

**INVESTIGATING THE FUNCTIONAL AND
STRUCTURAL NEURAL CORRELATES ASSOCIATED
WITH DANCE EXPERTISE**

Prabhjot Dhami

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

GRADUATE PROGRAM IN BIOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO

April 2016

© PRABHJOT DHAMI, 2016

ABSTRACT

We investigated the structural and functional plasticity associated with dance expertise in a cross-sectional pilot study, comparing ballet dancers to controls. Using fMRI, the whole-brain functional activation maps of dancers and controls engaged in motor imagery of dance movements were compared. Controls were found to show greater activity in numerous regions relative to dancers, including in the superior frontal gyrus, hippocampus, and cerebellum. Anatomically, dancers exhibited greater cortical thickness in areas such as the inferior occipital gyrus, inferior frontal gyrus, and superior temporal gyrus. We also found years of dance training to be correlated with cortical thickness in various regions, including positive correlations being reported in the fusiform gyrus and parahippocampal gyrus. These preliminary results suggest that dance expertise is associated with a functional reorganization that corresponds to the reduced activity reported in other motor expertise groups, as well various putative changes in structure.

ACKNOWLEDGEMENTS

First and foremost, I would like to say thank you to Dr. Joseph DeSouza and Dr. Sylvain Moreno, for both giving me an opportunity to be a part of their respective labs and a student under their supervision. Aside from being able to learn an incredible amount from with two wonderful researchers, I have felt lucky to have two supervisors who whenever I felt lost or confused, were always willing to listen and offer sound advice. Their mentorship and guidance went well beyond the work presented here, and for that, I will always be grateful.

Thank you to Dr. Thilo Womelsdorf for his critiques and consistent willingness to offer comments and advice during the course of this masters. Also, a thank you to the numerous lab mates I've had the absolute joy of working with and learning from, with a special thank you to Michael Olshansky and Paula Di Nota, as well as to Karolina Bearss and Nevena Savija. Finally, a thank you to my family and friends who have helped me in ways that I cannot even begin to put into words how much I appreciate.

TABLE OF CONTENTS

Abstract	ii
Acknowledgments	iii
Table of Contents	iv
List of Tables	vi
List of Figures	vii
List of Abbreviations	viii
1. Introduction	1
1.1 Investigating the plasticity associated with motor expertise through dance	1
1.2 A brief history on neuroplasticity	3
1.3 Studying neuroplasticity in the context of skill learning and expertise	5
1.4 Neuroplasticity associated with motor skill learning and expertise	7
1.4.1 Properties of motor skill learning	7
1.4.2 Structural plasticity associated with motor expertise	12
1.4.3 Functional plasticity associated with motor expertise	16
1.5 Current study	22
2. Methods	25
2.1 Participants	25
2.2 Functional task procedure	25
2.3 fMRI acquisition	27
2.4 fMRI data preprocessing	27
2.5 fMRI data analysis	28
2.6 Structural data analysis	32
3. Results	35
3.1 Activation during motor imagery in dancers and controls	35
3.2 Differences in activity during motor imagery in dancers and controls	36
3.3 Non-rotated PLS analysis – task, interaction, and group effects	37
3.4 Cortical thickness differences between dancers and controls	45
3.5 Correlation between cortical thickness and years of dance experience in dancers	47
4. Discussion	49
4.1 Functional activity associated with motor imagery of dance movements in dancers and controls	49
4.2 Functional activity differences between dancers and controls during motor imagery of dance movements	53
4.3 Dance expertise and cortical thickness: differences between dancers and controls, and correlation with dance experience	64
4.4 Limitations and future directions	75
4.5 Conclusion	80

LIST OF TABLES

Table 1: Cluster list for the mean activation map of controls for the contrast between motor imagery and baseline (pg. 36)

Table 2: Cluster list for the mean activation map of expert ballet dancer for the contrast between motor imagery and baseline (pg. 37)

Table 3: Cluster list for the functional activity group contrast between dancers and controls (pg. 39)

Table 4: Cluster list of Task-PLS testing for task main effect (pg. 41)

Table 5: Cluster list of Task-PLS testing for an interaction effect between task and group (pg. 43)

Table 6: Cluster list of Task-PLS testing for a group main effect (pg. 45)

LIST OF FIGURES

Figure 1: Functional activity contrast between motor imagery and baseline (pg. 35)

Figure 2: Functional activity contrast between dancers and controls during motor imagery (pg. 38)

Figure 3: Task-PLS contrast for task main effect (pg. 40)

Figure 4: Task-PLS contrast for interaction effect (pg. 42)

Figure 5: Task-PLS contrast for group main effect (pg. 44)

Figure 6: Cortical thickness differences between dancers and controls (pg. 46)

Figure 7: Correlation between cortical thickness and years of dance training (pg. 48)

LIST OF ABBREVIATIONS

BOLD – Blood-Oxygen-Level Dependent

fMRI – Functional Magnetic Resonance Imaging

GLM – General Linear Model

LV – Latent Variable

MRI – Magnetic Resonance Imaging

PLS – Partial Least Squares

SMA – Supplementary Motor Area

VBM – Voxel-Based Morphometry

1. Introduction

1.1 Investigating the Plasticity Associated with Motor Expertise through Dance

Neuroplasticity, the ability of the brain to modify itself or through experiences with the external environment (Moreno and Bidelman, 2014), is of major interest in modern neuroscience, particularly due to its ability to provide insight into the fundamental mechanisms of learning and memory (Jancke, 2009). Today, as to what phenomena constitute as being a form of neuroplasticity is wide in scope, and can refer to various complex processes studied from a molecular, cellular, synaptic or network levels approach in animals, to a systems and cognitive levels approach in humans (Herholz and Zatorre, 2012). Accordingly, brain plasticity has been studied through a variety of experimental paradigms. With respect to humans, one of the most influential models to study experience-related plasticity has been that of probing the structural and functional changes that occur as a result of motor skill learning and expertise (Hamaide et al., 2015; Luft and Buitrago, 2002).

Motor skill learning may be defined as the process by which movements are executed more quickly and accurately with practice to achieve proficiency (Willingham, 1998). One way in which this has been studied in humans includes having subjects in a laboratory setting learn simple motor tasks, which although offers strict experimental control, often includes little practice needed to reach asymptotic levels in performance, and places little demand on cognitive resources; this makes it difficult to generalize the findings from such studies to

the more complex motor skills that humans are capable of (Wulf and Shea, 2002). In contrast, other studies have focused on the plasticity associated with the learning and expertise of more complex motor skills that take extensive time and practice to learn, such as the ability to play an instrument (Hill and Schneider, 2006; Yang, 2015). Such studies, particularly those that have studied musicians, have been pivotal in elucidating the neuroplastic changes associated with motor expertise. Yet, many of these studies have focused on expert groups whose motor expertise is commonly restricted to finger or single limb movements. Thus, there has been a noted lack of studies, particularly in the context of functional neuroimaging, that have investigated the plasticity associated with motor expertise in skills that require whole-body movements (Bezzola et al., 2012; Hetu et al., 2013; Wei and Luo, 2010). A group that may be used to investigate such questions on the plasticity associated with expertise in complex whole-body movements is that of dancers.

Dance may be defined as the act of one or more bodies moving in a rhythmic manner through space, often cued by music. Even in its simplest form, it requires a complex and simultaneous engagement in various physical and cognitive domains, and in order to become an expert in requires extensive training over long periods of time (Hanggi et al., 2010). It thus provides an advantageous, yet underutilized model to study the structural and functional plasticity associated with motor expertise in complex whole-body movements. Studies have investigated the relationship between dance expertise and various behavioral measures, including with specific memory domains (Hufner et al.,

2011; Smyth and Pendleton, 1994; Starkes et al., 1987), as well as with physical fitness performance such as posture control (Rein et al., 2011; Simmons, 2005) and balance (Bruyneel et al., 2010; Crofts et al., 1996; Gerbino et al., 2007). However, few studies have investigated the neural basis of dance expertise (Karpati et al., 2015). Here, we sought to investigate the structural and functional plasticity associated with dance expertise through a cross-sectional comparison between professional ballet dancers and controls.

1.2 A Brief History on Neuroplasticity

The term plasticity itself has been used in the field of brain sciences for well over a century, and although it has undergone significant evolution over that time to adapt to new postulations and discoveries, it has generally been used to refer to the suspected neural reorganization that occurs in relation to the modification of behaviour under various circumstances (for a detailed review on the history of the term, see Berlucchi and Buchtel, 2009). The historical roots of the term plasticity, in context of the brain, can be traced back to William James (1890), who first used it in reference to the association between changes in nervous pathways and habitual behaviour in animals. Other milestones in the development of the term include the work of Eugenio Tanzi (1893), who first postulated that in the context of learning and memory, the connections between neurons, which would later become known as synapses, may be possible sites of plasticity, and Santiago Ramon y Cajal (1894), who hypothesized that neural plasticity may be the result of new connections being formed between neurons

(Berlucchi and Buchtel, 2009). Although the idea of neural and synaptic plasticity would attenuate earlier on in the 20th century (Berlucchi and Buchtel, 2009), Donald Hebb is often credited for revitalizing the notion in his *The Organization of Behavior* (1949), which featured his famous postulation that is now commonly referred to as "Hebbian learning" (Draganski and May, 2008; Jancke, 2009). The pith of Hebb's theoretical framework, in the context of adult learning, was that an increase in synaptic strength, via growth processes or metabolic changes, occurs between neurons that fire together (Buonomano and Merzenich, 1998), an idea which is now commonly expressed in the maxim "neurons that fire together wire together" (Jancke, 2009). In the following years after Hebb's reintroduction of the term, brain plasticity would become a focus of experimental investigation, although early studies focused on plasticity in the context of development. This was due to staunch support for the notion that the brain was highly transmutable during the development stage of an organism, particularly during epochs known as critical periods, but that the adult brain was static, meaning that whatever neural connections were formed during development were fixed post development (Jancke, 2009; Ramachandran et al., 1992). However, it would eventually be found that the adult brain is not static, but instead plastic throughout ones life (Boyke et al. 2008; Jancke, 2009; Pascal-Leone et al., 2005).

Initial studies to uncover that the adult brain was indeed plastic investigated the effects of altered sensory and motor experiences on the adult animal brain, such as through lesions or micro-stimulation, and found substantial

neural reorganization of related cortical maps to occur as a result (Jenkins et al., 1990; Nudo and Milliken, 1996; Nudo et al., 1990). Early studies pertaining to adult brain plasticity in humans followed similar paradigms, focusing on patients who had undergone limb amputations, and similar to their animal study counterparts, were able to show massive cortical reorganization as a result of the amputations, reinforcing the notion that the brain was plastic in adulthood (Cohen et al., 1991; Ramachandran et al., 1992). From the studies discussed thus far, it may seem implied that brain plasticity is restricted to occurring as a response to injury or disease; such studies were indeed critical in investigating the phenomenon that is neural plasticity, particularly in the adult brain. However, other different experimental models have also been employed to study experience-dependent plasticity. Of such, one of the most insightful paradigms has been that of investigating how life experiences, and specifically skill learning, can induce neural reorganization (Draganski and May, 2008).

1.3 Studying Neuroplasticity in the Context of Skill Learning and Expertise

The experimental paradigm of skill learning has been paramount in the field of brain plasticity. Skill learning can be generally defined as a change, often an improvement, in perceptual, cognitive or motor performance that comes about as a result of training (Green and Bavelier, 2008), with expertise being achieved through extensive periods of deliberate and intensive practice, ultimately leading to proficiency in the related skill (Debarnot et al., 2014; Ericsson, 2008).

Numerous studies have revealed the singular finding that training in an activity

not only changes one's related performance, but can alter the neural correlates subserving the activity.

Early evidence for learning-dependent plasticity were based on animal studies (Black et al., 1990; Kleim et al., 1998), but faced limitations due to the techniques used, which were of an invasive nature and spatially restrictive, in that they were only capable of examining neural changes in very localized regions (Draganski and May, 2008). It was not until the advent of modern neuroimaging techniques, which allowed for imaging of the human brain in vivo, that the field of brain plasticity in the context of humans quickly burgeoned (Jancke, 2009); in particular, magnetic resonance imaging (MRI) became a mainstay imaging technique due to its ability to provide both structural and functional information across the entire human brain in a non-invasive manner (Draganski and May, 2008; Hamaide et al., 2015; Zatorre et al., 2012). Studies in this field have commonly utilized cross-sectional or longitudinal designs in order to infer just how the brain may be altered in correspondence to the training of a skill or task, with the use of various expert groups or training regimens. The fundamental takeaway from such studies is that the brain can change in a pertinent fashion in response to the environmental demands, with examples from seminal papers including the enlargement of the hippocampus in taxi drivers being attributed to their dependence on navigational skills and thus spatial representation of the environment (Maguire et al., 2000), and changes in regions involved in visuo-motor coordination following training in juggling (Draganski et al., 2004). Such studies have also established that the potential for plastic

changes to occur via training is not restricted to earlier ages as once was thought, but can occur in adulthood as well (Boyke et al. 2008; Jancke, 2009; Pascal-Leone et al., 2005). It is important to note that the term skill learning is broad in scope and used here to include the various forms that skill learning can take. Indeed, it is not difficult for one to imagine the various tasks that may fall under such a definition, and accordingly, this field of research is profuse with the use of various types of tasks. However, studying the plasticity associated with training and expertise in motor skills has been one of the most influential models in brain plasticity research (Hamaide et al., 2015; Luft and Buitrago, 2002), providing insight into how the learning and achieved expertise of a motor task can induce structural and functional plasticity on both cortical and subcortical levels (Chang, 2014; Dayan and Cohen, 2011; Debarnot et al., 2014).

1.4 Neuroplasticity Associated with Motor Skill Learning and Expertise

1.4.1 Properties of Motor Skill Learning

Motor skill learning may be defined as the process by which movements are executed more quickly and accurately with practice (Willingham, 1998), with the ultimate goal being to achieve automaticity of said movements (Debarnot et al., 2014). Motor skill learning itself is often studied in two disparate forms (Doyon and Benali, 2005); one is referred to as motor sequence learning, and involves the incremental acquisition of movements and proficient execution of said movements in a set sequence (e.g. learning to play a specific sequence of notes on a piano) (Dayan and Cohen, 2011; Ungerleider et al., 2002). The other

paradigm is referred to as motor adaptation, and involves adaptation to environmental changes (Ungerleider et al., 2002), which often comes in the form of externally induced perturbations while subjects are engaged in executing simple motor tasks (Dayan and Cohen, 2011). Of the two, motor sequence learning has played a much larger role in studying the neuroplasticity associated with motor skill learning and expertise (Dayan and Cohen, 2011), particularly due to its greater emphasis on learning taking place over multiple training sessions (which may span long intervals of time such as months depending on the task) in order to become proficient in the motor skill. Thus, from here on forward, our discussion on motor expertise and neuroplasticity will be in the context of motor sequence learning.

Motor skills are typically learned slowly over multiple training sessions, accompanied by a continuous reduction in reaction time and number of errors made (Ungerleider et al., 2002), until performance in the specific tasks reaches near asymptotic levels (Dayan and Cohen, 2011). These explicit gains achieved in motor skill learning can be divided into two stages: fast and slow learning. Fast learning consists of the typical significant improvements that occur in a single training session, whereas slow learning refers to the incremental gains that are achieved over multiple training sessions (Dayan and Cohen, 2011; Doyon and Benali, 2005; Ungerleider et al., 2002). These two stages are seen as being followed by an implicit consolidation stage, in which spontaneous improvements in performance occur while one is not engaged the practice of the task, an automatic stage, in which the learned motor skill behaviour can be executed with

minimal cognitive resources, and finally a retention stage, in which the motor skill can be executed as desired without the need for continuous practice of the task (Doyon and Benali, 2005). It is important to note that for the stages described above, particularly that of fast and slow learning, the temporal scale of events must be interpreted in the context of the task being learned; for example, the fast learning of a simple keyboard sequence may only last a few minutes, whereas the fast learning stage of a much more complex musical piece may last for months (Dayan and Cohen, 2011).

Although the exact mechanisms behind such motor skill learning remains unknown, various models have been proposed to provide a general framework of which brain regions are involved in initial motor skill learning. An influential model proposed by Doyon et al. (2003; 2005), primarily based on functional neuroimaging studies, suggests that during fast motor learning, both a cortico-striatal and cortico-cerebellar system are recruited, regardless of whether the task is of a motor sequence learning or motor adaptation nature. The specific structures believed to be involved include the striatum, cerebellum, limbic areas, and motor, prefrontal and parietal cortical regions, and the interaction between such regions is suggested to be necessary for successful motor learning in the early stages (Doyon and Benali, 2005). Following this early learning period, consolidation of the motor skills begins to occur, but the motor representation of a learned motor sequence shifts to the striatum, whereas the representation of a learned adaptation shifts to the cerebellum (Doyon and Benali, 2005, Penhune and Steele, 2012). Once slow learning has passed and retention is successful,

the representation of a learned motor sequence is supported by a unique cortico-striatal network, consisting of the striatum, motor cortical regions, and parietal cortices, whereas a learned motor adaptation is supported by a unique cortico-cerebellar network, consisting of the cerebellum, motor cortical regions, and parietal cortices (Doyon and Benali, 2005). Another prominent framework provided by Hikosaka et al. (2002) suggests that for early sequence motor skill learning, two parallel circuits are involved in the learning of what are two distinct features of a motor skill: the spatial (or sequential) order of movements and the actual motor movements, with the former involving a cortico-striatal circuit, and the latter a cortico-cerebellar circuit. Ultimately, the general theme in such models is that the learning of a motor skill depends on the dynamic interaction between various cortical and subcortical networks, and such interactions change over the learning period (Dayen and Cohen, 2011; Hikosaka et al., 2002).

The experience-dependent plasticity associated with motor expertise in humans has often been studied through investigating how extensive training and expertise in a motor skill is associated with neural reorganization (Debarnot et al., 2014). Researchers have commonly utilized cross-sectional or longitudinal designs, where comparisons are either drawn between experts (e.g. musicians) and controls, or over time as one becomes proficient in a motor task, allowing inferences to be made on the neural changes that occurs with becoming an expert in said motor skill (Jancke, 2009). Some of the first studies on neuroplasticity associated with complex motor expertise investigated the cortical representation of digits that were deemed to be pertinent in musical-related

motor skills; for example, a five day period of training on a piano finger exercise was found to lead to an enlargement of cortical motor areas related to the long finger flexor and extensor muscles (Pascual-Leone et al., 1995); another study found an enlargement of the finger cortical representations in string instrument players compared to controls (Elbert et al., 1995). However, as previously noted, it was not until the emergence of whole-brain neuroimaging techniques, and in particular MRI, that research on brain plasticity and motor expertise would flourish (Hikosaka et al., 2002). Through the use of MRI, how the brain changes as a result of motor training has primarily been studied through the two distinct but complementary perspectives of structural and functional plasticity. Structural neuroimaging provides great insight into the structural plasticity, or anatomical changes, associated with motor training and expertise. Due to only requiring subjects to remain stationary, structural neuroimaging has allowed researchers to study practically any motor expertise group, allowing insight into the broad structural changes that are associated with motor training and expertise. However, it cannot provide insight into the activity of the brain during a motor task, and how such activity changes over the course of learning to the point where expertise is achieved. Functional neuroimaging in contrast can provide such insight into how the activity of the brain during performance of a motor task changes as one learns and eventually achieves expertise in said task. Both have been instrumental in unveiling the finding that expertise in complex motor skills can be associated with substantial neuronal reorganization, on both a structural (Draganski et al., 2004; Gaser and Schlaug, 2003; Hanggi et al., 2010; Jancke et

al., 2009) and functional level (Doyon and Benali, 2005; Haslinger et al., 2004; Lotze et al., 2003). We first discuss the structural plasticity associated with motor expertise, and then shift focus to that of functional plasticity.

1.4.2 Structural Plasticity Associated with Motor Expertise

A prevalent finding associated with extensive motor skill learning and expertise is the occurrence of structural plasticity. Initial animal studies have shown motor skill learning to be associated with various neural structural changes, including the reorganization of task-related cortical maps (Kleim et al., 1998) as well as synaptogenesis in motor cortices (Black et al., 1990; Jones et al., 1999; Kleim et al., 1996; Kleim et al., 2002). Through the use of MRI, studies with humans have also demonstrated complex motor skill learning and expertise to be associated with significant structural changes, as commonly measured through changes in gray matter (Draganski and May, 2008; May, 2011). Here, the relationships between various types of motor expertise, such as proficiency in the playing of a musical instrument, and brain anatomy have been investigated. For example, Gaser and Schlaug (2003) found the gray matter volume of various regions to be significantly greater in keyboard musicians compared to non-musicians, including in the auditory, sensorimotor and premotor cortex, as well as in the cerebellum. Indeed, musicians, due to being a popular model to study neuroplasticity (Herholz and Zatorre, 2012; Wan and Schlaug, 2010), have commonly been reported to exhibit significantly greater amounts of gray matter in comparison to controls, including greater gray matter volume in the primary

sensorimotor cortex and cerebellum (Han et al., 2009), as well as greater gray matter volume and cortical thickness in the auditory cortex (Bermudez et al., 2009; Bermudez and Zatorre, 2005; Schneider et al., 2002). Aside from the ability to play a musical instrument, the structural correlates of expertise in a variety of other motor skills have also been investigated. Examples include: skilled golfers exhibiting increased gray matter volumes in parietal and premotor cortices (Jancke et al., 2009), the enlargement of gray matter volume in the vermian lobules VI-VII of the cerebellum (Park et al., 2009) and the striatum (Park et al., 2011) in basketball players, competitive judo players having increased gray matter volumes in the frontal and prefrontal cortex (Jacini et al., 2009), time as a professional typist being positively correlated with an increase in gray matter volume in regions such as the cerebellum (Cannonieri et al., 2007), professional divers having greater cortical thickness in the right orbitofrontal cortex, right parahippocampal gyrus and the left superior temporal sulcus (Wei et al., 2011), and professional handball players exhibiting increased gray matter volume in the SMA, cingulate motor area, right primary motor area, somatosensory cortex, and intraparietal sulcus (Hanggi et al., 2015). It is however important to note that the studies listed above are cross-sectional, and face the dilemma of being incapable of discerning whether such changes in structure are a direct consequence of training or due to some sort of predisposition; however, longitudinal studies have provided similar findings as those reported by their cross-sectional counterparts.

In their seminal work, Draganski et al. (2004) investigated the training effects of learning to juggle on the brain structure of young adults. Subjects were scanned at baseline prior to learning how to juggle, once after 3 months of training, and 3 months after training and practice had ceased. At the end of the 3-month training period, there was an expansion of gray matter in the mid-temporal area (MT/V5) and posterior intraparietal sulcus, areas involved in motion perception and visuomotor processing, and thus likely heavily involved in the complex visuo-motor task that is juggling. However, 3 months after training had ceased, the expansions in gray matter decreased back to near baseline levels, suggesting the increase and decrease of juggling skill to be tied to increases and decreases of gray matter in areas related to the task. Such results have also been supported by other studies using the same juggling paradigm, including the finding the juggling can induce gray matter expansion in the MT/V5 as early as after seven days of practice (Driemeyer et al., 2008), and that older adults show a similar expansion of gray matter in the MT/V5 after 3 months of juggling training, as well as in the hippocampus and nucleus accumbens (Boyke et al., 2008). In regards to musicians, Hyde et al. (2009) conducted a longitudinal study investigating the effects of musical instrument training on brain structure in children. Following 15 months of training, children who learned to play an instrument were found to exhibit greater relative voxel size in areas including in the right precentral gyrus (primary motor area), corpus callosum and the right primary auditory region; such changes were also found to be correlated with improvements in musically relevant motor and auditory skills, suggesting that

training is not only capable of inducing significant changes to brain structure, but such structural changes are also related to improvements in the skills being trained in. Other longitudinal studies have also shown an expansion of gray matter to occur following training in a complex motor task, including the increase of gray matter volume in frontal and parietal regions following 2 weekly practice sessions of a whole-body balancing task (Taubert et al., 2010), and 40 hours of golf training being associated with an increase of gray matter in areas deemed as task-relevant, including in sensorimotor regions and areas part of the dorsal stream (Bezzola et al., 2011). Thus, evidence from both cross-sectional and longitudinal studies suggest that motor expertise is associated with an increase in gray matter in regions deemed as pertinent to the motor skill that expertise is achieved in (Chang, 2014; Debarnot et al., 2014). However, there are studies, albeit few, that have reported the opposite finding that motor expertise is related to a decrease in gray matter (Draganski et al., 2006). Hanggi et al. (2010) compared the brain structure of professional ballet dancers to controls, and found dancers to exhibit decreased gray matter volumes in the left premotor cortex, SMA, putamen, and superior frontal gyrus, areas reported as key structures involved in dancing. It has also been suggested that gray matter increases or decreases may depend on factors such as the motor skill trained in, the brain region of interest, and the time spent training; for example, James et al. (2014) compared gray matter volume between controls, amateur musicians, and professional musicians, and found changes in gray matter to be function of expertise level; greater musical training experience was associated with an

increase of gray matter volume in regions related to higher-order cognitive processing, but associated with a decrease of gray matter volume in regions related to sensorimotor functions. Thus, although most studies suggest motor expertise to be associated with an increase of gray matter in task-relevant regions, there are studies that suggest this may not always be the case. Indeed, the question of whether training should be associated with an increase or decrease of gray matter in pertinent brain regions remains unclear due to the complex relationship that exists between brain structure and function (Zatorre et al., 2012).

1.4.3 Functional Plasticity Associated with Motor Expertise

Studies have shown skill training and expertise to be associated with substantial functional reorganization of the skill-related functional activity patterns, but such studies are not in agreement as to what these changes should consist of. Both increases and decreases of activity in task-related regions have been reported to be associated with practice of a skill, as well as changes in what regions are involved in performing the skill once expertise is achieved (Kelly and Garavan, 2005). In the context of motor skills, initial motor skill learning is believed to involve interactions between cortical and subcortical regions, including the motor and pre-motor cortical areas, striatum, cerebellum, as well as parietal and limbic areas (Doyon and Benali, 2005; Penhune and Steele, 2012). The interactions between such regions are also believed to change over the training period as the motor skill improves (Doyon et al., 2009; Hikosaka et al.,

2002). Thus, how activation patterns of a motor skill change due to intensive training, and once expertise is achieved, remains unclear due to inconsistent findings (Penhune, 2013; Reithler et al., 2010; Wiestler and Diedrichsen, 2013; Yang, 2015). To investigate such changes, functional neuroimaging has commonly been used to provide insight into the spatial activation patterns that arise when one is engaged in a motor task, and how such patterns differ as a function of expertise.

Longitudinal studies have tracked the functional patterns of activity associated with sequential motor task training, such as a finger-tapping task, as well as how such patterns change during the training period. Such studies have shown motor skill training to be associated with an increase of activity in task-related regions, including in the primary motor cortex (Floyer-Lea and Matthews, 2005; Karni et al., 1995), primary somatosensory cortex (Floyer-Lea and Matthews, 2005), putamen (Floyer-Lea and Matthews, 2005; Lehericy et al., 2005), striatum (Penhune and Steele, 2012), and SMA (Lehericy et al., 2005). However, there have also been contradictory reports that training in a motor skill leads to a general decrease of activity in task-related areas, including in regions such as the SMA (Reithler et al., 2010; Steele and Penhune, 2010), intraparietal sulcus (Reithler et al., 2010), insula (Reithler et al., 2010), premotor cortex (Gobel et al., 2011), precuneus (Gobel et al., 2011; Steele and Penhune, 2010), basal ganglia (Steele and Penhune, 2010), and the cerebellum (Lehericy et al., 2005; Steele and Penhune, 2010). It may also be that both increases and decreases, depending on the region, occur with motor training (Lafleur et al.,

2002; Lohse et al., 2014; Steele and Penhune, 2010), or the motor network related to the skill itself changes, recruiting different sets of brain regions (Kelly and Garavan, 2005). It is important to note that in an attempt to encompass the entire training period needed to achieve proficiency, such longitudinal studies commonly employ finger-tapping tasks, which consists of training periods that are often limited to several days or weeks. Such training is not entirely analogous to the more complex motor tasks that humans are capable of, such as the playing of an instrument, which can take years to become proficient in (Dayan and Cohen, 2011). In order to address this, cross-sectional studies have been conducted to compare novices to experts who have had extensive training in their motor skill of expertise.

Cross-sectional studies have commonly compared brain activity during relevant task performance between experts, who have trained intensively in the related motor skill for an extensive amount of time, and novices (Yang, 2015). The functional activity of musicians, and particularly pianists, have commonly been compared to matched non-musicians while executing finger-tapping motor tasks that highly resemble that of playing a piano. The common finding here is that musicians exhibit general patterns of reduced activity, in that they usually display fewer areas of activity or smaller hemodynamic responses in task-related areas compared to controls during motor execution; this includes in regions such as the primary motor cortex (Jancke et al., 2000; Krings et al., 2000), premotor cortex (Haslinger et al., 2004; Krings et al., 2000; Meister et al., 2005), SMA (Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Meister et al.,

2005), and temporoparietal junction (Berkowitz and Ansari, 2010), as well in the prefrontal cortex, cerebellum, insula, and basal ganglia (Haslinger et al., 2004). Similar findings of experts exhibiting lesser activity compared to novices during motor execution have also been reported in other expertise groups, including in violinists (Lotze et al., 2003) and professional racecar drivers (Bernardi et al., 2013).

Findings from both longitudinal and cross-sectional studies suggest that expertise in a motor skill is associated with a general decrease of activation in task related regions during execution, as well as fewer areas of activity. However, it is important to note that certain regions may show greater activity as a result of expertise; this has been a common finding in particular for the striatum, which is believed to be critical for the long term retention of well-learned sequence of movements (Debarnot et al., 2014; Doyon and Benali, 2005; Doyon et al., 2009; Lacourse et al., 2004; Lohse et al., 2014; Penhune and Steele, 2012; Yin et al., 2009). The reduced pattern of activity commonly associated with motor expertise is often attributed to the notion of neural efficiency; expertise may lead to increased motor efficiency in the task at hand, and thus reduced neural activity is needed to perform the related motor movements (Baeck et al., 2012; Bezzola et al., 2012; Diedrichsen and Kornysheva, 2015; Haslinger et al., 2004; Jancke et al., 2000; Jancke, 2009; Krings et al., 2000). It has also been suggested that such lower levels of activation found in experts may be related to the lesser involvement of attentional and executive resources needed to commit the motor movements, or may be due to task difficulty differences found between

experts and novices (Floyer-Lea and Matthews, 2005; Landau and D'esposito, 2006; Yarrow et al., 2009).

Various studies, including those mentioned above, have commonly drawn comparisons between experts and novices while engaged in simple motor exercises, such as finger tapping. This is in part due to such tasks being easy to perform while being confined in a MRI scanner, as well as not being associated with large movement artefacts (Bezzola et al., 2012). This offers the advantage of having subjects physically engaged in the motor task during neuroimaging, and depending on the expert group, such tasks can be extremely similar to those that are related to their area of expertise, such as pianists engaging in a finger-tapping task on a keyboard (Haslinger et al., 2004; Jancke et al., 2000; Meister et al., 2005). Investigating functional activation patterns during performance of more complex motor movements however can be problematic due to physical limitations of what a person can do while undergoing neuroimaging (Bezzola et al., 2012; Yarrow et al., 2009); this has been a critical reason as to why research on neuroplasticity and motor skill expertise has favoured structural neuroimaging over functional (Hamaide et al., 2015). Thus, groups with motor expertise in complex whole-body movements have commonly been overlooked due to such reasons. Yet, principles derived from studies using simple motor tasks may not generalize to the more ecological and complex motor skills humans are capable of (Wolf and Shea, 2002), thus reinforcing the need to independently investigate the functional activity associated with engagement in complex motor tasks compared to simpler tasks. In order to make such inquiries, the use of motor

imagery, a state in which one simulates an action mentally without producing any physical body movement (Debarnot et al., 2014), has been proposed as a tool to do so. This is due to substantial evidence that motor imagery of a movement produces similar functional activation patterns as when physically executing the same movement (Jeannerod and Frank, 1999; Lacourse et al., 2005; Lafleur et al., 2002; Lotze and Halsband, 2006; Meister et al., 2004; Pfurtscheller and Neuper, 1997; Porro et al., 1996). Other evidence includes motor imagery evoking similar physiological responses as those found in physical execution of a movement (Milton et al., 2008), as well as the functional activity changes that occurs following physical training to be also found during the motor imagery of the same trained movement (Lafleur et al., 2002). Indeed, motor imagery has been shown to consistently recruit large fronto-parietal networks in addition to subcortical and cerebellar regions, patterns congruent to those found during physical execution of the imagined motor movements (although there is still debate around the activation of the primary motor cortex during motor imagery; see Munzert et al., 2009) (Hetu et al., 2013). Accordingly, motor imagery has been used to probe the functional plasticity associated with expertise in complex motor skills. Milton et al. (2007) compared the functional activity during motor imagery of a pre-shot golf routine between expert golfers and novices, and reported the task-related network in experts to be more focused and efficiently organized, based on reduced overall brain activation and fewer regions involved during the motor imagery task compared to novices. Motor imagery has also been used to investigate the task-related functional activity differences between

controls and high jumpers (Olsson et al., 2008), divers (Wei and Luo, 2010), archers (Chang et al., 2011), as well as to explore how such functional patterns change via training in shooting (Baeck et al., 2012) and golf (Bezzola et al., 2012), with some of these studies supporting the notion of neural efficiency being associated with motor training (Bezzola et al., 2012; Chang et al., 2011). However, even some of these studies which have used motor imagery have only studied groups whose motor skill of expertise primarily involves the upper-limbs (e.g. archery and shooting); there remains a noticeable lack of studies that have investigated the functional plasticity associated with expertise in whole-body movements (Hetu et al., 2013; Wei and Luo, 2010).

1.5 Current Study

In the current study, we sought to investigate the important but understudied research topic of plasticity associated with whole-body movements by investigating both the functional and structural neural correlates associated with expertise in ballet dance. This gap in research is particularly prominent in the context of functional plasticity, where much of the literature has focused on elucidating the differences between experts and novices when engaged in the motor imagery of simple motor tasks (e.g. movements with fingers or certain limbs). Dance offer an advantageous model to study such neuroplasticity due to the intensive and long-term training it requires in whole-body movements (Di Nota et al., 2016; Hanggi et al., 2010; Karpati et al., 2015; Olshansky et al.,

2015), with such training placing a great demand on both cognitive and physical abilities (Blasing et al., 2012; Sevdalis and Keller, 2011).

In the context of functional neuroimaging, dancers have been used to investigate topics such as the neural basis of dance (Brown et al., 2006), as well as the neural correlates of action observation (Calvo-Merino et al., 2005; Cross et al., 2006). However, to our knowledge, no study has yet explored how the functional activity of expert dancers and controls differ during the performance of dance movements. To investigate this, we had both expert ballet dancers and controls perform motor imagery of dance movements while undergoing 8 minutes of functional neuroimaging. Due to dance being a highly complex motor and cognitive task, both groups were expected to recruit an extensive functional network that included motor-related cortical and subcortical areas, as well as fronto-parietal regions during motor imagery (Hetu et al., 2013). We also compared the functional activity maps of motor imagery of dance movements between the dancers and controls to investigate any potential differences. In line with the neural efficiency reported in other studies on motor expertise (Berkowitz and Ansari, 2010; Bernardi et al., 2013; Chang et al., 2011; Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Lotze et al., 2003; Meister et al., 2005), we predicted expert dancers to demonstrate a general pattern of reduced functional activity relative to controls during the motor imagery of dance movements.

We also investigated the structural correlates associated with dance expertise by comparing the cortical thickness between dancers and controls.

Various studies have reported motor learning and expertise to be associated with alterations in gray matter, with the common finding being an increase in gray matter in regions believed to be task relevant (Bezzola et al., 2011; Draganski et al., 2004; Gaser and Schlaug, 2003; Jancke et al., 2009). To our knowledge, only two studies have investigated gray matter differences between dancers and controls. One of these conducted a region-of-interest analysis, focusing solely on the hippocampus (Hufner et al., 2011). The other reported the aberrant finding of dancers showing a reduction in gray matter volume in various regions compared to controls (Hanggi et al., 2010). Thus, we also decided to investigate any potential structural differences between dancers and controls through cortical thickness, an alternative to volume for measurement of gray volume, which has not been examined in dancers to our knowledge.

2. Methods

2.1. Participants

The current MRI dataset pool had a total of 22 participants. For the expert dancer group, 17 professional ballet dancers (6 females, mean age = 19.00, SD = 1.17 years old, range = 18 - 22 years old, mean years of dance experience = 11.25, SD = 3.21 years, range = 6 - 16 years) were included. The expert dancers were recruited from three separate cohorts of the National Ballet of Canada's Apprenticeship Program. At the initial time of scanning, each cohort was set to learn and rehearse a new, and thus unfamiliar, dance piece in the upcoming semester. The current control group consisted of 5 subjects, recruited from the York University community (2 females, mean age = 26.00, SD = 10.07 years old, range = 18 - 43 years old, with no self-reported dance experience). It is important to note that a partial set of data in this thesis (5 functional scans from 5 subjects) was sampled from the 46 functional scans in Bar and DeSouza (2016).

Independent sample t-test through SPSS confirmed a significant difference between both groups for years of dance experience, $t(20) = 7.74$, $p < 0.001$, as well as for age, $t(20) = -2.97$, $p = 0.007$. Exclusion criteria for both groups included any history of neurological disorders, and for the control group, any self-reported professional dance experience or training.

2.2. Functional Task Procedure

Prior to the fMRI scanning procedure, participants received a 20-45 minute tutorial on motor visualization, in which they learned the difference

between visualizing movements from an internal (kinesthetic motor imagery) and external (visual motor imagery) perspective; this was done to ensure that the participants engaged in the motor imagery task from an internal perspective, which has been shown to induce similar activation patterns as when actually physically executing the same task (Jeannerod and Frank, 1999; Lotze and Halsband, 2006). The tutorial also included time for the participants to practice motor visualization from an internal perspective, such as being asked to visualize common dance movements.

Participants were then placed in the MRI scanner to undergo the visualization task. While in the scanner, participants wore a pair of headphones, which allowed them to hear the piece of music that they had no experience performing to, but one that the dancers were going to learn in the upcoming semester (J.S. Bach's *Concerto in C Major* for the first dance cohort, Marius Petipa's *Raymonda* for the second dance cohort, and D. Shostakovich's *Allegro Non Troppo* for the third dance cohort). Participants were instructed to visualize themselves dancing to the music from an internal perspective. Scanning followed a block design, consisting of five 60 second long dance imagery task blocks, interleaved by six 30 second long rest blocks.

Following the scanning session, participants completed two items, a post-scanning questionnaire and a visualization test, in order to gauge how accurately participants thought they visualized themselves dancing to their respective piece of music, if visualization was done from an internal or external perspective, if

visualization was continuous and timed to the music, and whether eyes were open or closed during visualization.

2.3 fMRI Acquisition

The following is a description of the fMRI acquisition that was used at the Sherman Health Science Research Centre, York University. A 3T Siemens Tim Trio MRI scanner was used to acquire functional and anatomical images using a 32-channel head coil. T2*-weighted echo planar imaging using parallel imaging (GRAPPA) with an acceleration factor of 2X with the following parameters was used: 32 slices, 56 Å~ 70 matrix, 210 mm Å~ 168 mm FOV, 3 Å~ 3 x 4 mm slice thick, TE = 30 ms, flip angle of 90°, volume acquisition time of 2.0 seconds.

Based on previous scanning following a similar paradigm, there were a total of 240 volumes per scan. High-resolution (1 mm³) anatomical scan of each subject's brain was taken at the end of each scanning session (spin echo, TR = 1900 ms, TE = 2.52 ms, flip angle = 9°, 256 X 256 matrix). Each subject's head was restrained while in the scanner with padded cushions to reduce movement artefacts. A vitamin E capsule was also placed near the right ear to clearly indicate later on the right hemisphere.

2.4 fMRI Data Preprocessing

All preprocessing steps for the functional data were done using tools from the FMRIB software library (FSL, version 5.0.4). For the anatomical data, non-brain tissue was removed using FSL's Brain Extraction Tool. Preprocessing of

the functional data for each subject followed the standard procedure as implemented in FSL's FEAT. A high pass filter of 90 seconds was applied, based on the total length of the rest and task block combined. Functional images were motion corrected using MCFLIRT, corrected for slice timing (with the option of interleaved applied due to how the functional data was collected), spatially smoothed using a Gaussian kernel of full-width half-maximum of 5 mm, and high pass filtered. Independent component analysis (ICA), as implemented through MELODIC in FSL, was applied to the preprocessed data of each subject in order to further denoise the data of any remaining artifacts, with the goal to improve the results of FEAT. Here, components were visually inspected, and classified as either noise or signals of interest, based on each component's activation map, time course and corresponding power spectrum, with judgement based on established criteria of what noise artefacts may appear as (Kelly et al., 2010). Components that were of particular interest for removal included those related to physiological noise, head movements, ventricle activity, and scanner artifacts. Such components that were classified as noise were then removed from each individual's functional data.

The functional data was then co-registered with its corresponding BET processed anatomical image. The anatomical images were also registered to standard structural Talairach standard images, defined by the Montreal Neurological Institute (MNI) standard brain; the same transformation matrices used for the structural to standard transformation were then applied to the functional images, resampled at 2 x 2 x 2 mm, to bring them into standard space.

2.5 fMRI Data Analysis

As previously mentioned, the expert dancer group consisted for 17 participants in total. However, for the motor imagery fMRI analysis, 3 participants from this group were excluded, due to being first scanned at the second time point, when all expert dancers had gained movement experience performing to the music pieces used for the motor imagery task. In order to avoid the musical pieces evoking any previously learned choreography during motor imagery, comparisons between dancers and controls were done with music that neither group had any experience performing to. Thus, these three dancers were excluded.

Primary statistical analysis of the functional data was through FSL's FEAT; specifically, a whole-brain general linear model was used to investigate the overall functional activation patterns that occurred during motor imagery in expert dancers and controls, and how the two groups differed during this task. For the first level analysis (individual subject level), the motor imagery block was defined as an explanatory variable for each subject, and was contrasted with the rest blocks. Cluster detection thresholding, which includes intrinsic correction for multiple comparisons, was applied, with a cluster p threshold of $p = 0.05$ and Z threshold of 2.3. For the second level analysis (group level), the group related explanatory variables defined were the effects of the groups (expert dancers vs. controls). Age was also added as a covariate and treated as a nuisance variable. Thus, a two-sample unpaired t -test was conducted, using mixed effects through FSL's FLAME, in order to compare the functional activation between the two

groups during the motor imagery task. Group activation maps were produced for four different experimental contrasts: two for the mean activation of each group for the motor imagery > baseline contrast, and two to assess any differences between the groups for this motor imagery contrast (contrasts: dancers > controls and controls > dancers). All resulting Z statistic images were thresholded using clusters determined by $Z > 2.3$ and a corrected cluster significance threshold of $p = 0.05$, and overlaid on a MNI305 high-resolution template (through the MRICroGL software) for visualization purposes in the neurological convention (left = left).

We also analyzed the functional data using Partial Least Squares (PLS), a multivariate technique that identifies whole brain patterns of activity that are correlated with the experimental design (i.e. Task-PLS) (Krishnan et al., 2011; McIntosh and Lobaugh, 2004). Whereas univariate methods (as used in the initial analysis described above) are optimal for the identification of signal changes at specific points in time or space, multivariate methods allow insight into whole-brain network patterns across space and/or time (McIntosh and Lobaugh, 2004). Thus, both were used here as they not only complement each other, but in particular, there has been a lack of studies assessing distributed whole-brain networks associated with motor expertise and motor imagery (Debarnot et al., 2014).

For this analysis, we specifically used the non-rotated version of Task-PLS, which allows the user to specify *a priori* contrasts (Krishnan et al., 2011; McIntosh and Lobaugh, 2004). Here, three different contrasts were used. The

first contrast examined any group main effect, the second examined any task main effect, and the third examined any interaction between group (dancers vs. controls) and task (motor imagery vs. rest). The interaction contrast allowed us to potentially identify brain networks that showed a cross-over interaction (i.e. regions recruited by controls during motor imagery and by dancers during baseline, or vice-versa). PLS identifies a set of spatial patterns, or latent variables (LV), that optimally relate the exogenous data and the functional imaging data. The statistical significance of each LV is assessed through permutation testing. Also, the reliability of the voxel weights, or salience, which characterizes the whole brain pattern identified by each LV, is estimated through a bootstrapping procedure, expressed as a bootstrap ratio (BSR). Each salience has a weighted value that can either be positive or negative, depending on whether the voxel exhibits a positive or negative relation to the specified contrast (Addis et al., 2012). Finally, brain scores for each condition in each contrast for each subject are also derived. These scores indicate how much of the spatiotemporal brain pattern is expressed by a subject within a specific condition. From these individual brain scores, a mean brain score with confidence intervals for each group for each condition is calculated. This allows one to assess how reliable each condition in each group is when contributing to the spatiotemporal pattern associated with the contrast (Addis et al., 2012). It also allows insight into whether separate groups express the pattern to differing degrees (as based on whether the confidence intervals of each group overlap or not). Here, statistical significance of the LVs were determined through 1000 permutation tests.

Reliability of the voxel saliences were computed independently using bootstrap estimation, which was also carried out 1000 times. A cluster threshold of 50 voxels was set, and only voxels which had a BSR of great than ± 3 (equivalent to a Z-score of 3, and a p-value of $p < 0.003$) were considered reliable and were included in the results. The resulting maps were then overlaid on a MNI305 high-resolution template (through the MRICroGL software) for visualization purposes in the neurological convention (left = left).

2.6 Structural Data Analysis

Along with the functional analyses, we also set out to investigate if dance expertise was associated with any gray matter structural differences. For this analysis, all 22 participants were included to test for group differences, as time point of when the dancers were scanned would not influence this analysis. The relationship between motor expertise and gray matter has commonly been investigated through VBM, which provides measurements of gray matter volume. To our knowledge, only two studies have investigated the gray matter volume correlates of dance expertise, with one study being a region-of-interest analysis on the hippocampus (Hufner et al., 2011), and the other being a whole brain analysis, but reporting the peculiar finding of reduced gray matter volume in dancers when compared to controls (Hanggi et al., 2010). An alternative gray matter measurement to volume is that of assessing cortical thickness, which has also been shown to be sensitive to the effects of training (Engvig et al., 2010; Wei et al., 2010). Some have suggested that cortical thickness may be more

precise than VBM in detecting changes in gray matter, due to reasons including that VBM results may be erroneously influenced by the degree of smoothing, registration techniques and choice of template (Bookstein, 2001; Jones et al., 2005; Li et al., 2015; Pereira et al., 2010). To our knowledge once again, no study has investigated potential differences in cortical thickness between expert dancers and controls. Thus, our primary goal here was to assess the relationship between dance expertise and gray matter, as measured through cortical thickness measurements.

We used Freesurfer (version 11.4.2) to compare the cortical thickness across the whole brain between dancers and controls. As previously mentioned, due to the focus of the analysis being on the gray matter structure and thus cortical thickness, subcortical structural differences were not analyzed here. The standard Freesurfer preprocessing pipeline was applied for each subject (Dale et al., 1999; Fischl and Dale, 2000). In brief, the preprocessing steps for cortical reconstruction of each subject included the removal of non-brain tissue, an automated Talairach transformation, intensity normalization, skull stripping, the segmentation of white matter, the generation and tessellation of the white matter surface, providing a boundary between white and gray matter, the deformation of the white matter surface into a pial surface, and the automatic correction of any defects in the surface. The whole cortex was then visually inspected, with manual corrections to surface errors made if warranted. Extensive detail on the Freesurfer pipeline has been published elsewhere (Dale et al., 1999; Fischl and Dale, 2000). The cortical reconstruction was used to create a cortical thickness

map for each subject. Thickness measurements at each vertex were based on the mean of the shortest distance between the gray/white matter surface and the pial surface, and from the pial surface to the gray/white matter surface (Fischl and Dale, 2000). Surface-based registration was then used to align all individual cortical thickness maps to a common surface, which was then smoothed with a Gaussian kernel of full-width half-maximum of 20 mm, with the resulting group maps submitted for statistical analysis.

For the between groups analysis, a surface-based independent t-test analysis was done using Freesurfer's GLM tools, allowing the comparison between the cortical thickness of each group on a vertex-by-vertex basis. Age was included as a nuisance covariate in the GLM. A threshold of $p < 0.01$ was used to define clusters; to correct for multiple comparisons, the resulting cortical thickness maps were thresholded with an expected false discovery rate of 0.05. A separate correlation analysis was done to assess the relationship between cortical thickness and years of dance experience; only the professional ballet dancers were included in this analysis ($n = 17$; mean years of dance experience = 11.25, SD = 3.21 years, range = 6 - 16 years; Shapiro-Wilk Test p -value = 0.178). Once again, a threshold of $p < 0.01$ was used to define the initial clusters, which were then corrected for multiple comparisons by the application of a threshold with an expected false discovery rate of 0.05.

3. Results

3.1. Activation During Motor Imagery in Dancers and Controls

We first assessed the whole brain functional activation that the controls and dancers exhibited in the context of the motor imagery > baseline contrast. Both groups demonstrated similar activation patterns (Figure 1, Table 1 and Table 2), which included the bilateral activation of the temporal gyrus, and motor-related cortical activation that included the SMA, a consistent area of activity in motor imagery (Hetu et al., 2013). However, a notable difference was that for the contrast of motor imagery > baseline, expert dancers exhibited bilateral activation

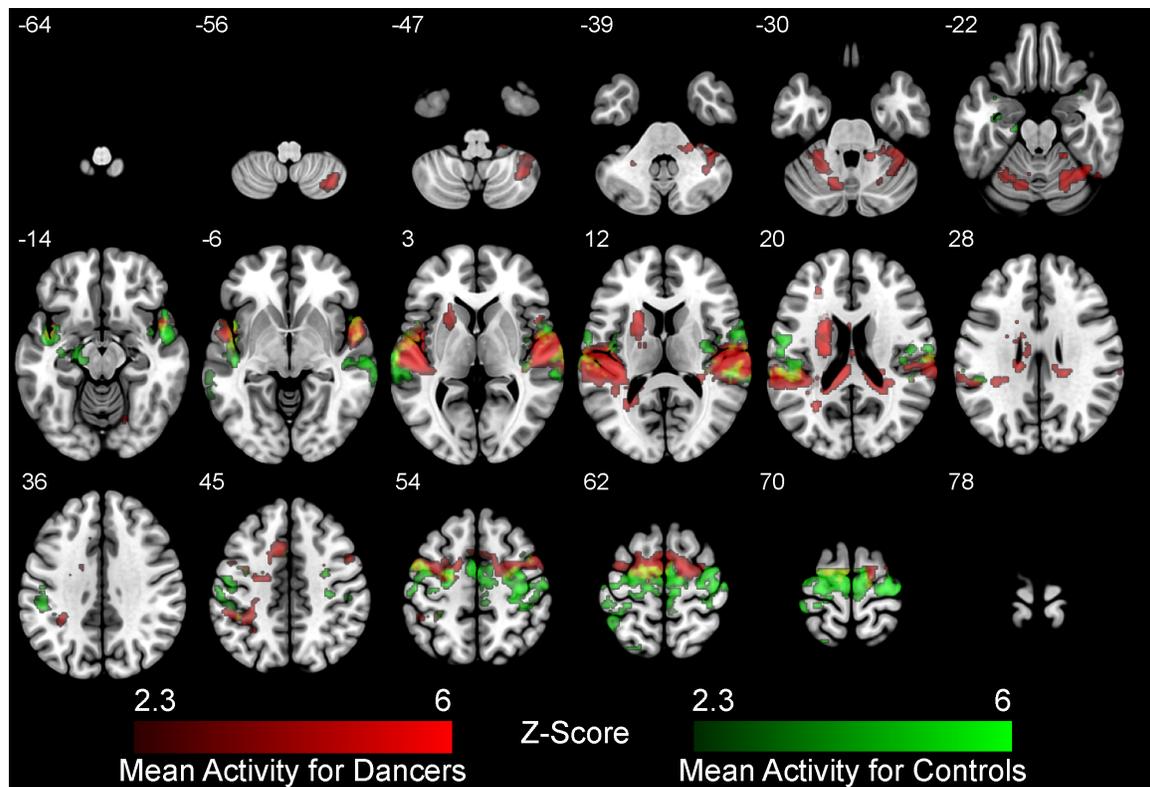


Figure 1. Significant activation for the motor imagery > baseline contrast in both the control and expert ballet dancer groups ($p < 0.01$ corrected for multiple comparisons using cluster detection). Areas in red correspond to the contrast activation map of the dancers, and areas in green for the controls. Areas in yellow represent an overlap of the activation maps for each group (this was simply done for visualization purposes, and was not a statistical conjunction analysis). Axial slices are reported with their Z MNI coordinates in the neurological convention (left = left).

of the cerebellum, whereas the controls showed no significant cerebellar activity.

Table 1. Cluster list for the mean activation map of controls for the contrast of motor imagery > rest (cluster correction with $Z > 2.3$ and $p < 0.05$). Coordinates are reported in MNI space. Regions associated with their respective coordinates were determined through the use of the SPM Anatomy Toolbox.

Cluster Index	Total Voxels for Cluster Index	Region	X (mm)	Y (mm)	Z (mm)	Z-max
2	6793	Left Middle Temporal Gyrus	-66	-32	2	9.80
2		Left Superior Temporal Gyrus	-66	-16	2	8.69
2		-	-64	-28	6	8.07
2		-	-46	0	-6	7.37
2		Left Precentral Gyrus	-44	-2	58	7.85
2		Left SMA	0	-10	64	6.87
1		2017	Right Postcentral Gyrus	66	-10	14
1	-		64	-12	18	7.5
1	Right Rolandic Operculum		56	0	6	10.1
1	-		52	0	0	8.89
1	-		62	-14	14	8.45
1	Right Superior Temporal Gyrus		60	-28	10	8.29

3.2. Differences in Activity During Motor Imagery in Dancers and Controls

The between-group analysis was done to assess the potential brain activity differences between controls and dancers during the motor imagery task. The controls were found to exhibit significantly greater activity in numerous brain regions during motor imagery of dance movements when compared to the expert dancers (Figure 2). These areas included the superior frontal and medial gyrus, anterior cingulate cortex, hippocampus, precuneus, and left cerebellum (Table 3). In contrast, no regions were found to be significantly more active in the expert dancers during the motor imagery task relative to controls.

Table 2. Cluster list for the mean activation map of expert ballet dancer for the contrast of motor imagery > rest (cluster correction with $Z > 2.3$ and $p < 0.05$). Coordinates are reported in MNI space. Regions associated with their respective coordinates were determined through the use of the SPM Anatomy Toolbox.

Cluster Index	Total Voxels for Cluster Index	Region	X (mm)	Y (mm)	Z (mm)	Z-max
5	4525	Left Superior Temporal Gyrus	-44	-26	10	5.96
5		-	-50	-12	0	5.30
5		-	-50	-12	4	5.08
5		-	-56	-32	14	5.03
4	2989	Right Superior Temporal Gyrus	52	-6	2	6.29
4		-	64	-28	12	4.76
4		-	58	-18	8	4.74
4		-	70	-20	10	4.61
4		Right Temporal Pole	54	4	-4	5.19
3	2620	Right SMA	14	0	60	3.69
3		Left SMA	-10	2	68	3.67
2	1147	Right Cerebellum	41	-55	-42	4.26
2		-	34	-58	-24	4.24
2		-	20	-64	-26	4.00
2		-	40	-42	-32	3.72
2		-	31	-36	-40	3.69
2		-	34	-64	-56	3.65
1	489	Left Cerebellum	-16	-66	-26	4.26
1		-	-24	-48	-28	4.07
1		-	-16	-64	-30	3.29
1		-	-28	-62	-24	3.17

3.3. Non-rotated PLS Analysis – Task, Interaction, and Group Effects

For the non-rotated Task-PLS analysis, three contrasts of interest were defined a priori; one for a group main effect, the second for a task main effect, and the third for an interaction effect between group (dancers and controls)

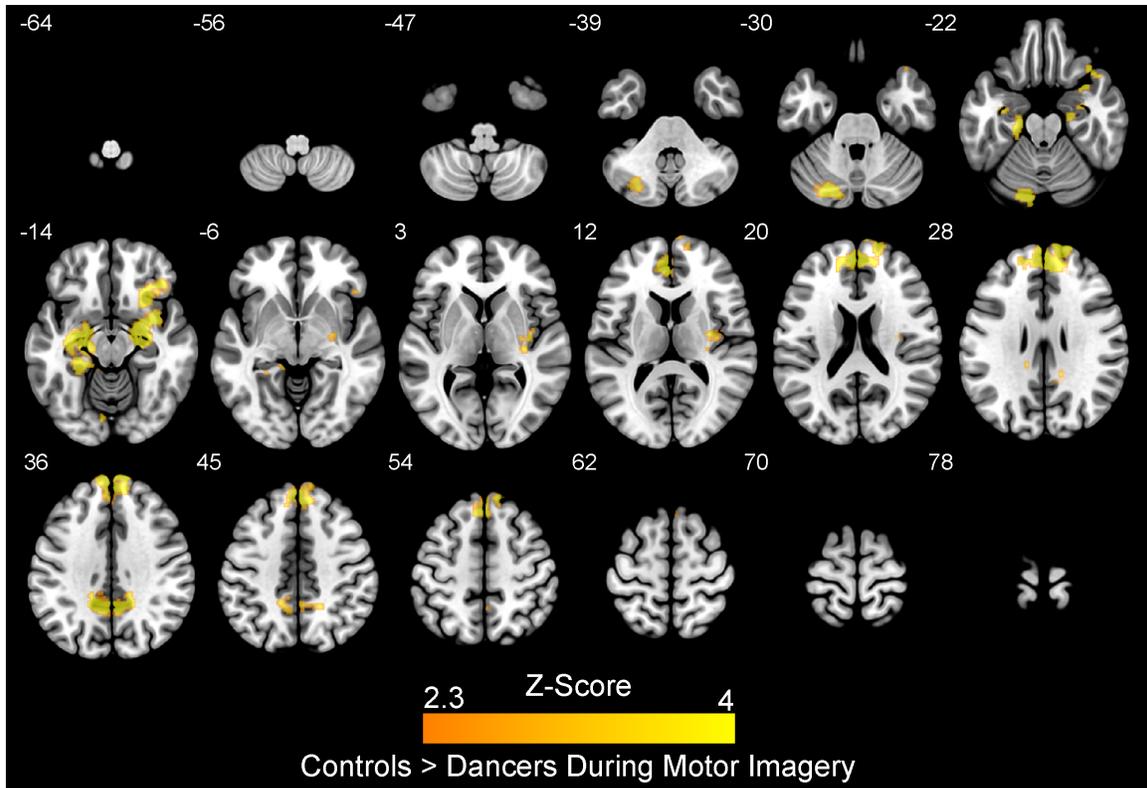


Figure 2. Areas of significant activation for the contrast of controls > expert dancers during motor imagery ($p < 0.01$ corrected for multiple comparisons using cluster detection). No areas were found to be significantly more active in the dancers compared to the controls during motor imagery; thus, only the control > dancer contrast is shown. Axial slices are reported with their Z MNI coordinates in the neurological convention (left = left).

and task (motor imagery and rest conditions). Thus, three latent variables were produced, one for each contrast. However, it is crucial to note that none of the latent variables were found to be significant, as determined through permutation testing (task main effect: $p < 0.426$; interaction effect: $p < 0.994$; group main effect: $p < 0.827$), which may have been due to the small sample size of the control group (Button et al., 2013). Nonetheless, the results are still interpreted below.

The first LV ($p < 0.426$), accounting for 59.96% of the covariance, was related to the contrast testing for a task main effect, and thus identified a set of

Table 3. Results of the functional group contrast, which consisted of comparing the motor imagery > baseline activation maps between dancers and controls (effects after cluster correction with $Z > 2.3$ and $p < 0.05$). Coordinates are reported in MNI space. Regions associated with their respective coordinates were determined through the use of the SPM Anatomy Toolbox.

Contrast	Cluster Index	Total Voxels for Cluster Index	Region	X (mm)	Y (mm)	Z (mm)	Z-Max
Controls > Dancers	5	2053	Right Superior Frontal Gyrus	18	62	24	4.65
	5		Left Superior Medial Gyrus	0	58	32	4.6
	5		-	0	42	42	4.26
	5		-	2	48	24	4.13
	5		-	0	44	48	4.06
	5		Left Anterior Cingulate Cortex	-6	48	12	4.07
	4	1037	Right Hippocampus	24	-16	-16	5.72
	4		Right Inferior Frontal Gyrus	26	24	-16	4.00
	4		Right Hippocampus	18	-10	-12	3.94
	4		Right Insula Lobe	38	8	-12	3.93
	3	623	Left Hippocampus	-32	-12	-16	4.38
	3		-	-34	-18	-16	4.16
	3		Left Parahippocampal Gyrus	-26	-38	-14	4.10
	3		-	-20	-22	-22	4.05
	3		-	-22	-28	-20	3.79
	3		Left Amygdala	-18	-6	-16	3.98
	2	501	Left Middle Cingulate Cortex	-14	-48	38	4.33
	2		Right Middle Cingulate Cortex	16	-46	34	4.04
	2		Left Precuneus	-10	-50	36	3.96
	2		-	-4	-48	38	3.27
	2		-	-6	54	38	3.19
	2		Right Precuneus	2	-50	50	3.28
	1	463	Left Cerebellum	-16	-80	-26	4.72
	1		-	-16	-82	-22	4.71
	1		-	-22	-78	-32	4.49
	1		-	-8	-78	-16	3.25
	1		-	-28	-70	-38	3.04
1	-		-20	-90	-26	2.46	
Dancers > Controls	-	-	-	-	-	-	-

disparate brain regions that in both groups, either showed greater activity during the motor imagery task or baseline (Table 4, Figure 3). The functional network

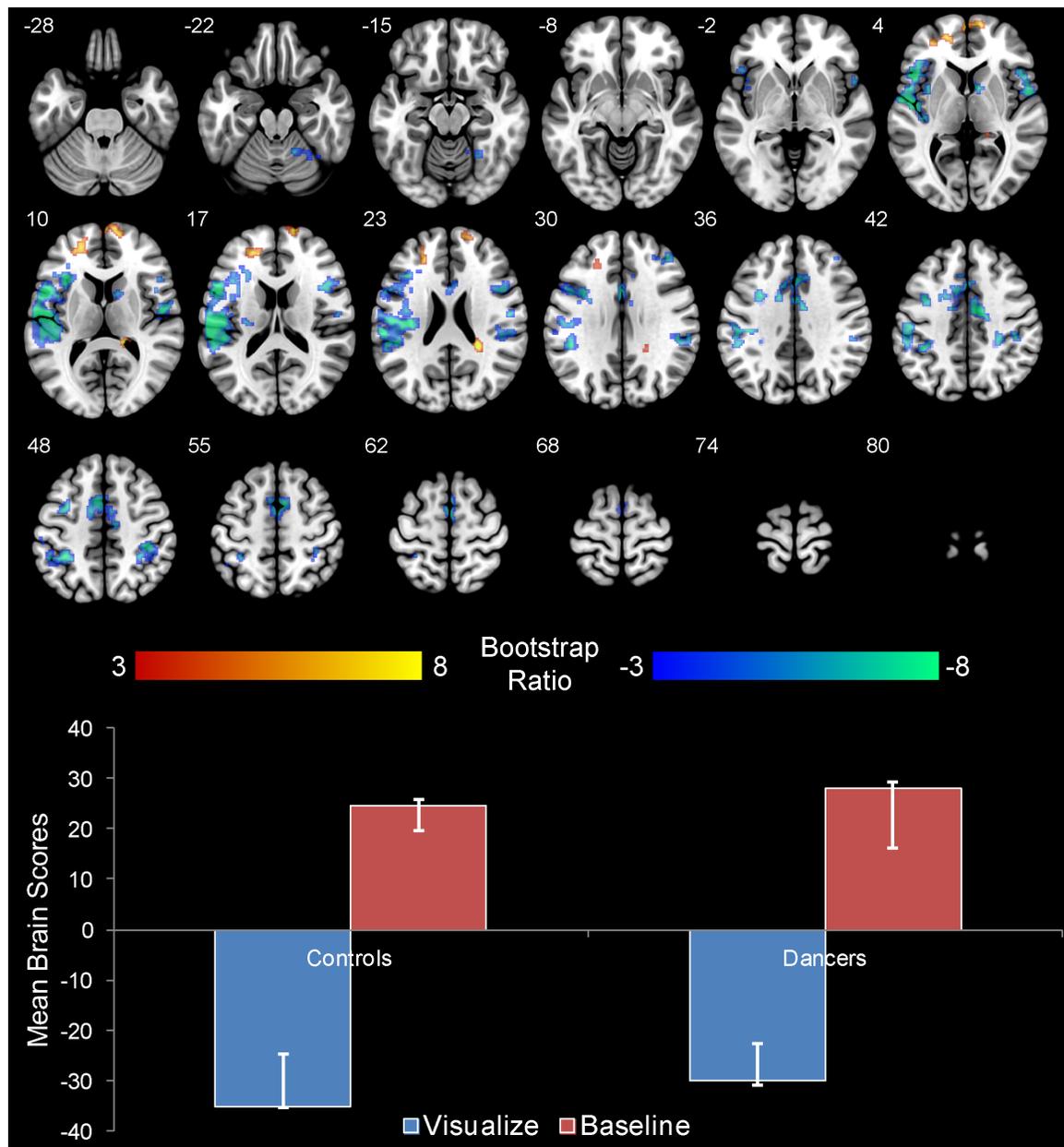


Figure 3. Latent variable 1 from the non-rotated Task-PLS, representing the contrast between motor visualization and baseline across both controls and dancers. The axial slices (reported with their z-coordinates in MNI space) represent which regions (minimum voxel threshold of 50 and bootstrap ratio of ± 3) exhibited greater activity during the motor visualization task (cool colours and associated with negative mean brain scores), and in contrast, regions which showed greater activity during baseline (warm colours and associated with positive mean brain scores). The graph below provides the mean-centered mean brain score of each group for this latent variable (with error bars representing 95% confidence intervals).

Table 4. Results of the functional non-rotated PLS analysis, testing for a task main effect. Results listed are clusters that were at least 50 voxels in size and had a minimum bootstrap ratio of ± 3 . Coordinates are reported in MNI space. Bootstrap ratio reported is that of the peak voxel in each cluster. Regions associated with their respective coordinates were determined through the use of the SPM Anatomy Toolbox.

Region	Voxel Size	X (mm)	Y (mm)	Z (mm)	Bootstrap Ratio
Right Superior Medial Gyrus	175	14	52	20	7.23
Left Middle Frontal Gyrus	199	-23	47	15	5.51
Left Superior Temporal Gyrus	3453	-54	-11	9	-11.59
Right Middle Cingulate Cortex	1023	10	-10	44	-6.90
Right Caudate Nucleus	73	10	7	5	-5.93
Right Rolandic Operculum	402	54	-8	10	-5.84
Right Postcentral Gyrus	198	40	-32	50	-5.58
Right Supramarginal Gyrus	129	54	-25	24	-5.21
Right Cerebellum	68	28	-55	-20	-4.95
Right Middle Frontal Gyrus	58	44	42	30	-4.38

of brain regions that were found to exhibit greater activity during the motor imagery task included the bilateral activation of the frontal gyrus and temporal lobes, as well as the right cerebellum, right caudate nucleus and right middle cingulate cortex; such areas have commonly been reported to be a part of the motor imagery functional network (Hetu et al., 2013). Only two clusters were found to be associated with the baseline condition: the right superior medial gyrus and the left middle frontal gyrus. Both the expert dancers and controls expressed the motor visualization and baseline networks (Figure 3) in a similar manner, as indicated by the overlapping confidence intervals between each group for each condition.

The second latent variable ($p < 0.994$), which accounted for 26.77% of the covariance, was related to the contrast that tested for an interaction effect between group (expert dancers and controls) and condition (motor visualization and baseline) (Table 5 and Figure 4). This contrast was of particular interest, due to potentially identifying brain networks that were recruited by the expert dancers

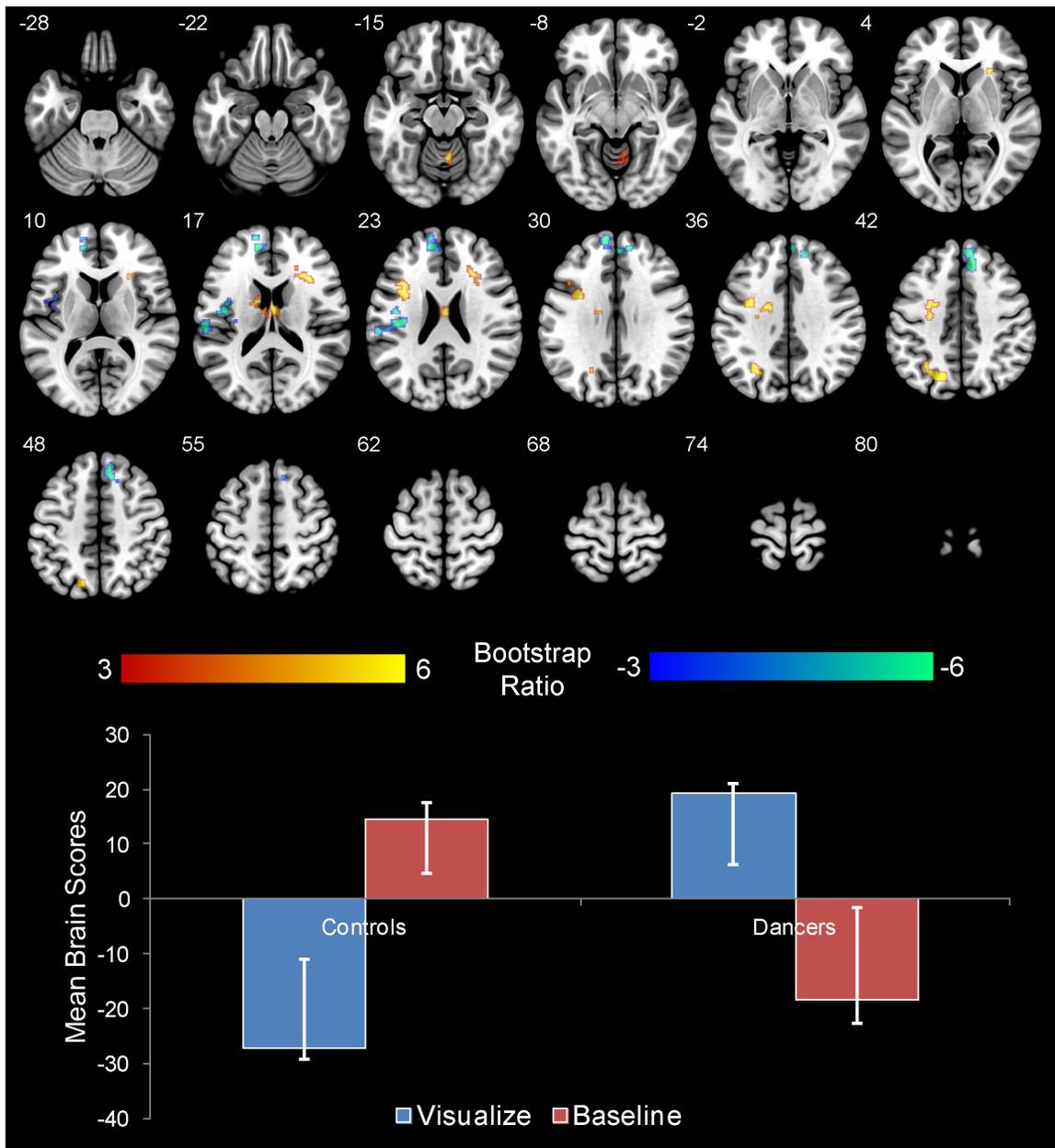


Figure 4. Latent variable 2 from the non-rotated Task-PLS, testing for an interaction between group (expert dancers and controls) and condition (motor visualization and baseline). The axial slices (reported with their z-coordinates in MNI space) represent brain regions identified by the interaction contrast (minimum voxel threshold of 50 and bootstrap ratio of ± 3). The graph below provides the mean-centered mean brain score of each group for this latent variable (with error bars representing 95% confidence intervals). Regions in warm colours (associated with positive mean brain scores) were regions that were recruited by the controls during baseline and by the dancers during motor visualization. Regions in cool colours (associated with negative mean brain scores) were regions that were recruited by the controls during motor visualization and by dancers during baseline.

Table 5. Results of the functional non-rotated PLS analysis, testing for an interaction effect between task and group. Results listed are clusters that were at least 50 voxels in size and had a minimum bootstrap ratio of ± 3 . Coordinates are reported in MNI space. Bootstrap ratio reported is that of the peak voxel in each cluster. Regions associated with their respective coordinates were determined through the use of the SPM Anatomy Toolbox.

Region	Voxel Size	X (mm)	Y (mm)	Z (mm)	Bootstrap Ratio
Left Inferior Frontal Gyrus	150	-32	4	28	5.57
Left Superior Parietal Lobule	201	-19	-63	40	5.33
Right Middle Frontal Gyrus	90	34	30	22	5.27
Right Cerebellum	54	8	-52	-10	4.95
Right Superior Medial Gyrus	433	10	38	44	-7.75
Left Rolandic Operculum	118	-40	-18	24	-7.18
Left Precentral Gyrus	85	-50	-6	22	-4.74

during motor imagery and by controls during baseline, and vice-versa. Regions associated with the baseline activity in controls and motor imagery in dancers (corresponding to warm colours and positive mean brain scores in Figure 4) included the left inferior frontal gyrus, left superior parietal lobule, right middle frontal gyrus, and right cerebellum; both groups engaged in this network of activity in a similar manner during their respective conditions, as implicated by the overlapping confidence intervals. Regions associated with motor imagery activity in controls and baseline activity in expert dancers (corresponding to cool colours and negative mean brain scores in Figure 4) included the right superior medial gyrus, left rolandic operculum and left precentral gyrus, and once again, both groups engaged in this network in a similar manner due to overlapping confidence intervals.

The third latent variable ($p < 0.827$), which accounted for 13.27% of the covariance, reflected the group main effect contrast (Table 6 and Figure 5). A spatial pattern was found which showed greater activity in controls for both the motor visualization and baseline task (regions in warm colours in Figure 5). This

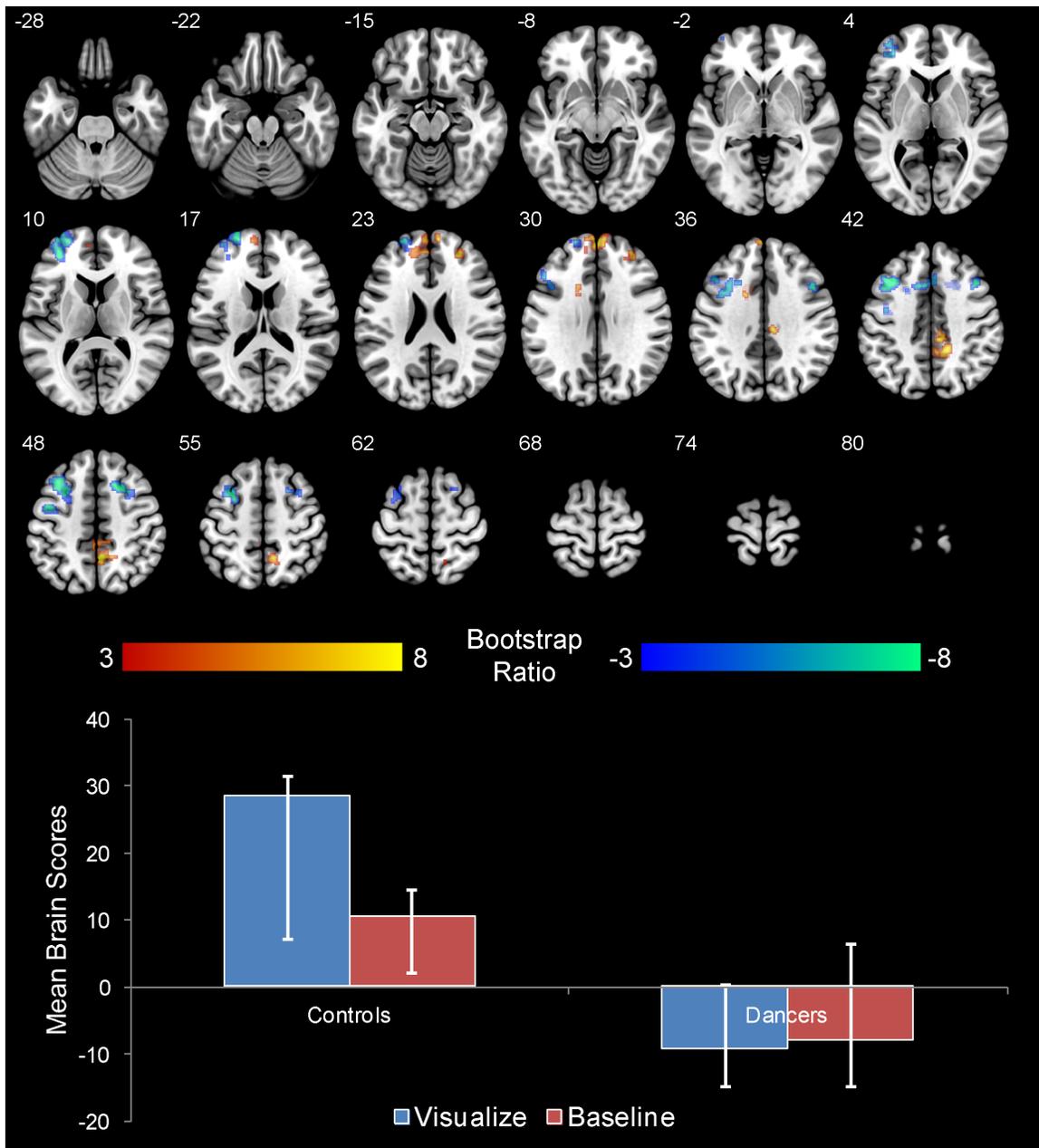


Figure 5. Latent variable 3 from the non-rotated Task-PLS, representing a group main effect. The axial slices (reported with their z-coordinates in MNI space) represent brain regions that were associated with either the controls or the expert dancers, regardless of task (minimum voxel threshold of 50 and bootstrap ratio of ± 3). The graph below provides the mean-centered mean brain score of each group for this latent variable (with error bars representing 95% confidence intervals). Regions in warm colours (associated with positive mean brain scores) were regions that were recruited by the controls during both the baseline and motor visualization. Regions in cool colours (associated with negative mean brain scores) were regions that were recruited by the expert dancers during both conditions.

included the right superior medial gyrus, right precuneus, left middle cingulate cortex, and right middle frontal gyrus. Both the motor imagery and baseline

Table 6. Results of the functional non-rotated PLS analysis, testing for a group main effect. Results listed are clusters that were at least 50 voxels in size and had a minimum bootstrap ratio of ± 3 . Coordinates are reported in MNI space. Bootstrap ratio reported is that of the peak voxel in each cluster. Regions associated with their respective coordinates were determined through the use of the SPM Anatomy Toolbox.

Region	Voxel Size	X (mm)	Y (mm)	Z (mm)	Bootstrap Ratio
Right Superior Medial Gyrus	234	8	50	24	8.57
Right Precuneus	310	4	-50	45	5.55
Left Middle Cingulate Cortex	52	-8	12	33	5.25
Right Middle Frontal Gyrus	75	30	45	25	5.03
Left Middle Frontal Gyrus	587	-38	20	44	-12.50
Right Middle Frontal Gyrus	140	24	15	45	-9.32
Left Middle Frontal Gyrus	420	-34	44	10	-8.45
Right Middle Frontal Gyrus	80	42	20	44	-8.00
Left Precentral Gyrus	58	-44	-2	48	-5.53
Left Middle Cingulate Cortex	55	-8	12	33	-5.19

conditions in the control group expressed this pattern of activity in a similar manner based on the overlapping of confidence intervals. The regions that were associated with an increase in activity during both conditions in the expert dancer group are shown in cool colours in Figure 5, and include the left and right middle frontal gyrus, left precentral gyrus, and the left middle cingulate cortex. However, it is important to note that neither of these two conditions reliably contributed to this spatial pattern of activity, based on their confidence intervals crossing zero.

3.4. Cortical Thickness Differences between Dancers and Controls

The cortical thickness between dancers and controls was compared through a whole-brain (vertex by vertex) analysis. Eleven significant clusters were found ($p < 0.01$) (Figure 6), with each exhibiting greater cortical thickness in dancers compared to controls. No regions were found to show thinner cortical thickness in dancers relative to controls. However, it is important to note that none of these clusters survived the correction for multiple comparisons

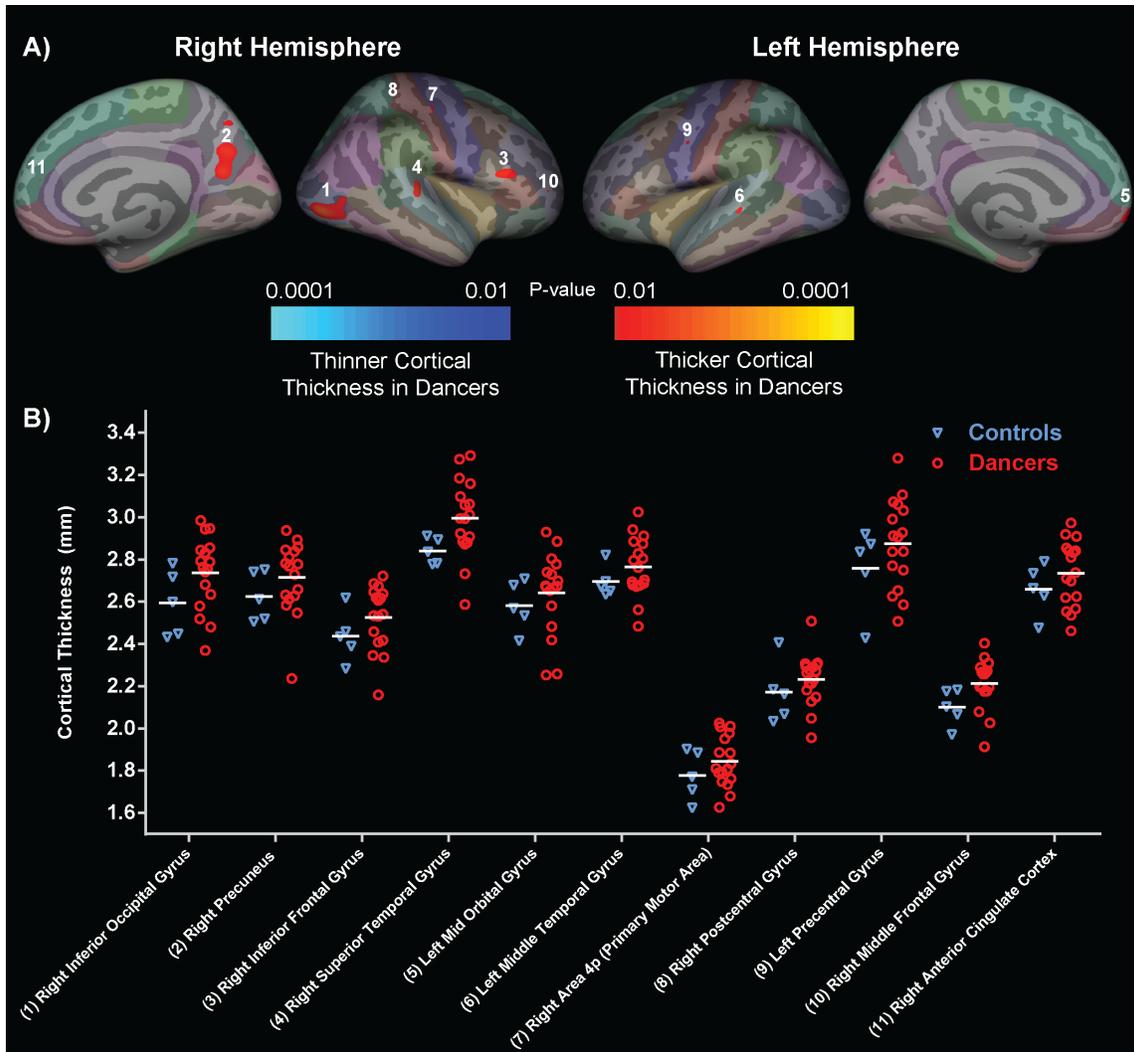


Figure 6. Results of surface-based cortical thickness analysis contrasting for significant differences between dancers and controls. Results are those of an uncorrected p-value of $p < 0.01$. No clusters survived the correction for multiple comparisons. Figure A) presents the eleven distinct clusters that were found to be thicker in dancers compared to controls. No regions were found to be thinner in dancers compared to controls. Results are displayed on the FSaverage inflated surface, with the Desikan-Killiany cortical atlas overlaid to allow visual distinction between regions. Figure B) provides a dot plot visualization of the cortical thickness measurements of each subject in the eleven regions that were found to be significantly different between the two groups. The white line represents the mean cortical thickness for each group. The number in brackets for each cluster on the x-axis correspond to the number labels found in figure A), which were determined through the use of the SPM Anatomy Toolbox. The order of clusters on the x-axis is in descending order from greatest cluster size (mm^2) to least.

through the application of a false discovery rate of 0.05. Regions with greater cortical thickness ($p < 0.01$, uncorrected for multiple comparisons) in dancers compared to controls included the right inferior occipital gyrus (surface area of cluster = 607 mm^2), right precuneus (surface area of cluster = 486 mm^2), right

inferior frontal gyrus (surface area of cluster = 187 mm²), right superior temporal gyrus (surface area of cluster = 142 mm²), left middle orbital gyrus (surface area of cluster = 136.7 mm²), left middle temporal gyrus (surface area of cluster = 35 mm²), right primary motor area (surface area of cluster = 18 mm²), right postcentral gyrus (surface area of cluster = 11 mm²), left precentral gyrus (surface area of cluster = 6 mm²), right middle frontal gyrus (surface area of cluster = 3 mm²), and right anterior cingulate cortex (surface area of cluster = 2 mm²).

3.5. Correlation between Cortical Thickness and Years of Dance Experience in Dancers

A correlation analysis was completed between cortical thickness and years of dance experience in the expert dancer group (n = 17). Seven clusters were found to be significant at a p-value of $p < 0.01$ (Figure 7); however, once again, none of these clusters survived the correction for multiple comparisons through the application of a false discovery rate of 0.05. Regions that exhibited a positive correlation between years of dance experience and cortical thickness included the left middle frontal gyrus (surface area of cluster = 81 mm²), left middle occipital gyrus (surface area of cluster = 19 mm²), left fusiform gyrus (surface area of cluster = 302 mm²), right parahippocampal gyrus (surface area of cluster = 29 mm²), and the right inferior temporal gyrus (surface area of cluster = 7 mm²). Regions of negative correlation included the right superior temporal

gyrus (surface area of cluster = 79 mm²) and the right middle frontal gyrus (surface area of cluster = 66 mm²).

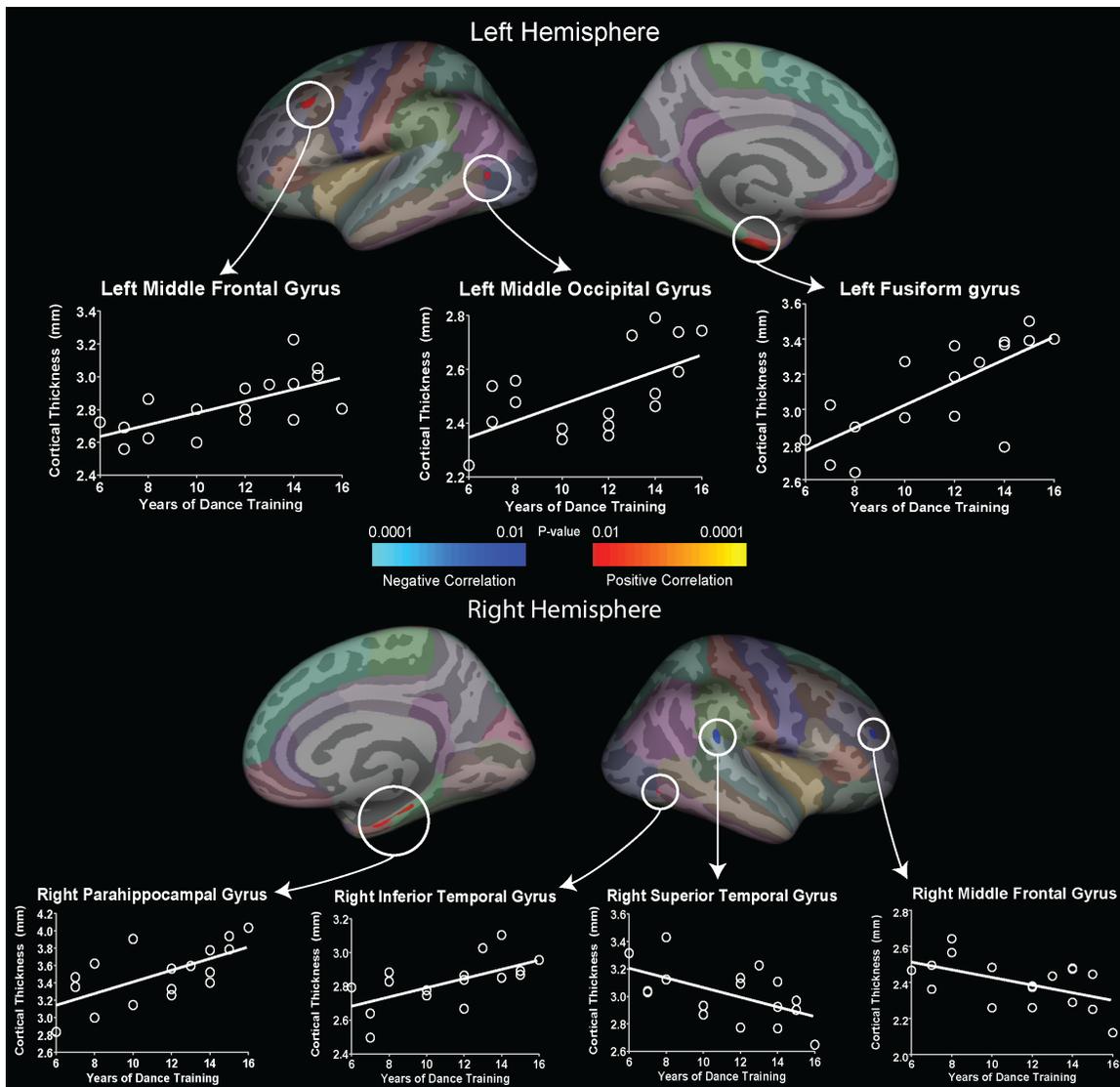


Figure 7. Correlation analysis results between cortical thickness and years of dance experience in expert dancers. Seven regions were found to exhibit a correlation, including both positive and negative relationships. Scatter plots for each one of these regions are provided. Results are those of an uncorrected p-value of $p < 0.01$. No clusters survived the correction for multiple comparisons. Results are displayed on the FSaverage inflated surface, with the Desikan-Killiany cortical atlas overlaid to allow visual distinction between regions. Regions were determined through the use of the SPM Anatomy Toolbox.

4. Discussion

4.1 Functional Activity Associated with Motor Imagery of Dance Movements in Dancers and Controls

The initial within-group fMRI analysis revealed the functional activation patterns associated with motor imagery of dance movements in both controls and expert dancers (Figure 1); many of these regions were found to be common in both groups, which was also implied by the task-PLS results (which were however non-significant) (Figure 3). Interestingly, the list of regions reported as being associated with the motor imagery of dance movements in both groups (Tables 1, 2, and 4) were similar to those reported by Brown et al. (2006), to which to our knowledge, is the only study which has investigated the functional activity associated with physical execution of dance movements within a scanner. Prominent regions that were common between experts and controls in our study (as implied by the overlap from the GLM analysis, as well as the task-PLS analysis), which also happened to be reported by Brown et al. (2006), included the superior temporal gyrus and the SMA (Brodmann's area 6).

Activity of the superior temporal gyrus as found in both groups can be partially attributed to the participants listening to musical pieces while in the scanner. The superior temporal gyrus is believed to be involved in the auditory processing of various features found in musical stimuli, including metre, rhythm, and melody (Brown et al., 2006; Chen et al., 2008; Liegeois-Chauvel et al., 1998; Zatorre et al., 2007). The superior temporal gyrus has also been proposed to be involved in auditory-motor interactions by disentangling the complex features

found in music, and selecting which features of the stimuli are motor relevant and thus needed to be transformed into motor representations by other brain regions, a feature that would be evoked during the imagery of movements cued by music (Zatorre et al., 2007).

Both groups also exhibited significant activation of the SMA during motor imagery, a region of particular interest due to its various functions that are relevant to the imagery of dance movements. The SMA is one the most consistently reported regions to be active not only during motor execution, but also during motor imagery, including during imagery of both simple (Guillot et al., 2008; Guillot et al., 2014; Hanakawa et al., 2003; Hetu et al., 2013; Lacourse et al., 2005; Lotze et al., 1999; Munzert et al., 2009; Naito et al., 2002) and complex motor movements (Baeck et al., 2012; Bezzola et al., 2012; Chang et al., 2011; Lotze et al., 2003; Meister et al., 2004; Olsson et al., 2008; Szameitat et al., 2007). The SMA is believed to hold various functional motor roles, including being involved in motor action planning (Baeck et al., 2012; Guillot et al., 2012; Lotze and Halsband, 2006), choosing the correct motor response to specific conditions or cues (Nachev et al., 2008), internally generated movements (Nachev et al., 2008), as well as in executing actions that involve performing a sequence of movements (Nachev et al., 2008; Tanji and Shima, 1994; Zatorre et al., 2007). With the critical role of the SMA in motor action initiation and performance of sequential movements, all while keeping in mind the extensive functional activity similarity between motor imagery and execution (Guillot et al.,

2014; Lotze and Halsband, 2006), the activation of the SMA during imagery of dance movements in both groups is not be surprising.

Although explored to a lesser extent in the literature, the SMA has also been proposed to be involved in the visuo-spatial transformations required in tasks such as mental rotation (Leek and Johnston, 2009). An example of such transformations may include the rotation of limbs during a motor imagery task (Hetu et al., 2013), which may represent another relevant role of the SMA in the context of imagery of dance movements, which commonly requires the mental manipulation of the spatial orientation of bodies (Blasing et al., 2012). The SMA activation found in both groups may also be related to its somatotopic properties. The SMA contains a somatotopically arranged map of the body, with movements of the hindlimbs being elicited from the caudal areas of the SMA, while forelimb movements from rostral areas (Nachev et al., 2008; Picard and Strick, 1996). Accordingly, Brown et al. (2006) suggested that the functional activation of the SMA during performance of dance movements (which in their study consisted of strictly bipedal movements) was related to the leg representation found in this region, and thus involved in the encoding of the parameters related to muscle group, contractile force, beginning and ending position, and movement direction. As previously mentioned, SMA activity has most commonly been reported during motor imagery of complex upper-limb motor movements (Baeck et al., 2012; Bezzola et al., 2012; Chang et al., 2011; Lotze et al., 2003; Meister et al., 2004; Olsson et al., 2008; Szameitat et al., 2007). However, in their meta-analysis, Hetu et al. (2013) noted that activation of the SMA was consistently found in

studies requiring the motor imagery of only lower-limb movements, whereas its activity was sparse in studies involving motor imagery of only upper-limb movements. This distinction may in part be due to the representation of upper-limb movements not only being restricted to the SMA, but may also be found in the premotor cortex (Graziano, 2006). However, if examining the SMA activity reported in this study solely in the context of its somatotopic properties, the activity found in both groups was likely related to both upper and lower limb movement imagery due to participants being instructed to engage in whole-body dance movements.

Other regions that were identified (although from non-significant results) as being common between the two groups during motor imagery included the middle cingulate cortex and cerebellum, regions previously shown to be active during the execution of dance movements (Brown et al., 2006). Both of these regions have also been consistently reported to be a part of the motor imagery network associated with both simple and more complex tasks (Hetu et al., 2013). Aside from being involved in the prediction of movement outcomes, temporal processing of movements, and the correction of movements based on feedback, the cerebellum may also be involved in the internal representation of movement, a crucial cognitive process during motor imagery (Guillot et al., 2014). The cingulate cortex is often implicated to be involved in motor control (Paus, 2001), corroborated by it having direct anatomical and functional connections to motor regions including the ventral horn of the spinal cord, the primary motor cortex, and premotor cortex (Amiez and Petrides, 2014). Its activity in the context of this

study was perhaps influenced by the complexity of the motor movements that were imagined by subjects; although active in more basic motor tasks, the cingulate cortex has also been shown to be modulated by the complexity of the motor task, with complex spatial motor coordination tasks eliciting greater activity in this region compared to when engaged in simpler tasks (Wenderoth et al., 2005). Aside from their individual functions described above, the cerebellum and cingulate cortex, along with the SMA, have also been suggested to be involved in supporting the coordination of different limbs during complex movements such as the playing of an instrument or engaging in dance movements (Brown et al., 2006; Jancke et al., 2000).

4.2 Functional Activity Differences between Dancers and Controls During Motor Imagery of Dance Movements

In the context of functional neuroimaging and motor expertise, much of the current literature has focused on investigating the functional activity differences between experts and novices when engaged in the execution or motor imagery of simple motor movements. In contrast, such comparisons in the context of expertise in complex whole-body movements, like dance, have been noticeably lacking (Hetu et al., 2013; Wei et al., 2010). Accordingly, the primary goal of this study was to investigate how the functional activity during motor imagery of dance movements potentially differs between expert ballet dancers and controls. The preliminary findings here support our hypothesis, with expert dancers exhibiting a general pattern of reduced functional activity compared to controls

during the motor imagery task. No regions were found to be significantly more active in dancers compared to controls, whereas various regions, including the superior frontal gyrus, hippocampus, middle cingulate cortex, and the left cerebellum (Figure 2, Table 3), were found to be more active in controls relative to dancers during the imagery of dance movements.

Controls were found to exhibit greater activity relative to the expert dancers during the imagery task in various frontal regions, particularly in the superior frontal gyrus and anterior cingulate cortex, regions that are thought to be jointly involved in cognitive control and attention during motor tasks (Debarnot et al., 2014). Although not a consistent finding in the pertinent literature, there are some studies that have reported a similar finding of a reduced or more focused activation of frontal regions being associated with motor expertise (Chang et al., 2011; Wei and Luo, 2010). Such results are in agreement with longitudinal studies that have reported slow motor skill learning to be characterized by a shift in functional activity from anterior to more posterior regions (Dayan and Cohen, 2011; Floyer-Lea and Matthews, 2005). However, such patterns of change in the frontal cortex may not be strictly related to motor expertise, but may instead reflect a more general pattern of functional change associated with general skill learning and expertise. It has been proposed that when faced with novel demands during unskilled performance, a particular set of regions involved in general attention and control tasks, including the prefrontal cortex and anterior cingulate cortex, are recruited and actively engaged in as a way to cope with such demands (Kelly and Garavan, 2005). Thus, a coordinated increase of

activity in such areas is associated with the performance of a new task. However, as one practices the task and proficiency is achieved, this pattern of frontal activity is reduced, as activity is shifted predominately towards pertinent posterior regions of the brain, such as in motor cortical regions for a motor skill. This reduction in frontal activity associated with skill expertise is ultimately thought to reflect a decrease in dependence on attention-related resources and executive functioning (Dayan and Cohen, 2011; Kelly and Garavan, 2005). Indeed, skilled performance is often defined by an increase in automaticity, a state in which relevant processes are rapid, smooth and require little attentional capacity (Yarrow et al., 2009). To reiterate, such changes in frontal activity are believed to be associated with the general acquisition and learning of all types of skills, which includes those that are motor-related. Thus, such activity differences may be related to the expert dancers placing a lesser demand on attentional and executive functioning resources due to their extensive practice in performing dance movements. In contrast, controls would be expected to extensively recruit these frontal attention and control regions due to the novel demands placed on them during the imagery task.

The middle cingulate cortex and precuneus were also a part of another significant cluster that was found to be more active in controls relative to dancers, with both regions being previously reported to be active during physical execution of dance movements (Brown et al., 2006). As previously mentioned, activity of the cingulate cortex may be modulated by the complexity of a motor task, with complex spatial motor coordination tasks inducing greater activity of the cingulate

cortex compared to simpler tasks (Wenderoth et al., 2005). However, previous studies have also shown an inverse relationship to exist between activity of the cingulate cortex and expertise level, with lower motor skill being associated with greater activity, and vice versa for those with motor expertise (Jancke et al., 2000; Milton et al., 2007). It follows that although the cingulate cortex was active in both groups, as would be expected due to the complexity of the motor imagery task as well as being a region shown to be active during the performance of dance movements (Brown et al., 2006), the difference in activity in this region may ultimately reflect the difference in dance skills between the two groups. This finding must be qualified however by the possibility that this difference in activity may not be strictly associated with a difference in dance motor skill between the two groups, but may instead be related to the motor imagery ability of each group. Individuals can vary greatly in motor imagery ability, which is based on criteria such as vividness and ability to match the temporal characteristics of the actual movements during imagery (Guillot et al., 2008). In contrast to skilled imagers, poor imagers have been found to exhibit different functional activation patterns when engaged in the same imagery task, including the recruitment of the cingulate cortex (Guillot et al., 2008). With the extensive use of motor imagery in dance training (Blasing et al., 2012), it is possible that this functional activity difference between the two groups in the cingulate cortex may not only be a reflection of dance motor skill, but may also reflect a difference in motor imagery ability, or even a conflation of these two potential explanations.

The activity of the cerebellum was found to be different between controls and dancers during the motor imagery task, with controls exhibiting greater functional activity relative to dancers. This was expected as a reduction of cerebellar functional activity in experts relative to novices, as was reported here, is one of the most consistent findings associated with motor expertise (Yang, 2015). Longitudinal studies involving simple finger-tapping tasks learned over a span of 5 days have shown the cerebellum to be significantly active during the early learning phase when the task is new, but over long term, as familiarity and proficiency in the task is achieved, a decrease in activity occurs (Parsons et al., 2005; Steele and Penhune, 2010). Cross-sectional studies between novices and motor experts have also reported experts to show lesser cerebellar activity when engaged in their task of expertise, including pianists during performance of finger movements (Haslinger et al., 2004; Koeneke et al., 2004), and archers during motor imagery of archery shooting (Chang et al., 2011). As previously mentioned, the cerebellum is involved in various processes related to motor performance, including motor learning, prediction of movement outcomes, temporal processing of movements, and the correction of movements based on feedback (Guillot et al., 2014). However, our findings, along with those mentioned above, suggest that cerebellar activity differs as a function of expertise in the motor task being performed (or imagined). This difference is in agreement with prominent models of motor skill learning in which the involvement of the cerebellum changes over the course of learning (Dayan and Cohen, 2011; Doyon and Benali, 2005; Doyon et al., 2003; Doyon et al., 2009). When first

performing and learning a novel motor task, regardless if the task is of a sequential learning or adaptation nature, a general motor-learning network is recruited, which includes motor cortical regions, prefrontal, parietal, and limbic areas, the striatum, and the cerebellum (Doyon and Benali, 2005). However, as learning of a sequential motor skill continues and retention and proficiency is achieved, the representation of the skill shifts to only include the basal ganglia and associated motor cortical regions, as the cerebellar functions related to motor learning, timing, and correction of movements minimized, thus leading to a reduction in activity (Doyon et al., 2009). That is not to say the cerebellum completely ceases to be active during motor execution a practiced motor skill. Brown et al. (2006) reported significant bilateral cerebellar activity in amateur dancers while physically executing bipedal dance movements, as did our dancers when performing motor imagery of dance movements. Rather, the cerebellum simply exhibits a reduction in activity over time as proficiency in the motor skill is achieved (Dayan and Cohen, 2011), which our findings support. The expert dancers in our study had extensive training, and were likely extremely familiar with the movements they imagined, having had years to practice and perform them. In contrast, the controls had no previous dance experience, and thus presumably no experience in performing ballet movements, which would have led to greater cerebellar functional activity compared to the dancers during imagery of dance movements, as was found in the results of our study. It is also important to note that there was a laterality effect found, with the cluster of functional activity difference between dancers and controls being found

specifically in the left cerebellum. Although some previous cross-sectional comparisons between novices and motor expert groups have found novices to exhibit greater activity bilaterally in the cerebellum (Chang et al., 2011; Haslinger et al., 2004), it has also been hypothesized that the left cerebellum is particularly influential only in the early stages of motor skill learning (Gaser and Schlaug, 2003; Hu et al., 2008). Longitudinal studies involving learning of bimanual coordination tasks have found cerebellar decreases to occur during learning, but only in the left side (Debaere et al., 2004). Other studies have also reported that novice performance is associated with bilateral activation of the cerebellum, where as only right cerebellar activity is found in motor experts (Koenke et al., 2004). Thus, our findings seem to support the notion that not only is the cerebellum a region of functional activity difference between motor experts and controls, but this difference may be confined to the left cerebellum.

A surprising finding was that of greater activity in the hippocampus of controls relative to dancers during the motor imagery task. The hippocampus has been noted as playing a role in the encoding and consolidation of new sequential motor skills, but only during the very early stages of learning (i.e. first 24 hours) (Albouy et al., 2008). No studies to our knowledge have reported differences in hippocampal activity when comparing controls to motor experts, with recent meta-analyses on this topic also failing to report such findings (Hardwick et al., 2013; Hetu et al., 2013; Yang, 2015). An exception comes from Lacourse et al. (2005), who did find greater activity in the hippocampus of participants when first performing imagery of a novel button-pressing task compared to when they

imagined performing the same task following a week of practice, once again suggesting that hippocampal activity is only significant during the very early stage of learning. However, the task was a simple finger motor task that involved only one week's worth of practice, making it inappropriate to compare with other studies that include complex motor expert groups who have trained in their skills for an extensive period of time. It is unlikely that the difference in hippocampal activity is an exclusive reflection of the dancers' motor expertise. If this were indeed the case, other studies with different motor expert groups should have reported similar differences in the hippocampus, but no such findings are to be found. Instead, the difference in hippocampal activity might be a reflection of how each group engaged in topographical representations during the imagery of dance movements.

Motor imagery of dance requires not only the visualization of appropriate limb movements, but also the imagining of one's body moving through space, which requires one to be aware of their orientation with respect to their mental surroundings (e.g. visualizing dancing on a performance stage) (Blasing et al., 2012). This is a unique feature of dance that may not be found in the other motor expert groups that have been studied thus far, such as musicians. Thus, it is possible that the imagery task in this study led to participants engaging in spatial mental imagery in order to create an internal representation of their orientation in an environment that they imagined moving through. Accordingly, the hippocampus is believed to be a crucial structure in such topographical processing (Poirel et al., 2010). This suggested role of the hippocampus in

topographical representations is primarily based on place cells being found in the hippocampus, which are neurons that the activity of are modulated based on the spatial position of an animal in its environment (Moser et al., 2008). We speculate that the difference in hippocampal activity may not be related to the motor expertise of the dance group, but rather to their familiarity of the environment in which they were likely imagining their dance movements. Wolbers and Buchel (2005) reported that during the initial spatial learning of a complex environment, subjects exhibited significant hippocampal activity. However, as the environment became better known and navigational performance improved, hippocampal activity decreased, implying it was only necessary when learning and incorporating new spatial information. Other studies have also suggested that the hippocampus is required only during the consolidation stage of topographical information (Barrash et al., 2000), as well as only being required when engaging in spatial memory of recently learned environments, and not for recalling spatial information that was encoded long before (Rosenbaum et al., 2004). Due to the extensive use of mental rehearsal in dance training (Blasing et al., 2012), it may be that during the motor imagery task, the dancers visualized their movements in the familiar environment of their dance school. This spatial familiarity may have thus led to lesser hippocampal activity in the dancers compared to controls, who may have imagined their movement in spatial environments that they are not familiar with.

The finding of controls exhibiting greater activity during imagery of dance movements relative to the dancers is in agreement with the hypothesis that motor

expertise is associated with neural efficiency, or a reduction in functional activity, a finding which has been commonly reported in other motor expert groups (Berkowitz and Ansari, 2010; Bezzola et al., 2012; Bernardi et al., 2013; Chang et al., 2011; Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Lotze et al., 2003; Meister et al., 2005; Milton et al., 2007). The neural efficiency hypothesis suggests that individual motor regions act in a more efficient manner during automatic and proficient motor performance, thus requiring less energy (Doyon et al., 2009). The exact mechanisms behind such a reduction of functional activity remain unknown, but various theories have been proposed to account for such findings. It may be that as a motor skill increases, more effectors are continuously linked, thus reducing the number of individual motor elements to be controlled via motor commands. This linkage of motor elements through practice may allow complex movements to occur in a much more automatic and efficient manner, which would be reflected by experts having smaller and less active neural networks while engaged in the motor task (Bezzola et al., 2012; Jancke, 2009). Diedrichsen and Kornysheva (2015) propose a similar model to potentially account for this reduced functional activity; motor skill learning involves various levels of the motor hierarchy, including that of the selection level, which represents movement goals. It is the selection level that activates the appropriate motor primitives, or the spatial and temporal patterns of muscle activity that occur across a wide range of desired complex movements. When first learning a motor task, the selection level can be a time and energy consuming process, due to the need to first consider various

alternatives of performing an action, and then eventually choosing the most appropriate set of motor primitives. However, as one becomes proficient in a motor skill, a dynamic network may emerge which consists of the different motor elements necessary for the desired movement linked together. Thus, when an expert wishes to initiate such a motor skill, only this single network “stream” needs to be activated, meaning minimum input from the selection level is required, which may ultimately result in a reduction of functional activity compared to the earlier stages of learning (Diedrichsen and Kornysheva, 2015).

Although we believe our findings support the hypothesis of neural efficiency being associated with complex motor skill expertise, it is important to note that the use of this term has drawn criticism. When referring to neural efficiency in the context of functional neuroimaging, it is often used to refer to the result that experts exhibit fewer areas of activity, or smaller hemodynamic responses in task-related areas, compared to novices. The findings of a reduction of functional activity are not necessarily the issue; instead, the criticism is primarily directed at how stating that one group demonstrates “neural efficiency” compared to another simply redescribes the data without providing an explanation as to the biological basis of such differences, which unfortunately are currently unknown (Poldrack, 2015). In an attempt to explain such results, one is faced with the confound that such differences may not actually reflect differences in efficiency, as in motor experts are using less neural energy to execute the same task as compared to controls, but may be related to each group engaging in a different set of cognitive processes or different neural computations for the

same task (Poldrack, 2015). The lack of a single verified explanation affirms the difficulty in interpreting the functional plasticity associated with skill learning. Recent animal studies have however taken a step towards providing evidence that the reduced functional activity associated with motor expertise may indeed reflect neural efficiency. Picard et al. (2013) had primates learn a sequential motor task for up to 6 years, with their performance then compared between the learned task and an untrained motor task. Recordings of neuronal firing and metabolic activity via 2DG ($[^{14}\text{C}]$ 2-deoxyglucose) uptake were taken in the primary motor cortex. Although neuronal firing was found to be similar between the two tasks, metabolic activity was significantly reduced during performance of the practiced motor skill, suggesting that motor training and expertise may lead to a state in which less synaptic activity is required to generate a given amount of neural activity while engaged in the practiced skill (Picard et al., 2013). Of particular importance is how such findings are translational to the field of fMRI and motor expertise; the authors noted the tight coupling that previous studies have demonstrated between metabolic processes and hemodynamic measures, and thus suggested that functional activity measured via the BOLD signal should be modulated in a similar fashion by motor expertise (i.e. a reduction of functional activity) as was their 2DG measurements, giving credence to the often-made conclusion that reduced functional activity (as measured by fMRI) in motor experts may indeed be a reflection of achieved neural efficiency (Picard et al., 2013), as was implied by the results of our study.

4.3 Dance Expertise and Cortical Thickness: Differences Between Dancers and Controls, and Correlation with Dance Experience

Several studies have investigated the structural differences between motor experts, such as musicians or athletes, and novices, with the common finding being greater gray matter in various regions, often deemed to be task-relevant, in the motor expert group (Bermudez et al., 2009; Bermudez and Zatorre, 2005; Gaser and Schlaug, 2003; Hanggi et al., 2015; Jacini et al., 2009; Jancke et al., 2009; Park et al., 2009; Park et al., 2011; Schneider et al., 2002; Wei et al., 2010). Here, we also explored for structural differences between expert ballet dancers and controls, with the results supporting our initial hypothesis as dancers were found to exhibit greater cortical thickness in various regions relative to controls; no regions were found to be thinner in dancers. Dance training involves the learning and correction of movements, thus leading to the consistent recruitment of regions that are related to functions such as motor control, timing and synchronization, visuo-motor imagery, spatial transformations, and action observation and imitation (Blasing et al., 2012). The regions found to differ in cortical thickness between dancers and controls, which included the right inferior occipital gyrus, right precuneus, right inferior frontal gyrus, and right superior temporal gyrus, correspond well with the functions described above that would be critical in achieving dance expertise.

The extensive use of motor imagery in dance training may have influenced the greater cortical thickness found in the precuneus and inferior occipital gyrus of dancers. Visual imagery, which has in common many of the neural substrates

found in kinaesthetic imagery, has been noted to elicit activity in occipital regions and in the precuneus, particularly when performed by skilled imagers (Guillot et al., 2009). It is possible that dancers, who may be skilled imagers due to their training (Blasing et al., 2012), extensively recruit these regions when they themselves are engaged in visual imagery of dance movements. The precuneus in particular has been shown to be implicated in various types of mental imagery tasks, including in motor imagery, where it is believed to be involved in the processing of spatial relationships for body movement control (Cavanna and Trimble, 2006; Hanakawa et al., 2003; Wenderoth et al., 2005). Outside the context of imagery, significant activity of the precuneus has also been reported during both the execution and preparation of spatially guided behaviours, with its activity particularly pronounced during tasks that require the coordination of multiple limbs while following complex spatiotemporal patterns (Astafiev et al., 2003; Cavanna and Trimble, 2006; Hanakawa et al., 2003). For example, Wenderoth et al. (2005) reported greater activity of the precuneus during a spatially complex bimanual coordination task compared to a unimanual coordination task, suggesting its activity to be influenced by the complexity of the motor task. Interestingly, not only was the precuneus one of the regions to have a greater cortical thickness in dancers, but it was also one of the regions in our functional study to exhibit reduced functional activity in dancers during motor imagery compared to controls. Accordingly, with being a region to differ on both structural and functional measures between dancers and controls, as well as its various implied roles in mental imagery and complex motor movement execution,

the precuneus may be one of the more pronounced regions to undergo plasticity via dance training.

Dancers were also found to exhibit greater cortical thickness in the frontal lobe, specifically in the left middle orbital frontal gyrus and right inferior frontal gyrus (pars opercularis). An increase of gray matter in such regions has previously been reported in other motor expertise groups, including in judo players (Jacini et al., 2009), divers (Wei et al., 2010), golfers (Bezzola et al., 2011), and musicians (James et al., 2014). Such similar region-specific structural plasticity reported across a wide variety of motor expert groups may reflect the involvement of critical frontal associative regions in the higher-order cognitive aspects required in the learning and consolidation of complex motor skills (Doyon and Benali, 2005). Structural plasticity of the middle orbital frontal gyrus has been found to be associated with long-term training and expertise in complex motor skills such as diving or playing of an instrument (James et al., 2014; Wei et al., 2010), but recent studies also imply that it is one of the initial regions to exhibit significant gray matter expansion following short-term motor training. Taubert et al. (2010) had participants train on a complex whole-body balancing task, and only after 6 weeks of practice (with one 45-minute session each week), they reported an increase of gray matter volume in various frontal regions, including in the left middle orbital frontal gyrus. Considering a balancing task used by Taubert et al. (2010) as their motor skill of interest, their results provide an intriguing overlap with the increased cortical thickness of the left middle orbital frontal gyrus found in our results, as dance requires extensive balancing ability, as

corroborated by various studies that have found dancers to perform significantly better than non-dancers on various measures of balance (Bruyneel et al., 2010; Crotts et al., 1996; Gerbino et al., 2007). Taubert et al. (2010) suggested that the gray matter expansion reported in the orbital frontal gyrus might reflect a building and maintenance of a learned optimal strategy for proficient task execution, which in this case was a balancing task. However, it is ultimately difficult to assess the potential role of the orbital frontal gyrus in dance training or even in general motor expertise, as it is considered one of the more least understood regions, with no consensus yet achieved as to its exact functions (Cavada and Schultz, 2000; James et al., 2014). Studies thus far have suggested it to be implicated in a variety of different functions, including in the control of mood, memory, processing and regulation of response to rewards and punishment, as well as in other emotional and social behaviours (Bechera et al., 2000; Cavada and Schultz, 2000; Kringelbach, 2005; O'Doherty et al., 2001).

The inferior frontal gyrus (pars opercularis) was also found to exhibit greater cortical thickness in dancers compared to controls, with similar reports of gray matter increase in this region being associated golf (Bezzola et al., 2011) and musical instrument (Gaser and Schlaug, 2003; James et al., 2014; Sluming et al., 2002) training. In the context of dance, the increase of cortical thickness in the inferior frontal gyrus may reflect its consistent involvement in action observation and imitation (Molnar-Szakacs et al., 2005), with it being consistently reported as a major node in the primate (human and non-human) mirror neuron circuit (Kilner et al., 2009; Rizzolatti et al., 1996). In such a network, it has been

suggested that the inferior frontal gyrus (pars opercularis) may be critical for the organization of higher-level and complex motor actions, including the selection or inhibition of action chunks (Schubotz and von Cramon, 2004; Zatorre et al., 2007). Accordingly, this region, along with other mirror neuron-related areas, have been shown to exhibit increased functional activity in dancers when viewing dance movements that they have previously learned, or movements similar to their style of dance expertise, in comparison to movements that they are not familiar with (Calvo-Merino et al., 2005; Cross et al., 2006). Similar domain-specific expertise effects have also been reported in musicians, who have been found to exhibit greater activity in mirror neuron related brain regions, including in the inferior frontal gyrus, during the perception of music compared to non-musicians (Bangert and Schlaug, 2006). Although only speculation, it may be that dance training requires a consistent engagement in this mirror-neuron network, and thus the inferior frontal gyrus, due to action observation and imitation being a crucial component in the learning of dance movements (Blasing et al., 2012; Sevdalis et al., 2011). This would be in contrast to non-dancers who putatively would not engage in motor learning through action observation and imitation to the same extent as professional dancers in their daily lives.

Greater cortical thickness was also found in the right superior temporal gyrus and left middle temporal gyrus of dancers relative to controls. Aside from music perception, the superior temporal gyrus is also involved in auditory-motor interactions through disentangling the complex features found in an auditory stimuli like music, and selecting which features of the stimuli are motor relevant

and thus needed to be transformed into motor representations by other brain regions (Zatorre et al., 2007). One of these regions that the superior temporal gyrus directly projects to includes the inferior frontal gyrus (Pandya and Yeterian, 1996). Such auditory-motor transformations are undoubtedly a critical component in dance, as dance movements are often executed in a temporal pattern while in synchrony to music (Brown et al., 2006; Sevdalis et al., 2011). However, another feature of the superior and medial temporal cortices that may be relevant to dance training is their critical role in biological motion (Saygin, 2007; Vaina et al., 2001). Following the functional plasticity reported in biological motion related regions of dancers during action observation (Calvo-Merino et al., 2005), as dancers become more proficient at the perception of body movements, structural plasticity may also occur in such areas as in the superior and medial temporal gyrus.

Finally, we turn to the correlation analysis, in which we investigated the relationship between years of dance training and cortical thickness. Of particular interest were the positive correlations found between years of dance experience and cortical thickness in the right parahippocampal gyrus and left fusiform gyrus. In a subcortical focused region of interest analysis, Hufner et al. (2011) compared the gray matter volume between professional dancers and slackliners, and found greater volume in dancers in regions such as the parahippocampal gyrus and the fusiform gyrus (Hufner et al., 2011). In our cross-sectional cortical thickness comparison, neither of these regions were found to differ between dancers and controls. However, our correlational results still imply a similar

relationship to that found by Hufner et al. (2011) between the structure of these regions and dance, as the cortical thickness of both the parahippocampal gyrus and fusiform gyrus were found to be positively correlated with dance experience. In comparison to the hippocampus, the parahippocampal gyrus has consistently been reported to be active in human navigational studies (Poirel et al., 2010). Although the exact type of navigational representation processed by the parahippocampal gyrus is still unclear, it is most often implicated in the perception and mental imagery of spatial scenes and places (Poirel et al., 2010), and in particular the acquisition (Aguirre et al., 1996; Epstein et al., 1999) and retrieval (Ekstrom et al., 2003; Gron et al., 2000) of spatial information. In a similar fashion, the fusiform gyrus is also believed to play a critical role in visually guided spatial memory (Shipman and Astur, 2008). Drawing from fMRI studies as well, the functional activity of the right parahippocampal activity has been reported as being modulated by expertise, with dancers exhibiting greater activity in this region when observing familiar dance movements versus those that are unfamiliar (Calvo-Merino et al., 2005). Similarly, it was also reported as a region of activity difference between dancers and novices during imagery of dance movements in our fMRI study. During dance movement rehearsal over 5 weeks, the fusiform gyrus and parahippocampal gyrus were also found to increase in activity over the training period during dance simulation (Cross et al., 2006). Thus, it appears as though the parahippocampal gyrus and fusiform gyrus are two regions that demonstrate pronounced structural and functional plasticity in relation to dance training and expertise.

Our main result of expert ballet dancers exhibiting greater cortical thickness in various regions corresponds well with other studies which have reported motor learning and expertise to be associated with greater gray matter in various regions (Bermudez et al., 2009; Bermudez and Zatorre, 2005; Gaser and Schlaug, 2003; Hanggi et al., 2015; Jacini et al., 2009; Jancke et al., 2009; Park et al., 2009; Park et al., 2011; Schneider et al., 2002; Wei et al., 2010). Extending beyond experience-dependent structural plasticity in the strict context of motor training, the learning of skills in other various domains has also been found to be associated with increases in gray matter (Aydin et al., 2007; Engvig et al., 2010; Kuhn et al., 2014; Maguire et al., 2000; Mechelli et al., 2004), suggesting that in general, skill learning is associated with an increase of gray matter in what are believed to be task-relevant regions (May, 2011). It is important to note that the underlying biological mechanisms responsible for the increases in cortical gray matter as reported through MRI are currently unknown; potential candidates include neurogenesis, gliogenesis, synaptogenesis and other changes in other cellular properties, with any one of these potentially capable of influencing MRI signals (May, 2011; Zatorre et al., 2012). These potential candidates are derived from animal studies which have found various types of skill learning, including motor-related, to be associated with a quantitative increase in distinct neural properties and processes, including as previously listed, neurogenesis (Gould et al., 1999; Tronel et al., 2010), gliogenesis (Dong and Greenough, 2004), and synaptogenesis (Black et al., 1990; Chklovskii et al., 2004; Holtmaat et al., 2006; Jones et al., 1999; Kleim et

al., 1996; Kleim et al., 2002), with it being possible, if not likely, that increased gray matter as detected through MRI is due to a combination of these factors (Zatorre et al., 2012).

Although a vast majority of studies have found motor expertise to be associated with an increase of gray matter, there are some studies, albeit few, that have reported the aberrant finding that motor expertise is associated with a decrease of gray matter in various task-related regions (James et al., 2014; Vaquero et al., 2016). An example of such a study is that by Hanggi et al. (2010), who by comparing professional ballet dancers to non-dancers, found decreased gray matter volumes in the premotor cortex, SMA, putamen, and superior frontal gyrus of dancers. Indeed, their peculiar result was a motivating factor in us investigating for potential structural differences between controls and the dancers in our study, to determine whether dance expertise is unique in that it is associated with a reduction of gray matter. However, our findings of dancers exhibiting greater cortical thickness relative to non dancers is in contradiction to the findings reported by Hanggi et al. (2010), and instead corresponds well to what a majority of the literature suggests, and that is motor expertise is associated with an increase of gray matter in what are believed to be task-relevant regions (Bermudez et al., 2009; Bermudez and Zatorre, 2005; Gaser and Schlaug, 2003; Hanggi et al., 2015; Jacini et al., 2009; Jancke et al., 2009; Park et al., 2009; Park et al., 2011; Schneider et al., 2002; Wei et al., 2010). In a follow up analysis not reported here, we also compared the gray matter volume between dancers and controls, which was the same measurement used by

Hanggi et al. (2010), and similar to our cortical thickness results, we only found greater volume in various regions of dancers relative to controls, with no regions exhibiting smaller volumes in dancers.

As for their unusual finding, Hanggi et al. (2010) suggested that potential factors may include the weight of the dancers, or what stage of training they were in, although as admitted by the authors, such reasons were unlikely to drastically influence the brain anatomy of the dancers in their study. For example, the particular stage of training a motor group is at may affect whether any significant anatomical differences are found between such a group and controls. By comparing the brain anatomy of professional golfers, nonprofessional golfers, and novice or non-golfers, Jancke et al. (2009) reported greater gray matter volumes in the nonprofessional golfers in comparison to the novice golfers, but found no differences between professional and nonprofessional golfers. It may be that significant gray matter changes only occur in the early stages of training, with no significant structural changes occurring past this point, regardless of time spent training or proficiency gained in the motor skill (Driemeyer et al., 2008). It has also been suggested that depending on the brain region, smaller increases in gray matter are associated with greater performance improvements (Taubert et al., 2010). Such studies only suggest that the potential for gray matter increase may plateau or even return to baseline once past the initial training period and expertise is achieved, but do not offer support for motor expertise to be associated with a decrease of gray matter relative to baseline (Hanggi et al., 2010). Others have suggested that whether an increase or decrease of gray

matter occurs following training depends on various factors such as the brain region, stage of training, and the motor skill itself that is being trained in (James et al., 2014). If dance expertise is truly associated with a decrease of gray matter, one potential confound that may have influenced our main result is the difference in age between our dancers and controls, with the controls being significantly older. Thinner cortical thickness has been reported in middle aged adults across various areas compared to younger adults (Salat et al., 2004), but the process of cortical thinning itself may begin during the teenage period and may continue to decrease into adulthood depending on the region (Shaw et al., 2008). It is possible that the result of greater cortical thickness being found in the dancers compared to controls was influenced by the significant difference in age between the two groups. Having said that, our results ultimately supported our hypothesis that expertise in ballet dance, a complex sensorimotor skill that requires extensive and intensive practice to become proficient in, is associated with an increase of gray matter.

4.4 Limitations and Future Directions

There are various limitations associated with the present work that must be kept in mind. Arguably the most glaring is the sample size of the control group, which only had five subjects. Low sample sizes can diminish the statistical power of a study, thus negatively affecting the likelihood that a significant finding is a reflection of a true effect (Button et al., 2013). In the context of neuroimaging, suggestions for the optimal sample size to detect an appropriate effect include

between 16 to 32 subjects (Friston, 2012), if not more (Yarkoni, 2009). Regardless, the control group size did not meet such proposed standards, which may have influenced the various non-significant results that were found, specifically from the PLS and cortical thickness analyses. Other issues included the control group being significantly older than the dancer group, including an adult with the age of 43 as one of the five control subjects. This may have obscured both the structural and functional analysis. As previously discussed, cortical thinning of various regions is associated with aging, and may begin to occur during early adulthood (Salat et al., 2004; Shaw et al., 2008). In the context of the functional analysis, the older age of subjects in the control group may have also influenced their motor imagery ability (Schott, 2012). Different features of motor imagery, such as accuracy and timing of movements, have been reported to be well persevered in older adults during the imagery of simple motor tasks. However, the motor imagery ability of older adults may be potentially worse when imagining complex and difficult movements (Saimpont et al., 2013), which dance may be considered as. In regards to functional activity during motor imagery, older adults have also been reported to exhibit similar areas of activity, but greater activity in such regions when compared to younger adults (Zwergal et al., 2012). Another potential confound that other studies focusing on the plasticity associated with motor expertise often fail to mention is that of exercise. With a typical ballet dance training session capable of evoking physiological responses that correspond to aerobic intensities levels that range from moderate to extremely strenuous (Schantz and Astrand, 1984), the aerobic fitness of dancers

has been noted to be similar to that of other non-endurance athletes (Cohen et al., 1981). There is now substantial evidence that exercise can induce both structural and functional plasticity (Hillman et al., 2008), predominantly in frontal and parietal regions (Colcombe et al., 2004; Colcombe et al., 2006) as well as in medial temporal lobe structures (Erickson et al., 2011). Thus, when investigating the plasticity associated with motor expertise in a skill that is also an athletic activity, it is possible that some differences may be attributable not to the complex sensorimotor learning involved in the motor skill, but perhaps to the fitness-related training that the motor skill requires.

The use of a motor imagery task in this study also carries several caveats. If the requested motor task to be imagined is simple, and participants have previous experience performing such actions, there is confidence to be had in that all participants imagined similar movements. However, as the movements to be imagined become more complex, there is in a sense, a greater degree of freedom for subjects in regards to which movements they may imagine during the task. In this study, although general guidelines were provided in regards to the ballet movements to be imagined, it is possible that the participants performed different movements throughout the task. It would also be expected that dancers, due to their training, would have a greater repertoire of dance movements, and thus potentially performed a greater variety of movements, some of which the controls had no knowledge of. Extending on this, there are also potential issues when comparing experts with controls who have no prior experience in the motor skills that the expert group has expertise in. With

complex motor skills, it may be the case that controls are not capable of performing such movements, making it difficult to address how experts and controls differ when engaged in the movement of interest (Jancke, 2009). As alluded to previously, there is also the potential confound related to the participant's skill in motor imagery. Individuals may differ in regards to their motor imagery ability, with those considered as having either poor or expert motor imagery ability having been found to exhibit slightly different functional activation patterns when engaged in the imagery of the same movement, including poor imagers recruiting the cerebellum and cingulate cortex (Guillot et al., 2008). However, motor imagery skill can also be improved through consistent practice (Milton et al., 2008). Motor imagery is frequently used in dance training as an aid with the learning and optimizing of movements, as well as with the mental rehearsal of such movements (Blasing et al., 2012). Due to their extensive use of motor imagery, dancers may be better at it than controls that have not engaged in motor imagery to the same extent. This then leads to a potential confound in regards to the functional activity differences found between dancers and controls, as to what extent was this finding influenced by differences in motor imagery ability between the two groups.

Another limitation included the lack of recording of muscle activity during imagery. As stated previously, motor imagery is commonly defined as a state in which one simulates an action mentally without producing any physical body movement (Debarnot et al., 2014). Thus, if there is an actual motor output during the imagery task, some regard this as not being actual motor imagery (Hetu et

al., 2013). To control for muscle activity during motor imagery, the recording of electromyography activity has been proposed; however, to date, very few neuroimaging motor imagery studies have done so due to the technical complications that arise when attempting to acquire electromyography recordings during MRI scanning (Hetu et al., 2013). It is important to reiterate that we did engage in visual inspection of potential motor movements during scanning with video recordings, a procedure that has been used in the literature to control for movements in motor imagery studies (Sharma et al., 2006). Finally, the study design itself was that of a cross-sectional, which ultimately carries the limitation of being unable to distinguish whether functional and structural differences found were due to dance training or to a predisposition (Zatorre et al., 2012).

Dance remains an advantageous but underutilized model to investigate the plasticity associated with complex motor expertise, and thus there are numerous future directions of interest that may be taken. One critical step going forward would be to conduct a longitudinal study to investigate the functional and structural plasticity associated with dance training (Bar and DeSouza, 2016). As previously mentioned, cross-sectional studies cannot discern whether any differences found between expert groups and controls are due to training or some sort of predisposition, a limitation that longitudinal studies can overcome. Attempting to conduct such a study however is faced with the logistical challenges of having to scan the same participants over very long periods of time. Unlike simple motor tasks that can be learned over the course of minutes or days, to achieve expertise in a complex motor skill like dance requires extensive

and intensive practice that usually takes place over the course of years (Hanggi et al., 2010).

In the context of functional neuroimaging, our primary questions of interest were evaluated through conventional univariate fMRI analysis, meaning each voxel was independently assessed in regards to its modulation by the task design, and thus there was no consideration for interregional relationships. Future studies may investigate the difference between expert dancers and controls during imagery of dance movements from a network perspective; for example, based on the areas that were found to more active in controls relative to dancers during the imagery task, functional connectivity analyses can be conducted with these regions of interest. This would elucidate how the functional networks associated with these regions potentially differs between dancers and controls when engaged in imagery of dance movements, and ultimately provide further insight into the functional plasticity associated with dance expertise.

It is also imperative for future studies to correlate the changes in structure and function associated with dance training to various dance-related behavioural measures, in an attempt to establish relationships between the neural changes to the changes in behaviours and skills associated with dance. The significance of neuroplasticity being associated with expertise is often hindered by a lack of pertinent behavioural correlations that can help establish relationships between changes in the brain and behaviour (Zatorre et al., 2012). Dance training has been found to be associated with various changes in both cognitive (Hufner et al., 2011; Smyth and Pendleton, 1994; Starkes et al., 1987) and motor measures

(Bruyneel et al., 2010; Crotts et al., 1996; Gerbino et al., 2007; Rein et al., 2011; Simmons, 2005), and thus provides an abundance of behavioural measures that can be used in future studies to correlate with changes in brain function and structure, with the goal to ultimately elucidate the brain-behaviour relationship associated with dance expertise.

4.5 Conclusion

In this thesis, we explored the functional and structural plasticity associated with dance expertise by comparing expert ballet dancers to controls in a cross-sectional fashion. This was done in part to address the noticeable lack of studies investigating the neuroplasticity associated with expertise in motor skills that require complex whole-body movements, particularly in the field of functional neuroimaging. It is important to once again reiterate that the control group was undersized by only having 5 subjects, and thus the results here are of a preliminary nature and must be interpreted with caution. Many of the findings reported in this study were either not significant, or were only so when uncorrected for multiple comparisons. Nonetheless, our findings still supported our hypothesis; dancers were found to demonstrate reduced functional activity relative to controls during the motor imagery of dance movements, and dancers were found to exhibit greater cortical thickness in various regions compared to controls. Both of these findings correspond with the current literature, which suggests that motor expertise is associated with neural efficiency, or reduced functional activity, during engagement in the relevant motor skill (Berkowitz and

Ansari, 2010; Bezzola et al., 2012; Bernardi et al., 2013; Chang et al., 2011; Haslinger et al., 2004; Jancke et al., 2000; Krings et al., 2000; Lotze et al., 2003; Meister et al., 2005; Milton et al., 2007), and an increase of gray matter in task-relevant regions (Bermudez et al., 2009; Bermudez and Zatorre, 2005; Gaser and Schlaug, 2003; Hanggi et al., 2015; Jacini et al., 2009; Jancke et al., 2009; Park et al., 2009; Park et al., 2011; Schneider et al., 2002; Wei et al., 2010).

As continuously asserted throughout this thesis, the neuroplasticity associated with motor expertise, and skill expertise in general, can be studied from both a functional or structural perspective, with each providing a distinct insight into how the brain changes by means of training. An encompassing question in this field then becomes what is the relationship between the structural and functional changes that are associated with motor skill learning and expertise. Some have coupled the reduction of functional activity with decreased gray matter, suggesting that the expertise-related reduction in functional activity reflects an improved efficiency in regions involved in the task, which in turn, leads to a reduction of gray matter as some sort of optimization response (Hanggi et al., 2010; James et al., 2014; Vaquero et al., 2016). Although our study did not investigate any potential relationships between the patterns of functional and structural differences found between dancers and controls, we still explored both of these neural properties independently, and our results suggest that although dance expertise is associated with neural efficiency in the context of functional activity, this decrease in activity is not accompanied by a reduction of gray matter; instead, expertise in dance is associated with an increase of cortical

thickness in various regions which may or may not have shown any functional activity differences. Ultimately, this thesis attempted to address a gap in the field of motor expertise and neuroplasticity by investigating both the functional and structural plasticity associated with dance expertise, as well as provide an initial first step to using dance as a model to study experience-dependent plasticity and to gain insight into the relationship between the brain and behaviour.

5. References

- Addis, D. R., Knapp, K., Roberts, R. P., & Schacter, D. L. (2012). Routes to the past: neural substrates of direct and generative autobiographical memory retrieval. *Neuroimage*, *59*(3), 2908-2922.
- Aguirre, G. K., Detre, J. A., Alsup, D. C., & D'Esposito, M. (1996). The parahippocampus subserves topographical learning in man. *Cerebral cortex*, *6*(6), 823-829.
- Albouy, G., Sterpenich, V., Balteau, E., Vandewalle, G., Desseilles, M., Dang-Vu, T., ... & Peigneux, P. (2008). Both the hippocampus and striatum are involved in consolidation of motor sequence memory. *Neuron*, *58*(2), 261-272.
- Amiez, C., & Petrides, M. (2014). Neuroimaging evidence of the anatomo-functional organization of the human cingulate motor areas. *Cerebral cortex*, *24*(3), 563-578.
- Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *The Journal of Neuroscience*, *23*(11), 4689-4699.
- Aydin, K., Ucar, A., Oguz, K. K., Okur, O. O., Agayev, A., Unal, Z., ... & Ozturk, C. (2007). Increased gray matter density in the parietal cortex of mathematicians: a voxel-based morphometry study. *American Journal of Neuroradiology*, *28*(10), 1859-1864.
- Baek, J. S., Kim, Y. T., Seo, J. H., Ryeom, H. K., Lee, J., Choi, S. M., ... & Chang, Y. (2012). Brain activation patterns of motor imagery reflect plastic changes associated with intensive shooting training. *Behavioural brain research*, *234*(1), 26-32.
- Bangert, M., & Schlaug, G. (2006). Specialization of the specialized in features of external human brain morphology. *European Journal of Neuroscience*, *24*(6), 1832-1834.
- Bar, R. & DeSouza, J.F.X. (2016). Tracking plasticity: effects of long-term rehearsal in expert dancers encoding music to movement. *PLoS One*, *11*(1).
- Barrash, J., Damasio, H., Adolphs, R., & Tranel, D. (2000). The neuroanatomical correlates of route learning impairment. *Neuropsychologia*, *38*(6), 820-836.
- Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral cortex*, *10*(3), 295-307.

Berkowitz, A. L., & Ansari, D. (2010). Expertise-related deactivation of the right temporoparietal junction during musical improvisation. *Neuroimage*, *49*(1), 712-719.

Berlucchi, G., & Buchtel, H. A. (2009). Neuronal plasticity: historical roots and evolution of meaning. *Experimental Brain Research*, *192*(3), 307-319.

Bermudez, P., & Zatorre, R. J. (2005). Differences in gray matter between musicians and nonmusicians. *Annals of the New York Academy of Sciences*, *1060*(1), 395-399.

Bermudez, P., Lerch, J. P., Evans, A. C., & Zatorre, R. J. (2009). Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cerebral Cortex*, *19*(7), 1583-1596.

Bernardi, G., Ricciardi, E., Sani, L., Gaglianese, A., Papasogli, A., Ceccarelli, R., ... & Pietrini, P. (2013). How skill expertise shapes the brain functional architecture: an fMRI study of visuo-spatial and motor processing in professional racing-car and naïve drivers. *PloS One*, *8*(10).

Bezzola, L., Mérillat, S., & Jäncke, L. (2012). The effect of leisure activity golf practice on motor imagery: an fMRI study in middle adulthood. *Front. Hum. Neurosci*, *6*(67), 10-3389.

Bezzola, L., Mérillat, S., Gaser, C., & Jäncke, L. (2011). Training-induced neural plasticity in golf novices. *The Journal of Neuroscience*, *31*(35), 12444-12448.

Black, J. E., Isaacs, K. R., Anderson, B. J., Alcantara, A. A., & Greenough, W. T. (1990). Learning causes synaptogenesis, whereas motor activity causes angiogenesis, in cerebellar cortex of adult rats. *Proceedings of the National Academy of Sciences*, *87*(14), 5568-5572.

Blasing, B., Calvo-Merino, B., Cross, E. S., Jola, C., Honisch, J., & Stevens, C. J. (2012). Neurocognitive control in dance perception and performance. *Acta psychologica*, *139*(2), 300-308.

Bookstein, F. L. (2001). "Voxel-based morphometry" should not be used with imperfectly registered images. *Neuroimage*, *14*(6), 1454-1462.

Boyke, J., Driemeyer, J., Gaser, C., Büchel, C., & May, A. (2008). Training-induced brain structure changes in the elderly. *The Journal of neuroscience*, *28*(28), 7031-7035.

Brown, S., Martinez, M. J., & Parsons, L. M. (2006). The neural basis of human dance. *Cerebral cortex*, *16*(8), 1157-1167.

- Bruyneel, A. V., Mesure, S., Paré, J. C., & Bertrand, M. (2010). Organization of postural equilibrium in several planes in ballet dancers. *Neuroscience letters*, 485(3), 228-232.
- Buonomano, D. V., & Merzenich, M. M. (1998). Cortical plasticity: from synapses to maps. *Annual review of neuroscience*, 21(1), 149-186.
- Button, K. S., Ioannidis, J. P., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S., & Munafò, M. R. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, 14(5), 365-376.
- Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an fMRI study with expert dancers. *Cerebral cortex*, 15(8), 1243-1249.
- Cannonieri, G. C., Bonilha, L., Fernandes, P. T., Cendes, F., & Li, L. M. (2007). Practice and perfect: length of training and structural brain changes in experienced typists. *Neuroreport*, 18(10), 1063-1066.
- Cavada, C., & Schultz, W. (2000). The mysterious orbitofrontal cortex. Foreword. *Cerebral cortex*, 10(3), 205-205.
- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*, 129(3), 564-583.
- Chang, Y. (2014). Reorganization and plastic changes of the human brain associated with skill learning and expertise. *Front. Hum. Neurosci*, 8, 35.
- Chang, Y., Lee, J. J., Seo, J. H., Song, H. J., Kim, Y. T., Lee, H. J., ... & Kim, J. G. (2011). Neural correlates of motor imagery for elite archers. *NMR in Biomedicine*, 24(4), 366-372.
- Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Listening to musical rhythms recruits motor regions of the brain. *Cerebral cortex*, 18(12), 2844-2854.
- Chklovskii, D. B., Mel, B. W., & Svoboda, K. (2004). Cortical rewiring and information storage. *Nature*, 431(7010), 782-788.
- Cohen, J. L., Segal, K. R., Witriol, I., & Mcardle, W. D. (1981). Cardiorespiratory responses to ballet exercise and the VO₂max of elite ballet dancers. *Medicine and science in sports and exercise*, 14(3), 212-217.
- Cohen, L. G., Bandinelli, S., Findley, T. W., & Hallett, M. (1991). Motor reorganization after upper limb amputation in man. *Brain*, 114(1), 615-627.

Colcombe, S. J., Erickson, K. I., Scalf, P. E., Kim, J. S., Prakash, R., McAuley, E., ... & Kramer, A. F. (2006). Aerobic exercise training increases brain volume in aging humans. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *61*(11), 1166-1170.

Colcombe, S. J., Kramer, A. F., Erickson, K. I., Scalf, P., McAuley, E., Cohen, N. J., ... & Elavsky, S. (2004). Cardiovascular fitness, cortical plasticity, and aging. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(9), 3316-3321.

Cross, E. S., Hamilton, A. F. D. C., & Grafton, S. T. (2006). Building a motor simulation de novo: observation of dance by dancers. *Neuroimage*, *31*(3), 1257-1267.

Crotts, D., Thompson, B., Nahom, M., Ryan, S., & Newton, R. A. (1996). Balance abilities of professional dancers on select balance tests. *Journal of Orthopaedic & Sports Physical Therapy*, *23*(1), 12-17.

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis: I. Segmentation and surface reconstruction. *Neuroimage*, *9*(2), 179-194.

Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, *72*(3), 443-454.

Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., & Swinnen, S. P. (2004). Changes in brain activation during the acquisition of a new bimanual coordination task. *Neuropsychologia*, *42*(7), 855-867.

Debarnot, U., Sperduti, M., Di Rienzo, F., & Guillot, A. (2014). Experts bodies, experts minds: how physical and mental training shape the brain. *Front Hum Neurosci*, *8*, 280.

Diedrichsen, J., & Kornysheva, K. (2015). Motor skill learning between selection and execution. *Trends in cognitive sciences*, *19*(4), 227-233.

Di Nota, P. M., Levkov, G., Bar, R., & DeSouza, J. F. (2016). Lateral occipitotemporal cortex (LOTc) activity is greatest while viewing dance compared to visualization and movement: learning and expertise effects. *Experimental brain research*, 1-17.

Dong, W. K., & Greenough, W. T. (2004). Plasticity of nonneuronal brain tissue: roles in developmental disorders. *Mental retardation and developmental disabilities research reviews*, *10*(2), 85-90.

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current opinion in neurobiology*, *15*(2), 161-167.

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., ... & Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioural brain research*, 199(1), 61-75.

Doyon, J., Penhune, V., & Ungerleider, L. G. (2003). Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia*, 41(3), 252-262.

Draganski, B., & May, A. (2008). Training-induced structural changes in the adult human brain. *Behavioural brain research*, 192(1), 137-142.

Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., & May, A. (2004). Neuroplasticity: changes in grey matter induced by training. *Nature*, 427(6972), 311-312.

Draganski, B., Gaser, C., Kempermann, G., Kuhn, H. G., Winkler, J., Büchel, C., & May, A. (2006). Temporal and spatial dynamics of brain structure changes during extensive learning. *The Journal of Neuroscience*, 26(23), 6314-6317.

Driemeyer, J., Boyke, J., Gaser, C., Büchel, C., & May, A. (2008). Changes in gray matter induced by learning—revisited. *PLoS One*, 3(7).

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, 425(6954), 184-188.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, 270(5234), 305-307.

Engvig, A., Fjell, A. M., Westlye, L. T., Moberget, T., Sundseth, Ø., Larsen, V. A., & Walhovd, K. B. (2010). Effects of memory training on cortical thickness in the elderly. *Neuroimage*, 52(4), 1667-1676.

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: Recognition, navigation, or encoding?. *Neuron*, 23(1), 115-125.

Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., ... & Wojcicki, T. R. (2011). Exercise training increases size of hippocampus and improves memory. *Proceedings of the National Academy of Sciences*, 108(7), 3017-3022.

Ericsson, K. A. (2008). Deliberate practice and acquisition of expert performance: a general overview. *Academic emergency medicine: official journal of the Society for Academic Emergency Medicine*, 15(11), 988-994.

Fischl, B., & Dale, A. M. (2000). Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proceedings of the National Academy of Sciences*, 97(20), 11050-11055.

Floyer-Lea, A., & Matthews, P. M. (2005). Distinguishable brain activation networks for short-and long-term motor skill learning. *Journal of neurophysiology*, 94(1), 512-518.

Friston, K. (2012). Ten ironic rules for non-statistical reviewers. *Neuroimage*, 61(4), 1300-1310.

Gaser, C., & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *The Journal of Neuroscience*, 23(27), 9240-9245.

Gerbino, P. G., Griffin, E. D., & Zurakowski, D. (2007). Comparison of standing balance between female collegiate dancers and soccer players. *Gait & posture*, 26(4), 501-507.

Gobel, E. W., Parrish, T. B., & Reber, P. J. (2011). Neural correlates of skill acquisition: decreased cortical activity during a serial interception sequence learning task. *NeuroImage*, 58(4), 1150-1157.

Gould, E., Beylin, A., Tanapat, P., Reeves, A., & Shors, T. J. (1999). Learning enhances adult neurogenesis in the hippocampal formation. *Nature neuroscience*, 2(3), 260-265.

Graziano, M. (2006). The organization of behavioral repertoire in motor cortex. *Annu. Rev. Neurosci.*, 29, 105-134.

Green, C. S., & Bavelier, D. (2008). Exercising your brain: a review of human brain plasticity and training-induced learning. *Psychology and aging*, 23(4), 692.

Gron, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nature neuroscience*, 3(4), 404-408.

Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2008). Functional neuroanatomical networks associated with expertise in motor imagery. *Neuroimage*, 41(4), 1471-1483.

Guillot, A., Di Rienzo, F., & Collet, C. (2014). The neurofunctional architecture of motor imagery. *Functional magnetic resonance imaging/Book*, 1.

Hamaide, J., De Groof, G., & Van der Linden, A. (2015). Neuroplasticity and MRI: A perfect match. *NeuroImage*.

Han, Y., Yang, H., Lv, Y. T., Zhu, C. Z., He, Y., Tang, H. H., ... & Dong, Q. (2009). Gray matter density and white matter integrity in pianists' brain: a combined structural and diffusion tensor MRI study. *Neuroscience letters*, 459(1), 3-6.

Hanakawa, T., Immisch, I., Toma, K., Dimyan, M. A., Van Gelderen, P., & Hallett, M. (2003). Functional properties of brain areas associated with motor execution and imagery. *Journal of Neurophysiology*, 89(2), 989-1002.

Hanggi, J., Koeneke, S., Bezzola, L., & Jancke, L. (2010). Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. *Human brain mapping*, 31(8), 1196-1206.

Hanggi, J., Langer, N., Lutz, K., Birrer, K., Mérillat, S., & Jäncke, L. (2015). Structural brain correlates associated with professional handball playing. *PloS One*, 10(4).

Hardwick, R. M., Rottschy, C., Miall, R. C., & Eickhoff, S. B. (2013). A quantitative meta-analysis and review of motor learning in the human brain. *Neuroimage*, 67, 283-297.

Haslinger, B., Erhard, P., Altenmüller, E., Hennenlotter, A., Schwaiger, M., Gräfin von Einsiedel, H., ... & Ceballos-Baumann, A. O. (2004). Reduced recruitment of motor association areas during bimanual coordination in concert pianists. *Human brain mapping*, 22(3), 206-215.

Hebb, D. O. (1949). The organisation of behaviour: a neuropsychological theory. *Wiley*.

Herholz, S. C., & Zatorre, R. J. (2012). Musical training as a framework for brain plasticity: behavior, function, and structure. *Neuron*, 76(3), 486-502.

Hetu, S., Grégoire, M., Saimpont, A., Coll, M. P., Eugène, F., Michon, P. E., & Jackson, P. L. (2013). The neural network of motor imagery: an ALE meta-analysis. *Neuroscience & Biobehavioral Reviews*, 37(5), 930-949.

Hikosaka, O., Nakamura, K., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current opinion in neurobiology*, 12(2), 217-222.

Hill, N. M., & Schneider, W. (2006). Brain changes in the development of expertise: Neuroanatomical and neurophysiological evidence about skill-based

adaptations. *The Cambridge handbook of expertise and expert performance*, 653-682.

Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: exercise effects on brain and cognition. *Nature reviews neuroscience*, 9(1), 58-65.

Holtmaat, A., Wilbrecht, L., Knott, G. W., Welker, E., & Svoboda, K. (2006). Experience-dependent and cell-type-specific spine growth in the neocortex. *Nature*, 441(7096), 979-983.

Hu, D., Shen, H., & Zhou, Z. (2008). Functional asymmetry in the cerebellum: a brief review. *The Cerebellum*, 7(3), 304-313.

Hufner, K., Binetti, C., Hamilton, D. A., Stephan, T., Flanagin, V. L., Linn, J., ... & Strupp, M. (2011). Structural and functional plasticity of the hippocampal formation in professional dancers and slackliners. *Hippocampus*, 21(8), 855-865.

Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., & Schlaug, G. (2009). Musical training shapes structural brain development. *The Journal of Neuroscience*, 29(10), 3019-3025.

Jacini, W. F., Cannonieri, G. C., Fernandes, P. T., Bonilha, L., Cendes, F., & Li, L. M. (2009). Can exercise shape your brain? Cortical differences associated with judo practice. *Journal of Science and Medicine in Sport*, 12(6), 688-690.

James, C. E., Oechslin, M. S., Van De Ville, D., Hauert, C. A., Descloux, C., & Lazeyras, F. (2014). Musical training intensity yields opposite effects on grey matter density in cognitive versus sensorimotor networks. *Brain Structure and Function*, 219(1), 353-366.

James, W. (1890). *The principles of psychology*.

Jancke, L. (2009). The plastic human brain. *Restorative neurology and neuroscience*, 27(5), 521-538.

Jancke, L., Koeneke, S., Hoppe, A., Rominger, C., & Hänggi, J. (2009). The architecture of the golfer's brain. *PLoS One*, 4(3).

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

Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current opinion in neurobiology*, 9(6), 735-739.

- Jenkins, W. M., Merzenich, M. M., Ochs, M. T., Allard, T., & Guic-Robles, E. (1990). Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *Journal of neurophysiology*, 63(1), 82-104.
- Jones, D. K., Symms, M. R., Cercignani, M., & Howard, R. J. (2005). The effect of filter size on VBM analyses of DT-MRI data. *Neuroimage*, 26(2), 546-554.
- Jones, T. A., Chu, C. J., Grande, L. A., & Gregory, A. D. (1999). Motor skills training enhances lesion-induced structural plasticity in the motor cortex of adult rats. *The journal of neuroscience*, 19(22), 10153-10163.
- Karni, A., Meyer, G., Jezzard, P., Adams, M. M., & Ungerleider, L. G. (1995). Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature*, 377(6545), 155-158.
- Karpati, F. J., Giacosa, C., Foster, N. E., Penhune, V. B., & Hyde, K. L. (2015). Dance and the brain: a review. *Annals of the New York Academy of Sciences*, 1337(1), 140-146.
- Kelly, A. C., & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cerebral Cortex*, 15(8), 1089-1102.
- Kelly, R. E., Alexopoulos, G. S., Wang, Z., Gunning, F. M., Murphy, C. F., Morimoto, S. S., ... & Hoptman, M. J. (2010). Visual inspection of independent components: defining a procedure for artifact removal from fMRI data. *Journal of neuroscience methods*, 189(2), 233-245.
- Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *The Journal of Neuroscience*, 29(32), 10153-10159.
- Kleim, J. A., Barbay, S., & Nudo, R. J. (1998). Functional reorganization of the rat motor cortex following motor skill learning. *Journal of neurophysiology*, 80(6), 3321-3325.
- Kleim, J. A., Barbay, S., Cooper, N. R., Hogg, T. M., Reidel, C. N., Remple, M. S., & Nudo, R. J. (2002). Motor learning-dependent synaptogenesis is localized to functionally reorganized motor cortex. *Neurobiology of learning and memory*, 77(1), 63-77.
- Kleim, J. A., Lussnig, E., Schwarz, E. R., Comery, T. A., & Greenough, W. T. (1996). Synaptogenesis and Fos expression in the motor cortex of the adult rat after motor skill learning. *The Journal of Neuroscience*, 16(14), 4529-4535.

Koeneke, S., Lutz, K., Wüstenberg, T., & Jäncke, L. (2004). Long-term training affects cerebellar processing in skilled keyboard players. *Neuroreport*, *15*(8), 1279-1282.

Kringelbach, M. L. (2005). The human orbitofrontal cortex: linking reward to hedonic experience. *Nature Reviews Neuroscience*, *6*(9), 691-702.

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

Krishnan, A., Williams, L. J., McIntosh, A. R., & Abdi, H. (2011). Partial Least Squares (PLS) methods for neuroimaging: a tutorial and review. *Neuroimage*, *56*(2), 455-475.

Kuhn, S., Gleich, T., Lorenz, R. C., Lindenberger, U., & Gallinat, J. (2014). Playing Super Mario induces structural brain plasticity: gray matter changes resulting from training with a commercial video game. *Molecular psychiatry*, *19*(2), 265-271.

Lacourse, M. G., Orr, E. L., Cramer, S. C., & Cohen, M. J. (2005). Brain activation during execution and motor imagery of novel and skilled sequential hand movements. *Neuroimage*, *27*(3), 505-519.

Lacourse, M. G., Turner, J. A., Randolph-Orr, E., Schandler, S. L., & Cohen, M. J. (2004). Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. *Journal of rehabilitation research and development*, *41*(4), 505.

Lafleur, M. F., Jackson, P. L., Malouin, F., Richards, C. L., Evans, A. C., & Doyon, J. (2002). Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. *Neuroimage*, *16*(1), 142-157.

Landau, S. M., & d'ESposito, M. (2006). Sequence learning in pianists and nonpianists: an fMRI study of motor expertise. *Cognitive, Affective, & Behavioral Neuroscience*, *6*(3), 246-259.

Leek, E. C., & Johnston, S. J. (2009). Functional specialization in the supplementary motor complex. *Nature Reviews Neuroscience*, *10*(1), 78.

Lehericy, S., Benali, H., Van de Moortele, P. F., Péligrini-Issac, M., Waechter, T., Ugurbil, K., & Doyon, J. (2005). Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(35), 12566-12571.

- Li, Y., Yuan, K., Cai, C., Feng, D., Yin, J., Bi, Y., ... & Qin, W. (2015). Reduced frontal cortical thickness and increased caudate volume within fronto-striatal circuits in young adult smokers. *Drug and alcohol dependence*, *151*, 211-219.
- Liegeois-Chauvel, C., Peretz, I., Babai, M., Laguitton, V., & Chauvel, P. (1998). Contribution of different cortical areas in the temporal lobes to music processing. *Brain*, *121*(10), 1853-1867.
- Lohse, K. R., Wadden, K., Boyd, L. A., & Hodges, N. J. (2014). Motor skill acquisition across short and long time scales: a meta-analysis of neuroimaging data. *Neuropsychologia*, *59*, 130-141.
- Lotze, M., & Halsband, U. (2006). Motor imagery. *Journal of Physiology-paris*, *99*(4), 386-395.
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., ... & Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal of cognitive neuroscience*, *11*(5), 491-501.
- Lotze, M., Scheler, G., Tan, H. R., Braun, C., & Birbaumer, N. (2003). The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *Neuroimage*, *20*(3), 1817-1829.
- Luft, A. R., & Buitrago, M. M. (2005). Stages of motor skill learning. *Molecular neurobiology*, *32*(3), 205-216.
- Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences*, *97*(8), 4398-4403.
- May, A. (2011). Experience-dependent structural plasticity in the adult human brain. *Trends in cognitive sciences*, *15*(10), 475-482.
- McIntosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: applications and advances. *Neuroimage*, *23*, S250-S263.
- Mechelli, A., Crinion, J. T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R. S., & Price, C. J. (2004). Neurolinguistics: structural plasticity in the bilingual brain. *Nature*, *431*(7010), 757-757.
- Meister, I. G., Krings, T., Foltys, H., Boroojerdi, B., Müller, M., Töpper, R., & Thron, A. (2004). Playing piano in the mind—an fMRI study on music imagery and performance in pianists. *Cognitive Brain Research*, *19*(3), 219-228.

- Meister, I., Krings, T., Foltys, H., Boroojerdi, B., Müller, M., Töpper, R., & Thron, A. (2005). Effects of long term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: Implications for cortical motor organization. *Human brain mapping, 25*(3), 345-352.
- Milton, J., Small, S. L., & Solodkin, A. (2008). Imaging motor imagery: methodological issues related to expertise. *Methods, 45*(4), 336-341.
- Milton, J., Solodkin, A., Hluštík, P., & Small, S. L. (2007). The mind of expert motor performance is cool and focused. *Neuroimage, 35*(2), 804-813.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. *Cerebral Cortex, 15*(7), 986-994.
- Moreno, S., & Bidelman, G. M. (2014). Examining neural plasticity and cognitive benefit through the unique lens of musical training. *Hearing research, 308*, 84-97.
- Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Neuroscience, 31*(1), 69.
- Munzert, J., Lorey, B., & Zentgraf, K. (2009). Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain research reviews, 60*(2), 306-326.
- Nachev, P., Kennard, C., & Husain, M. (2008). Functional role of the supplementary and pre-supplementary motor areas. *Nature Reviews Neuroscience, 9*(11), 856-869.
- Naito, E., Kochiyama, T., Kitada, R., Nakamura, S., Matsumura, M., Yonekura, Y., & Sadato, N. (2002). Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum. *The Journal of neuroscience, 22*(9), 3683-3691.
- Nudo, R. J., & Milliken, G. W. (1996). Reorganization of movement representations in primary motor cortex following focal ischemic infarcts in adult squirrel monkeys. *Journal of neurophysiology, 75*(5), 2144-2149.
- Nudo, R. J., Jenkins, W. M., & Merzeniech, M. M. (1990). Repetitive microstimulation alters the cortical representation of movements in adult rats. *Somatosensory & motor research, 7*(4), 463-483.

O'Doherty, J., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature neuroscience*, 4(1), 95-102.

Olshansky, M. P., Bar, R. J., Fogarty, M., & DeSouza, J. F. (2015). Supplementary motor area and primary auditory cortex activation in an expert break-dancer during the kinesthetic motor imagery of dance to music. *Neurocase*, 21(5), 607-617.

Olsson, C. J., Jonsson, B., Larsson, A., & Nyberg, L. (2008). Motor representations and practice affect brain systems underlying imagery: an fMRI study of internal imagery in novices and active high jumpers. *The open neuroimaging journal*, 2(1).

Pandya, D. N., Yeterian, E. H., Fleminger, S., & Dunnett, S. B. (1996). Comparison of prefrontal architecture and connections [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 351(1346), 1423-1432.

Park, I. S., Lee, K. J., Han, J. W., Lee, N. J., Lee, W. T., & Park, K. A. (2009). Experience-dependent plasticity of cerebellar vermis in basketball players. *The cerebellum*, 8(3), 334-339.

Park, I. S., Lee, K. J., Han, J. W., Lee, N. J., Lee, W. T., & Park, K. A. (2011). Basketball training increases striatum volume. *Human movement science*, 30(1), 56-62.

Parsons, M. W., Harrington, D. L., & Rao, S. M. (2005). Distinct neural systems underlie learning visuomotor and spatial representations of motor skills. *Human brain mapping*, 24(3), 229-247.

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annu. Rev. Neurosci.*, 28, 377-401.

Pascual-Leone, A., Nguyet, D., Cohen, L. G., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of neurophysiology*, 74(3), 1037-1045.

Paus, T. S. (2001). Primate anterior cingulate cortex: where motor control, drive and cognition interface. *Nature Reviews Neuroscience*, 2(6), 417-424.

Penhune, V. B. (2013). Neural encoding of movement sequences in the human brain. *Trends in cognitive sciences*, 17(10), 487-489.

Penhune, V. B., & Steele, C. J. (2012). Parallel contributions of cerebellar, striatal and M1 mechanisms to motor sequence learning. *Behavioural brain research*, 226(2), 579-591.

Pereira, J. M., Xiong, L., Acosta-Cabronero, J., Pengas, G., Williams, G. B., & Nestor, P. J. (2010). Registration accuracy for VBM studies varies according to region and degenerative disease grouping. *Neuroimage*, 49(3), 2205-2215.

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neuroscience letters*, 239(2), 65-68.

Picard, N., & Strick, P. L. (1996). Motor areas of the medial wall: a review of their location and functional activation. *Cerebral cortex*, 6(3), 342-353.

Picard, N., Matsuzaka, Y., & Strick, P. L. (2013). Extended practice of a motor skill is associated with reduced metabolic activity in M1. *Nature neuroscience*, 16(9), 1340-1347.

Poirel, N., Zago, L., Petit, L., Mellet, E., Guillot, A., & Collet, C. (2010). Neural bases of topographical representation in humans: Contribution of neuroimaging studies. *The Neurophysiological foundations of mental and motor imagery*, 17-30.

Poldrack, R. A. (2015). Is “efficiency” a useful concept in cognitive neuroscience?. *Developmental cognitive neuroscience*, 11, 12-17.

Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., ... & Di Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *The Journal of neuroscience*, 16(23), 7688-7698.

Ramachandran, V. S., Stewart, M., & Rogers-Ramachandran, D. C. (1992). Perceptual correlates of massive cortical reorganization. *Neuroreport*, 3(7), 583-586.

Ramon y Cajal, S. (1894) La Wne structure des centres nerveux. *Proc Roy Soc London*, 55:444–468

Rein, S., Fabian, T., Zwipp, H., Rammelt, S., & Weindel, S. (2011). Postural control and functional ankle stability in professional and amateur dancers. *Clinical Neurophysiology*, 122(8), 1602-1610.

Reithler, J., van Mier, H. I., & Goebel, R. (2010). Continuous motor sequence learning: cortical efficiency gains accompanied by striatal functional reorganization. *NeuroImage*, 52(1), 263-276.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive brain research*, 3(2), 131-141.

Rosenbaum, R. S., Ziegler, M., Winocur, G., Grady, C. L., & Moscovitch, M. (2004). "I have often walked down this street before": fMRI studies on the hippocampus and other structures during mental navigation of an old environment. *Hippocampus*, 14(7), 826-835.

Saimpont, A., Malouin, F., Tousignant, B., & Jackson, P. L. (2013). Motor imagery and aging. *Journal of motor behavior*, 45(1), 21-28.

Salat, D. H., Buckner, R. L., Snyder, A. Z., Greve, D. N., Desikan, R. S., Busa, E., ... & Fischl, B. (2004). Thinning of the cerebral cortex in aging. *Cerebral cortex*, 14(7), 721-730.

Saygin, A. P. (2007). Superior temporal and premotor brain areas necessary for biological motion perception. *Brain*, 130(9), 2452-2461.

Schantz, P. G., & Astrand, P. O. (1984). Physiological characteristics of classical ballet. *Med Sci Sports Exerc*, 16(5), 472-6.

Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature neuroscience*, 5(7), 688-694.

Schott, N. (2012). Age-related differences in motor imagery: working memory as a mediator. *Experimental aging research*, 38(5), 559-583.

Schubotz, R. I., & Von Cramon, D. Y. (2004). Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. *The Journal of Neuroscience*, 24(24), 5467-5474.

Sevdalis, V., & Keller, P. E. (2011). Captured by motion: Dance, action understanding, and social cognition. *Brain and cognition*, 77(2), 231-236.

Sharma, N., Pomeroy, V. M., & Baron, J. C. (2006). Motor imagery a backdoor to the motor system after stroke?. *Stroke*, 37(7), 1941-1952.

Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., ... & Giedd, J. N. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *The Journal of Neuroscience*, 28(14), 3586-3594.

Shipman, S. L., & Astur, R. S. (2008). Factors affecting the hippocampal BOLD response during spatial memory. *Behavioural Brain Research*, 187(2), 433-441.

Simmons, R. W. (2005). Neuromuscular responses of trained ballet dancers to postural perturbations. *International journal of neuroscience*, 115(8), 1193-1203.

Sluming, V., Barrick, T., Howard, M., Cezayirli, E., Mayes, A., & Roberts, N. (2002). Voxel-based morphometry reveals increased gray matter density in Broca's area in male symphony orchestra musicians. *Neuroimage*, 17(3), 1613-1622.

Smyth, M. M., & Pendleton, L. R. (1994). Memory for movement in professional ballet dancers. *International Journal of Sport Psychology*.

Starkes, J. L., Deakin, J. M., Lindley, S., & Crisp, F. (1987). Motor versus verbal recall of ballet sequences by young expert dancers. *Journal of Sport Psychology*, 9(3), 222-230.

Steele, C. J., & Penhune, V. B. (2010). Specific increases within global decreases: a functional magnetic resonance imaging investigation of five days of motor sequence learning. *The Journal of neuroscience*, 30(24), 8332-8341.

Szameitat, A. J., Shen, S., & Sterr, A. (2007). Motor imagery of complex everyday movements. An fMRI study. *Neuroimage*, 34(2), 702-713.

Tanji, J., & Shima, K. (1994). Role for supplementary motor area cells in planning several movements ahead. *Nature*, 371, 29.

Tanzi, E. (1893). I fatti e le induzioni dell'odierna istologia del sistema nervoso. *Riv Sper Fren Med Leg*, 19:419-472

Taubert, M., Draganski, B., Anwander, A., Müller, K., Horstmann, A., Villringer, A., & Ragert, P. (2010). Dynamic properties of human brain structure: learning-related changes in cortical areas and associated fiber connections. *The Journal of Neuroscience*, 30(35), 11670-11677.

Tronel, S., Fabre, A., Charrier, V., Olier, S. H., Gage, F. H., & Abrous, D. N. (2010). Spatial learning sculpts the dendritic arbor of adult-born hippocampal neurons. *Proceedings of the National Academy of Sciences*, 107(17), 7963-7968.

Ungerleider, L. G., Doyon, J., & Karni, A. (2002). Imaging brain plasticity during motor skill learning. *Neurobiology of learning and memory*, 78(3), 553-564.

Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences*, 98(20), 11656-11661.

Vaquero, L., Hartmann, K., Ripollés, P., Rojo, N., Sierpowska, J., François, C., ... & Münte, T. F. (2016). Structural neuroplasticity in expert pianists depends on the age of musical training onset. *NeuroImage*, *126*, 106-119.

Wan, C. Y., & Schlaug, G. (2010). Music making as a tool for promoting brain plasticity across the life span. *The Neuroscientist*, *16*(5), 566-577.

Wei, G., & Luo, J. (2010). Sport expert's motor imagery: Functional imaging of professional motor skills and simple motor skills. *Brain research*, *1341*, 52-62.

Wei, G., Zhang, Y., Jiang, T., & Luo, J. (2011). Increased cortical thickness in sports experts: a comparison of diving players with the controls. *PLoS One*, *6*(2).

Wenderoth, N., Debaere, F., Sunaert, S., & Swinnen, S. P. (2005). The role of anterior cingulate cortex and precuneus in the coordination of motor behaviour. *European Journal of Neuroscience*, *22*(1), 235-246.

Wiestler, T., & Diedrichsen, J. (2013). Skill learning strengthens cortical representations of motor sequences. *Elife*, *2*.

Willingham, D. B. (1998). A neuropsychological theory of motor skill learning. *Psychological review*, *105*(3), 558.

Wolbers, T., & Buchel, C. (2005). Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations. *The Journal of neuroscience*, *25*(13), 3333-3340.

Wulf, G., & Shea, C. H. (2002). Principles derived from the study of simple skills do not generalize to complex skill learning. *Psychonomic bulletin & review*, *9*(2), 185-211.

Yang, J. (2015). The influence of motor expertise on the brain activity of motor task performance: A meta-analysis of functional magnetic resonance imaging studies. *Cognitive, Affective, & Behavioral Neuroscience*, *15*(2), 381-394.

Yarkoni, T. (2009). Big correlations in little studies: Inflated fMRI correlations reflect low statistical power—Commentary on Vul et al.(2009). *Perspectives on Psychological Science*, *4*(3), 294-298.

Yarrow, K., Brown, P., & Krakauer, J. W. (2009). Inside the brain of an elite athlete: the neural processes that support high achievement in sports. *Nature Reviews Neuroscience*, *10*(8), 585-596.

Yin, H. H., Mulcare, S. P., Hilário, M. R., Clouse, E., Holloway, T., Davis, M. I., ... & Costa, R. M. (2009). Dynamic reorganization of striatal circuits during the acquisition and consolidation of a skill. *Nature neuroscience*, *12*(3), 333-341.

Zatorre, R. J., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: auditory–motor interactions in music perception and production. *Nature reviews neuroscience*, 8(7), 547-558.

Zatorre, R. J., Fields, R. D., & Johansen-Berg, H. (2012). Plasticity in gray and white: neuroimaging changes in brain structure during learning. *Nature neuroscience*, 15(4), 528-536.

Zwergal, A., Linn, J., Xiong, G., Brandt, T., Strupp, M., & Jahn, K. (2012). Aging of human supraspinal locomotor and postural control in fMRI. *Neurobiology of aging*, 33(6), 1073-1084.