauscher, Shaw & Ky, 1993; Stoesz, Jakobson, Kilgour & Lewycky, 2007), and mathematical abilities . Additionally, musical training has been shown to change neural processing across the cortex (Chen, Penhune & Zatorre, 2008; Kaganovich et al., 2013; Musacchia, Sams, Skoe & Kraus, 2007), as well as brain morphology (Hyde et al., 2009).

1.3 Dancers

Dancers, like musicians, often develop their art through years of highly structured rehearsal and instruction. It is most common for the best performers in music and dance to start their training from a young age (Parviainen, 1998). Whereas musicians receive their exposure to music through both critical listening and music production, expert dancers typically gain substantive experience with critical listening alone (arguably this may not be entirely true for tap-dancers or other percussive styles of dance; additionally, there are often cases of individuals with both dance and musical training). It is important for dancers to critically evaluate the pieces of music to which they are performing or choreographing a dance for a few reasons. Firstly, the tempo and rhythm of a given piece of music acts as the timing mechanism for dancers' movements. Movement sequences are often tightly coupled with the rhythmic structure of a song, particularly the song's underlying beat (Brown, Martinez & Parsons, 2006; Grahn & Brett, 2007; Phillips-Silver & Trainor, 2005). Secondly, it is often important for dancers, when choreographing or performing a dance to consider the underlying emotional tone of the accompanying song (Christensen, Gaigg, Gomila, Oke & Calvo-Merino, 2014). A song's emotional

valence is not conveyed by one aspect of the music in particular, but it is conveyed by the song's key signature, melody, tempo and rhythm together (Koelsch, Fritz, V Cramon, Müller & Friederici, 2006). For a dancer to perform movements that are aesthetically congruent with a musical piece, it is important for them to evaluate these properties thoroughly, and to shape their dance to their music.

As both musicians and dancers master their crafts, they not only develop significant expertise with the sensorimotor transformations involved in producing their art, they also develop expertise processing familiar sensory stimuli (i.e., the musical pieces they perform and their related musical genres) (Ali & Peynircioğlu, 2010; Olshansky, Bar, Fogarty & DeSouza, 2015; Satoh, Takeda, Nagata, Shimosegawa & Kuzuhara, 2006; van den Bosch, Salimpoor & Zatorre, 2013; Vatakis & Spence, 2006).

1.4 Expertise

Expertise is a common term used to describe an individual's ability to perform a highly mastered action. Typical examples of experts are medical specialists, cab drivers, shepherds, chess players, actors, athletes and musicians (Bourne, Kole & Healy, 2014; Woollett, Spiers & Maguire, 2009). Regardless of the field of expertise, skilled proficiency is the result of structured learning and extensive experience (Ericsson, 2008). Within an expert's area of specialization, their familiarity with sensory events, including their physical properties (Gorman, Abernethy & Farrow, 2013; James & James, 2013), and their knowledge of contextual information regarding expected outcomes influence experts' observational strategies, and their interpretation of sensory events (Dick, Lee, Nusbaum & Price, 2011).

An example of this is the observation of a familiar sport (in this case baseball). To a seasoned baseball fan or athlete, following a game is relatively easy. The experienced observer knows where to look, and when, as well as relevant contextual information (e.g., rules, structure and significance). Conversely, an individual with little or no experience with baseball, even after being exposed to the rules and strategies within the game, would not have this information internalized and would have difficulties following the game without the efficient observational strategies of baseball experts.

Experience driven knowledge and strategy formation considerably influences how people process and interact with their environment, providing experts with unique

skills and capacities (Bourne, Kole & Healy, 2014; Ericsson, 2008; Williams & Ericsson, 2005). As specialized experience increases, individuals tend to make judgments about associated sensory events more quickly and accurately (Gorman, Abernethy & Farrow, 2013; Karni et al., 1995). A baseball umpire who has spent many years judging whether a pitch is a 'strike' or a 'ball' has the *expertise* to outperform (in terms of accuracy and speed of processing) even the most passionate of fans. Expertise is the mechanism that produces a high level of task relevant performance in an expert, within a constrained range of events (Bourne, Kole & Healy, 2014). Expertise typically arises from deliberate practice or training with an activity or situation (Ericsson, 2008), and results in rapid intuitive judgments to stimuli (Dreyfus & Dreyfus, 2005). One can become an expert in virtually any kind of event (or object), which provides some sort of consistent information regarding stimuli and responses.

Along with these effects of expertise, there are additional behavioural consequences of extensive musical experience. The deliberate practice of musical performance requires the training of both multisensory and motor skills that are correlated with improved performance (Hyde et al., 2009). Expert musicians, such as percussionists, are better than novice musicians at perceiving incongruence in rhythmic structures (Petrini et al., 2009), as well as temporal reproduction (Cicchini, Arrighi, Cecchetti, Giusti & Burr, 2012). Additionally, musicians have been found to outperform non-musicians (i.e., shorter reaction times) in tasks that require the judgment of both semantic and metric congruency (Marie, Magne & Besson, 2011). Investigating memory recall in an expert pianist, Chaffin and Imreh (2002) showed that following extensive practice with a piece of music, a concert pianist utilized declarative memory to guide skilled motor performance in the free recall of the practiced piece 27 months following practice (Chaffin & Imreh, 2002). This expertise is argued to be similar to that of an expert chess-player, requiring conceptual representations of the previously mastered song.

Top-down processes are another factor that may impact the effect of familiarity on music processing. Research has shown reduced neural activity in auditory processing areas such as the superior temporal cortex as a result of repetition suppression (Bergerbest, Ghahremani & Gabrieli, 2004), and stimulus expectation (Andics, Gál, Vicsi, Rudas & Vidnyánszky, 2013). By simply having extensive experience

with a stimulus (i.e., a song) neural activation to subsequent presentations of the same stimulus have been shown to be modulated by cognitive factors such as memory and anticipation.

The neuropsychological organizational mechanism called “chunking” is a related, yet distinct concept to stimulus expectation (Gobet et al., 2001). Chunking is the psychological phenomenon where individuals tend to group information into “chunks” in order to organize their mental representations (Mayzner & Adler, 1965). Although it is often described as a mnemonic technique or a neuropsychological property of human memory, chunking has also been described and investigated in the context of perception and learning (Gobet, 2005). Chunking is therefore important for expert performance, and has been shown to reflect two mechanisms. *Goal-oriented chunking*, which is the deliberate, conscious process of chunking information, and *perceptual chunking*, which is the automatic involuntary process of chunking perceptual information (Gobet et al., 2001). It has been argued that both perceptual as well as goal-oriented chunking are critical for expert performance (Bartlett, Boggan & Krawczyk, 2013; Gobet, 2005; Waters & Gobet, 2008).

1.5 Multisensory Integration

Our environments are busy and chaotic, yet we usually navigate them with ease. From the moment you wake up in the morning, you are exposed to a battery of interactions, events, and ever-changing environments. On our daily commute, walking through the hallways of buildings and busy public spaces, we are continuously taking in huge amounts of information from the senses. Indeed information from all five senses is constantly coming into our bodies, yet we effortlessly are quite efficient at only attending to those inputs that are most pertinent and salient, while ignoring distractions. This is a very important skill to have if one wishes to function in social settings, and engage in their environment. It is crucial for social interaction, and an inevitable hurdle in modern cities where transportation, infrastructure and advertisements alone generate limitless sensory events.

When we consider the nature of our environments, and the sensory information that we are exposed to (for example, watching our favorite musician perform live in a loud and crowded theater), it is typically evident that the various modalities we perceive (auditory and visual features) originate from unified source (the musician we are

observing). Given a noisy environment, we often need to rely on information from multiple senses in order to perceive and interpret events properly.

When we hear, our nervous system is taking signals from the hair cells in the ears, via the brainstem and subcortical areas, and then finally to the auditory cortex (A1) (Demanez & Demanez, 2003). When we see, our brain is taking signals from the ganglion cells in the retina, again through subcortical areas, and then to the visual cortex (V1) (Schiller, 1986). These are examples of *unisensory* perception, and a similar pathway can be outlined for all of our senses. Often these pathways are discussed and investigated separately and there have been countless seminal experiments examining these sensory mechanisms individually (Dowling & Boycott, 1966; Hubel & Wiesel, 1977; Hudspeth & Gillespie, 1994; Kanwisher, McDermott & Chun, 1997).

Investigations into the mechanisms underlying unisensory processing have led to the vast majority of scientific knowledge on human perception. This research has resulted in significant knowledge into the functional role of much of the occipital, temporal and parietal lobes, as well as various key perceptual subcortical structures such as the colliculus and thalamus (DeSouza et al., 2011; DeSouza, Menon & Everling, 2003; Mishkin & Ungerleider, 1982; Schiller, 1986). What has become increasingly evident is that a detached investigation of each of our senses individually is an inadequate strategy for explaining the entirety of human perception (Cappe, Rouiller & Barone, 2009; Meredith & Stein, 1986; Spence & Driver, 2004; Stein, Huneycutt & Meredith, 1988; Stein & Stanford, 2008). A holistic description of human sensation and perception necessarily includes not only the investigation of each of these senses, but additionally the investigation of how, why, and where these senses interact and influence each other, and moreover what these interactions mean for human cognition and neurobiology.

Multisensory integration is the mechanisms, neurons and networks in the brain that combine the signals from two or more sensory pathways (Avillac, Ben Hamed & Duhamel, 2007; Beauchamp, 2005; Calvert, 2001; Cappe, Rouiller & Barone, 2009; Stein & Stanford, 2008; Stevenson et al., 2012). Multisensory integration is believed to function on three main principles. The spatial principle dictates that unisensory stimuli that appear in the same spatial location are more strongly integrated than stimuli that appear in two separate locations. Similarly, the temporal principle states that unisensory

stimuli that appear at the same moment in time are more strongly integrated than stimuli that appear at two separate moments in time. Finally, the principle of inverse effectiveness states that multisensory integration becomes stronger as responsiveness to the component unisensory stimuli reduces (Holmes & Spence, 2005).

At the behavioural level, multisensory integration has been shown to enhance performance on a variety of tasks, including stimulus detection tasks, improving individuals' ability to detect stimuli at varying levels of saliency, as well as improving accuracy in both humans (Calvert, Campbell & Brammer, 2000; Gillmeister & Eimer, 2007; Lovelace, Stein & Wallace, 2003; Vroomen & de Gelder, 2000), and animals (Stein, Meredith, Huneycutt & McDade, 1989; Stein & Rowland, 2011). Additionally, during experiments that require rapid responses to stimuli, multisensory inputs can result in faster reaction times when compared to unisensory stimuli (Calvert, Campbell & Brammer, 2000; Liu, Zhang, Campos, Zhang & Sun, 2011). Because of its role in enhancing both stimulus saliencies as well as behavioural responses, multisensory integration is an incredibly important perceptual mechanism.

At the neural level, multisensory integration is defined as a significant difference in neural activity evoked by multisensory stimuli, compared to the resultant neural activity of individual unisensory stimuli (Meredith & Stein, 1983; Stein & Stanford, 2008). This integration can only occur in bimodal neurons, which respond to multiple sensory modalities and cross-modal stimuli. In order to be considered a meaningful processing unit of multisensory signals, the combination of cross-modal signals ought to have a distinct influence on neurons' activity when compared to unisensory components. This can come in the form of either multisensory enhancement, or multisensory depression (Calvert, Spence & Stein, 2004; Gillmeister & Eimer, 2007; Spence & Driver, 2004) (Figure 1). Enhancements can be the result of additive and superadditive effects, where two cross-modal inputs have a greater effect on a neuron (i.e., in terms of cellular depolarization or hemodynamics) than either one of the unisensory inputs alone (Stevenson, Geoghegan & James, 2007; Werner & Noppeney, 2010). The additive response of a bimodal neuron to an auditory stimulus in combination with a visual stimulus would be the sum of the two unisensory responses, whereas the superadditive response to the same combination of stimuli would be greater than the sum of the two unisensory responses. Multisensory depression on the other hand is the result of

subadditive effects, where the response of a bimodal neuron to a combination of stimuli is less than the combined response to each input alone (Cappe, Thut, Romei & Murray, 2010; Werner & Noppeney, 2010) (Figure 1).

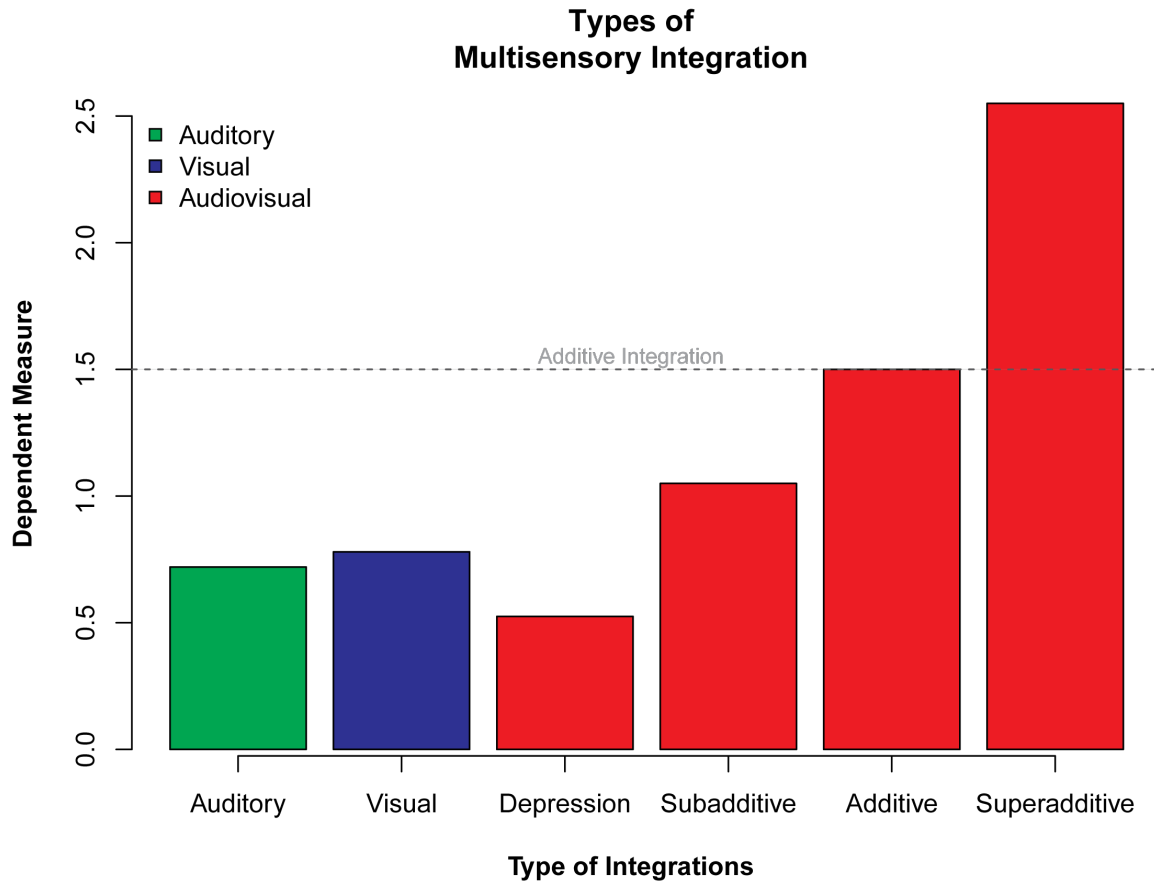


Figure 1. Types of Multisensory Integration. An example of the various outcomes of multisensory integration within a neuronal or behavioural measure (e.g., number of spikes, hemodynamic signals, performance accuracy ...etc.) depicting the integration of Auditory (green) and visual (blue) sensory signals. Forms of multisensory integration (red) include: Depression – where the measured outcome is less than either unisensory outcome; Subadditive – where the outcome is less than the linear summation of each of the unisensory outcomes; Additive – where the outcome is equal to the linear summation of each of the unisensory outcomes; and Superadditive - where the multisensory outcome is greater than the linear summation of each of the unisensory outcomes.

One of the most studied multisensory areas in the brain, the parietal cortex, particularly the posterior parietal cortex (PPC), has been shown to be instrumental in integrating visual, auditory, tactile and vestibular sensory inputs. In addition, the PPC has been shown to play a large role in sensorimotor transformation for visually guided movements, in both animal models (Andersen, Snyder, Bradley & Xing, 1997; Avillac, Denève, Olivier, Pouget & Duhamel, 2005; Schlack, Sterbing-D'Angelo, Hartung,

Hoffmann & Bremmer, 2005; Stricanne, Andersen & Mazzoni, 1996), and humans (Cohen & Andersen, 2002; DeSouza et al., 2000; Molholm et al., 2006) . The PPC has long been considered part of the primate *association cortex* (Mountcastle, Lynch, Georgopoulos, Sakata & Acuna, 1975), which is believed to be critical for higher order perception and cognition. Since roughly 2002, due partially to the accessibility of functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) technology, as well as a handful of human electrophysiological studies, there has been an influx of research on multisensory processing in the human PPC. Hadjikhani (1998), as well as Calvert and colleagues (2000, 2001) conducted some of the first neuroimaging studies attempting to demonstrate the same multisensory effects observed in animal electrophysiology (enhancements and depressions) in humans (Calvert, 2001; Calvert, Campbell & Brammer, 2000; Calvert, Hansen, Iversen & Brammer, 2001; Hadjikhani & Roland, 1998). What they found was that indeed there are analogous parietal areas in humans to those outlined in the monkey cortex (for a review of non-human primate findings, see (Andersen, Snyder, Bradley & Xing, 1997; Cohen, Cohen & Gifford, 2004; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann & Bremmer, 2005)

As a sensorimotor transformation area, sensory integration in the human PPC has largely been investigated within the context of reaching and grasping tasks involving the integration of visual and tactile information (Binkofski et al., 1998; Culham, 2004; Culham et al., 2003). In terms of auditory and visual sensory integration, Cappe and colleagues (2010) discovered subadditive, non-linear interactions occurring roughly 50–60 ms after stimulus onset in the PPC area (Brodmann's area 39/40) using event-related potentials (ERP) (Cappe, Thut, Romei & Murray, 2010). In this study, audiovisual stimuli produced significantly lower evoked potentials than would be expected if there were additive effects within a specific time window. Previous research using ERP measures resulted in data that was difficult to interpret under the additive model of multisensory integration, which had been well established in both the electrophysiological and fMRI literature. These earlier studies (Giard & Peronnet, 1999; Molholm et al., 2002) have been criticized due to their lack of control for common activity between unisensory and multisensory tasks, such as anticipatory potentials and motor responses. Cappe and colleagues (2010) were among the first to identify the timing, topographic stability,

directionality (i.e., enhancement vs. depression) and sources of audiovisual integration in humans using ERP's.

The temporal lobes are major processing centers of several different cognitive faculties, such as audition (Zatorre, 2001), speech and language (Ghazanfar, Chandrasekaran & Logothetis, 2008; Tervaniemi & Hugdahl, 2003), and memories (Nadel & Peterson, 2013). In addition to these cognitive functions, the temporal lobes have received quite a bit of attention as a major multisensory processing area. Within the temporal lobes, there are different regions where bimodal cells have been identified, including the superior temporal sulcus (STS), A1 and belt areas (Beauchamp, Argall, Bodurka, Duyn & Martin, 2004; Bizley, Nodal, Bajo, Nelken & King, 2007; Werner & Noppeney, 2010). The STS has been shown to be an important cortical processing area for speech perception in particular, integrating auditory and visual sensory signals in both superadditive (Barracough, Xiao, Baker, Oram & Perrett, 2005; Crosse & Lalor, 2014; Stevenson, Geoghegan & James, 2007) and subadditive manners (Beauchamp, Argall, Bodurka, Duyn & Martin, 2004). In addition to responding to the presence of multisensory stimuli, the STS is also sensitive to the congruency (synchrony) of audiovisual events (i.e., whether or not the audio and visual components occurred together, or with delay) (Barracough, Xiao, Baker, Oram & Perrett, 2005; Bishop & Miller, 2009; Meienbrock, Naumer, Doehrmann, Singer & Muckli, 2007). The superior temporal cortices have also been implicated in the processing of somatosensory stimulation, showing superadditive effects when combined with auditory stimuli (Sperdin, Cappe, Foxe & Murray, 2009).

Non-human primate research investigating mirror neuron networks have given rise to an extensive literature describing bimodal neurons in the pre-motor (PM) cortex (particularly in the ventral PM) located in the frontal lobes (Bremmer et al., 2001; Graziano & Gandhi, 2000; Graziano, Hu & Gross, 1997; Keysers et al., 2003; Meredith & Stein, 1986). Neurons in this region have been described as “audiovisual mirror neurons” by Keysers and colleagues (Keysers et al., 2003). Graziano and colleagues though, have additionally found the PM to be responsive to tactile stimulation (Graziano & Gandhi, 2000; Graziano, Taylor & Moore, 2002). In monkeys and human alike, the PM has been shown to play a role in multisensory integration, particularly in relation to one's sense of their own body (Gentile, Petkova & Ehrsson, 2011; Zeller, Gross, Bartsch,

Johansen-Berg & Classen, 2011), in sensory perception relevant to motion and motor behaviour (Bremmer et al., 2001; Graziano, Taylor & Moore, 2002; Kaplan & Iacoboni, 2007; Kuchenbuch, Paraskevopoulos, Herholz & Pantev, 2014), and in bimodal divided attention (Johnson, Strafella & Zatorre, 2007). Furthermore, a handful of human electrophysiological studies have reported mirror neuron activity (Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010), as well as multisensory processing (Quinn et al., 2014) which closely matches the findings from animal research, suggesting a close degree of similarity between humans and monkeys.

Several different areas in the human prefrontal cortex have repeatedly been shown to be modulated by multisensory stimuli. The dorsolateral prefrontal cortex has been shown to be involved in the binding of audiovisual stimuli (Johnson, Strafella & Zatorre, 2007; Meienbrock, Naumer, Doehrmann, Singer & Muckli, 2007) with the supplementary motor area (SMA) (Paraskevopoulos, Kuchenbuch, Herholz & Pantev, 2012) and other frontal areas similarly responsive to audiovisual stimuli (Kaplan & Iacoboni, 2007; Laurienti et al., 2003; Liu, Zhang, Campos, Zhang & Sun, 2011). Both audio-tactile (Kuchenbuch, Paraskevopoulos, Herholz & Pantev, 2014) and visual-tactile (Gentile, Petkova & Ehrsson, 2011; Quinn et al., 2014) integration regions have also been discovered in the human prefrontal cortices, indicating that the frontal lobes are involved in numerous types of multisensory stimulus processing.

One of the most researched 'unisensory' cortical areas, the occipital lobes have long been believed to exclusively process vision, including early low-level visual features such as colour perception, as well as higher level features such as object recognition, which are split into two major pathways, the dorsal ("Where") and ventral ("What") streams (Goodale & Milner, 1992). Over the past two decades, researchers have begun studying areas within the occipital lobes in order to determine its involvement in multisensory processing. There have been numerous human neuroimaging studies which have shown evidence of significant connections between inferior and lateral occipital cortices and regions within the temporal (Beer, Plank, Meyer & Greenlee, 2013; Bishop & Miller, 2009) and parietal (Molholm et al., 2006; Quinn et al., 2014) lobes. Connections between the occipital lobe and the STS in particular have been implicated in multisensory processing of speech, with evidence of auditory modulation within occipital areas (Barutchu, Freestone, Innes-Brown, Crewther & Crewther, 2013;

Gougoux, Zatorre, Lassonde, Voss & Lepore, 2005; Paraskevopoulos, Kuchenbuch, Herholz & Pantev, 2012). Whereas ventral occipital regions appear to respond to all audiovisual stimuli, dorsal and lateral regions have been shown to be preferentially responsive to spatially synchronous audiovisual stimuli (Macaluso, George, Dolan, Spence & Driver, 2004). Furthermore, the lateral occipital cortices have been shown to respond to both visual as well as tactile information regarding objects shape (Beauchamp, 2005), suggesting an important role in coordinating visually guided movements. In addition to higher order visual processes, multisensory influences have also been shown to produce non-linear interaction within early visual processing areas, which have been shown to influence behavioural responses (Romei, Murray, Merabet & Thut, 2007).

Whether in terms of highly specialized professional contexts, or simply in terms of navigating and interacting with our every-day environment, it is often advantageous (or at times critical) to have quick and accurate responses to sensory events. Part of our capacity to interact with our environments and to respond to stimuli comes from our ability to organize objects, events and places into unified mental representations.

1.6 The Effects of Musical Expertise on Sensory Processing

This thesis is aimed at elucidating the role of musical expertise on aspects of sensory processing. Musical expertise can mean numerous things, and experts themselves can come from vastly diverse background, with unique abilities and experiences. Here two of the most common examples of musical experts are investigated.

Experiment #1 is a cross-sectional psychophysics experiment investigating multisensory integration, and is designed to examine whether multisensory integration is modulated by musical experience. This experiment compares the multisensory integration of a naturalistic musical stimulus between experienced musicians and non-musician controls.

Experiment #2 is a neuroimaging case study investigating neural activity as measured through fMRI of the KMI of dance accompanied by music in dancers. This experiment is aimed at understanding the role of sensorimotor expertise and familiarity on neural activity during sensorimotor transformations of naturalistic musical stimuli.

Together these experiments provide behavioural and neuroimaging evidence of the role of musical expertise on naturalistic sensory processing. This research explores a largely under-studied field of musical expertise using real-world musical stimuli. The goal of this thesis is to assess whether sensorimotor musical experience has a significant impact on the way that individuals perceive and interact with musical stimuli. These experiments represent just the beginning of a research line that should be conducted in the future, and inform us about the role that music plays in influencing our sensory experiences.

2. Experiment #1

2.1 Background

In experiment #1, we examined how musicians and non-musicians differ in their behavioural response to naturalistic multisensory stimuli, such as the observation of a musical instrument being played with the accompanying congruent sound. This stimulus is naturalistic as it contains a musician generating congruent visual and auditory stimuli together, producing a strong multisensory event (Lee & Noppeney, 2011; Pynn & DeSouza, 2010; Schutz & Kubovy, 2009; Stein & Stanford, 2008). This stimulus is additionally beneficial as a multisensory stimulus as it can be considered more ecologically valid than the typical stimuli used in the literature (e.g., the flashes of light coupled with sounds such as in (Stein, Meredith, Huneycutt & McDade, 1989).

Psychophysical experiments exploring multisensory enhancement typically test participants on a perceptual task during two or more unisensory conditions, followed by the testing of the same task during a multisensory condition that integrates the stimuli previously presented during the unisensory conditions. Each participant's performance on the unisensory tasks is then compared with their performance on the multisensory task in order to ascertain any performance enhancements provided by the multisensory stimuli. Additionally, participants' observed multisensory enhancement is often compared to modeled estimates of multisensory enhancement, such as Bayesian based models of optimal cue integration. This is where using a musical paradigm provides additional benefits over more conventional simplistic multisensory paradigms. By utilizing both experienced musicians as well as non-musician controls, we can test the effects of expertise on individuals' ability to process a naturalistic audiovisual scene, as well as how this impacts their multisensory enhancement.

Over the past decade, several groups of researchers have begun examining multisensory integration within musicians, using musical stimuli. Some of these experiments have begun to examine more basic perceptual mechanisms, such as temporal binding windows of sensory events (Lee & Noppeney, 2014; Lee & Noppeney, 2011), temporal-order judgements (Hodges, Hairston & Burdette, 2005; Vatakis & Spence, 2006), sensitivity to asynchrony (Petrini, Holt & Pollick, 2010), and duration judgements (Schutz & Kubovy, 2009; Schutz & Lipscomb, 2007). Other research has

been focused on elucidating the role of multisensory musical stimuli on higher order cognitive aspects of music, such as regulating emotional responses to music and expressivity (Krahé, Hahn & Whitney, 2015; Vuoskoski, Thompson, Clarke & Spence, 2014) as well as the listener's sense of phrasing and tension (Vines, Krumhansl, Wanderley & Levitin, 2006). Even with the considerable recent advancements in research on the multisensory processing of musical stimuli, there are still some fundamental questions which remain unanswered. One unanswered question is whether musical experience influences musicians' ability to discriminate multisensory musical notes (i.e., notes that we both hear and see being performed) and whether experience impacts the way in which musicians integrate multisensory stimuli?

Experiment #1 investigates whether a musician's extensive experience perceiving and interacting with naturalistic musical performances impacted the degree to which they experience multisensory enhancement, as compared to both modeled estimates and the multisensory enhancement of non-musicians. In order to accomplish this, we tested both musicians and non-musicians in a two-alternative forced choice pitch discrimination task using the method of constant stimuli.

We hypothesized that, due to their perceptual and motor experience (i.e., top-down prior knowledge about the stimulus and contextual information - see Liu, Zhang, Campos, Zhang & Sun, 2011), musicians would experience greater multisensory cue reliability than their predicted maximum likelihood estimates (MLE) of optimal cue integration values, which are solely based on bottom-up perceptual integration. This hypothesis predicts that musicians would employ additional information from a multisensory stimulus that they could not have utilized during unisensory perception, which is inaccessible to those without extensive exposure to musical stimuli. Experience dependent perceptual cues such as timber/location relationships (i.e., knowledge regarding the connection between a notes location on an instrument and its timber) would be irrelevant and imperceptible without both auditory and visual cues. Thus, due to musicians' prior knowledge about music production, they would use experience dependent perceptual cues (such as knowledge about pitch / location or timber / location relationships), and as a result would be more successful at discriminating between two multisensory cues than controls, and would deviate from their modeled enhancement. Alternatively, our null-hypothesis was that this same prior knowledge would not impact

musicians' multisensory performance, and thus musicians would perform equally well during multisensory perception as was predicted by their MLE values.

We predicted that non-musicians would experience equivalent multisensory gains to their predicted MLE values, as they should rely solely on stimulus driven information and should lack any experience dependent cues. Thus, top-down experiential priors ought to have less influence on multisensory performance.

The results of experiment #1 allowed us to compare the multisensory enhancement of musicians and non-musicians in order to evaluate the influence of musical experience on multisensory processing.

2.2 Methods

2.2.1 Participants

This study was comprised of two groups of participants. The first group consisted of individuals with less than five years musical training; these participants formed the non-musician control group (NM). The second group of participants formed the musician group (M) if they met at least one of the following criteria: i) 5 or more years of formal musical training, ii) professional performance experience (i.e., touring, or paid performances), or iii) session musician (paid recording musician). Participants were recruited through the Undergraduate Research Participant Pool at York University, the Psychology Department at York University, as well as the Toronto music community.

A total of 45 participants were tested during the course of the experiment. As the experiment was designed to assess multisensory integration, participants' performance needed to fall within specific criteria in order to allow for proper analyses of multisensory cue integration. Firstly, performance on all conditions needed to be well above chance, as chance performance would produce no useable information. If a participant either a) could not perform the task at all, or b) was simply guessing their responses, there would be no way of properly assessing any changes in performance between conditions. Secondly, performance across all conditions could not be at ceiling (i.e., perfect), as this would allow for no potential examination of multisensory enhancement in performance due to multisensory cue integration. As such, all participants' data were sorted following data acquisition to ensure that each participant's met the criteria above. A complete

description of the elimination criteria and procedure are described in the *Statistical Analysis* section.

Of the 26 non-musicians tested, 16 participants required elimination from the study due to chance performance during at least one of the experimental conditions, resulting in 10 remaining participants (6 male; mean age = 22.8 years, SD = 4.57; mean years of musical experience = 3.8 years). Of the 19 musicians tested, 5 participants required elimination from the study due to chance performance during at least one of the experimental conditions, which resulted in 14 remaining participants (6 male; mean age = 24.14 years, SD = 5.67; mean years of musical experience = 14.36 years). Given the high proportion of non-musicians that required exclusion, the experimental task appeared to be more challenging for non-musicians than for the musicians. Because this screening process may have biased the results, it is important to note that the results and inferences of experiment #1 may only characterize individuals with the ability to perform the current task, and that this may differ from those individuals who found the task excessively difficult. These issues are further addressed in the *Limitations* section.

In order to access the level and nature of participants' musical history, including training, recreational listening, and demographic information, we used a questionnaire provided by Dr. L.J. Trainor (Auditory Development Lab at McMaster University) (Appendix 1). Ethical approval was received from the Office of Research Ethics at York University (Certificate #: 2013 – 296; valid 11/07/13 – 03/03/16). Thus, all participants were asked to provide written consent. Additional exclusion criterion included: abnormal vision (if uncorrected), and deficits in auditory processing (self-reported).

2.2.2 Stimuli

A set of five neighboring notes (i.e., one semi-tone separating each note) was recorded using an acoustic guitar (*Simon and Patrick - CW GT Vintageburst*). This set of notes range from G3 (196.0 Hz) to B3 (246.94 Hz) (Figure 2). In order to emulate real-world noise, constant gaussian white noise was played during the recording of all stimuli. This was added to the guitar recordings in order to emulate the background noise that is often present in a live musical performance (e.g., a crowded theater or bar). All stimuli were recorded using a Sony HDR-SR1 high-definition camcorder secured to a tripod. Recordings were then edited to a length of 200 ms using MAGIX Movie Edit Pro 2014 Premium, with stimulus onset aligned to 100 ms (i.e., the onset of the notes being played

within each recording), and were reduced to a resolution of 240 X 180 pixels. Stimulus duration, onset and resolution were determined following extensive piloting of the experiment using various combinations of duration and resolution. The chosen combination resulted in a task that was challenging, without being overly difficult for the majority of pilot subjects.

Audio components from each video were extracted, resulting in one audiovisual file (MPEG-4), and one audio file (WAVE) for each stimulus. Psychtoolbox (version 3.0.10) in Matlab (MathWorks - R2013a) was used to present stimuli, along with the presentations of instructions, and the recording of participants' responses. For both audio and video components, four pairs of notes were then generated, all containing note 3 and one of notes 1, 2, 4 or 5 (Figure 2). All pairs of notes were duplicated in reverse order, resulting in eight possible pair/order combinations.

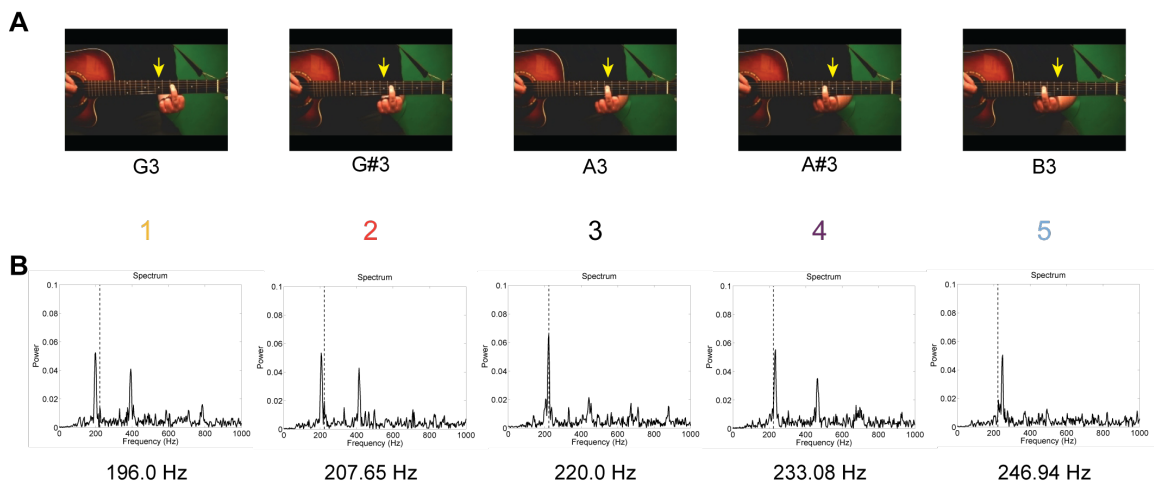


Figure 2. Stimulus set for experiment #1. This figure illustrates the complexity of the stimuli in experiment #1 as well as the relationship between each stimulus level. (A) Film frames from each of the five visual stimuli used for both visual [V] and audiovisual [AV] conditions. Notes (1 - 5) increase in pitch from left to right (i.e., G3 – B3). The yellow arrow indicates the location of note #3 (A3) for comparison to all other note locations. (B) Frequency power spectrum of each of the five auditory stimuli used for both auditory [A] and AV conditions. Notes (1 - 5) increase in pitch (i.e., frequency) from left to right (i.e., 196 Hz – 246.94 Hz). The dashed line indicates the frequency of note #3 (220 Hz) for comparison to all other notes.

2.2.3 Task Procedure

There were three experimental conditions: unisensory auditory discrimination (A), unisensory visual discrimination (V), and multisensory audiovisual discrimination (AV). During each condition, participants performed two alternative forced-choice tasks. They were presented with two stimuli in succession (i.e., pairs), in the auditory, visual or

audiovisual sensory domains for each experimental condition respectively. Each of the pairs contained two musical notes played on a guitar, and/or positions on a guitar corresponding to two musical notes depending on experimental conditions (i.e., musical notes for the auditory condition, positions on an instrument for the visual condition, and a synchronized presentation of both for the audiovisual condition). Each pair contained note #3 (A3, 220 Hz) and participants were asked following each trial which note was “higher”, the first or the second note. ‘Higher’ here refers to either i) the note’s pitch, or ii) the location on the guitar (with positions closer to the body of the guitar representing higher pitches – Figure 3). For each condition, participants were asked to judge which note was higher, between one of the eight possible stimulus pairs presented in random order. Prior to beginning, the experimental tasks were thoroughly explained and demonstrated to each participant.

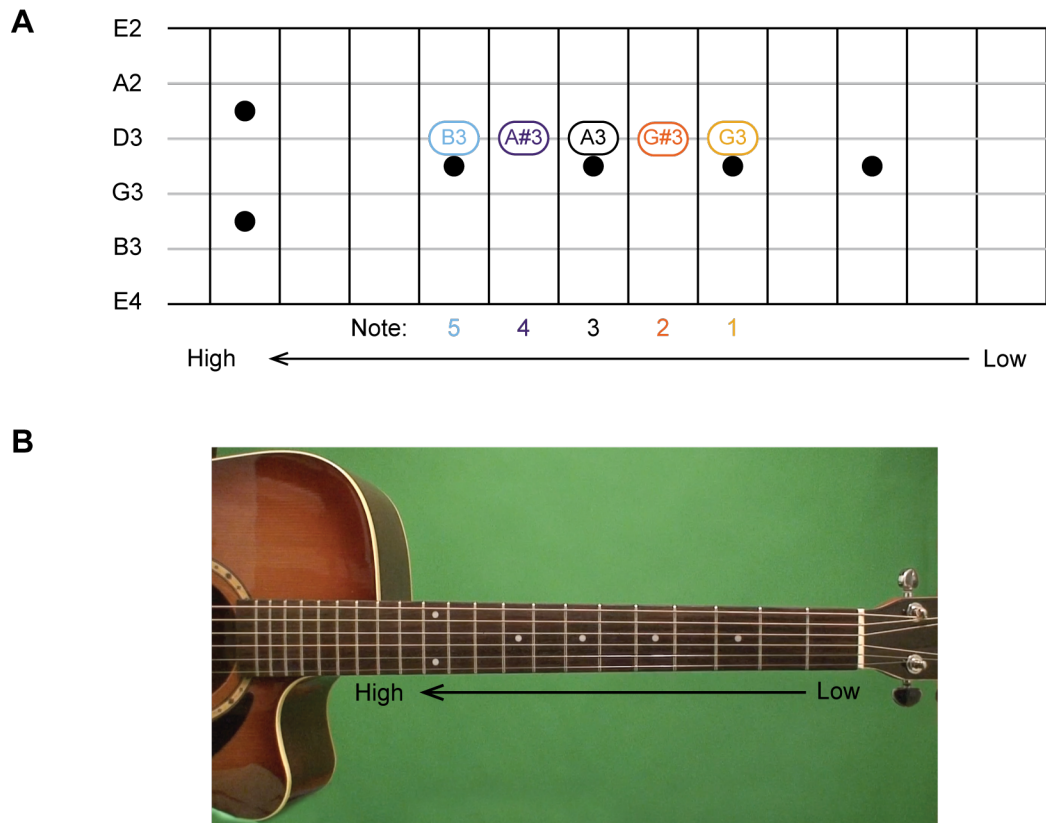


Figure 3. Layout of guitar fretboard. This figure illustrates the visual stimulus (i.e., an acoustic guitar) in experiment #1. (A) A schematic diagram identifying the placement of each of the five notes used in experiment #1, including the pitch directionality from low to high. (B) A photograph of the acoustic guitar used in experiment #1, including the pitch directionality from low to high.

Following an explanation of the experimental tasks, but prior to the collection of unisensory and multisensory trials, all participants were separately tested on the two unisensory conditions to determine their sensitivity threshold. Because the goal of experiment #1 was to assess multisensory enhancement, it was important for all participants to initially perform sub-optimally on both unisensory conditions in order to leave room for improvements in performance during the multisensory condition. Importantly, the goal of experiment #1 was to contrast the within-group multisensory enhancements (i.e., how each groups' observed multisensory cue reliability compares to their own modeled estimates), and not the between-group cue reliabilities themselves. Therefore, it was important for all participants to perform as uniformly as possible in the baseline unisensory conditions in order to establish a level "playing field" on which any experience driven differences in multisensory integration could be detected.

Using a staircase procedure, thresholds were determined for both auditory and visual stimulus intensity. Separately for each modality, stimuli were manipulated so that each participant performed between 60% - 85% accuracy (i.e., the proportion of correct responses). Incrementally, the volume of the auditory stimuli was lowered by multiplying the amplitude of the sound waves by a sizing factor (α) until participants' performance was at criteria. The gaussian blur intensity was augmented until participants' performance was at criteria. This was accomplished by increasing the kernel width (k) of the two-dimensional convolution shader used during video playback. These intensities were then used for the remainder of each participant's data collection.

Non-musicians' auditory thresholds ($M = 0.22 \alpha$, $SD = 0.22$) did not differ from musicians' auditory thresholds ($M = 0.13 \alpha$, $SD = 0.12$; $t(12.65) = 1.10$, $p = 0.29$). Similarly, non-musicians visual thresholds ($M = 18.20 k$, $SD = 2.15$) were similar to musicians' visual thresholds ($M = 17.57 k$, $SD = 2.53$; $t(21.24) = 0.65$, $p = 0.52$).

As shown in Figure 4, pair combinations containing adjacent notes ('adjacent pairs' containing either notes 2 or 4) were presented 30 times each as these pair combinations are most challenging to differentiate, and therefore ought to be most sensitive to multisensory enhancement. Combinations containing more distant notes ('distal pairs' containing either notes 1 or 5) were only presented 18 times each. Additionally, the 'exact pair' combinations '3-3' was not presented at all, as participants

could only perform at chance levels, as neither note is higher than the other and all pairs and note orders were completely randomized (Figure 4).

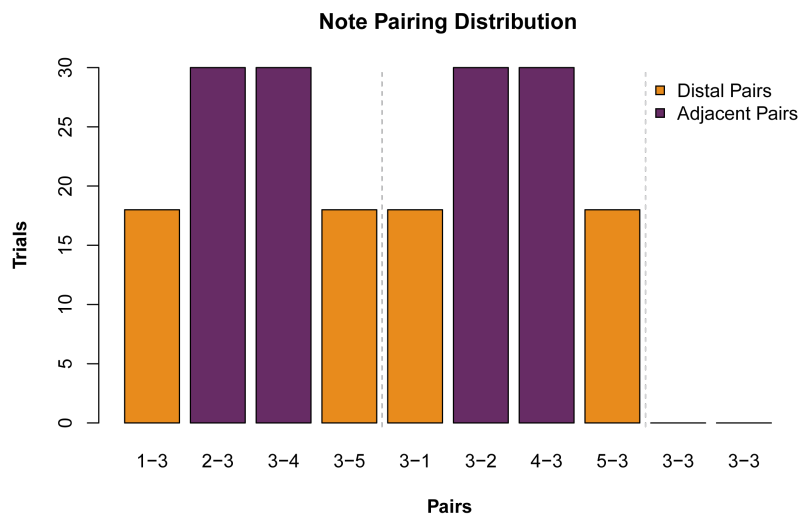


Figure 4. Distribution of note pairings. This histogram depicts the frequency of each of the eight note pairings presented to each participant in experiment #1. Additionally, both adjacent (i.e., pairs including notes 2 and 4) and distal (i.e., pairs including notes 1 and 5) pairs are identified.

2.2.4 Statistical Analysis

All participant data were sorted into non-musician and musician groups, followed by an initial analysis of each participant’s task performance for each level of each condition using Matlab. This initial analysis was accomplished by determining the percent of responses where each of the 5 stimulus levels were judged to be “higher” than stimulus 3. This analysis resulted in percentages for each stimulus level for each condition, for each participant (with the performance at stimulus level 3 always assumed to be 50%). These values were written into one text file (i.e., *.txt*) for each participant, and all subsequent data analyses were then analyzed using R version 2.15.3 (R Development Core Team).

Data exclusions: As indicated above, participants’ performance was evaluated based on specific elimination criteria. In order quantitatively assess whether performance was above chance, each participant’s percentage for each stimulus level (i.e., notes 1 through 5) was correlated with stimulus level using Pearson’s product-moment correlation (r). This was conducted because chance performance on one or more stimulus levels would cause a linear line of best fit to be flat (approaching $r = 0$), whereas optimal performance (i.e., if a participant responded that stimuli 1 and 2 were

always lower than 3, and stimuli 4 and 5 were always higher than 3) would result in a steeper linear line of best fit (approaching $r = 1$). Therefore, for each participant's dataset, for each condition, a correlation was computed. As a conservative estimate, if this correlation was lower than $r = 0.4$, the dataset was determined to reflect chance performance.

However, the possibility remained that participant data indicated positively correlated performance that was invalid; this would occur if either distal notes (i.e., 1 or 5) were judged to be higher than note 3 at or near chance levels. If this were to occur with one of the distal notes, particularly if performance on the remaining distal note was strong, a positive correlation would still be present, although this would not be an accurate indicator of overall performance. Therefore, for each participant's dataset, for each condition, note 1 had to be judged as lower than note 3 in a minimum of 60% of trial, and correspondingly, note 5 had to be judged to be higher than note 3 in a minimum of 60% of trials. This requirement ensured that all included data reflected participants who were able to perform the task above chance levels. This resulted in an inclusion of 53.3% ($N = 24/45$) of all the collected data

Following the data exclusion, individual data was sorted into the two experimental groups based on the grouping criterion listed above. Separately for each individual, the dependent measure (i.e., the proportion of trials that each stimulus level was judged to be higher than note 3) was fitted using a normal cumulative distribution function with a fixed threshold (i.e., point of subjective equality = 50% performance at stimulus level #3). These fit parameters produced a standard deviation value (σ) for each set of data that reflected the slope of the fitted line. Using equation #1, these standard deviations were then used to determine a measure of each individual's auditory, visual and audiovisual cue reliability (Angelaki, Gu & DeAngelis, 2009). A comparison of the distributions of pre and post-excluded reliability measures can be seen in Figure 5.

$$Cue\ Reliability_x = \frac{1}{\sigma_x^2} \quad [1]$$

All group cue reliability measures were then tested for assumption violations (i.e., homogeneity of variances and distribution normality) using the Bartlett test of

homogeneity of variances and the Shapiro-Wilk test for normality in order to determine the most appropriate statistical procedures for comparing both unisensory and multisensory performance within groups.

Mixed model analysis of variance (ANOVA) - A mixed model ANOVA was first conducted as an omnibus test to determine whether any significant interactions were present between the two independent variables, one between subject variable (i.e., experience) and one within subject variable (i.e., stimulus modality). Additionally the ANOVA indicated whether either independent variable resulted in any significant main effects. The mixed model ANOVA was conducted using the ezANOVA function, part of the ez package in R (Lawrence, 2013). A type II sum of squares was used as the sample sizes were unbalanced (Langsrud, 2003). In order to correct for sphericity violations, p -values were adjusted using a Greenhouse-Geisser epsilon (GGe) for the interaction effect and the effect of stimulus modality as these effects had greater than two levels and were therefore sensitive to sphericity violations. Effect sizes were calculated using the generalized Eta-Squared (η_G^2).

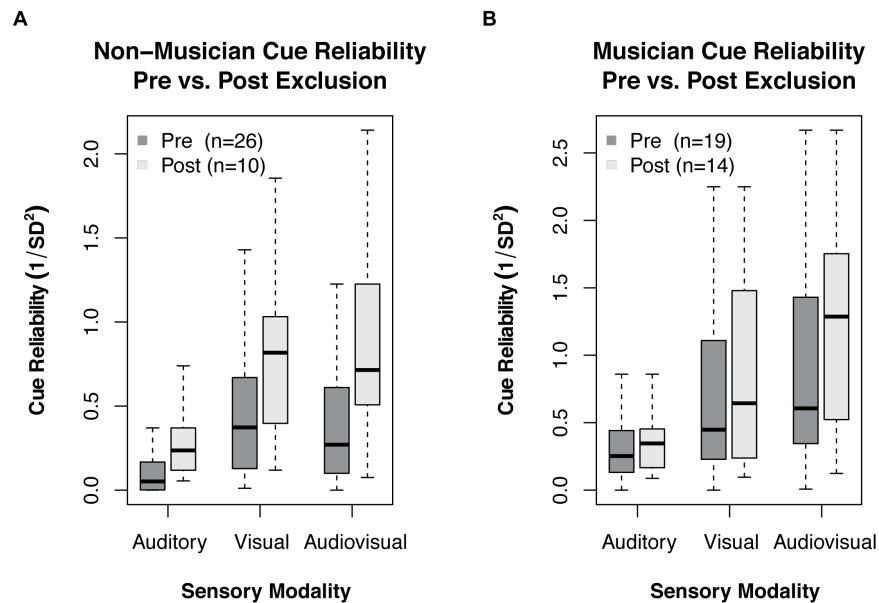


Figure 5. Cue reliability variability pre and post-exclusion. Boxplots illustrating the variability in cue reliability measures, comparing pre-exclusion datasets to post-exclusion datasets. (A) Non-musician measures for auditory, visual and audiovisual conditions for pre (n=26) and post (n=10) exclusion datasets. (B) Musician measures for all conditions for pre (n=19) and post (n=14) exclusion datasets.

Given that the goal of experiment #1 was to contrast the within-group multisensory enhancements (i.e., how each groups' observed multisensory cue reliability compares to their own modeled estimates), and not the between-group cue reliabilities themselves, this mixed model ANOVA was conducted for two reasons. Firstly, to verify the relative equivalence of performance of empirical data between non-musicians and musicians, as it was important for both groups' to begin with similar unisensory performances so that any multisensory differences could be attributed to possible expertise effect and not discrepancies in baseline performance. Secondly, this omnibus test was conducted to ensure that there were no interaction effects that may have influenced any main effects of condition.

Within-group analysis – Maximum likelihood estimates of optimal multisensory cue integration were calculated for each participant using their unisensory cue reliability measures (i.e., A and V) in order to model a predicted effect of multisensory enhancement using equation #2 (Angelaki, Gu & DeAngelis, 2009).

$$\sigma_{AV}^2 = \frac{\sigma_A^2 * \sigma_V^2}{\sigma_A^2 + \sigma_V^2} \quad [2]$$

Therefore, for each participant four measures of cue reliability were calculated using equation #1, one for each of the three experimental conditions (i.e., stimulus modalities), and one modeled MLE. Separately for each group, the observed multisensory cue reliability was then compared to the MLE predicted multisensory enhancement for each individual. Additionally, to assess whether each individual's observed multisensory cue reliability significantly deviated from his or her unisensory performance, multisensory performance was compared to both the auditory and visual cue reliability.

Tests for assumption violations revealed both non-normality and variance heterogeneity in our data. Gaussian kernel density plots were generated in order to visually assess the severity and nature of these assumption violations (Figure 6). Due to the small sample size of our data, kernel density plots were chosen in favor of histograms as they produced clear illustrations of sparse data. Along with the assumption violation test results, Figure 6 revealed severe differences in variances between conditions as well as slightly bimodal distributions. Therefore, non-parametric

analyses were determined to be required using Wilcoxon signed rank tests for all pairwise tests. Subsequent pairwise tests evaluating mean differences of within group cue reliabilities were controlled for multiplicity (multiple comparisons correction) using Holm stepwise correction procedure ($\alpha = 0.05$). For all pairwise comparisons, standardized effect sizes are reported using Pearson's r (Field, Miles & Field, 2012).

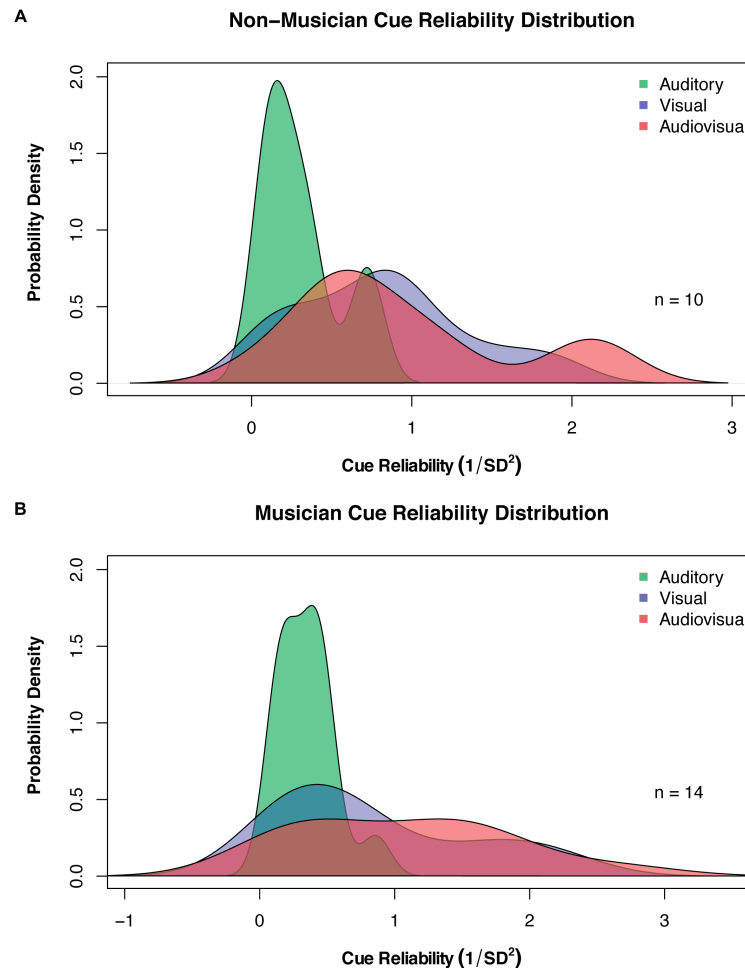


Figure 6. Cue reliability distributions. This figure visually compares the probability density distributions between all conditions for the purposes of illustrating statistical testing assumption violations. (A) Non-musician cue reliability distribution for all conditions. (B) Musician cue reliability distribution for all conditions.

Within-group correlations – In order to further explore the relative contributions of each of the unisensory stimuli in generating multisensory enhancement, for each group, cue reliability measures were correlated between conditions using Spearman's rank correlation coefficient (r_s). In this analysis, each groups' unisensory cue reliability measures (i.e., A and V separately) were correlated with their observed multisensory

cue reliability measures (e.g., A vs. AV, V vs. AV). This analysis elucidated how tightly each group's unisensory performance was coupled with their multisensory performance, and which unisensory cue had a stronger influence on multisensory cue integration.

2.3 Results

Before examining how the observed multisensory integration compared to the predicted integration, we first conducted a mixed-model ANOVA in order to determine whether there were a) significant interactions between the independent variables, b) a significant effect of group (experience), and most importantly c) whether there was a significant main effect of condition (stimulus modality), which there must necessarily be in order for multisensory enhancement to occur. The results of this ANOVA indicated that there was no significant interaction between experience and stimulus modality ($F(2,44) = 0.573$, $GGe = 0.744$, $p_{corrected} = 0.444$, $\eta_G^2 = .016$). As there was no significant interaction, main effects were evaluated. Our analysis revealed no main effect of group ($F(1,22) = 0.519$, $p = 0.479$, $\eta_G^2 = .012$). Our analysis of stimulus modality revealed a significant effect of condition ($F(2,44) = 10.482$, $GGe = 0.744$, $p_{corrected} < 0.001$, $\eta_G^2 = .182$) (Figure 7). Although there were no interaction effects, our analysis continued to a more sensitive pairwise analysis in order to examine the nature of the multisensory integration within each experimental group, given the main effect of condition.

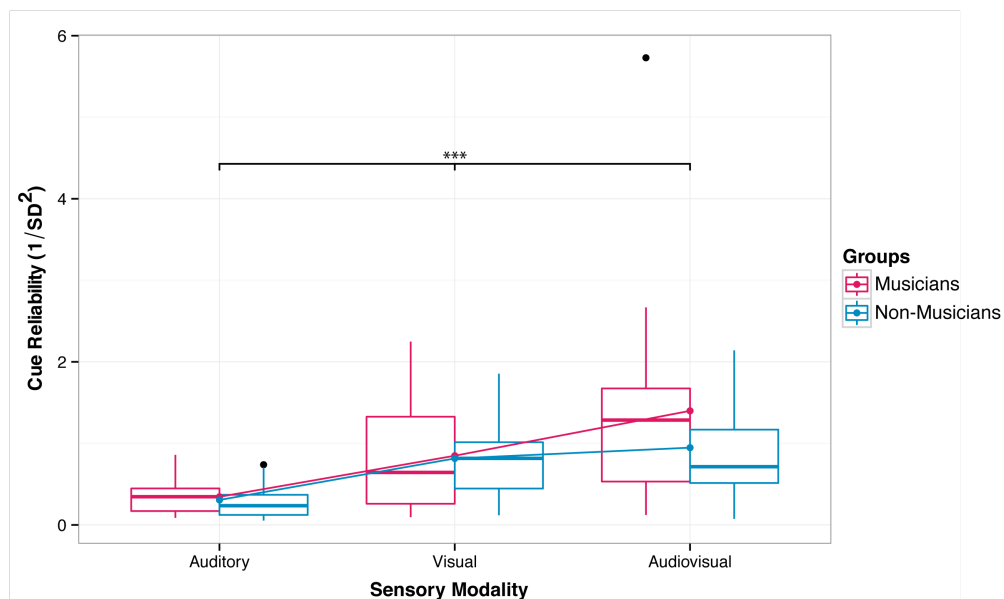


Figure 7. Cue reliability interaction plot. This graph depicts the cue reliability for each group, during all stimulus conditions. Coloured boxplots indicate the distribution and variability of

reliability measures (thick horizontal lines indicating median values), while coloured points and thin lines indicate mean reliability measures (red = musicians; blue = non-musicians). Black points indicate outlying values. *** indicates = $p < 0.001$.

In the comparison between modeled and observed multisensory enhancement, we expected that non-musicians would experience equivalent multisensory gains to their predicted values. Due to their perceptual expertise and situational experience, we predicted that musicians would utilize additional cues in their decision making process, such as knowledge about music production and the tonal characteristics of the guitar. Thus, we anticipated expert musicians would use this experience to combine multisensory cues better than controls, and would deviate from their modeled enhancement.

Our results indicated that the non-musicians' observed multisensory cue reliability ($M_{AV}=0.948$, $SD_{AV}= 0.693$) was not statistically different than their predicted MLE cue reliability value ($M_{PredictedAV}=1.223$, $SD_{PredictedAV}= 0.599$; $Z = 1.478$, $p_{corrected} = 0.641$, $r = .331$) (Figure 8C and 8E). Similarly, our results indicated that the musicians' observed multisensory cue reliability ($M_{AV}=1.399$, $SD_{AV}= 0.1.454$) was not statistically different than their predicted MLE cue reliability value ($M_{PredictedAV}=1.195$, $SD_{PredictedAV}= 0.817$; $Z = 0.157$, $p_{corrected} = 0.903$, $r = .171$) (Figure 8D and 8F). All Wilcoxon signed rank tests were two-sided. Thus, it appeared that both non-musicians and musicians were integrating auditory and visual cues in the expected way as predicted using maximum likelihood estimates of optimal cue integration. However, it remained to be determined whether each group's observed multisensory cue reliability deviated from their unisensory performances.

In order to distinguish whether each group's observed multisensory cue reliability was significantly different than their performance during either of the unisensory conditions, we compared each group's auditory and visual performance to their empirical audiovisual performance. Our results indicated that the non-musicians' observed multisensory cue reliability was significantly higher than their auditory cue reliability ($M_A=0.307$, $SD_A= 0.243$; $Z = 2.497$, $p_{corrected} = 0.049$, $r = .558$); however, their multisensory cue reliability was not statistically different than their visual cue reliability ($M_V=0.816$, $SD_V= 0.549$; $Z = 1.172$, $p_{corrected} = 0.649$, $r = .262$). Similarly, the musicians' observed multisensory cue reliability was found to be significantly higher than their auditory cue reliability value ($M_A=0.346$, $SD_A= 0.205$; $Z = 2.919$, $p_{corrected} = 0.010$, $r =$

.552), but was not statistically different than their visual cue reliability ($M_V = 0.849$, $SD_V = 0.722$; $Z = 1.287$, $p_{corrected} = 0.650$, $r = .243$). Therefore, our results indicate that both the musicians' and non-musicians' observed multisensory cue reliability significantly deviated from either of their auditory cue reliability, while visual cue reliability was found to be statistically equivalent to multisensory cue reliability.

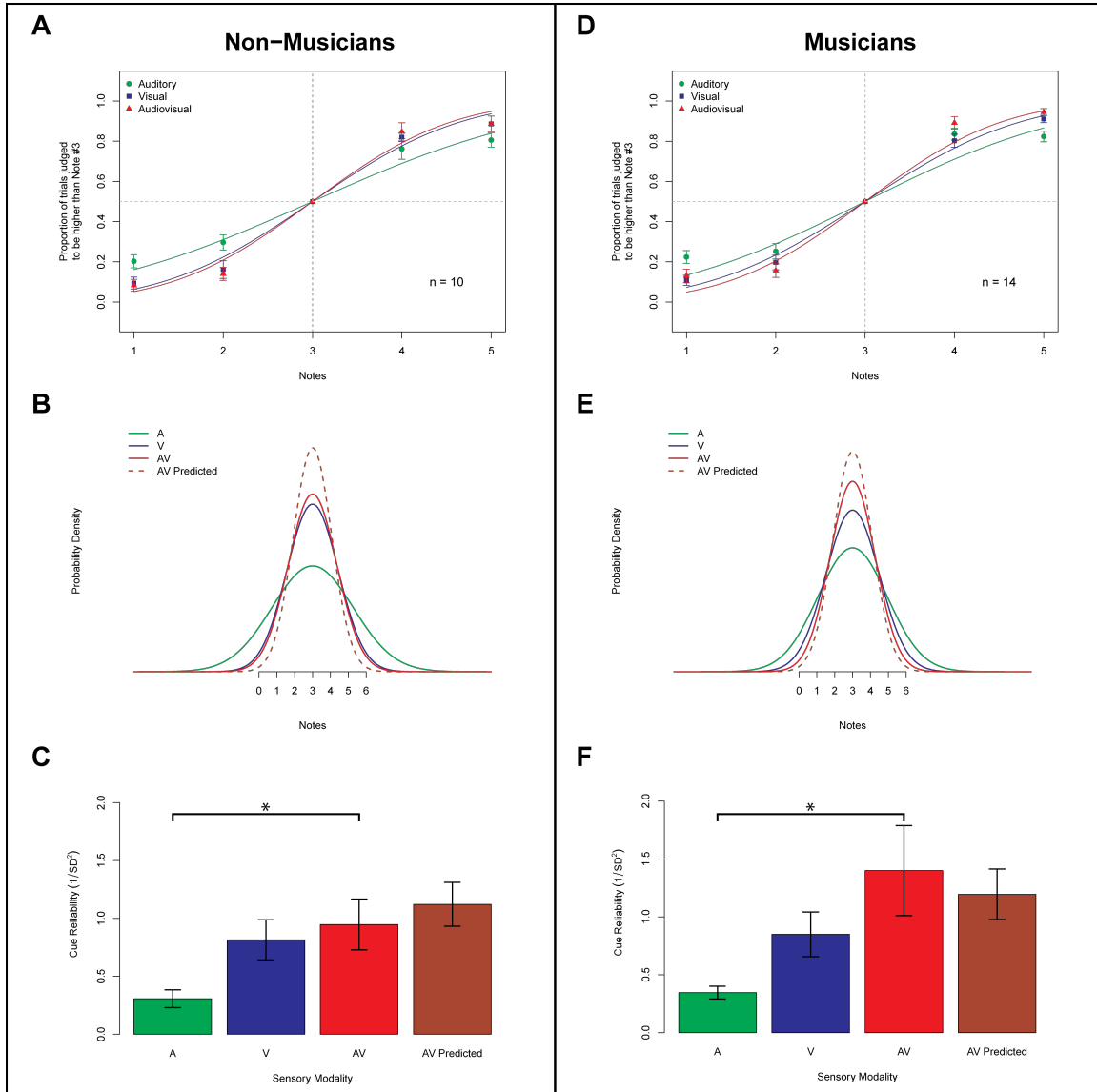


Figure 8. Multisensory integration results. This figure shows each groups cue reliability measures for each condition as well as their modeled MLE cue reliability. (A) Fitted psychometric functions for the non-musicians' empirical data ($n = 10$). (B) A kernel density plot illustrating non-musicians' cue reliability. (C) A bar graph comparing the non-musicians' cue reliability measures derived via the fitting parameters in A. (D) Fitted psychometric functions for the musicians' empirical data ($n=14$). (E) A kernel density plot illustrating musicians' cue reliability. (F) A bar graph comparing

the musicians' cue reliability measures derived via the fitting parameters in *D*. All error bars indicate the standard error of the mean (SEM). * indicates = $p < 0.05$.

In our correlation analysis of cue reliability measures between conditions for non-musicians, our results indicate that multisensory cue reliability was not significantly correlated with auditory cue reliability ($r_s = 0.31$, $p = 0.385$; Figure 9A), but it was significantly correlated with visual cue reliability ($r_s = 0.84$, $p = 0.002$; Figure 9B). For the musicians, our results indicate that multisensory cue reliability was significantly correlated with both auditory cue reliability ($r_s = 0.67$, $p = 0.008$; Figure 9C), as well as visual cue reliability ($r_s = 0.57$, $p = 0.034$; Figure 9D). These results indicate that both unisensory cues may have played a role in multisensory performance for the musicians. Conversely, it is possible that auditory cues may have contributed less to multisensory performance for non-musicians as auditory performance was not correlated with audiovisual performance.

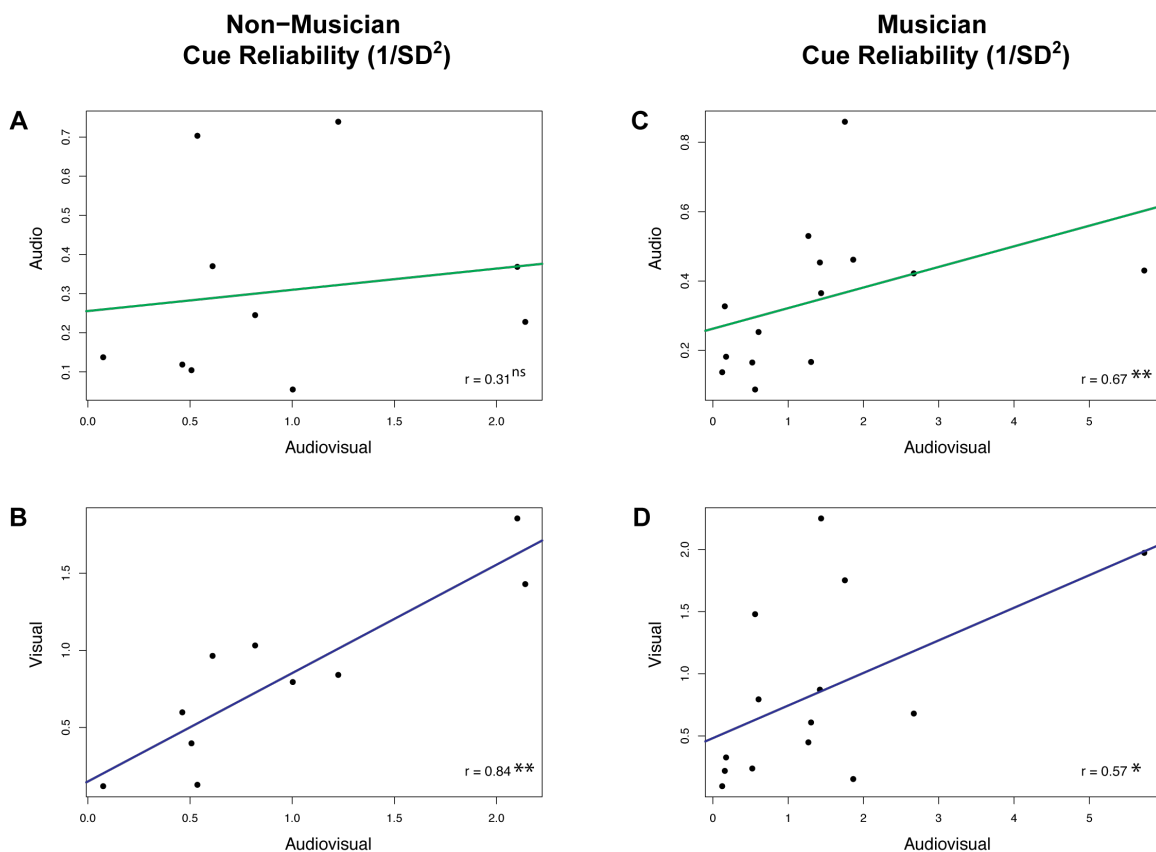


Figure 9. Unisensory vs. multisensory correlations. These scatterplots show the relationship between each participant's unisensory cue reliability and their multisensory cue reliability within each group. For each plot, a linear line of best fit is shown, and Spearman's rank correlation coefficient (r_s) is shown (audio = green; visual = blue). (A) Non-musicians' audio vs. audiovisual

cue reliability. (B) Non-musicians' visual vs. audiovisual cue reliability. (C) Musicians' audio vs. audiovisual cue reliability. (D) Musicians' visual vs. audiovisual cue reliability. * indicates = $p < 0.05$; ** indicates = $p < 0.01$; ns indicates = non-significant.

2.4 Discussion

Experiment #1 is one of the first to explore the influence of domain specific experience on the multisensory integration of naturalistic musical stimuli. Our between-group results indicate that there are no significant group differences between non-musicians and musicians in a two alternative forced choice discrimination task using audiovisual musical stimuli. Furthermore, our within-group results suggest that neither musicians nor non-musicians significantly deviated from their MLE of optimal cue integration, which would indicate that previous experience may not influence the outcomes of multisensory integration.

This statement holds true in the comparison of observed and predicted multisensory cue reliability measures, but in order to further assess the nature of each groups multisensory integration (e.g., whether either group were relying on one unisensory cue more than the other cue) we examined the relationships between each groups' unisensory performance and their multisensory performance. Although this analysis similarly suggest that there is no effect of experience in modulating multisensory integration, we do see a trend that may indicate differences in the way that non-musicians and musicians integrate auditory and visual cues in attaining their multisensory enhancements, within the current paradigm.

Beginning with the similarities, for both groups auditory cues were found to be significantly less reliable than audiovisual cues. Conversely, visual cues reliability was not found to be statistically different than multisensory cue reliability for either group. This result indicates that non-musicians and musicians are performing similarly throughout the experiment. Both groups found the discrimination task more difficult (i.e., they were less accurate) when provided with auditory cues, whereas their performance greatly ameliorated when provided with visual or audiovisual cues. Importantly, because audiovisual cue reliability did not significantly deviate from visual cue reliability, it can not clearly be concluded whether participants were integrating unisensory cues, or merely performing the visual task during the presentation of audiovisual stimuli.

Although unisensory and multisensory cue reliabilities are similar between the two groups, we further explored these pairwise relationships by conducting a correlation analysis. This analysis was performed in order to evaluate and visualize the influence of each unisensory cue on multisensory cue reliability on a participant-by-participant level. This investigation may have indicated subtle differences between musicians and non-musicians. The correlation analyses between auditory and audiovisual cue reliability (Figure 9A and 9C) indicated that only musicians' auditory cue reliability was significantly correlated with their multisensory cue reliability. Therefore, despite the finding that auditory cue were significantly less reliable than multisensory cues overall, this evidence seems to suggest that the musicians who perform poorly when given auditory cues tended to perform poorly when provided with audiovisual cues, and vice versa (Figure 9C). This is contrasted by non-musicians, for whom there were no discernible relationship between auditory and audiovisual performances (Figure 9A). Of course given that visual cues were found to be equally reliable as audiovisual cues (which were both highly reliable), it is not a surprise that both groups' visual cue reliability measures significantly correlated with their audiovisual cues reliability values (9B and 9D).

Given the relationship between the musicians' auditory and audiovisual cue reliability measures, it stands to reason that auditory cues at least partially influenced decision making during the audiovisual task. Therefore, even though the musicians' multisensory performance did not significantly deviate from their visual performance, there is reason to speculate that musicians were not merely using the same strategy during both conditions, and that both auditory and visual cues were being utilized during the multisensory condition. Yet for non-musicians, given the lack of relationship between auditory and audiovisual performance, in combination with the particularly strong correlation between visual and audiovisual cue reliabilities ($r_s = 0.84$; Figure 9B), it seems more likely that non-musicians may have focused exclusively on visual cues when performing the audiovisual task. Therefore, both groups were clearly relying heavily on visual cues when performing the audiovisual task, yet it appears that auditory stimuli may have still been valuable cues for musicians.

In experiment #1, we predicted that non-musicians would experience equivalent multisensory gains to their predicted values, and this postulation was found to be true. Non-musicians were found to have an observed multisensory cue reliability that matched

their MLE predicted values. We additionally predicted that musicians would experience greater multisensory gains to their predicted values due to their top-down knowledge about music production, including knowledge about pitch-location and timber-location relationships. This alternate hypothesis was found to not be the case; musicians, similarly to non-musicians, had observed multisensory cue reliabilities that were equivalent to their MLE predicted values. Although both groups' observed and predicted multisensory cue reliability were found to be equivalent, we still can not be certain whether participants were integrating both unisensory cues, or if they were simply relying on visual cues as they were consistently more reliable.

From experiment #1, we are unable to clearly conclude the exact mechanisms participants used in integrating multisensory cues or if multisensory integration occurred at all, but the evidence suggests that both groups heavily relied on their most reliable unisensory cue (i.e., visual cues). If participants were attempting to integrate both cues, this is a common strategy within multisensory integration and is the basis of the MLE calculation. The seemingly contradictory result that participants both integrated multisensory cues optimally, and that multisensory cue reliability was statistically equivalent to their visual cue reliability may not be inconsistent with probability based models of cue integration. Essentially, when integrating multiple cues we can only work with the stimuli we are given. Moreover, if a cue is simply not reliable for any reason (i.e., our auditory stimuli), and another cue is very reliable (i.e., our visual stimuli), then based on a weighted estimate of integration, the most optimal cue integration would weigh the reliable cue a great deal higher than the unreliable cue (Alais, Newell & Mamassian, 2010; Angelaki, Gu & DeAngelis, 2009). Thus, given unbalanced cue reliabilities, it is possible that the combined reliability to closely match the most reliable cue; however, within the current results it is unknown whether auditory cues were utilized at all.

It remains unclear is why participants found visual cues to be more reliable than auditory cues. Additionally, given the lack of any correlation between non-musicians' auditory and audiovisual cue reliabilities, why are auditory cues less utilized by non-musicians? It is quite possible that there are multiple forces driving this result and further testing in the future is required.

Firstly, given that both trained musicians and non-musicians found visual cues to be more reliable, there may be an overarching bias within the stimulus and design that

resulted in the visual cue being more reliable. Although every attempt was made during individual thresholding to balance each participant's auditory and visual performance, we consistently found that participants performed better on the visual task than the auditory task during the subsequent experimental blocks. Although their performance indicated that visual cues were more reliable than auditory cues, it is very interesting to note that anecdotally, many participants across both groups stated that they felt the auditory task was "*easier*" than the visual task, and that the auditory cues were more "*reliable*".

So, even though the data indicated that visual cues were more reliable than auditory cues for both groups on average (Figure 8C & 8F), subjectively participants felt that the opposite was true. It is possible that the visual task may have initially been more difficult for participants than the auditory task, which would result in the selection of an easier stimulus difficulty level during thresholding (i.e., higher signal to noise). However, after numerous trials participants may have adapted and become more acclimated and practiced with this task, which may have led to the visual task difficulty to be less challenging than the auditory difficulty. This would assume that participants generally improved their performance differently between the auditory and visual tasks. It is possible there was simply more "room for improvement" regarding the visual task given that anecdotally participants initially found the visual task to be more difficult. Of course within the current paradigm, it is difficult to conclude these mechanisms for certain, but these results lead us to question whether there are more fundamental differences in the way that participants adapt to naturalistic auditory and visual discrimination tasks, or if the chosen stimuli were simply flawed.

Secondly, even though both groups found visual cues to be more reliable, it is possible that musicians may have still been able to use auditory cues because of their exposure to music. More specifically, musicians routinely make judgment on pitch discrimination when both critically evaluating and producing music, and this is a skill that may allow an individual to utilize the auditory cues within the current experiment.

Recently, numerous researchers have begun examining the multisensory integration of musical stimuli. Many of these experiments explore more complex aspects of music, such as emotional responses to music and listener's sense of higher-order structure (Krahé, Hahn & Whitney, 2015; Vines, Krumhansl, Wanderley & Levitin, 2006; Vuoskoski, Thompson, Clarke & Spence, 2014). These lines of research differ from our

current research as they examine more complex and often abstract characteristics of music, whereas our current experiment investigates low level perceptual features of the music (i.e., pitch and position). Other experiments have begun to explore these fundamental perceptual mechanisms, such as temporal binding windows of sensory events, temporal-order judgments, sensitivity to asynchrony, and duration judgments (Lee & Noppeney, 2011; Petrini, Holt & Pollick, 2010; Schutz & Kubovy, 2009; Vatakis & Spence, 2006), yet no research to date has investigated the influence of musical experience on individuals ability to discriminate real-world multisensory musical stimuli. Understanding how individuals process and integrate these more basic aspects of music, including musical note discrimination, certainly enhance and aid our understanding of more complex musical characteristics such as emotion, emergent structures, and tension.

2.5 Limitation

There are several aspects of the current experiment which may have influenced the results, and which could be identified as possible limitations. These limitations can be organized in to two categories, design limitations, and technical limitations.

Design limitations – In experiment #1, the relatively small sample size, which was the result of the high proportion of participant data that did not meet the inclusion criteria, likely influenced the results. This is because small sample sizes can result in a) non-representative populations and b) a meaningful influence on the power of statistical test. We attempted to prevent these issues by collecting a large number of participants; however, given the high proportion of participants who were unable to perform the experimental task and were thus excluded, our final sample sizes were smaller than anticipated. Secondly, the two groups may not have been perfectly homogenous representations of “non-musicians” and “musicians”. Although all participants met the criteria for group membership, the groups could have been defined more stringently – if the groups, for example, consisted of individuals who had never touched an instrument in their lifetime, as well as a group of elite professional musicians, than there may have been more differences in performance between the each group. This would have been quite challenging to accomplish, as most individuals have at some point learned or played a musical instrument as part of their schooling, and it is additionally difficult to recruit large numbers of elite musicians.

Additionally, it is important to remember that both experimental groups were filtered during the exclusion process. This filter resulted in the removal of any individuals who were unable to perform the experimental tasks. Thus our results reflect the abilities of a subsection of individuals who poses the ability to perform a challenging perceptual task which may not be shared by all. Thus we need to be cautious with any generalizations made between the results of experiment #1 and abilities found outside the lab with the broad public. It is interesting to note that a much larger proportion of non-musicians than musicians had difficulties with the stimuli and tasks (excluded: NM = 61.5% vs. M = 26.3%). Since the current experiment contrasts the multisensory integrations of non-musicians and musicians, and does not directly compare their performance and abilities, a separate experiment would need to be conducted to determine if and why non-musicians are better at musical perceptual tasks.

Technical limitations – When designing the stimulus, it was originally planned that visual stimuli (i.e., the videos) would be convolved with a Gaussian kernel in order to render the stimulus more blurry, and thus to make the task more challenging. After extensive piloting, it became apparent that the computer (particularly the graphics card) being used might present some limitation. This was because once blur levels was raised above a particular limit the computer would begin to spontaneously freeze, which would crash the Matlab script. Fortunately however, during the thresholding block of the experiment, we found that the majority of participants required blur levels below this limit; still, this limited our ability to increase the blur (and therefore difficulty) for some participants. Because of this, it is possible that some participants may have required more difficult visual stimuli in order to balance auditory and visual task difficulty. This might have affected the difference in task difficulty found in our results, which made it difficult to assess multisensory integration.

2.6 Conclusion

Therefore, within the current experiment it appears that musical experience may not appear to alter the outcomes of multisensory integration, as both musicians and non-musicians performed equally well given audiovisual cues as would be predicted using a maximum likelihood estimate of optimal cue integration. Unfortunately, given the large discrepancy between auditory and visual cue reliability, we can not conclude whether participants were truly integrating unisensory cues, or merely attending to the more

reliable cue (i.e., visual cues). Our analysis of the relationship between each participant's unisensory and multisensory cue reliability measures revealed that there may be asymmetries between musicians and non-musicians in their use of auditory cues. However, this asymmetry may simply be the result of a small sample size and limited statistical power; therefore, further investigations need to be conducted. Thus, experience may enhance musicians' ability to utilize information from individual senses, yet it does not appear to fundamentally influence the product of multisensory integration.

3. Experiment #2

3.1 Background

Experiment #1 showed that musical expertise and sensorimotor experience may only subtly influence the multisensory processing of brief, distilled musical stimuli, if at all. In experiment #2, we explored the influence of this same experience in influencing the sensorimotor processing of longer, more complex musical stimuli.

Music can have a great effect on our bodies, and the way we move. This is particularly true in music with a salient underlying beat structure, which makes music an essential component of dance. Over roughly the past decade, researchers have begun examining neural responses to music in humans (Brown, Martinez & Parsons, 2006; Phillips-Silver et al., 2011; Zatorre, 2001), yet despite advancement in our knowledge about music processing, it still remains unclear how music is transformed from an auditory signal into complex movements (Bläsing et al., 2012; Grahn & Brett, 2007).

This ability seems to be quite fundamental in humans, as our ability to effortlessly synchronize our movements to auditory stimuli develops at an early age (Phillips-Silver & Keller, 2012; Phillips-Silver et al., 2011; Repp & Su, 2013). Music itself is integral in dance, as elements such as rhythm and timing shape dancers' sequences of movements (Adshead-Lansdale & Layson, 1994; Sachs, 1965). Dancers may begin learning several different forms and style of dance early in their careers; though, professional dancers often develop their expertise within a limited number of related dance styles if not one primary style. Each style of dance tends to be accompanied by a stereotypical musical genre. For example, an expert classical ballet dancer likely has lots of experience dancing to classical or romantic music; however, they may have little to no experience dancing to hip-hop music. This stylistic segregation results in dancers who have high familiarity moving to certain styles of music and little familiarity moving to others.

What remains unclear is how one's familiarity with a particular musical stimulus affects their ability to generate movements to said music. Thus, to explore this question, the aim of Experiment #2 was to investigate the effects of music familiarity on the cortical activity of an expert b-boy (i.e., a male breakdancer) during the kinesthetic motor

imagery (KMI) of dance accompanied by music, (as described in: (Guillot et al., 2009; Lotze, 2013; Lotze & Halsband, 2006).

In investigating the interaction of music and movement in the brain and the role of music familiarity during imagined movement, we chose to identify cortical brain regions that have been shown to be involved in both sensory and motor processing. Several auditory regions including A1 and the superior temporal gyri (STGs) have been implicated in motor processing (Kung, Chen, Zatorre & Penhune, 2013; Zatorre, Chen & Penhune, 2007). Additionally, motor areas such as the dorsal pre-motor cortex, the pre-SMA, the SMA, the intraparietal sulcus, and the cerebellum have correspondingly been shown to be involved in auditory processing, including improvised generation of rhythmic and melodic structures (de Manzano & Ullén, 2012; Liu et al., 2012), as well as during imagined and perceived familiar melodies (Herholz, Halpern & Zatorre, 2012).

The SMA (Brodmann's area 6) has repeatedly been shown to be critical for motor planning (Makoshi, Kroliczak & van Donkelaar, 2011; Thickbroom et al., 2000) and because of this, the SMA has is considered an important structure for both motor execution and imagery (Burianová et al., 2013; Jeannerod, 1995; Lotze et al., 1999; Lotze & Halsband, 2006). Historically, the SMA has been shown to be active during the mental imagery of simple motor tasks (Leonardo et al., 1995; Rao et al., 1993) and more recently in those which involve mental imagery accompanied by music, or of musical performances (Chen, Penhune & Zatorre, 2008; Cross, Hamilton & Grafton, 2006; Herholz, Halpern & Zatorre, 2012; Zvyagintsev et al., 2013). Furthermore, Grahn and Brett (2007) showed that musicians showed greater SMA activation as compared to the non-musicians in a study investigating beat perception and reproduction in both musicians and non-musicians (Grahn & Brett, 2007). Because of its involvement in several of the most fundamental components of dance, including beat perception, motor execution and imagery, as well as its role in music perception, the SMA is an ideal region of interest when examining the sensorimotor interactions during the KMI of dance to music.

The SMA is a prime example of a historically "motor" region that is actually quite involved in sensorimotor processing. Correspondingly, the primary auditory cortex, located within Heschl's gyrus (HG, Brodmann's area 41), is a stereotypically "sensory" region that is involved in the sensorimotor processing of music and dance. Preliminary

evidence has shown that bilateral primary auditory cortices are important during the learning of a dance through visualization over 8 months when cued by music (DeSouza & Bar, 2012), as well as music perception and mental imagery (Yoo, Lee & Choi, 2001; Zatorre, Chen & Penhune, 2007). HG is additionally believed to be an important processing area for elements of music that are important for dance, including rhythmic patterns (Penhune, Zatorre & Feindel, 1999), as well as melodies and timing (Tervaniemi & Hugdahl, 2003; Zatorre & Belin, 2001).

The processing of musical stimuli in HG has been shown to be lateralized (Koelsch, 2012; Tervaniemi & Hugdahl, 2003), yet there is little evidence of how learning influences this lateralization in HG (DeSouza & Bar, 2012). There have been a few studies investigating the structural roots of musical lateralization in HG. One such study by Bermudez, Lerch, Evans, and Zatorre (2009) used voxel-based morphometry to compare the concentration of gray matter of 71 expert musicians against that of 64 non-musicians. Their results showed that gray matter concentrations in the posterolateral aspect of HG in musicians were lateralized to the right hemisphere (Bermudez, Lerch, Evans & Zatorre, 2009). A second study performed by Hyde and colleagues (2009) investigated the development of music training in a group of first-graders using deformation based morphometry, showing lateralization of structural development as a function of training over a 15-month period (Hyde et al., 2009). Compared to structural changes previously seen in expert populations of musicians, Hyde and colleagues (2009) demonstrated that training-induced neuroplasticity could be detected in HG following musical rehearsal over a relatively short training regimen.

What both of these studies suggest is that neuroplastic changes in auditory processing areas occur as a result of specialized experience or training. Studies such as these have led us to question how lateralization of auditory processing in HG may be mediated by training, expertise and consequently familiarity. In Experiment #2, we investigated whether functional laterality was demonstrated in expert dancers.

Top-down processes, such as repetition suppression (Bergerbest, Ghahremani & Gabrieli, 2004) and stimulus expectation (Andics, Gál, Vicsi, Rudas & Vidnyánszky, 2013) are additional factors that may influence the effect of musical familiarity on auditory processing in the temporal cortices. By simply having extensive experience with a

stimulus (i.e., a song), neural activation to subsequent presentations of the same stimulus is modulated by cognitive factors such as memory and anticipation.

Experiment #2 was designed to investigate the effect of musical familiarity on neural activity underlying KMI when accompanied by music (Olshansky, Bar, Fogarty & DeSouza, 2015). The scope of this investigation was focused on two model cortical regions for sensory and motor processing, particularly in respects to musical processing and motor imagery, this being HG and the SMA respectively. Concentrating on the neural processing underlying KMI, we used functional magnetic resonance imaging (fMRI) to obtain blood-oxygen-level–dependent (BOLD) signals from an expert breakdancer during imagined dancing to both familiar and unfamiliar music. In order to accomplish this goal, KS's BOLD responses were contrasted between two experimental conditions: first, during imagined dance to self-selected breakdancing music (i.e., the familiar “breakdancing” condition), and second, during imagined dance to a novel piece of classical music (i.e., the unfamiliar “ballet” condition). So as to shed additional light on the influence of individual experience on the KMI of dance to music, an added contrast was conducted between KS and two dancers with corresponding experience - an expert ballet dancer (for whom the classical music was highly familiar), and a non-expert control (for whom neither music was substantially familiar as dance accompaniment).

We hypothesized two principal findings:

1. As a result of increased exposure to the highly familiar music through dance rehearsal, and the resulting increased ability to dynamically generate creative movements, KS would show greater SMA activity during kinesthetic motor imagery to a familiar piece of music and dancing style compared to an unfamiliar music and dancing style. Therefore, we hypothesized that increased exposure and practice would lead to the planning of more elaborate movements, which would be reflected by increased neural activity.
2. We expected that KS would exhibit decreased auditory processing of the familiar music during motor imagery, reflecting repetition suppression and stimulus expectation. Thus, we hypothesized that increased exposure and practice processing a highly familiar piece of music would minimize the effort required to process dance relevant musical elements

(i.e., rhythmic structures and emotionality), and this reduced need to dissect the music's features would be reflected by decreased neural activity.

Following from these hypotheses, we additionally hypothesized that due to KS's experience and familiarity they would exhibit greater SMA activity and would have less HG activity than control subjects during kinesthetic motor imagery to familiar music, with reverse results for the less familiar music.

3.2 Methods

3.2.1 Participant

This case study investigates an expert breakdancer KS (male, 47 years old, right handed) who had 35 years of professional breakdancing experience at the time of data acquisition. Participant KS has had a long and influential career as a dancer, and is widely recognized as one of the forefather of modern breakdancing. Control subject 1 (male ballet dancer, 51 years old, right-handed) has 45 years of professional ballet experience, including performance and teaching, and control subject 2 (male novice dancer, 44 years old, right-handed) has 6 months of beginner ballet experience. The necessary ethical approval was obtained from the Office of Research Ethics at York University (Certificate #: 2013 – 296; valid 11/07/13 – 03/03/16).

3.2.2 Materials and Scanning Procedure

All functional and anatomical data were acquired using a 3-Tesla Siemens Tim Trio MRI scanner (Siemens Medical Systems, Erlangen, Germany) with a 32-channel head coil at the Sherman Health Sciences Research Center at York University (Toronto, Ontario, Canada). High-resolution T1-weighted anatomical images of each participant were obtained (spin echo, matrix = 256×256 , voxel size = 1 mm^3 , TR = 1900 ms, TE = 2.52 ms, flip angle = 9°). T2*-weighted images were acquired using generalized autocalibrating partially parallel acquisitions (GRAPPA) echo planar imaging, with an acceleration factor of 2X (slices = 32, matrix = 56×70 , FOV = $210 \text{ mm} \times 168 \text{ mm}$, voxel size = $3 \text{ mm} \times 3 \text{ mm} \times 4 \text{ mm}$, TR = 2000 ms, TE = 30 ms, flip angle = 90°). All images were presented on a back projected screen, which participants viewed using a head coil mounted mirror (Avotec SV-6011. Stuart, Florida, U.S.A., visual angle 36°), and heard the stimulus via MR-compatible headphones (MR Confon, Magdeburg, Germany) while

their heads were padded with foam in order to restrict movement artifacts. A vitamin E capsule was placed near each participant's right ear in order to localize the right hemisphere.

3.2.3 Task Procedure

While in the scanner, participants performed three tasks: two KMI tasks and a motor localization task. All tasks were presented in a block design, with five 60-second stimulus blocks separated by 30-second baseline fixation blocks with a 30-second period before and after scanning. During the kinesthetic motor imagery tasks, participants were instructed to visualize themselves dancing from the internal, first-person perspective, as if they were going to complete movements (Ruby & Decety, 2001) to musical stimuli. Participants performed a motor localization task in order to functionally localize brain regions involved in movement. Participants were instructed to extend and contract the toes of their right feet at a rate of 1Hz when the word “*wiggle*” appeared on the screen (i.e., 60-second stimulus block). Each task lasted 480-seconds and resulted in a total of 240 functional volumes.

Data for the breakdancing motor imagery task was only obtained from subject KS and control 2. The data from control 1 were acquired previously (DeSouza & Bar, 2012) and were only used as a contrast for the ballet condition.

3.2.4 Stimulus

Two pieces of music were used during the experiment. Our exemplar breakdancing piece was selected by subject KS three days prior to the experiment, chosen specifically as a song which he had performed to many times over more than twenty years. This piece came from Grandmaster Flash's version of the Incredible Bongo Band's 1973 song entitled *Apache* (a 60-second section during the bongo solo). Our exemplar ballet piece was supplied to us from the director of the National Ballet of Canada Youth, Outreach and Understanding (YOU) Dance program, as a song which they were currently learning, and was identified as a novel piece by subject KS, to which he had never performed a dance. This piece came from the first 60-seconds of J.S. Bach's *Fugue* from *Concerto in C major [BWV 1061]*, as adapted for solo piano. Stimuli were not matched for acoustic properties (e.g. pitch, rhythm, tempo...etc.), as they were provided to us as exemplar musical stimuli and it was important for each stimulus to

reflect musical stimuli at varying levels of familiarity, and which have been practiced many times.

3.2.5 fMRI Pre-Processing

Brain Voyager QX (version 2.2.1, Brain Innovation, Maastricht, The Netherlands) was used for all data analyses (Goebel, Esposito & Formisano, 2006). Participants' structural data was normalized to Talairach space (Talairach & Tournoux, 1988). Functional data was coregistered to native anatomical space and pre-processed with motion correction (sinc interpolation) using reference volumes to correct for intra-session alignment, slice scan time correction (sinc), as well as high-pass temporal filtering (GLM - Fourier - 2 cycle sine/cosine). No spatial smoothing was performed.

Due to the nature of the experiment (i.e., participants were instructed to imagine moving without actually moving), participant data were thoroughly scrutinized for motion artifacts with the aid of video footage recorded during the scanning sessions (only in participants KS and control 2) to ensure that participants did not move during KMI. No data needed to be motion corrected more than 0.5 mm throughout any functional scans.

Three-dimensional anatomical images were generated from each participant's T1-weighted data using automatic tissue segmentation. Segmented gray-matter data were then inflated to produce cortical maps (smoothing force = 0.8; morphing iterations = 800) and surface maps using each participant's functional data. Because HG is an anatomically defined cortical region, all HG regions of interest (ROIs) were defined anatomically using inflated cortical maps (Figure 10A). In contrast, because of the anatomical variability between individuals, and as a functionally defined cortical region, SMA ROIs were independently and functionally defined for each participant. This was accomplished by identifying each participant's medial Brodmann's area 6, referencing the human motor area template coordinates outlined for the SMA in the meta-analysis by Mayka and colleagues (Mayka, Corcos, Leurgans & Vaillancourt, 2006). We then extracted the data from the active voxels within each participant's SMA during the motor localization task (statistical thresholds for all participants: $p < .05$; false discovery rate corrected) (see Figure 10B).

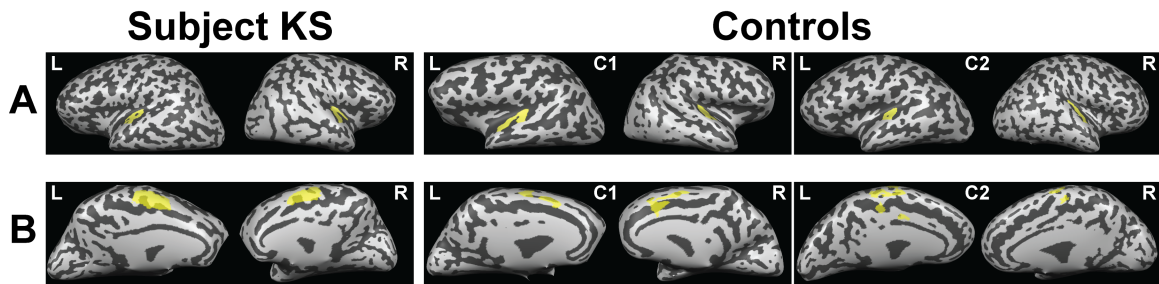


Figure 10. Regions of interest (ROIs). A depiction of the ROI's shown on inflated cortical surface maps. (A) Anatomically defined ROIs in yellow of Heschl's gyrus for subject KS and the two control subjects C1 and C2. (B) Functionally defined ROIs in yellow of the supplementary motor cortex for subject KS and the two control subjects C1 and C2 ($Q_{FDR} < 0.05$).

3.2.6 Statistical Analysis

Surface maps were created using single-subject GLMs contrasting stimulus-ON blocks with baseline fixation blocks for each subject. A two-gamma hemodynamic response function was modeled, and the five repeated stimulus-ON blocks were averaged, volume-by-volume for each subject and condition. The average percent change in BOLD signals during 31 functional volumes for each participant's individual ROIs were extracted and used for all statistical comparisons. Functional volumes correspond to the recorded hemodynamic signal during the stimulus-ON blocks.

The data were analyzed using R version 2.15.3 (R Development Core Team). Within-subject comparisons were conducted with paired-sample t -tests on 31 functional volumes (degrees of freedom = 30) that were averaged across stimulus-ON blocks. Two-sample Welch's t -tests were used for between-subject comparisons in order to account for unequal intra-subject variances. For all comparisons, we report the effect sizes calculated using Eta-squared (η^2). All results were then corrected for family-wise error rates using a Holm stepwise correction procedure in order to maintain an alpha level of 0.05.

3.3 Results

Heschl's gyrus – Our analysis of subject KS's primary auditory cortex (HG) unveiled significant differences in cortical activation bilaterally between the ballet and breakdancing KMI conditions (see Table 1 and Figure 11A). During the breakdancing condition, KS's average percent change in BOLD signal was significantly less than during the ballet condition, in both the left ($t(30) = 2.78, p < .05, \eta^2 = 0.204$) and right

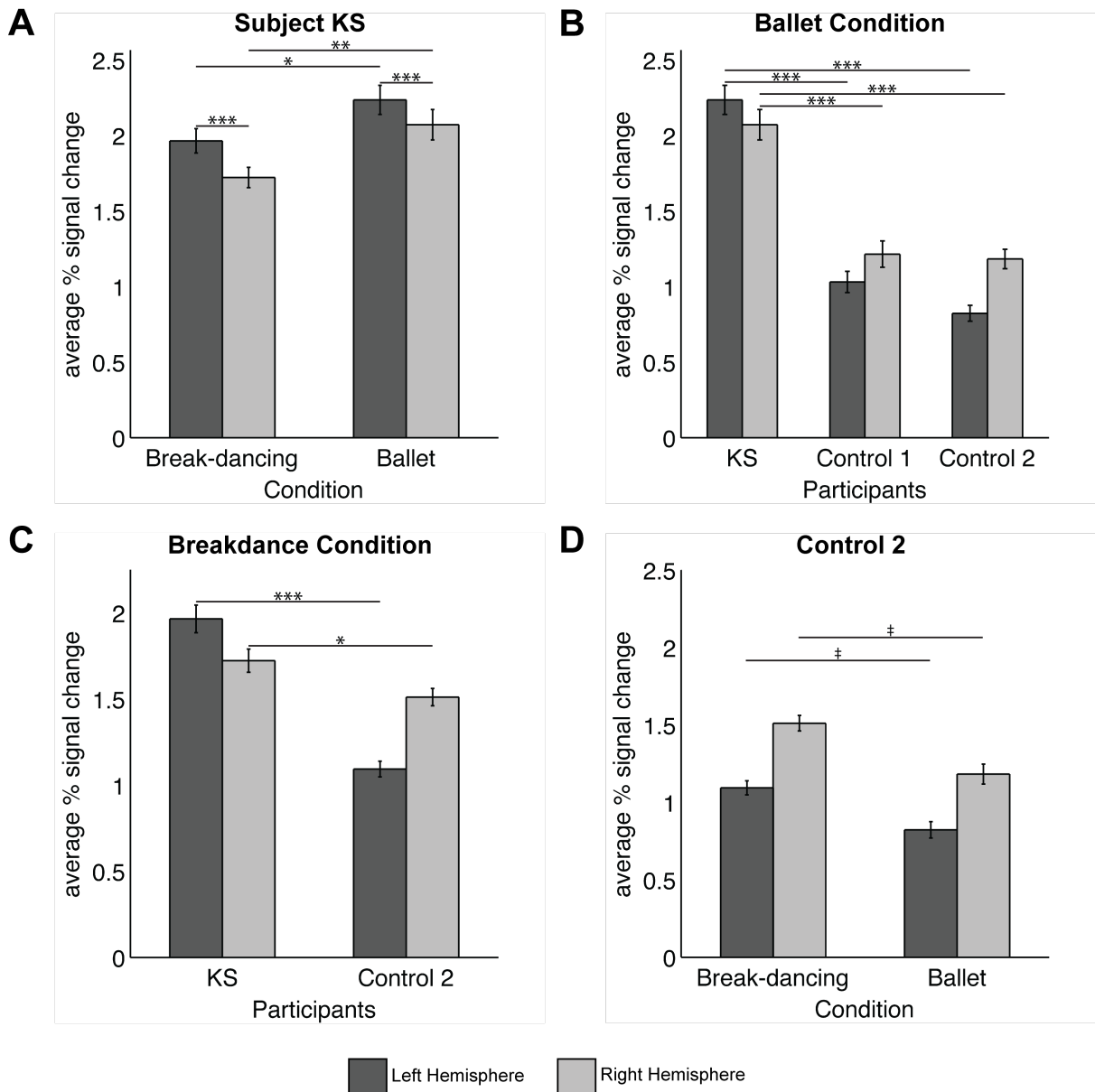


Figure 11. Kinesthetic motor imagery (KMI) in Heschl's gyrus (HG). All graphs indicate average blood-oxygen-level-dependent (BOLD) percent signal change between KMI and rest. (A). Subject KS's bilateral HG signals for the break-dancing condition and the ballet condition. Statistics show paired t-tests (one-tailed between conditions and two-tailed between hemispheres). (B). All subjects' bilateral HG signals during the ballet condition. Statistics indicate two-tailed Welch's t-tests. (C). Subject KS and control subject 2's bilateral HG signals during the break-dancing condition. (D). Control subject 2's bilateral HG signal during both break-dancing and ballet conditions. Statistics indicate two-tailed Welch's t-tests. * indicates = $p < 0.05$; ** indicates = $p < 0.01$; *** indicates = $p < 0.001$; ‡ indicates = $p < 0.001$ uncorrected.

hemispheres ($t(30) = 3.26, p < .01, \eta^2 = 0.262$), as revealed by one-tailed, paired-sample t -tests.

Table 1. Mean percent BOLD signal change from subject KS during kinesthetic motor imagery accompanied by familiar music (breakdance) music and unfamiliar music ballet)

Region of Interest		Experimental Condition		t -statistic	Effect Size (η^2)
		Breakdance	Ballet		
Heschl's Gyrus	<i>Left</i>	1.97 (0.08)	2.24 (0.10)	2.78*	0.204
	<i>Right</i>	1.72 (0.07)	2.07 (0.10)	3.26**	0.262
SMA	<i>Left</i>	0.74 (0.03)	0.61 (0.05)	2.54*	0.177
	<i>Right</i>	0.60 (0.01)	0.42 (0.04)	3.99**	0.347

Note. * = $p < 0.05$, ** = $p < 0.01$. All p -values were corrected using *Holm* multiplicity correction. Standard error of the means appear in parentheses below means. All comparisons were paired sample t -tests, $df = 30$. '*Left*' indicates the left cerebral hemisphere, and '*Right*' indicates the right cerebral hemisphere. t -statistics indicate separate comparisons for each cerebral hemisphere (i.e., *Left vs. Left; Right vs. Right*).

Our analyses of KS additionally revealed significant lateralization in left and right HG activation within each condition. Interestingly, for both the breakdancing condition ($t(30) = 7.48, p < .001, \eta^2 = 0.807$, two-tailed) and the ballet condition ($t(30) = 3.99, p < .001, \eta^2 = 0.590$, two-tailed), the left HG was significantly more active than the right HG (see Figure 11A).

To assess any effects of dance experience between different musical genres, we contrasted subject KS's BOLD signals against those from a professional ballet dancer (control 1) as well as a novice with beginner ballet experience (control 2). Data from both control subjects were obtained from the ballet visualization condition (see Table 2 and Figure 11B). The average BOLD signal from control 1 was significantly less than that of subject KS in both hemispheres ($t(54.96)_{\text{left}} = 10.06, p < .001, \eta^2 = 0.648$); $t(58.85)_{\text{right}} = 6.43, p < .001, \eta^2 = 0.413$). Average BOLD activity was also significantly less in control 2 when compared to KS ($t(46.37)_{\text{left}} = 12.83, p < .001, \eta^2 = 0.780$; $t(51.05)_{\text{right}} = 7.45, p < .001, \eta^2 = 0.521$). Only control 2 performed the breakdancing condition of the motor imagery task, and their average BOLD signals were significantly lower than subject KS

($t(47.42)_{\text{left}} = 9.42, p < .001, \eta^2 = 0.652$; $t(55.39)_{\text{right}} = 2.52, p < .05, \eta^2 = 0.103$ – see Table 3 and Figure 11C).

Table 2. Mean percent BOLD signal change from all participants during kinesthetic motor imagery accompanied by Concerto in C major [BWV 1061] (ballet condition).

Region of Interest		Participant			t-statistic		Effect Size (η^2)	
		KS	C1	C2	KS-C1	KS-C2	KS-C1	KS-C2
Heschl's Gyrus	<i>Left</i>	2.24 (0.10)	1.03 (0.07)	0.82 (0.05)	10.06*** (54.96)	12.83*** (46.37)	0.648	0.780
	<i>Right</i>	2.07 (0.10)	1.21 (0.09)	1.18 (0.06)	6.43*** (58.85)	7.45*** (51.05)	0.413	0.521
SMA	<i>Left</i>	0.61 (0.05)	0.48 (0.04)	0.02 (0.03)	1.98 ^{ns} (57.44)	9.59*** (49.88)	0.064	0.648
	<i>Right</i>	0.42 (0.04)	0.73 (0.05)	0.14 (0.03)	4.63*** (56.84)	5.60*** (53.18)	0.274	0.371

Note. *ns* = non-significant, *** = $p < 0.001$. All p-values were corrected using *Holm* multiplicity correction. Standard error of the means appear in parentheses below means. All comparisons were Welch's two sample *t*-tests. Degrees of freedom appear in parentheses below each t-statistic. '*Left*' indicates the left cerebral hemisphere, and '*Right*' indicates the right cerebral hemisphere. *t*-statistics and effect sizes indicate separate comparisons between subject KS and each control participant.

Together, our results indicate that subject KS demonstrates significantly less BOLD signal in HG during imagined dance to breakdancing music, as well as consistently greater BOLD signal in the left HG across both task conditions. Furthermore, KS shows significantly greater bilateral HG activity than both control subjects, across all conditions.

Supplementary motor area (SMA) – Analyses of SMA activation in subject KS revealed significant differences bilaterally between the ballet and breakdancing KMI conditions (see Table 1 and Figure 12A). KS's average percent change in BOLD signal during the breakdancing condition was significantly greater than during the ballet condition, in both the left ($t(30) = 2.54, p < .05, \eta^2 = 0.177$) and right hemispheres ($t(30) = 3.99, p < .01, \eta^2 = 0.347$) as revealed by one-tailed, paired-sample *t*-tests.

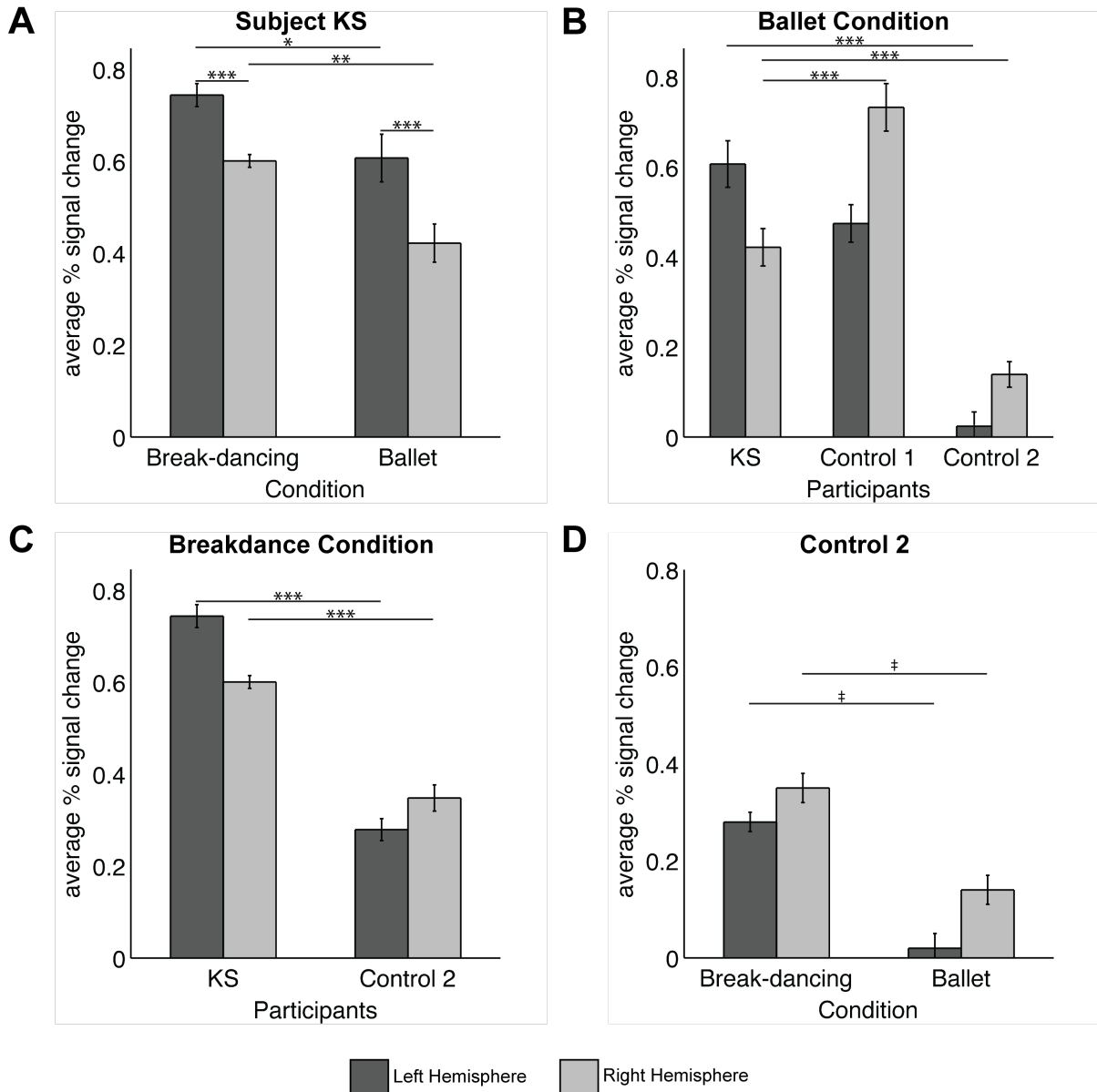


Figure 12. Kinesthetic motor imagery (KMI) in the supplementary motor area (SMA). All graphs indicate average blood-oxygen-level–dependent (BOLD) percent signal change between KMI and rest. (A). Subject KS’s bilateral SMA signals for the break dancing condition and the ballet condition. Statistics show paired t-tests (one-tailed between conditions and two-tailed between hemispheres). (B). All subjects’ bilateral SMA signals during the ballet condition. Statistics indicate two-tailed Welch’s t-tests. (C). Subject KS and control subject 2’s bilateral SMA signals during the break dancing condition. (D) Control subject 2’s bilateral SMA signal during both break-dancing and ballet conditions. Statistics indicate two-tailed Welch’s t-tests. * indicates = $p < 0.05$; ** indicates = $p < 0.01$; *** indicates = $p < 0.001$; ‡ indicates = $p < 0.001$ uncorrected.

Similar to our findings in HG, we observed significant differences between left and right SMA activation within each condition. Once again, BOLD activation was significantly greater in the left hemisphere than the right during the breakdancing condition ($t(30) = 8.59, p < .001, \eta^2 = 0.711$, two-tailed) and the ballet condition of the motor imagery task ($t(30) = 10.58, p < .001, \eta^2 = 0.789$, two-tailed – see Figure 12A).

Table 3. Mean % BOLD signal change from all participants during kinesthetic motor imagery accompanied by Apache (breakdance condition).

Region of Interest		Participant		t-statistic	Effect Size (η^2)
		KS	C2		
Heschl's Gyrus	<i>Left</i>	1.97 (0.08)	1.09 (0.05)	9.42*** (47.42)	0.652
	<i>Right</i>	1.72 (0.07)	1.51 (0.05)	2.52* (55.39)	0.103
SMA	<i>Left</i>	0.74 (0.03)	0.28 (0.02)	13.40*** (59.93)	0.750
	<i>Right</i>	0.60 (0.01)	0.35 (0.03)	7.94*** (43.52)	0.592

Note. * = $p < 0.05$, *** = $p < 0.001$. All p-values were corrected using *Holm* multiplicity correction. Standard error of the means appear in parentheses below means. All comparisons were Welch's two sample *t*-tests. Degrees of freedom appear in parentheses below each t-statistic. 'Left' indicates the left cerebral hemisphere, and 'Right' indicates the right cerebral hemisphere. *t*-statistics and effect sizes indicate separate comparisons between subject KS and each control participant.

Between-group comparisons of average SMA activity revealed significant differences between KS and both control subjects during the ballet motor imagery condition (see Table 2 and Figure 12B). The average BOLD signal from control 1 was significantly greater than subject KS in the right SMA ($t(56.84)_{\text{right}} = 4.63, p < .001, \eta^2 = 0.274$) but was non-significantly different in the left SMA ($t(57.44)_{\text{left}} = 1.98, p > .05, \eta^2 = 0.064$). For control 2, average BOLD activation was significantly less than subject KS bilaterally ($t(49.88)_{\text{left}} = 9.59, p < .001, \eta^2 = 0.648$; $t(53.18)_{\text{right}} = 5.60, p < .001, \eta^2 = 0.371$). Similar to HG, BOLD signals from the SMA in control 2 during breakdancing motor imagery were significantly less than subject KS in both hemispheres ($t(59.93)_{\text{left}} = 13.4, p < .001, \eta^2 = 0.750$; $t(43.52)_{\text{right}} = 7.94, p < .001, \eta^2 = 0.592$) (see Table 3 and Figure 12C).

In summary, these results show that subject KS demonstrates significantly greater BOLD signal in the SMA during the imagined dance to breakdancing music, as well as consistently greater BOLD signal in the left SMA across both task conditions. Additionally, KS shows significantly greater bilateral SMA activity than control 2 across both conditions, whereas KS had significantly less BOLD activity in the right SMA than control 1.

3.4 Discussion

The results of experiment #2 lend further evidence to the notion that experience and familiarity play a key role in modulating activity of select motor planning and primary sensory cortical areas (i.e., the SMA and HG, respectively) as revealed during imagined dance to music (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; DeSouza & Bar, 2012; Herholz, Halpern & Zatorre, 2012). We observed significantly less BOLD signal in HG during the imagined dance to the familiar music compared to unfamiliar music in an expert breakdancer (KS). This finding is potentially the result of the participants' past experiences, as the processing of a highly familiar stimulus may require less processing in primary sensory processing areas compared to unfamiliar songs. Moreover, our interpretation is in line with previous research by Jacobsen and colleagues, whose examinations of the effect of familiarity on auditory change detection suggest that familiar auditory stimuli result in enhanced preparatory processes (Jacobsen, Schröger, Winkler & Horváth, 2005), in order for the listener to effectively perceive characteristics of the music (i.e. beat, rhythm, melodies, and emotional valence), and thus facilitating faster and more efficient processing of overlearned stimuli. These findings are additionally in line with previous findings showing reduced hemodynamic responses in the superior temporal cortex as a result of repetition suppression (Bergerbest, Ghahremani & Gabrieli, 2004) as well as stimulus expectation (Andics, Gál, Vicsi, Rudas & Vidnyánszky, 2013). The interpretation that KS required less sensory processing as a result of exposure and familiarity is particularly plausible as subject KS chose their stimulus specifically because it was highly familiar and because they had extensive experience dancing to this piece for decades.

KS also displayed consistently greater BOLD signal in the left HG across both conditions, which may be explained by a few different factors. It is possible that the greater hemodynamic signal in their left HG originates from some sort of asymmetry

found in KS's early auditory pathway, such as a deficit in their right inner ear. Unfortunately, it is impossible to know whether there were any asymmetries, as the current experiment did not test for binaural auditory sensitivity or physiology. Another possible interpretation of this lateralization of activity could reflect the functional properties of the right and left primary auditory cortices. Neighboring areas to HG, such as the planum temporale (PT) have been shown to process speech vs. musical sounds differentially, with speech sounds being lateralized to the left PT and musical sounds to the right PT (Tervaniemi & Hugdahl, 2003). However, within HG the left hemisphere appears to be more involved in processing aspects of music such as harmony, timbre, and temporal variation, whereas the right hemisphere appears to be more sensitive to increased spectral variation and resolution, and pitch perception (Jamison, Watkins, Bishop & Matthews, 2006; Koelsch, 2012; Vuust, Brattico, Seppänen, Näätänen & Tervaniemi, 2012). Therefore, it is possible that the lateralization found in subject KS reflects their increased focus on aspects of the stimulus such as the rhythm, textures and tempo that have been shown to be preferentially processed in the left auditory cortex.

Very few researchers have investigated the effects of familiarity on music perception and motor planning, particularly during KMI within expert populations. One such study conducted by Calvo-Merino et al. (2005) investigated action observation of familiar versus unfamiliar dance styles and showed that experience with a given dance style resulted in increased activation of the superior temporal lobes when observing familiar movements compared to unfamiliar movements (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005). In this paradigm, participants were presented with brief (3 second) silent videos of dancers performing either ballet or capoeira dances. Our current investigation was considerably different than Calvo-Merino et al. (2005) in the following respects: First, subject KS had to imagine dancing instead of watching a video of another performer, therefore they performed KMI as opposed to passive observation. Second, KS performed the motor imagery for a substantially longer period of time (one minute). Third, KS was acoustically cued and paced using music. And fourth, our paradigm did not have any visual stimulus, with subject KS closing his eyes during KMI. This study by Calvo-Merino et al. (2005) presented visual stimuli in order to investigate the aspects of action observation, whereas we were interested in studying auditory

processing of music and movement during motor imagery in the absence of influence from visual processing networks.

Although the current experiment did not explore the neural processing involved in the passive listening of familiar vs. unfamiliar music, research investigating passive music listening has shown that auditory cortex activity is correlated with cognitive measures based on familiarity (Pereira et al., 2011). This research conducted by Pereira and colleagues measured individual's ratings of pleasantness and their emotional response to music while controlling for the participant's level of musical familiarity. They concluded that the less pleasant music was the greater activity in certain auditory areas, which include the left STG. Moreover, they found that familiarity appeared to be an important factor influencing the listeners' emotional connection with the music. Higher familiarity resulted in increased subcortical activity in both limbic and paralimbic regions believed to be crucial for emotional responses. From this, it is reasonable to suspect that the music people enjoy would typically encompass a portion of the music in which they are most familiar with (as people generally listen to music that they consider pleasant). This conclusion is in line with our finding that subject KS showed less primary auditory cortex activity during the familiar breakdancing conditions. Since we did not control for emotional responses to the stimuli, we are unable to verify whether these findings reflect similar mechanisms.

KS's numerous years of experience generating choreography to this particular musical piece may explain our findings of increased SMA activity during imagined dance of breakdancing. The greater SMA activity observed in KS during this condition compared to during the ballet condition may be the result of having a larger repertoire of available movements that have been practiced and dynamically combined for decades, as well as KS's familiarity to the music. It is possible that highly familiar music may result in significantly more SMA activity and larger movement repertoire when compared to imagined dance to less familiar music. Similar to our current findings, Pereira et al. (2011) found that the bilateral SMA was significantly more active during passive listening to familiar music, when compared to unfamiliar music.

Other evidence in support of the effects of familiarity on the SMA activation is scant, though one such study by Milton and colleagues (2007) showed that expert golfers had less SMA activity when compared to novice controls during imagined

movements (Milton, Solodkin, Hlustík & Small, 2007). Although this study appears to contradict our current findings, the motor imagery task used in Milton and colleagues (2007) involved a far less complex movement (the swinging of a golf club), and it is likely that the complex and dynamic movements required for dance necessitate more SMA involvement and thus may not be directly comparable. Additionally, our stimuli are cued by music and were presented for a longer duration (i.e., 60-s compared to the few seconds it takes to imagine a single golf swing). This is a plausible explanation for our current findings as this region has been implicated in the combination of several simpler component movements into a larger sequence (Picard & Strick, 1996; Tanji, 2001). Although once learned, swinging a golf club requires many movements, it still only requires one goal – to hit the ball into the hole. Dance similarly involves many different movements. However, unlike the golf example, dancing additionally requires many different goals such as keeping the beat, matching dynamic changes in the music, controlling your body in three-dimensional space, and paying attention to people nearby, all while executing ever-transforming movements. Taken together, our results support the notion that SMA may be central to movement processing when coupled with music.

Interestingly, one common trend in cortical activation between KS and both of the control subjects is the lateralization of BOLD signals. However, as shown in Figures 11B and 12B, subject KS had lateralized activity in the left hemisphere, whereas both control 1 and control 2 show the opposite trend, with greater activity in the right hemispheres. Additionally, the same trend continued during the breakdancing condition (Figures 11C and 12C), with only control 2 showing lateralization in the right hemisphere and KS again showing lateralized activity in the left hemisphere. There is considerable evidence suggesting that certain aspects of auditory processing are lateralized within the primary auditory cortex (Tervaniemi & Hugdahl, 2003; Zatorre, 2001). Because these trends persist across both conditions, it is unlikely that the patterns of lateralization are due to the different stimulus and likely reflect morphological differences unique to each subject. Further investigation into the lateralization of both HG and SMA, particularly during the KMI of dance accompanied by music, needs to be conducted in order to determine whether the lateralization observed in the present study reflects individual differences or the functional plasticity resulting from the subjects' experiences and familiarity with the stimuli.

3.5 Limitations

With the exception of the SMA in control 1 during ballet motor imagery, subject KS had higher BOLD signals than control subjects in both visualization conditions. It is possible that this enhanced signal is the result of years of choreography and dance experience; though, this is an unlikely explanation as control 1 has similar choreography experience to subject KS. A more robust investigation into the stability and perpetuity of this difference needs to be conducted in order to ascertain whether subject KS has a unique ability to process musical stimuli and to generate imagined motor commands. A potential confound with the current study lies in the participant's familiarity with the music; it is possible that subject KS's ability to imagine dance moves, and therefore their associated neuronal activity, may be a direct result of their level of familiarity with the stimulus. This in itself is an interesting question, and further research on the connection between stimulus novelty and one's ability to produce KMI of dance are necessary in order to determine if there is a direct influence of familiarity on the neural correlates of KMI.

Additionally, stimuli were not matched for physical properties, and it is possible that this factored into the differential neuronal activation between conditions. The current stimuli were chosen as the goal was for each stimulus to reflect extremely familiar and novel musical pieces, respectively, and as such personal experience was used as our primary criteria. Future research investigating KMI to music of various levels of familiarity should try and control for these acoustic properties.

3.6 Conclusion

The findings from experiment #2 suggest that kinesthetic motor imagery to familiar music and dance styles results in greater SMA activity in subject KS, and presumably more elaborate and complex imagined movements. Our results suggest that one's internal representations of dance moves can be specific to a musical stimulus. Motor plans used for one form of dance (and musical stimulus) may not necessarily carry over across multiple dance styles in those with high levels of expertise, however more research is required to support this theory. Furthermore, these findings indicate that motor imagery to less familiar music and dance styles results in greater primary auditory cortex activity. This can potentially be attributed to top-down cognitive factors such as memory, which influence stimulus expectation and repetition suppression.

These results highlight the importance of auditory stimuli when generating movements for dance and demonstrate the important link between dance and music – whereby a dancer’s level of familiarity to a piece of music can influence how they process and generate novel choreography.

4. General discussion

4.1 The Effects of Musical Expertise on Processing

Although music is such an important component of life (Clarke, Dibben & Pitts, 2010; Hagen & Bryant, 2003; Trainor & Corrigall, 2010), neuropsychological research has only recently begun investigating the neural basis of music perception and interactions. The study of those with musical expertise, as a method of investigating these questions, provides a valuable avenue for understanding the role of musical experience on sensory processing (Münste, Altenmüller & Jäncke, 2002). Because of music's universality and its power to influence our bodies and minds, this research is important to help us understand how we interact with and perceive music, and how we can utilize music throughout our lives.

The goal of this thesis was to explore the role of musical expertise on the sensory processing of music stimuli. Because musical expertise can be found in individuals with various backgrounds, there are many research questions that could be investigated on this topic, most of which have only begun to be studied, if at all. This thesis was aimed at investigating two major examples of musical experts. Firstly the musicians themselves, and secondly dancers, as both of these groups typically have extensive sensory and sensorimotor experience actively interacting with music. This research was aimed at investigating the role of musical experience on the sensory processing of ecologically valid (i.e., naturalistic) musical stimuli.

Experiment #1 focused on musical expertise in musicians. This investigation took the form of a psychophysics experiment exploring multisensory integration, and was designed to investigate whether musical experience influenced multisensory integration in a two alternative forced choice discrimination task. In order to accomplish this we examined how musicians and non-musicians differ in their behavioural responses to naturalistic multisensory stimuli, such as the discrimination of two notes being played on a musical instrument, comprised of their congruent auditory and visual components. In experiment #1, we were interested in exploring whether a musician's extensive experience perceiving and interacting with musical performances impacted the degree to which they experience multisensory enhancement, as compared to modeled estimates.

The findings from this experiment provide some of the first evidence of the influence of domain specific experience on the multisensory integration of musical stimuli, particularly as it pertains to low-level sensory discrimination. Our results may indicate that neither musicians nor non-musicians significantly deviated from their MLE of optimal cue integration, which suggests that previous experience may not significantly influence multisensory integration or enhancements. However, given the high degree of difference in unisensory cue reliability in this study, it remains unclear if participants were truly integrating both cues, or simply relying on visual cues in performing the multisensory task. When we examined the relationships between each of the group's unisensory performance and their multisensory performance, our results indicated that both non-musicians and musicians found auditory cues less reliable than visual cues when performing a multisensory task. Although all individuals appear to have integrated audio and visual cues similarly, our results present evidence which may suggest that both groups may have done so in distinct ways. Whereas non-musicians appear to have relied exclusively on visual cues when performing the multisensory task, our correlational evidence indicates that musicians may have additionally utilized auditory information in performing the multisensory task. Although, given that our results are inconclusive, further investigations are required to explore this inference. These findings are not without their limitations, however they are in line with the Bayesian based MLE model of optimal sensory cue integration, which predicts that the more reliable a cue is, the more weight it holds on influencing perception and decision making when combined with additional cues, and conversely, the less reliable a cue, the less weight it receives (Angelaki, Gu & DeAngelis, 2009).

Therefore, as both musicians and non-musicians performed equally well given audiovisual cues as would be predicted using a MLE of optimal cue integration, we can conclude that musical experience does not appear to influence the effects of multisensory integration. Our analysis of the relationship between each participant's unisensory and multisensory cue reliability measures revealed that there may be asymmetries between musicians and non-musicians in their use of auditory cues. Importantly, this asymmetry may be the result of limited statistical power and further investigations need to be conducted. Thus, experience may enhance musicians' ability to utilize information from individual senses, yet it does not appear to fundamentally influence the product of multisensory integration.

Experiment #2 focused on musical expertise in a professional dancer. This experiment was a case study investigating the neural activity (inferred via BOLD signals) of the kinesthetic motor imagery of dance accompanied by music in an expert breakdancer (KS). Whereas experiment #1 focused on the influence of musical expertise on multisensory integrations using brief distilled musical stimuli, experiment #2 explored similar influences on sensorimotor processing and transformations using longer more complex musical stimuli. Our results indicated that subject KS demonstrated significantly less BOLD signal in their primary auditory cortex (HG) during imagined dance to familiar (i.e., breakdancing) music, as well as consistently greater BOLD signal in the left HG as compared to the right HG across both familiar and unfamiliar conditions. KS also exhibited significantly greater bilateral HG activity than both control subjects, across all conditions. Furthermore, our results showed that subject KS demonstrated significantly greater BOLD signal in their SMA, an important motor planning region, during imagined dance to familiar music, as well as consistently greater BOLD signal in the left SMA across both task conditions. KS additionally showed significantly greater bilateral SMA activity than control 2 across both conditions, and less BOLD activity in the right SMA than control 1.

Building on the work of only a small number researchers, these results provide evidence that experience and familiarity play key roles in modulating activity of select primary sensory cortical and motor planning areas (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; DeSouza & Bar, 2012; Herholz, Halpern & Zatorre, 2012). We observed a relative reduction in BOLD signal in a primary sensory region during KMI to the familiar music compared to unfamiliar music. This may reflect a reduced requirement of feature processing, such as the conscious processing of rhythmic and melodic structure, in primary sensory processing areas during the perception of familiar music. This conclusion is in line with previous findings that familiar auditory stimuli likely result in enhanced preparatory processes (Jacobsen, Schröger, Winkler & Horváth, 2005), which may aid listeners to effectively perceive characteristics of the music, and thus facilitate faster and more efficient processing of familiar stimuli. These findings are additionally supported by previous research which has demonstrated reduced hemodynamic responses in the superior temporal cortex as a result of repetition suppression (Bergerbest, Ghahremani & Gabrieli, 2004) as well as stimulus expectation (Andics, Gál, Vicsi, Rudas & Vidnyánszky, 2013). This evidence suggests that familiar

music, at least in those with substantial musical expertise and experience, requires less neural processing of acoustic characteristics than novel music.

There has been little research investigating the effect of experience of any type on SMA activation, let alone musical expertise (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; Cross, Kirsch, Ticini & Schütz-Bosbach, 2011; Hänggi, Koeneke, Bezzola & Jäncke, 2010). Our results indicated that experience and familiarity with musical stimuli and genre result in greater SMA activation when generating imagined dance movements. It is assumed that KS would have a larger repertoire of internalized sequences of movement for familiar dance genres that they would possess for unfamiliar genres. This is assumed because they had practice dynamically combining individual movements into more elaborate choreography for decades, which would no doubt result in learnt and memorized motor sequences (Makoshi, Kroliczak & van Donkelaar, 2011; Rao et al., 1993). It is this substantial experience with the dance genre and the music itself that may have resulted in the greater SMA activity in KS during familiar dance compared to during unfamiliar dance.

4.2 Limitations

Using ecologically valid stimuli – When investigating any sensory phenomenon, it is important to carefully consider the ecological validity of your experiment. This is particularly true in the case of experiments that are intended to probe expert skills, as it should not be assumed that behavioural outcomes of context specific experience is generalizable. Now, it is entirely plausible that learned skills in one domain are quite generalizable to similar or related domains, but unless this transferability is itself the focus of an experiment, it becomes difficult to make clear conclusions regarding the direct influence of expert skills on expert activities unless the correct conditions are provided.

In conducting this thesis, steps were made to ensure that the paradigms and stimuli that were used were representative of real-world conditions for both the musicians in experiment #1, and the dancers in experiment #2. This presented certain difficulties. For instance, historically multisensory integration experiments utilized multiple artificial stimuli, such as light-emitting diodes, computer generated sounds (Stein, Huneycutt & Meredith, 1988), or mechanically generated vibrations (Spence, Shore & Klein, 2001); however, the growing trend within multisensory research, and the

aim of experiment #1 was to use meaningful naturalistic stimuli. The biggest difficulty in not using artificially produced stimuli is control. In experiment #1, we recorded five adjacent notes on an acoustic guitar with the expectation that these tones would have specific physical characteristics (i.e., sound pressure at a particular frequency). However, if you play an A3 (220 Hz) on a guitar, you get more than just sound waves at 220 Hz, you additionally get a complex spectrum of sound waves (see Figure 2). This occurs because the instrument's unique attributes (i.e., the materials it is constructed from, its shape and the humidity of the room it is stored in) produces a unique and complex acoustic signature. Likewise, this variability is also present in recorded commercial music, and this makes for a highly complex stimulus that is hard to accurately describe and difficult to control when designing an experiment. This complexity may introduce confounding variable which influence participants' performance. For instance in experiment #1, even though it ought to be easier to discriminate notes that are farther apart tonally (e.g., A3 vs. B3) , it's possible that two closer notes (e.g., A3 vs. A#3) may be discriminated not only by fundamental frequencies, but also by timbre, and this may result in the closer note pairing being easier to discriminate. Therefore, it is important when using naturalistic stimuli to keep in mind that results may not represent hypothetically ideal stimuli (e.g., Note A#3 recorded on a particular acoustic guitar recorded with a specific microphone and environment may not be a *perfect* example of A#3).

Difficulty controlling and describing naturalistic musical stimuli is not the only hurdle that we must overcome, complex naturalistic stimuli can be challenging to manipulate. In experiment #1 for instance, if we had used artificial stimuli in designing an analogous experiment (e.g. pure sine wave tones and a small square presented on a computer screen), it would have been extremely easy to create a continuum of stimulus levels by simply manipulating the sound frequency and the location of the square on the screen. However, using the notes and note positions from an actual guitar, there is a fixed minimum distance between stimulus levels both sonically and visually. The problem with this is that our resolution of stimulus level's (independent variable) influence on performance (dependent variable) is fairly coarse, and this can impact our ability to accurately capture and interpret behaviour.

In order to overcome these limitations while continuing to perform an ecologically valid experiment we could do a few things. Music information retrieval packages that implement signal processing operations such as the *MIR toolbox* for Matlab (Lartillot & Toivainen, 2007) provide analysis techniques that allow users to extract and describe musical features such as spectral and component analysis, rhythmic, key, tempo and emotional feel. Furthermore, certain musical instruments such as classical stringed instruments (e.g. violin, cello, bass) that are fretless (i.e., notes can be produced at a continuum of positions along the instrument) may be easier to manipulate in designing stimuli, and choosing stimulus levels.

4.3 Future Directions

Although researchers have long been studying the psychology of music production and perception and have begun exploring its neuroscience over the past several decades, there remain numerous mysteries about how we perceive and interact with music as a complex stimulus and an art.

Future research on naturalistic music perception needs to factor into their models and theories the high degree of stimulus variability. Building on the experiments presented in this thesis, future research should include systematic investigations into the KMI of music on a group level. This research would examine the influence of familiarity between groups of dancers performing KMI to more numerous and strictly controlled stimuli. Furthermore, the addition of a passive listening control condition would allow us to parse out the BOLD responses to the physical properties of the stimuli, in order to more accurately assess the effects of experience. A similar experiment could be conducted on groups of musicians, as it would be fascinating to investigate the KMI of music production in musicians. In this research, we could explore the sensorimotor processing of familiar vs. improvised or newly learnt music, and provide some of the first information on the motor planning involved in music as a complex sensorimotor transformation and an art.

Building on experiment #1, future investigations of the naturalistic multisensory integrations of musical stimuli should attempt to utilize instruments and methods that allow for finer control of stimulus levels. This would allow for greater control of experimental manipulations and may provide a more reliable and accurate platform for investigating multisensory enhancement. Additionally, these experiments could be

expanded to investigate spatial and temporal multisensory integration, as has been widely studied in the non-musical multisensory literature. The use of eye tracking paradigms would provide a valuable behavioural measure of attention in order to assess the influence of multisensory cues on visuospatial processing.

Combining the focus of both experiments presented in this thesis, future research could also aim to investigate whether instrument specific experience (as opposed to general musical experience) produces behavioural advantages or neurological gains with familiar vs. unfamiliar naturalistic stimuli. Furthermore, this type of research should aim to explore whether or not any expertise effects are transferable across musical instruments or sub-classes of instruments (i.e., stringed, woodwind, brass and percussive instruments). This research would provide insight into the mechanisms that allow for expert musical performance, and how adaptable these mechanisms may be across instruments and domains.

4.4 Conclusion

Together these experiments have begun to provide behavioural and neurological evidence of the role of musical experience on sensory processing. From the two experiments presented in this thesis, it can be concluded that sensorimotor musical experience may have an impact on the way that individuals perceive and interact with musical stimuli. Additionally, this thesis advocates that further research is needed to elucidate the influence of specialized expertise on ecologically valid stimuli and tasks. The finding that context and content specific experience observing, creating and interacting with particular stimuli produced task relevant effects on performance and neural responses in experts indeed makes sense, and should not come as a surprise to most. Those with musical expertise develop specialized abilities to evaluate music, whether in terms of simple pitch discrimination of brief musical sounds, or their neural processing of complex sensorimotor transformations of complete musical pieces.

The development of these specialized abilities are not exclusively found in musicians, but are likely no different than comparable abilities any practiced expert might develop, whether they be musicians, cab drivers, baseball umpires, golfers or scientists. When an individual gains substantial experience interacting with all the individual stimuli within an environment, at some point they develop specialized abilities to perceive and interact with familiar stimuli. This in itself is a large part of what it means to be an expert,

to gain a meaningful advantage in perceiving, evaluating and performing within a specific context.

Therefore, the findings presented in this thesis provide new evidence using real-world complex stimuli, which support a well-established and intuitive conclusion, that our experiences shape the way we perceive and interact with our environments (Moreno & Besson, 2006; Münte, Altenmüller & Jäncke, 2002). The purpose of this thesis was to examine how the claim that specialized experience modulates perception functions within ecologically valid framework. Specifically, this thesis builds on the developing field of music cognition and neuroscience, and investigates how sensorimotor musical expertise impacts the multisensory processing of real-world stimuli.

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APPENDIX A

PARTICIPANT INFORMATION FORM

The following information will be kept confidential.

First Name: _____ **Age:** _____ **Sex:**

1. Do you **currently** play a musical instrument (including voice)?
_____ Yes (go to question #2) _____ No (skip to question #3)

2. Please provide the following information for each instrument you **currently** play, starting with the one that you consider your primary instrument.

Instrument	Ages during which you have played this instrument	Ages during which you took music lessons on this instrument	Hours per week that you play this instrument currently

Please describe the situations in which you play (e.g., alone, in a small ensemble or band, in a large orchestra or choir, etc.)

3. Have you **previously** played an instrument (including voice) that you no longer play (e.g., as a child)?
_____ Yes (go to question #4) _____ No (skip to question #5)

4. Please provide the following information for each instrument that you **used to play**.

Instrument	Ages during which you played this instrument	Ages during which you took lessons on this instrument	Hours per week that you played this instrument

--	--	--	--

Please describe the situations in which you played (e.g., alone, in a small ensemble or band, in a large orchestra or choir, etc.)

5. Please indicate the highest formal music levels (instrumental/vocal performance, dance or theory) that you have achieved (e.g. Royal Conservatory, Theory, Suzuki Books, etc).

Instrument/Course/Subject	Level

6. Describe your **current** recreational music and dance activities (e.g., “jam sessions” with friends, singing karaoke, dancing at nightclubs, etc.):

7. How often do you attend musical or dance concerts or performances?

8. Have you had any formal ear training*? Yes (years) No
 Not sure

* In ear training or “aural skills” lessons, musicians learn to identify musical elements such as intervals, chords and rhythms, simply by hearing them.

9. Do you play by ear*? Yes No

* playing or learning to play a piece of music by listening to a musical rendition, without the aid of printed material

10. Do you have absolute/”perfect” pitch*? Yes No
 Not sure

* absolute pitch is the ability to name notes without a reference, e.g. to hear a tone and immediately know it was a “C”

11. To the best of your knowledge, are you tone deaf*? Yes No
 Not sure

* tone deafness is when you are unable to perceive differences of musical pitch accurately

12. How many hours per week do you spend listening to music? _____
hours/week

13. Please describe your regular listening habits (e.g., listen to mp3/iPod on the bus, play stereo at home, etc.):

14. What styles of music do you listen to (e.g., rock, r&b, classical, traditional/folk, etc.)

15. Please briefly describe your other main activities or interests (e.g., sports, outdoor activities, art, reading, video game playing, etc.).

16. Do you **currently** speak any other languages besides English? Yes
 No

If yes, please indicate which language(s) including English, the percentage of time that you use them, and the situations in which you speak each language.

Language	Percentage (%) of time that you use this language	Situations in which you use the language

17. Did you **previously** speak any languages other than English that you no longer speak? If yes, please list and describe the ages and situations in which you used these languages:

18. Have you lived in North America for all your life? Yes
 No

If not, please describe where else you have lived, and for how long.

Location	How old were you (age range) when you lived there?

19. Do you have any hearing problems that you are aware of? If yes, please specify.

20. Please indicate whether you are left or right handed when performing the following tasks:

	Left	Right	Both
Writing	_____	_____	_____
Drawing	_____	_____	_____
Using a Spoon	_____	_____	_____
Throwing	_____	_____	_____
Kicking	_____	_____	_____

21. Do you wear glasses or contacts? Yes
 No

22. Do you currently have a cold? Yes
 No

Thank you for your assistance!

APPENDIX B



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RENEWAL

Certificate #:	2013 - 296
Renewal Approved:	03/03/15
Approval Period:	03/03/15-03/03/16

Memo

To: Professor Joseph DeSouza, Faculty of Health, ~~XXXXXXXXXX~~;
~~XXXXXXXXXX~~

From: Alison M. Collins-Mrakas, Sr. Manager and Policy Advisor, Research Ethics
(on behalf of Denise Henriques, Chair, Human Participants Review Committee)

Date: **Tuesday, March 03, 2015**

Re: Ethics Approval

The effects of attention on multisensory processing: Comparing experts and non-experts

With respect to your research project entitled, "The effects of attention on multisensory processing: Comparing experts and non-experts", the committee notes that, as there are no substantive changes to either the methodology employed or the risks to participants in the research project or any other aspect of the project, a renewal of approval re the above project is granted.

Should you have any questions, please feel free to contact me at: ~~416-736-5914~~ or via email at: ~~XXXXXXXXXX~~.

Yours sincerely,

Alison M. Collins-Mrakas M.Sc., LLM
Sr. Manager and Policy Advisor,
Office of Research Ethics