White Matter Plasticity in Dancers and Musicians

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ABSTRACT

White Matter Plasticity in Dancers and Musicians

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This dissertation examined training-related brain plasticity by comparing white matter (WM) structure between dancers and musicians and relating the structural changes to dance and music abilities. We focused on the primary motor pathways, to identify potential structural differences between whole-body dance training and specific-effector music training.

To this purpose, highly trained dancers and musicians, matched for years of training, were tested on a novel dance imitation task, melody discrimination, and rhythm reproduction. Participants were scanned using magnetic resonance imaging (MRI). WM was analyzed at a whole-brain level in Study 1, using diffusion tensor imaging (DTI). Study 2 used probabilistic tractography to examine the descending motor pathways from the hand, leg, trunk and head regions. In Study 1, dancers showed increased diffusivity and reduced anisotropy in comparison to musicians in regions including the descending motor pathways, the superior longitudinal fasciculus and the corpus callosum, predominantly in the right hemisphere. Consistent with this, in Study 2, dancers had increased diffusivity and greater volume in all portions of the right descending motor pathways, whereas musicians had increased anisotropy, especially in the right hand and trunk/arm tracts. Importantly, in both studies, DTI metrics were positively related with dance and negatively with melody performance. In Study 2, DTI metrics also were negatively associated with age of training start, indicating a direct relation between the structural changes observed and training.

Our findings indicate that different types of long-term training have distinct effects on brain structure. In particular, dance training, which engages the whole body, appears to enhance connectivity among a broad range of cortical regions, possibly by increasing axonal diameter and the heterogeneity of fiber orientation. In contrast, music training seems to increase the coherence and packing of the connections linked to the trained effector(s).

This dissertation is novel in comparing brain structure between two groups of highly trained performers and in examining multiple DTI metrics concurrently. Further, in Study 2, we developed a novel methodology to segregate the motor cortex into regions corresponding to four main body parts, which could be used by other researchers interested in motor connectivity.

RÉSUMÉ

La Plasticité de la Matière Blanche chez le Danseurs et les Musiciens

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Cette thèse examine la plasticité cérébrale associée à l'entrainement à long terme. La structure de la matière blanche de danseurs a été comparée à celle de musiciens. Les changements structurels ont été mis en relation avec les capacités liées à la danse et à la musique. Nous nous sommes concentrés sur les voies motrices primaires pour identifier les éventuelles différences structurelles entre l'entrainement du danseur mobilisant tout le corps et celui du musicien mobilisant un effecteur spécifique.

Pour cela, des danseurs et des musiciens expérimentés, ayant un nombre d'années de formation comparable, ont été évalués sur une tâche d'imitation de danses, une tâche de discrimination de mélodies et une tâche de reproduction de rythmes. Les participants ont été ensuite soumis à l'imagerie à résonance magnétique (IRM). Dans une première étude, la matière blanche a été analysée au niveau global du cerveau en utilisant l'imagerie par tenseur de diffusion (DTI). Dans une deuxième étude, les voies motrices descendantes des régions de la main, de la jambe, du tronc et de la tête ont été analysées à l'aide de la tractographie probabilistique.

La première étude a montré que les danseurs avaient des valeurs plus élevées de diffusivité et des valeurs inférieures d'anisotropie par rapport aux musiciens, dans des régions qui incluent les voies motrices descendantes, le fascicule longitudinal supérieur et le corps calleux, surtout dans l'hémisphère droit. En accord avec ces résultats, la deuxième étude a révélé chez les danseurs, une augmentation de diffusivité et de volume dans toutes les portions des voies motrices descendantes, alors que les musiciens avaient une augmentation d'anisotropie, notamment dans les traits de la main et du tronc/bras. Il faut noter que dans les deux études, les métriques de DTI étaient corrélées négativement avec l'âge du début de l'entrainement, ce qui indique une relation directe entre les changements structurels observés et l'entrainement.

Nos études montrent que les différents types d'entrainement à long terme ont des effets différents sur la structure cérébrale. En particulier, la formation en danse, faisant travailler tout le corps, semble renforcer la connectivité entre une vaste gamme de régions corticales, probablement en accroissant le diamètre des axones et l'hétérogénéité de l'orientation des fibres. Au contraire, la formation musicale semble augmenter la cohérence et le tassement des connections liées aux effecteurs entrainés.

Cette thèse introduit une nouveauté en comparant la structure du cerveau entre deux groupes d'artistes expérimentés et en étudiant plusieurs métriques de DTI simultanément. En outre, dans la deuxième étude, nous avons développé une nouvelle approche méthodologique pour ségréguer le cortex moteur en quatres régions qui correspondent à quatre parties du corps. Cette approche pourrait être utilisée dans de futures études s'intéressant à la connectivité des voies motrices.

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All my efforts are for my beloved children, who give meaning to my life. I dedicate this thesis to you.

Study 1

We would like to thank our participants for their time, Jennifer Bailey, Emily Coffey and Jamila Andoh for their assistance in the recruiting and testing process, and Ilana Leppert for technical counselling. This work was funded by a grant from the Natural Sciences and Engineering Council of Canada (NSERC) to Dr. Krista Hyde and Dr. Virginia Penhune (238670); NSERC CREATE in Auditory Cognitive Neuroscience and Quebec Bioimaging Network fellowships to Chiara Giacosa.

Study 2

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Conflicts of interest

The authors declare that they have no conflicts of interest.

Ethical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and research committee and were approved by the Research Ethics Board at the Montreal Neurological Institute and Hospital.

Informed consent

Written informed consent was obtained from all participants included in the study. Participants were compensated for their participation.

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CONTRIBUTIONS OF THE AUTHORS

This dissertation includes two studies, the first already published and the second in revision. Both studies are part of a bigger project that was conceived by Dr Krista Hyde and Dr. Virginia Penhune, with my participation in the final steps of its design. This project included also the analyses of behavioral performance (Appendix C.C) as well as gray matter (Karpati et al., 2016, 2018) in the same sample.

Introduction and Discussion I authored the general introduction and discussion with the supervision of Dr. Virginia Penhune and all it entails (reading of drafts and provision of feedback, suggestions, and guidance leading to the final product).

Study 1 I was involved in the development of the behavioral test battery, the design of the MRI protocol and the adaptation of a music survey to dance and its translation into French. I collected the data in collaboration with Dr. Falisha Karpati and I conducted all the WM analyses, including the coding of scripts. I wrote the manuscript with the supervision and collaboration of Dr. Virginia Penhune. Dr. Krista Hyde, Dr. Falisha Karpati and Dr. Nicholas Foster provided feedback to the final manuscript.

Study 2 I conceived and realized Study 2 under the supervision of Dr. Virginia Penhune. I conducted the neuroimaging, behavioral and statistical analyses and coded the necessary scripts in multiple scripting languages. I self-taught and combined all the methods in an original manner, successfully developing a novel methodology. I authored the manuscript with the supervision and collaboration of Dr. Virginia Penhune. The manuscript received feedback by Dr. Nicholas Foster and Dr. Christopher Steele.

Appendix A.A This section includes two supplementary tables to Study 1 and were authored by myself.

Appendix B.B This section includes the Supplementary Material that explains the methods of Study 2 in details. It was entirely developed and written by myself with feedback from Dr. Virginia Penhune.

Appendix C.C This study includes the behavioural analyses of the project, which design I took part in, together with Dr. Penhune and Dr. Hyde. Dr. Karpati is the first author of this paper, she ran the analyses and wrote the paper. However, I fully collaborated with Dr. Karpati the recruiting and testing and gave feedback on the analyses. I also ran the same analyses aside in the reduced sample presented in Study 1 and 2, even where not explicitly presented, and took part in the manuscript review, together with the other co-authors.

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CHAPTER 1

General Introduction

1.1 Overview

Dance and music are universal forms of human expression that developed across cultures. Although everyone has danced at a party or sung with friends, professional dancers and musicians are able to produce extraordinarily complex sequences of extremely fast, precisely timed and demanding movements that remain inaccessible to laymen. Why? Because both dancers and musicians to achieve their abilities need to follow many years of intense and regular training. Training, which primarily consists of learning, repeating, correcting and perfecting movements, dynamically modifies brain structures in an adaptive process, called neuroplasticity (Zatorre et al., 2012; Zilles, 1992). Neuroplasticity can occur in both the gray (GM) and the white matter (WM). Gray matter is predominantly composed of the neuronal cell bodies and forms the external cortical portion of the brain, in addition to some subcortical structures. White matter is composed of axons that connect cortical regions and is organized in distinct pathways or tracts. Given the specificity but also the similarity and measurability of their training, dancers and musicians provide ideal populations to investigate the distinct structural brain changes associated with their specific skills. There is a large body of existing research examining the structural neural correlates of music (see Penhune, 2019; Schlaug, 2015 for reviews) but relatively little information about the structural correlates of dance (Hänggi et al., 2010). Therefore, examining the distinct structural correlates of dancers in comparison to musicians contributes to deepen the understanding of the specific plasticity processes related to long-term training of the whole body *versus* specific body parts and of the visual-auditory-motor integration functioning.

The purpose of this dissertation was to compare WM structure between dancers and musicians and to investigate its relations with dance and music skills. WM has been previously shown to be altered by physical and music training (Engel et al., 2014; Scholz et al., 2009; Steele et al., 2012; Taubert et al., 2010), as well as expertise (Hänggi et al., 2010; Huang et al., 2013). Three groups of dancers, musicians and control were tested on a battery of dance- and music-related tasks and underwent a magnetic resonance (MR) scan using diffusion-weighted imaging to assess WM structure. Study 1 examined WM at the whole brain level to identify all regions that differed between groups. Guided by these results, Study 2 examined the specific portions of the descending motor pathways that link the head, hand, trunk and leg motor brain regions to the brainstem. These analyses were designed to distinguish the effects of whole-body training (dance) *versus* the training of specific effectors (music). While a more standard approach for whole brain WM investigation was used for Study 1, a novel approach, which combined a method to consistently create subject-specific seed masks with multi-tensor probabilistic tractography, was developed in Study 2. Correlations of WM metrics with behavioral and demographic measures were also reported in both studies.

1.2 Neural correlates of dance and music

Dancing and playing music are disciplines that, despite their specificities, have a lot in common. The most obvious element that they share is music itself, since dance consists of rhythmical body movements that usually follow musical sounds (Bläsing et al., 2012; Karpati et al., 2016). The ability to produce movements in synchrony to other performers or to sounds is therefore a characteristic that is clearly shared by dance and music performers. Dance and music similarly require the integration of visual, auditory and proprioceptive stimuli to produce motor outputs. However, the relevance of each of these systems differs between these two disciplines. For instance, dancers perform complex sequences of demanding movements that activate their entire body, whereas musicians train specific effectors (e.g., fingers, arms or lips) to produce complex sequences of fine movements. Therefore, dance requires the extraordinary development of physical skills, such as strength, flexibility, static and dynamic whole-body balance (Bläsing et al., 2012; Krasnow et al., 2011) . Conversely, music demands the development of fine-motor skills with metric precision, such as very rapid finger shifting, as well as higher cognitive aspects of rhythm, pitch and melody manipulation (Zatorre et al., 2007; Schlaug, 2015).

There are relatively few studies that have investigated the neural basis of dance (see Karpati et al., 2015 for a review). Nonetheless, interest has grown in the last 10 years (Krasnow et al., 2011), as the rapidly increasing body of literature shows (Dordevic et al., 2018; Burzynska et al., 2017; Meier et al., 2016; Karpati et al., 2015, 2017, 2018; Orlandi et al., 2017; Cruz-Garza et al., 2014; Amoruso et al., 2017; Poikonen et al., 2016, 2018; Orlandi and Proverbio, 2019). Structural studies have been used to identify the neuroanatomical correlates of long-term training, whereas functional studies have investigated brain networks involved in dance-specific functions. Although the focus of this thesis is the WM structural correlates of dance training, functional research can provide supplemental information about the regions involved in dance and music processing, especially given the small number of structural studies available (Hänggi et al., 2010; Nigmatullina et al., 2015).

In the functional domain, both electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) have been used to examine the brain activity during the observation or imaging of dance movements (Orgs et al., 2008; Cross et al., 2006, 2009b,a; Calvo-Merino et al., 2006, 2005; Fink et al., 2009; Olshansky et al., 2015; Fujioka et al., 2015; Bar and DeSouza, 2016). A network of regions, including frontal sensorimotor and temporo-parietal regions, has been shown to be modulated by experience and familiarity, i.e. stronger activity was observed in trained *versus* untrained subjects during the observation of dance movements and for physically trained *versus* unfamiliar movements. This "action observation network" (AON), which includes the "mirror neuron system" (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004), is known to be engaged, not only in movement observation but also in action execution and plays a key role in learning by imitation (Rizzolatti et al., 2001; Krüger et al., 2014; Caspers et al., 2010; Buccino et al., 2001).

The use of functional imaging to examine the neural activity during dance performance is limited because most brain imaging techniques are not mobile and are susceptible to motion artifacts caused by body movements. In the first study that overcame these issues, Brown et al. (2006) developed a device that allowed dancers to perform leg movements during positron emission tomography (PET) scanning, without moving other body parts. Beyond the sensorimotor activity observed in all leg movement tasks, with such a procedure it was possible to link distinct aspects of dance movement, such as metric movement and spatial patterning, to the specific activity of basal ganglia and parietal regions. Two other studies used functional near infrared spectroscopy (fNIRS), which measures changes of blood oxygenation levels in the cortex to infer temporal and spatial dynamics of cortical activity. fNIRS is portable and has reduced sensitivity to body movement, thus brain activity was recorded during the whole-body imitation of lower-limb dance-like steps. The timing of brain activity differed between parietal and temporal regions and as function of task difficulty (Tachibana et al., 2011); further, temporal accuracy in the task performance differentiated fronto-polar from middle-temporal regions (Ono et al., 2014). Resting-state fMRI has also been used to investigate the long-lasting changes in network connectivity in dancers. Resting-state connectivity is thought to reflect changes in connectivity that result from the coactivation of functionally connected regions that are recurrently recruited during training (Cantou et al., 2018). In particular, resting-state fMRI was used to show enhanced functional connectivity in sensorimotor regions of dancers compared to non-dancers (Li et al., 2015). Using resting state measures from EEG, Ermutlu et al. (2015) showed increased power in frequencies linked to the network associated with motor activity, imagery and memory of dancers in comparison to fast ball athletes. Taken together, these findings show that distinct aspects of dance training implicate a variety of fronto-temporo-parietal regions belonging to multiple, partly interconnected, networks, with a particular enhancement of sensorimotor regions.

Few studies have investigated the structural brain correlates of dance training (Hänggi et al., 2010; Nigmatullina et al., 2015). Hänggi et al. (2010) were the first to use MRI to compare brain structure between professional dancers and untrained controls. Their sample of female ballet dancers showed reduced GM and WM volumes, as well as reduced fractional anisotropy (FA) – an index of white matter coherence – in regions including the supplementary motor and premotor cortex, the internal capsule and the corpus callosum. GM density reductions were also observed in the vestibular cerebellum and these volumes were correlated to total hours of dancing experience (Nigmatullina et al., 2015). Together, these findings demonstrate that dance training affects brain structure, particularly pointing toward GM and WM reductions, which might reflect the increased efficiency or complexity of connections of their training-related networks. However, dancers in this study had lower body-mass indices than controls, a factor known to influence brain structure. That, together with the all-female sample, made it important to replicate their findings.

In contrast to dance, the body of research that has investigated the neural correlates of music is much larger (Penhune, 2019; Schlaug, 2015). Functional studies comparing musicians and non-musicians on musically relevant tasks showed a variety of changes in sensorimotor, frontal, temporal and parietal regions (see Zatorre et al., 2007; Herholz and Zatorre, 2012 for reviews). These regions are part of the auditory-motor dorsal stream network important for linking sound and action (see Rauschecker and Scott, 2009 for a review). Evidence for musicians enhanced auditory-motor interaction comes also from studies that showed coactivation of motor and auditory regions during motor imagery of well-known pieces, during passive listening to rhythms or to rehearsed pieces, and in pianists observing a pianist playing or playing a silent keyboard (Baumann et al., 2007; Chen et al., 2008; Grahn and Rowe, 2009). Consistent with these findings, resting-state functional studies (see Cantou et al., 2018 for a review) add evidence to the enhanced functional connectivity in sensorimotor and auditory regions in musicians (Luo et al., 2012; Klein et al., 2016).

Structural imaging studies consistently showed enhancements in GM density, gyrification or cortical thickness of musicians in comparison to controls, especially in auditory and motor regions, including the Heschl's gyrus (Schneider et al., 2002, 2005; Bermudez et al., 2009; Foster and Zatorre, 2010b; Gaser and Schlaug, 2003) and the planum temporale (in posterior part of the superior temporal gyrus) (Schlaug et al., 1995b; Schlaug, 2001; Zatorre et al., 1998). The length of the central sulcus, often used as indicator of the size of primary motor cortex (M1), was expanded in musicians compared to non-musicians and correlated with age of training start (Amunts et al., 1997). Furthermore, specific structural (Bangert et al., 2006) and functional (Pantev et al., 2001) enlargements of the hand and finger representations were observed in keyboard and string players, especially in the hemisphere mostly relevant to their training. Other regions where musicians showed increased GM measures compared to non-musicians are the frontal (Abdul-Kareem et al., 2011; Sluming et al., 2002; James et al., 2014) and parietal regions (Foster and Zatorre, 2010b; Gaser and Schlaug, 2003; James et al., 2014). The picture for white matter structure is more complicated (see Moore et al., 2014 for a review). The size of the mid-sagittal corpus callosum (CC) has been repeatedly observed to be larger in musicians compared to non-musicians, particularly in those who started before age seven (Schlaug et al., 1995a; Oztürk et al., 2002; Lee et al., 2003; Steele et al., 2013). Other modifications in WM have been consistently associated with musicianship in regions including the descending motor pathways – including the corticospinal tract (CST) and the internal capsule (IC) – as well as in the superior longitudinal fasciculus (SLF) and the arcuate fasciculus (AF). Data predominantly point to increases in FA, commonly used as a measure of fiber coherence, in the tracts of musicians (Bengtsson et al., 2005; Han et al., 2009; Schmithorst and Wilke, 2002; Acer et al., 2018; Rüber et al., 2013; Halwani et al., 2011), however some authors have also found FA reductions (Imfeld et al., 2009; Schmithorst and Wilke, 2002; Acer et al., 2018). These discrepancies may be due to the different cohorts compared or the regions of interest (ROI) chosen (Halwani et al., 2011; Rüber et al., 2013). In sum, music training has been generally associated with GM and WM increases, especially in auditory-motor networks. However, the direction of training-induced changes is not always consistent, in particular for FA. Given that FA is sensitive to a variety of microstructural properties of WM, changes in this metric should not be interpreted only as indicators of fiber coherence. Thus, lower FA values might be also due to the enhancement of a specific fiber bundle in a region where multiple bundles cross, or to the enlargement of axon diameters (Zatorre et al., 2012; Schlaug, 2015).

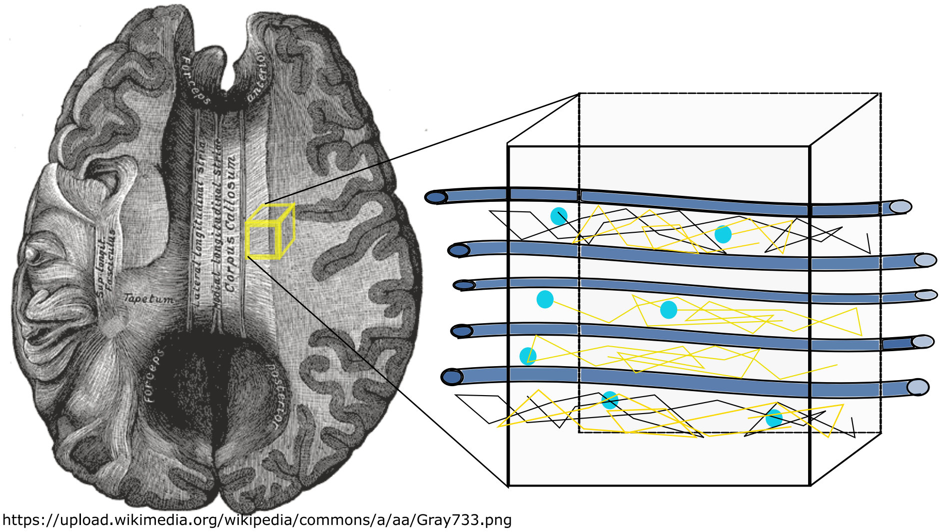
Taken together, the available literature shows evidence for brain plasticity associated with long-term dance and music training especially in visual- and auditory-motor networks respectively. It further suggests that WM might be differently modified by these two types of training such that dance reduces while music increases GM volume and fiber coherence. Therefore, in the present thesis, highly-trained dancers and musicians were compared to each other with the aim 1) to identify both the common and distinct regions that are affected by different types of training and 2) to understand the physiological and structural WM features that characterize each type of training. In Study 1, the WM structures of dancers were examined at a whole-brain level to identify the regions that were modified by dance training in comparison to music or no training. Importantly we also wanted to establish an association between training-induced structural changes and specific dance and music skills. Driven from Study 1 findings, in Study 2, the analyses focussed on the descending motor pathways – which include the corticospinal tracts (CST) –, crucial for the enhanced motor skills of the motor experts assessed. In particular, we aimed at verifying whether whole-body dance training enhanced connectivity across all body regions in contrast to the specific-effector music training enhancing more focussed trained-related connections. Such knowledge can deepen the insight into the mechanisms of the brain to control and execute movement.

1.3 Why white matter?

Most recent models of brain function emphasize the importance of interacting neural networks (Zatorre et al., 2012). Examining WM architecture allows us to study neural networks at the structural level. Importantly, changes in WM have been observed after both short- and long-term training. For example, short periods of training – lasting for few weeks – have been previously observed in activities, such as juggling (Scholz et al., 2009) and playing music (Chen et al., 2012), as well as training in specific laboratory-controlled tasks involving the whole body (Taubert et al., 2010) or specific effectors (Wang et al., 2013; Reid et al., 2017; Palmer et al., 2013). These studies demonstrate that physical training induces structural alterations to WM, and in particular to the descending motor pathways. WM structural modifications after long-term training have also been observed in highly trained athletes (Huang et al., 2013; Wang et al., 2013; Jäncke et al., 2009), as well as in musicians (Schlaug et al., 1995a; Lee et al., 2003; Imfeld et al., 2009; Schmithorst and Wilke, 2002; Han et al., 2009; Halwani et al., 2011; Rüber et al., 2013) and dancers (Hänggi et al., 2010) as described above. Such changes were correlated with hours of practice during childhood (Bengtsson et al., 2005) and age of training start (Steele et al., 2013). Moreover, studies investigating brain-behaviour correlations provide evidence of the relations between WM changes and skill acquisition. Sensorimotor synchronization abilities and maximum tapping rate were positively correlated with FA in temporal and sensorimotor WM pathways of samples including both musicians and non-musicians (Steele et al., 2013; Rüber et al., 2013). In visuo-motor and auditory-motor learning and short training paradigms with naïve subjects, FA was positively correlated with learning speed and performance (Engel et al., 2014; Tomassini et al., 2011; Blecher et al., 2016; Della-Maggiore et al., 2009), although negative relationships were also observed between FA and performance on a sensorimotor finger tapping task (Steele et al., 2012) and a whole-body balance task (Taubert et al., 2010). Taken together this literature shows increased fiber coherence (FA) after short periods of training or in musicians with long-term training, and lower FA, maybe due to increased crossing fibers or axon diameter, in athletes and dancers who consistently trained the whole body for many years.

1.4 What is DTI?

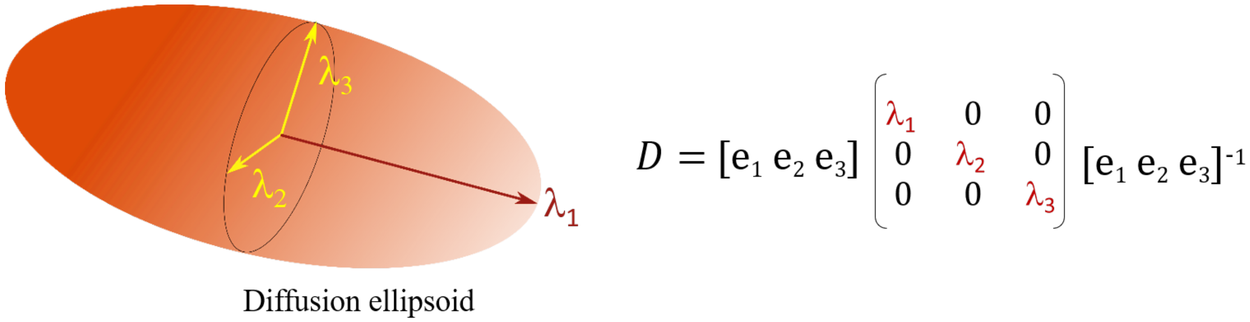
Our understanding of WM structure in the human brain has been promoted by the development of *in vivo* diffusion weighted imaging (DWI) techniques (Zatorre et al., 2012). DWI is a form of MR imaging that measures the diffusion (random thermal motion) of water molecules in the brain and uses this information to infer the underlying structure. Water molecules constitute a large part of the volume of the brain, and their diffusion is differently constrained depending on the type of tissue in which they are located. In GM, water molecules are relatively unconstrained, and tend to move in a random pattern; in WM, water molecules are constrained by fiber bundles, and tend to move along the direction of those fibers. DWI measures this diffusion motion and fits it to a model.



https://upload.wikimedia.org/wikipedia/commons/a/aa/Gray733.png

Figure 1.1 Diffusion motion of water molecules through brain fibers.

The most widely used model for studying diffusion in WM is diffusion tensor imaging (DTI), which describes water diffusion within each voxel with an ellipsoid (See Fig. 1.2). This ellipsoid characterizes the shape and direction of diffusion motion: a more spherical ellipsoid indicates more unrestricted diffusion with lower directionality (isotropic motion), whereas a narrower and elongated ellipsoid indicates more hindered diffusion with greater directionality (anisotropic motion) (Fig. 1.3). The shape, size and orientation of the ellipsoid are described by three eigenvalues corresponding to three eigenvectors, which respectively indicate the lengths and directions of its main axes (Fig. 1.2); such measures are integrated in a tensor, hence the name DTI. The eigenvalues represent the magnitude of diffusion along the principal (λ_1) and two secondary perpendicular directions of motion (λ_2, λ_3) and characterize the shape of the ellipsoid, whereas the eigenvectors describe its spatial orientation (Bahn, 1999).



$$D = [e_1\ e_2\ e_3] \begin{bmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{bmatrix} [e_1\ e_2\ e_3]^{-1}$$

Figure 1.2 Ellipsoid and its relation with diffusion tensor.

D = diffusion tensor; e_i = eigenvector components indicating the eigenvector orientation in space; λ_i = eigenvalues.

The most common DTI metric is FA, which is calculated as a combination of the three eigenvalues and is interpreted as an index of the ellipsoid elongation, or linearity. In voxels where the water motion is more isotropic, FA is lower and tends to 0; conversely, where the water motion is more anisotropic, FA is higher and tends to 1. Beyond FA, the eigenvalues are other metrics frequently reported to examine the diffusion ellipsoid. The highest eigenvalue, λ_1, is usually called axial diffusivity (AD), while the average of λ_2 and λ_3 is named radial diffusivity (RD).

Like FA, other metrics, calculated from different combinations of the eigenvalues, describe global features of the diffusion ellipsoid. For instance, the mean diffusivity (MD), as its name suggests, is the mean of the eigenvalues and connotes the overall magnitude of the diffusion tensor. However, the tensor shape can be fully described only by three orthogonal and invariant metrics (Ennis and Kindlmann, 2006). The three eigenvalues

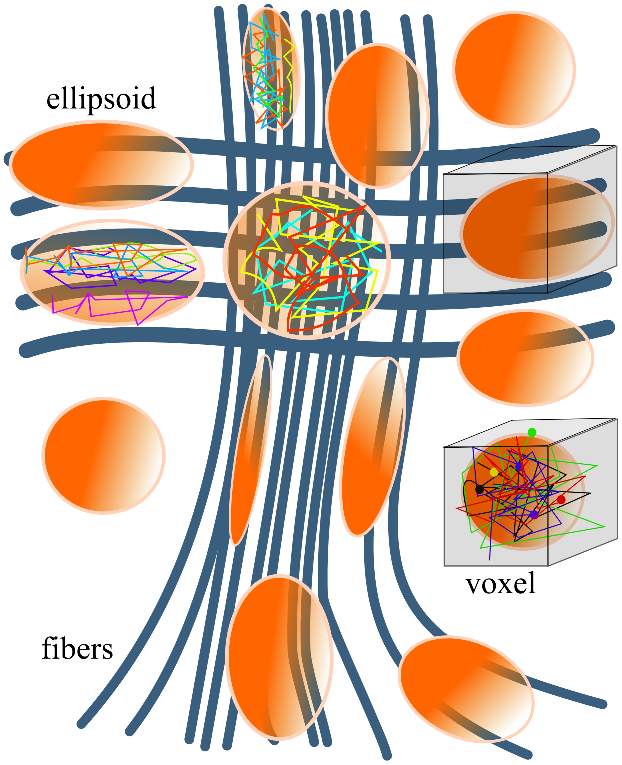


Figure 1.3 Shape of the ellipsoid and fiber organization.

Fibers are shown in blue. The diffusion motion of water molecules within a voxel is shown on the right. The ellipsoid is more spherical in absence of obstacles and in regions of crossing fibers. The shape of the ellipsoid changes with different fiber configurations, becoming more elongated where the fibers are densely packed and coherent and more spherical with less dense, crossing, twisting, bending or fanning fibers.

correspond to an orthogonal basis of eigenvectors (Bahn, 1999) and therefore are independent from one another. Although together they specify the magnitude of diffusivity, eigenvalues are not spatially invariant, as their order in the tensor diagonal depends on the orientations of the eigenvectors, which determines the frame of reference. In contrast, FA is a directionally invariant metric of the tensor shape. However, on its own, FA is not sufficient to define the diffusion tensor anisotropy. It needs to be combined with the other two orthogonal and invariant measures to convey all the information contained in the set of the three eigenvalues, in a way that is independent of the orientation of the frame of reference. It has been proposed that FA could be complemented by the norm of the tensor and the mode of anisotropy (MO) (Ennis and Kindlmann, 2006); the norm representing the tensor magnitude and MO the ellipsoid planarity. Ranging from -1, which indicates a planar anisotropic tensor with two large axes and one small (pancake shape), to 1, which indicates a linearly anisotropic tensor with one long and two small axes (cigar shape), MO permits to distinguish between the linearity and the planarity of the ellipsoid (see Fig. 1.4). In this invariant set, the norm of the tensor can be reasonably substituted by MD. Indeed, both MD and the norm represent the tensor magnitude and MD becomes orthogonal to FA for low FA values (Ennis and Kindlmann, 2006).

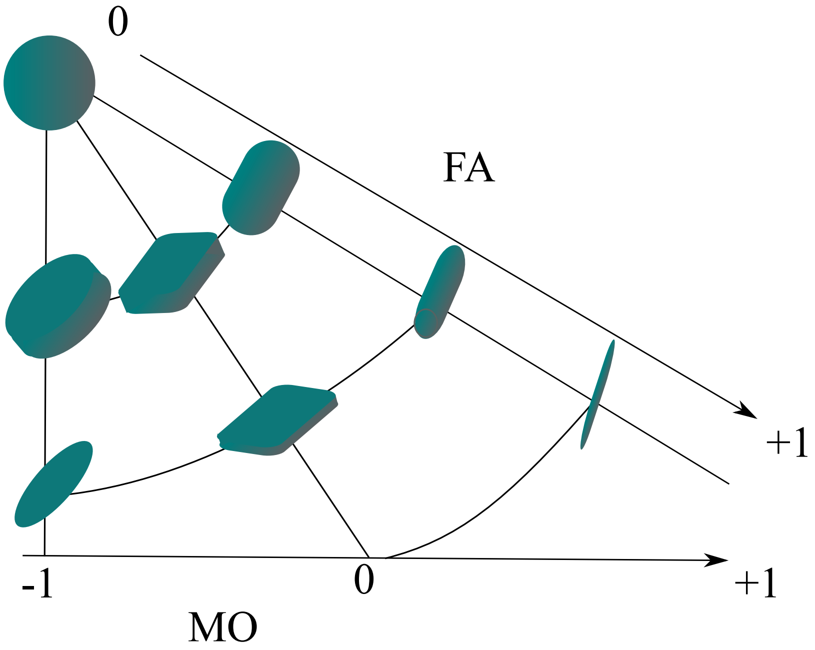


Figure 1.4 Shape of the diffusion tensor as a function of MO and FA.

The ellipsoid becomes more linear with higher FA and more planar with lower MO. Image inspired from (Ennis and Kindlmann, 2006).

Therefore, in Study 1, beyond the eigenvalues, reported in terms of AD and RD as is customary in the field, the full set of invariant metrics (FA, MD and MO) were analysed. This allowed us to fully characterize the tensor shape, thus enhancing the precision and reliability of our interpretations. All metrics presented so far (FA, AD, RD, MD, MO) were non-directional, meaning that they were not related to any fiber bundle orientation. In Study 1, additional directional measures of the relative proportion (partial volume fractions) of primary and secondary fibers were also examined. These directional metrics, named F1 and F2, are based on the "ball and stick model" (Behrens et al., 2003) and represent the orientation of the two most prominent fibers within a voxel.

The parameters estimated in each brain voxel by fitting the selected model depend on the microstructural characteristics of the underlying tissues and are used to infer macrostructural anatomical features. For instance, the more densely packed and parallel the fibers are, the higher FA; conversely, the bigger the axon diameter and the less coherent the fiber directions, the lower FA and the higher RD. However, each voxel contains hundreds of thousand neurons, possibly belonging to multiple fiber bundles, each following its own direction, and even more glial cells. Myelin sheaths, which frequently surround the biggest axons, constitute a barrier to water molecules, hindering their motion along the longitudinal direction of the fibers. Microstructural properties, such as axonal density, diameter and membrane permeability, neurofibrils within the axons and internode Ranvier distance all affect the global water motion within a voxel (Beaulieu, 2002; Alexander et al., 2007; Zatorre et al., 2012; Sampaio-Baptista and Johansen-Berg, 2017). Given the huge scale gap between the microstructural factors influencing the estimated parameters across the entire voxel and the macrostructural features that are inferred across the entire brain, great care is needed in the interpretation of such studies.

1.4.1 DTI for voxel-based analysis

Among the various approaches used to analyze WM, Tract-Based Spatial Statistics (TBSS) is the most popular. TBSS is a fully-automated method specifically designed to examine WM at a whole brain level, voxel-by-voxel. The FA maps of each subject, obtained by fitting the DTI model, are first nonlinearly aligned (co-registered) in a target space; then, the common WM tracts, identified as the regions with the highest mean FA values, are "thinned" and thresholded to create a skeletonized mean FA map. Each individual FA image is then projected onto the mean FA skeleton by aligning voxel-by-voxel the individual highest FA values of the closest relevant tract to the common skeleton. Voxelwise statistical analyses are then conducted on the DTI metrics of choice, restricted to the skeleton map. The non-linear alignment and superposition among individual WM images and the restriction of the analyses to the main WM regions (thinned FA skeleton) between subjects provide a common space where the principal WM areas can be compared, with reduced risk of incorrect alignment between tracts or partial volume effects at the border with GM. The voxelwise analysis of DTI metrics in such WM regions constitutes a valuable quantitative approach for a comparison at the whole-brain level, without the need to define the tracts or regions of interest (ROIs) a priori.

1.4.2 DTI for tractography

However, with TBSS it is only possible to identify the regions where groups differ, but not to distinguish the specific tracts involved. Tract identification with such an approach involves the use of a template-based atlas, which is not always sensitive nor specific enough to identify the tracts truly affected. Although group differences occurring within a voxel may actually involve one or more of the several fiber bundles that traverse it, DTI models the global diffusion across the entire voxel as coming from one coherent bundle with homogeneous physiological properties. Unfortunately, it has been estimated that between 63% and 90% of WM voxels contain crossing fibers (Jeurissen et al., 2013), which might vary in several characteristics, such as fiber orientation, axon diameter or density. Therefore, TBSS gives only a global indication of the WM voxels where the changes occur but cannot provide any specific information about the characteristics of each traversing tract.

In contrast, tractography aims to identify the fiber trajectory of a selected tract that links two anatomically meaningful regions of interest (ROIs), known to be crossed by the tract, “by following a continuous path of greatest diffusivity (or least hindrance)” (Catani et al., 2002). For example, the uncinate fasciculus was isolated from the inferior-fronto-occipital fasciculus by carefully identifying two regions of interest (ROIs), one including both fiber bundles, and the other one including only the fibers of the uncinate fasciculus (Catani et al., 2002) (see Fig. 1.5). By joining the most likely fiber orientations across voxels, tractography is able to limit the analysis to the voxels containing the tract of interest. Moreover, it permits the visualization of morphological differences between individual subjects or groups within the same tract (Johansen-Berg and Behrens, 2009).

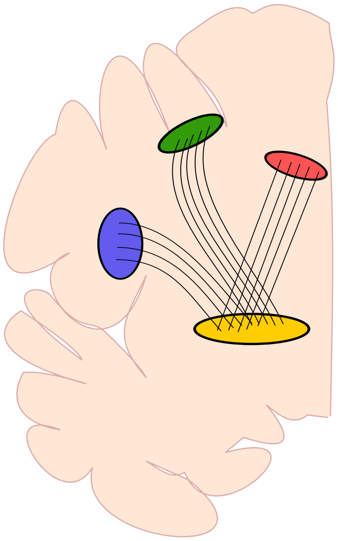


Figure 1.5 Segregation of parallel or crossing fiber bundles with an appropriate selection of the seed ROIs for tractography.

The image shows a graphic visualization of 3D tract reconstruction from a start region (seed) to an arrival region (target), disentangling two partially overlapping tracts.

Various tractography algorithms that have been proposed. When fiber tracking is based on the diffusion single-tensor model, only one main fiber bundle is modeled in each voxel, often introducing errors in tract reconstruction that can fail to identify portions of a big bundle or miss entire secondary bundles (Behrens et al., 2007). Multi-tensor tractography is a more advanced model that accounts for the multiple fiber orientations within a voxel. In Study 2, we chose to implement a multi-tensor probabilistic tractography approach. The advantage of choosing a probabilistic *versus* a deterministic approach is that it accounts for the uncertainty in local fiber orientation caused by the incompleteness of the diffusion model (e.g. DTI) (Behrens et al., 2007). When using deterministic tractography, the errors due to uncertainty can propagate along the entire pathway, potentially resulting in erroneous tract reconstructions. On the contrary, probabilistic tractography draws a full representation of uncertainty in voxels that are more susceptible to tracking errors and calculates the path of greatest diffusivity (least hindrance) with a percent confidence. This allows tracking through regions of uncertainty due, for example, to crossing fibers. In probabilistic tractography, thousands of streamline samples are started in each seed voxel. A streamline is any line whose tangent is parallel to the field (Johansen-Berg and Behrens, 2009); therefore, in tractography, the streamlines are the lines formed by joining in sequence all the orientations – contained in contiguous voxels –, sampled from the posterior distribution of principal diffusion directions (Behrens et al., 2003, 2007). The streamline samples so obtained describe a probability distribution of the connectivity from the seed to the target that accounts for the uncertainty in the local fiber orientations (Johansen-Berg and Behrens, 2009). The probability of the dominant streamline is then calculated, in each voxel, as the ratio between the number of streamlines passing through that voxel and the total number of samples drawn from the same seed. A direct extension of the single-fiber tractography, based on the "ball and stick model", is multiple-fiber tractography (Behrens et al., 2007). The "ball and stick" model is based on a partial volume approach in which diffusion is modelled as the combination of an isotropic component (ball) and multiple totally anisotropic components (sticks) (Behrens et al., 2003). The two-fiber tractography, used in Study 2, extends the single-fiber "ball and stick model" to the case where two fibers (sticks) are modeled in each voxel, where relevant (Fig. 1.6).

A Bayesian approach, called automatic relevance determination (ARD), was used to infer multiple fibers only in voxels where their existence is highly probable and create the map of fiber orientations (Behrens et al., 2007). The reason why only two fiber orientations were included in the model of both Study 1 and 2 is because, in our sample, the map of the different fiber orientations did not show continuity of voxels containing a third fiber orientation. In sum, the two-fiber probabilistic tractography approach allowed us to identify a tract of interest and compare the metrics of interest within that tract between different groups.

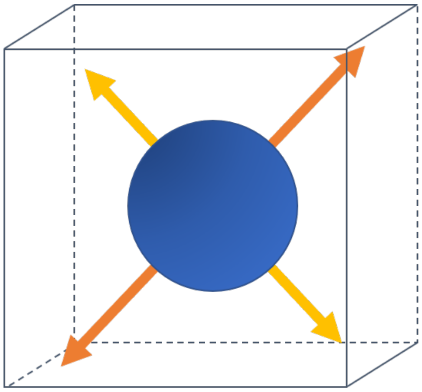


Figure 1.6 Ball and stick model of diffusion for two fiber orientations.

Crucially, a careful choice of the seed and target regions can permit us to separately analyze specific subcomponents of one tract, even when they overlap with other subcomponents or tracts. For instance, among all the interhemispheric connections, specific callosal fibers, linking the hand motor and sensory regions, have been previously identified by tracking between hand WM ROIs through a portion of the medial body of the CC (Sehm et al., 2016). Similarly, Meier and colleagues tracked the fibers of the CST seeded respectively in the foot/leg and hand GM regions (Meier et al., 2016). Both the studies reported above, however, created the seed ROIs around coordinates obtained from other studies. In Study 2, using sample specific ROIs, identified based on anatomical landmarks, which allowed us to track each portion of the primary motor pathways seed in the hand, head, trunk and leg separately for both hemispheres.

In conclusion, DTI is the most common approach used to quantitatively examine WM microstructure in order to infer its regional properties. For the purpose of this thesis, TBSS was used to identify across the whole brain which regions distinguished dancers from musicians or untrained controls; tractography allowed for more specific analyses of selected components of the motor tracts.

1.5 Research Project

1.5.1 General Procedures

The research described in this dissertation aimed at comparing WM structure in highly trained dancers with those of equally trained musicians and untrained controls. We also aimed to assess the relationship between brain structure and measures of training and domain-specific task performance. Participants were practicing dancers or musicians with at least ten years of formal training in their own discipline and less than three years in the other one. Control subjects were not currently enrolled in and had less than three years of training in dance, music or similar disciplines (such as gymnastics or figure skating) and yet were physically active (running, yoga, biking, etc.). The only other previous study on brain structure in dancers examined a sample of ballet dancers who were all female and who had low body-mass indices, which is known to affect brain structure (Bobb et al., 2014; Lavagnino et al., 2016; Seitz et al., 2015; Bär et al., 2015; Katzman et al., 1996; Kennedy et al., 2016; Repple et al., 2018; Hu et al., 2017; Gaudio et al., 2017; Nagahara et al., 2014). To address these potential biases, we targeted contemporary dancers where there are a larger number of males and where low body weight is less common.

All participants were tested on a battery of behavioural tests designed to reflect a range of dance- to music-related skills. A complete description of the tasks and behavioural results is reported in the Appendix C.C. They also underwent an MRI scanning to obtain standard T1-weighted images, used to examine GM (Karpati et al., 2017), and DWI images used to examine WM. Behavioural tasks included the Dance Imitation Task which was developed in our laboratory based on the Dance Central video game. In this task participants were required to imitate in real-time a selection of dance choreographies of variable complexity. This task assesses the ability to observe and imitate in real-time whole-body dance movements synchronised with music. Music-related tasks included the Melody Discrimination (Foster and Zatorre, 2010a) and Rhythm Synchronization tasks (Chen et al., 2008), which have previously been used to test these abilities in both musicians and non-musicians. To control for and examine potential groups differences in relevant cognitive functions, the battery also included a test of global cognitive function (Matrix Reasoning) and auditory working memory (Letter Number Sequencing and Digit Span), drawn from the WAIS (Wechsler and Assessment, 1997; Wechsler and Company, 1999).

1.5.2 White Matter Approaches

In Study 1, a DTI TBSS approach was used to compare the WM structure between dancers, musicians and controls at the whole brain level. In Study 2, a combination of multi-tensor probabilistic tractography and ROI approach was used to specifically examine the descending motor pathways of dancers and musicians. To verify whether dancers and musicians had differential connectivity enhancements related to their specific training. To do this I developed a novel approach to separately examine the components of the motor pathways that descend from each cortical motor representation of four main body parts (head, hand, trunk and leg) bilaterally. Importantly, similar to Study 1, relevant brain measures were correlated with measures of behavioural performance as well as with age of training start, showing the association between the WM structural changes and training.

CHAPTER 2

Dance and music training have different effects on white matter diffusivity in sensorimotor pathways

Chiara Giacosa, Falisha J. Karpati, Nicholas E.V. Foster, Virginia B. Penhune, Krista L. Hyde

2.1 Abstract

Dance and music training have shared and distinct features. Both demand long and intense physical training to master. Dance engages the whole body, and requires the integration of visual, auditory and motor information. In comparison, music engages specific parts of the body and primarily requires the integration of auditory and motor information. Comparing these two forms of long-term training offers a unique way to investigate brain plasticity. Therefore, in the present study we compared the effects of dance and music training on white matter structure using diffusion tensor imaging (DTI), and examined the relationship between training-induced brain changes and specific measures of dance and music abilities. To this aim, groups of dancers and musicians matched for years of experience were tested on a battery of behavioural tasks and a range of DTI measures.

Our findings show that dancers have increased diffusivity and reduced fibre coherence in WM regions, including the corticospinal tract, superior longitudinal fasciculus and the corpus callosum. In contrast, musicians showed reduced diffusivity and greater coherence of fibres in similar regions. Crucially, diffusivity measures were related to performance on dance and music tasks that differentiated the groups. This suggests that dance and music training produce opposite effects on WM structure. We hypothesize that intensive whole-body dance training may result in greater fanning of fibres connecting different brain regions, an increase in crossing fibres, or larger axon diameter. In contrast, musical training may result in more focussed enhancements of effector-specific pathways. These findings expand our understanding of brain plasticity by emphasizing that different types of training can have different long-term effects on brain structure.

2.2 Introduction

Dance and music are universal forms of human expression that have both shared and distinct features. Both dance and music training require long, intense and quantifiable training to master. Dance training engages the whole body, and requires the integration of visual, auditory and motor information. It focuses on perfecting movement through observation and imitation. In comparison, music engages specific parts of the body, typically the hands and fingers, and primarily requires the integration of auditory and motor information. Music training emphasizes perfecting sound through listening and refining movement. Thus, the neural systems relevant for long-term dance training likely include those important for whole-body control, visual and auditory sensorimotor integration and the "action observation network" (AON) (Cross et al., 2009b; Grafton, 2009; Keysers and Gazzola, 2009; Caspers et al., 2010). Conversely, the neural systems relevant for long-term music training likely include the regions important for control of specific effectors and those engaged in auditory-motor integration (Bangert et al., 2006; Lahav et al., 2007; Zatorre et al., 2007). Therefore, comparing white matter structure between dancers and musicians provides a new window to investigate the neural correlates of long-term training. Examination of long-term training in a variety of domains has shown that it has lasting effects on brain structure and function (Maguire et al., 2000; Draganski et al., 2004; Driemeyer et al., 2008; Jäncke et al., 2009; Keller and Just, 2009; Taubert et al., 2010; Bezzola et al., 2011). Among these disciplines, music training has received particular attention (Hyde et al., 2009a,b; Schlaug et al., 2009; Herholz and Zatorre, 2012; Groussard et al., 2014; Schlaug, 2015). In contrast, research about the structural neural correlates of dance training is still at a very early stage and very few studies have specifically addressed this topic (Hänggi et al., 2010; Nigmatullina et al., 2015). However, these studies compared dancers only to untrained controls, and there were no behavioural measures of dance performance. Thus, our goals in the present study were to characterize the specific effects of dance training on WM structure in comparison with another group of experts with similar long-term sensorimotor training, and to relate those changes to their acquired skills. To do this, we directly compared expert dancers with equally well-trained musicians and untrained controls using both behavioural and a range of DTI measures.

2.2.1 Previous work on dance and music

The study of specialized training such as dance and music offers a unique way to study brain plasticity and its interaction with behaviour. The literature about the neural correlates of music training is much richer than the one about dance and has been previously reviewed (Moore et al., 2014); therefore, here, our main focus will be on dance training.

Previous research about dance has been largely behavioural. These studies have examined various components of dancers' acquired skills, such as postural, balance and motor control (Crotts et al., 1996; Golomer et al., 2010; Kiefer et al., 2011; Costa et al., 2013), timing, synchrony and choreography (Minvielle-Moncla et al., 2008; Waterhouse et al., 2014; Woolhouse and Lai, 2014), as well as memory (Poon and Rodgers, 2000; Vicary et al., 2014) and imagery for sequences of movements (Golomer et al., 2008) (see Bläsing et al., 2012 for a review). Further, dance expertise has been shown to improve skills that are closely related to the training received, such as balance, posture and sensitivity to the biological motion of familiar actions (Calvo-Merino et al., 2010; Kattenstroth et al., 2011).

Some recent research has investigated the functional correlates of dance (see Bläsing et al., 2012; Karpati et al., 2015 for review). A large part of this literature has focused on the AON, which includes temporo-parietal and frontal sensorimotor regions that are involved in visuo-motor integration and learning of actions performed with specific effectors (Caspers et al., 2010; Landmann et al., 2011; Krüger et al., 2014) or the whole body (Calvo-Merino et al., 2005; Cross et al., 2006, 2009b; Gardner et al., 2015). In both animal and human studies (Grèzes and Decety, 2001; Rizzolatti and Craighero, 2004; Hecht et al., 2013b), these regions have been found to be engaged during the observation and performance of mouth or single limb actions (Fadiga et al., 1995; Gallese et al., 1996; Rizzolatti et al., 1996a,b; Buccino et al., 2001; Gazzola and Keysers, 2009), as well as of whole-body movements (Cross et al., 2009a; Sevdalis and Keller, 2011). It has been shown that this network is particularly relevant for dance learning, which requires observing, simulating and imitating others' whole-body movements (Calvo-Merino et al., 2005; Cross et al., 2006, 2009b). In addition to studies of dance observation, a few experiments have examined lower limb dance-like movements which can be performed during brain imaging. Cortical, subcortical, and cerebellar regions have been shown to be involved in specific aspects of these dance-like movements (Brown et al., 2006; Tachibana et al., 2011; Ono et al., 2014). These studies are the first ones that identified the regions that are functionally relevant for dance execution as opposed to dance observation. However, these paradigms have limited generalizability to real whole-body dance training, and the participants in these studies were not experts.

There are only few studies that have examined the structural neural correlates of dance expertise (Hänggi et al., 2010; Nigmatullina et al., 2015). Hänggi et al. (2010) compared female ballet dancers and non-dancers using voxel-based morphometry (VBM) and diffusion tensor imaging (DTI). They found that dancers had decreased GM volumes in cortical and subcortical structures critical for motor control and sensorimotor integration, along with decreases in WM volume and fractional anisotropy (FA) in sensorimotor pathways and the corpus callosum. They hypothesized that reductions of WM volume and FA might be the result of greater efficiency, or enhancements in crossing fibre pathways. Although these changes in brain structure were found to be related to the age of commencement of training, no behavioural measures of dance performance were obtained. Further, the authors reported only two global DTI measures, which give little information about crossing fibres. Similar decreases in FA were also found in fronto-parietal and sensorimotor pathways of professional gymnasts (Huang et al., 2013). Just like dancers, gymnasts are experts in whole-body movements and their training focuses on visual-motor integration and action observation. Therefore, their similar training might result in similar changes in WM structure.

Structural brain imaging studies have shown that music training is associated with enhancements of grey (GM) and white matter (WM) in motor regions associated with effector-specific motor control, the corpus callosum, and the auditory cortex (Schlaug et al., 1995a; Sluming et al., 2002; Gaser and Schlaug, 2003; Bengtsson et al., 2005; Bermudez and Zatorre, 2005; Bermudez et al., 2009; Han et al., 2009; Hyde et al., 2009b; Abdul-Kareem et al., 2011; Groussard et al., 2014). Further, these brain differences have been linked to performance on music-related tasks (Foster and Zatorre, 2010a; Steele et al., 2013; Bailey et al., 2014; Elmer et al., 2014).

In summary, structural imaging studies in dancers and gymnasts showed a reduction in the WM volume and anisotropy localised in sensorimotor and commissural pathways, as well as fronto-parietal association fibres (Hänggi et al., 2010; Huang et al., 2013; Nigmatullina et al., 2015). In contrast, despite some inconsistencies (Schmithorst and Wilke, 2002; Imfeld et al., 2009), studies in musicians suggest that music training tends to increase fractional anisotropy, especially in the sensorimotor projection fibres (Bengtsson et al., 2005; Han et al., 2009) and in the corpus callosum (Schlaug et al., 1995a; Steele et al., 2013).

2.2.2 DTI measures

Currently, DTI is the most widely used method to investigate the micro-structural properties of WM. It measures the characteristics of diffusion of water molecules in brain tissues. This motion is modelled as an ellipsoid characterised by three axes. Biological features, such as axonal size, density, coherence and degree of myelination all constrain water molecule motion, and thus influence diffusivity measures (Moseley et al., 1990; Basser et al., 1994; Neil et al., 1998; Gulani et al., 2001; Beaulieu, 2002; Assaf et al., 2008). Because no one-to-one relationship exists between any DTI measure and the architecture of WM structure (Wheeler-Kingshott and Cercignani, 2009; Jones et al., 2013; Walhovd et al., 2014), a multi-parametric combined analysis of diffusion data is helpful. Therefore, in the present study we examined both non-directional and directional measures in order to have a better understanding of the different possible underlying biological configurations (Alexander et al., 2007). The most commonly used DTI measure is fractional anisotropy (FA), which gives a global estimate of the elongation of the ellipsoid or the linearity of diffusion. Other non-directional measures are: axial diffusivity (AD) which measures the amount diffusion along the principal axis; radial diffusivity (RD) which measures the diffusion perpendicular to the principal axis; mean diffusivity (MD) which quantifies the amount of diffusion in each voxel; and the mode of anisotropy (MO) which describes whether diffusion is more planar or linear (Basser and Pierpaoli, 1996; Beaulieu, 2002; Ennis and Kindlmann, 2006; Assaf et al., 2008). In addition, we assessed the partial volume fractions of primary and secondary fibres (F1 and F2). Based on the “ball and stick model” (Behrens et al., 2003), these directional measures give an estimation of the relative proportion of the primary and secondary fibres in the voxels where the co-existence of at least two fibre populations is detected.

2.2.3 Objectives and predictions of this study

Taken together, previous literature suggests that long-term dance training can have specific effects on the sensorimotor and action observation systems. The purpose of the present study is to investigate the effects of long-term dance training on WM structure by comparing dancers to musicians and untrained controls. Musicians are a useful comparison group for dancers because music and dance training are both long and intense, require similar integration of sensory and motor information, and the amount of training can be quantified. This can allow us to make more specific interpretations about any observed differences in WM structure. In addition, we wanted to relate any training-induced brain modifications to specific measures of dance and music abilities. Because previous DTI studies in dancers have found reductions in FA that are difficult to interpret, in this study, we decided to analyse multiple diffusivity measures in order to better understand the biological underpinnings of diffusivity changes. We tested groups of highly trained dancers and musicians who were matched for years of experience, and also compared them to controls with limited dance or music training. Importantly, we tested all participants on a battery of dance and music-related tasks, as well as tests of global cognitive function and auditory working memory. Based on previous research, we predicted that dancers would show reduced anisotropy in sensorimotor, fronto-parietal and callosal connections, whereas musicians would show higher anisotropy in the corticospinal tract and corpus callosum. We also expected that these changes would be related to group differences in behavioural performance on dance- and music-based tasks.

2.3 Materials and Methods

2.3.1 Participants

Three groups of participants (age 18-40) were recruited for this study: expert dancers (N=20), expert musicians (N=19) and a control group of non-musician/non-dancers (N=20). Dancers and musicians were either currently practicing as professionals, or students involved in professional training. Their training was assessed via a detailed questionnaire developed in our lab: the Montreal Dance and Music History Questionnaire (MDMHQ) (Karpati et al., 2016), based on (Bailey and Penhune, 2010; Coffey et al., 2011). Dancers and musicians had on average approximately 15 years of experience in their respective disciplines, controls had on average less than one year in dance, music, figure skating, and aerobics. All participants were physically active (biking, running or practicing other physical exercises). Dancers were currently practicing contemporary dance as their principal style, but had a variety of training backgrounds, including ballet, tap, jazz, swing, and ballroom. Dancers whose main style was too similar to the dance task used here (i.e., urban, street or hip-hop dance) were excluded. Analogously, musicians had various instrumental backgrounds, including keyboard instruments, strings, woodwinds, brass, and percussion. None of the musicians had absolute pitch. Since the dance task was based on a video-game, participants were also excluded if they had more than 2 years of experience with dance video-games. The groups did not differ in age, sex distribution, body-mass index (BMI) or years of education (See Table 2.1). Participants had no past or current learning or developmental disorder, neurological or psychiatric conditions, or reported current or past alcohol or substance abuse. One participant in each group was excluded due to artefacts in the DTI data (see DTI data analysis section below: 2.3.3). The experimental protocol was approved by the Research Ethics Board at the Montreal Neurological Institute and Hospital, and a written informed consent was obtained from all participants. All participants were compensated for their participation.

2.3.2 General procedures

Participants took part in two testing sessions distributed over two non-consecutive days: one behavioural and the other for MRI acquisition, including DTI. The behavioural battery included dance- and music-related tasks as well as tests of global cognitive and memory function. The Dance Imitation Task was developed in our laboratory based on the video game Dance Central 1 for the console Xbox Kinect 360 (Harmonix, http://www.harmonixmusic.com) using the Kinect infrared light sensor (http://www.xbox.com/en-ca/Kinect; US Patent No. 20100197399). Participants are required to imitate a selection of seven dance routines of increasing levels of complexity. Scoring is based on the percent of correct moves provided by the video game scoring system. This task assesses the ability to observe and imitate in real time whole-body dance movements synchronised with music. The Melody Discrimination Task (Foster and Zatorre, 2010a,b) requires participants to detect subtle pitch changes in a series of melodies. This task assesses auditory processing and pitch discrimination. Finally, the Rhythm Synchronisation Task has been used in a number of our previous studies and requires participants to tap in synchrony with a series of musical rhythms. It has been previously used with musicians and non-musicians (Chen et al., 2008; Bailey and Penhune, 2010; Bailey et al., 2014). This task assesses auditory-motor integration and fine motor response. Furthermore, a language task and three standardized cognitive tests were given to all participants to examine any possible group differences in global cognitive or memory function: the Syllable Sequence Discrimination Task (Foster and Zatorre, 2010b,a), that has the same design as the Melody Discrimination Task but uses syllables instead of tones, the Digit Span and Letter-Number Sequencing subtasks from the Wechsler Adult Intelligence Scale III (Wechsler and Assessment, 1997) and the Matrix Reasoning subtask from the Wechsler Abbreviated Scale of Intelligence (Wechsler and Company, 1999). Full behavioural results for these groups are reported in a previous paper (Karpati et al., 2016). For the purpose of this paper, only brief descriptions of the behavioural results and the relationships between behavioural performance and WM diffusivity measures will be reported.

2.3.3 Diffusion tensor imaging and analysis

Diffusion data acquisition

Diffusion-weighted images (DWI) were acquired for all participants at the Montreal Neurological Institute (MNI) on a 3T Siemens Trio MR scanner with a 32-channel head coil. The following parameters were applied: 99 diffusion-weighted gradient directions with a b-value of 1000 s/mm2, 10 b0 non-weighted images, TE of 88 ms, TR of 9340 ms, EPI factor 128, isotropic voxels of 2 x 2 x 2 mm3, 72 slices, FOV of 256 mm. Ear plugs and headphones, as well as foam pads were used to reduce noise perception and head motion, respectively.

Behavioural analysis

Behavioural analyses for the full sample are reported in detail in (Karpati et al., 2016). Here, similar analyses were conducted on the subjects used for the DTI analysis. Briefly, to allow for between-task comparisons, overall scores for the dance, melody and rhythm tasks were converted to z-scores. A linear fixed-effects model was conducted on these data, with group as a between-subjects fixed factor and task as a within-subjects repeated measure using an unstructured covariance matrix.

Each control task was separately analysed with univariate analyses, with group as the between subject factor. Raw scores on each cognitive task were converted to scaled scores using standard protocols. All analyses included age and sex as covariates of no interest.

Brain analysis

All the following analyses included age and sex as covariates of no interest. Results were considered significant at $p<0.05$, after family-wise error (FWE) correction for multiple comparisons.

Voxelwise group comparisons of diffusivity measures

Group comparisons between dancers, musicians and controls were performed on both non-directional (RD, AD, MD, FA and MO) and directional (F1 and F2) diffusivity measures following the Tract-Based Spatial Statistics (TBSS) procedure, using the FMRIB Software Library (FSL v5.0) (Smith et al., 2004).

TBSS for non-directional measures

Each subject's raw data were first corrected for eddy current distortions and head motion using the FMRIB's Diffusion Toolbox (FDT); then, the Brain Extraction Toolbox (BET) (Smith, 2002) was used to exclude non-brain voxels from the analyses, and the diffusion tensor model was applied, by means of FDT, to estimate the diffusivity measures in each voxel. From the three eigenvalues, axial (AD), radial (RD) and mean (MD) diffusivities were easily calculated as the highest eigenvalue (AD), the average between the other two eigenvalues (RD) and the tensor trace (MD). Fractional anisotropy (FA) and the mode of anisotropy (MO), representing the eccentricity and type of anisotropy respectively, were also calculated with FDT.

Individual data of each diffusivity measure were then averaged and compared to the other subjects' data of the same measure. If one subject had at least 3 diffusivity measures that fell 3 SD out of their own group distributions, that subject was considered an outlier and excluded from the rest of the analyses. According to this rule, two subjects were excluded, one dancer and one control. One musician had to be excluded due to scanning artefacts. Other vibration artefacts (Gallichan et al., 2010), which occurred especially with large x-directed gradients, were corrected by excluding the affected frames. After correction, all subjects had more than 70 gradient directed frames of good quality.

Data that survived the above quality control were analysed with the TBSS method (Smith et al., 2006), implemented in FSL. First, individual FA images were non-linearly aligned to the FMRIB58_FA target template, and transformed into the 1 x 1 x 1 mm MNI152 standard space. The resulting FA images were averaged and thinned to obtain a study-specific mean FA skeleton, which represents the centres of all fibre bundles that are common to all participants. Each subject's aligned FA image was then projected onto its individual FA skeleton, before entering the permutation-based non-parametric voxelwise statistical analyses. The mean FA skeleton was thresholded at the value of 0.25 in order to include only major tracts that existed in all individuals.

A similar procedure was then applied to the other diffusion measures, namely RD, AD, MD and MO. For each diffusivity measure, nonlinear registration to the common space and skeletonisation procedure were based on the steps accomplished for FA. Then, each individual measure map was projected onto the mean FA skeleton, before statistical analyses were performed.

TBSS for directional measures (FSL)

In order to increase the interpretability of the diffusivity scalar measures obtained with TBSS in crossing-fibre regions, TBSS was performed also on scalars associated with a specific direction of fibres in each voxel. The model applied assumed that two fibre populations existed for each voxel. The model with three fibres was tested, but gave an inconsistent distribution of tertiary fibre orientations across consecutive voxels (impossibility of reconstructing smooth fibre pathways).

After the pre-processing steps, common to the previous TBSS analyses, partial volume estimates for fibre orientations 1 and 2 (F1 and F2 respectively) were calculated in each voxel for each subject. F1 and F2 were reassigned within subject at each voxel in order to ensure consistency across voxels, such that adjacent voxels had the same label assigned to the same fibre population. Then, F1 and F2 were reassigned again in order to ensure that orientations were consistent across subjects. Both these steps were accomplished using the "tbss_x" software, part of FSL (Jbabdi et al., 2010).

Voxelwise statistical analyses

For all non-directional (RD, AD, MD, FA and MO) and directional (F1 and F2) diffusivity measures, non-parametric permutation tests (5000 permutations per analysis) were carried out using the FSL's tool Randomise (Winkler et al., 2014) for the general linear model (GLM). Three group comparisons were performed: 1) dancers versus musicians, 2) dancers versus controls, and 3) musicians versus controls.

Group comparisons of the subjectwise averaged extracted values of diffusivity measures

RD, FA and MO were further tested with univariate ANOVAs including age and sex as covariates of no interest. For each DTI measure, individual data were extracted and averaged either over the whole WM skeleton or the 'Dancers versus Musicians' ROIs. The 'Dancers versus Musicians' ROIs were selected to include all the voxels where each DTI measure differed between dancers and musicians, thus a different ROI was created for each measure. The resulting subjectwise averaged values were then used in the ANOVAs to compare each parameter between groups.

Brain-behaviour relations

All analyses included age and sex as covariates of no interest. Results were considered significant at $p<0.05$. Family-wise error (FWE) correction for multiple comparisons was applied to all voxelwise analyses.

Voxelwise regressions of diffusivity measures with behavioural performance

Independent linear regressions between each diffusivity measure (dependent variables) and performance on each behavioural task (independent variables) were calculated by inserting the appropriate general linear model (GLM) matrix in the FSL's Randomise tool. These analyses were performed over the whole WM skeleton and in the 'Dancers versus Musicians' ROIs, across all groups together and in each one separately.

Correlations of the subjectwise averaged extracted values with behavioural performance

Each of the non-directional and directional diffusivity measures were also correlated with performance on behavioural tasks. Partial correlations with age and sex as covariates of no interest were performed in SPSS over the whole WM skeleton and the 'Dancers versus Musicians' ROIs.

2.4 Results

2.4.1 Behavioural results

Group Characteristics

One-way ANOVAs conducted on age and BMI with group (dancer, musician or control) as the between-subjects factor did not reveal any significant differences between groups (see Table 2.1; Age: $F(2,53) = 2.12$, $p = 0.13$; BMI: $F(2,53) = 0.4$, $p = 0.67$). One-way ANOVAs conducted on years of dance and music training revealed significant group differences for both training types (Dance: $F(2,53) > 131$, $p < 0.0001$; Music: $F(2,53) > 0.201$, $p < 0.0001$). Post-hoc pair-wise comparisons confirmed that both dancers and musicians had significantly longer training in their own discipline compared to the other groups. Furthermore, both dancers and musicians had comparable training to controls in the other discipline, measured as years of music or dance training, respectively (see Table 2.1). Univariate analyses on years of dance and music training, including age and sex as covariates of no interest, consistently revealed significant differences for both training types (Dance: $F(2,51) > 136$, $p < 0.0001$; Music: $F(2,51) > 235$, $p < 0.0001$).

Dance and music tasks

Behavioural results for the full sample were reported previously (Karpati et al., 2016). As described above, three participants (one from each group) were excluded due to unreliable MRI data. For the current sample we followed the same procedure and obtained consistent results with (Karpati et al., 2016). To compare task performance between groups, we performed a linear fixed-effects analysis on the z-scores of the dance, rhythm and melody tasks (see Fig. 1.2) with group as a between-subjects factor and task as a within-subjects repeated measure; age and sex were considered in the model as variables of no interest. This analysis revealed a significant interaction between group and task

Group	**N**	**Age (yrs ± SD)**	**Sex**	**BMI (±SD)**	**Years of dance training (±SD)**	**Years of music training (±SD)**	**Level of education (±SD)**
Dancers	19	25.1 ± 3.9	13F, 6M	21.6 ± 2.3	15.5 ± 5.2	1.7 ± 1.9	2.37 ± 0.6
Musicians	18	22.9 ± 3.4	12F, 6M	22.5 ± 3.2	1.04 ± 1.8	15 ± 3.6	2.39 ± 0.98
Controls	19	25.4 ± 5.1	12F, 7M	22.1 ± 3.1	0.4 ± 0.9	0.4 ± 1.0	2.58 ± 1.12
Comparison between groups	56	D=M=C *ns*		D=M=C *ns*	D>M=C P < 0.0001	M>D=C P < 0.0001	D=M=C *ns*

Table 2.1 Participant characteristics.

Education levels for each group are calculated on a scale 1-5, where 1 is the lowest (completed high school) and 5 is the highest (completed PhD).
F= females, M= males, SD = standard deviation, BMI = Body Mass Index.

(F(4,53) = 26.4, p < 0.0001). Moreover, to compare behavioural performance between groups on each task separately, one-way ANOVAs and Bonferroni post-hoc tests were performed. As expected, for the Dance Imitation Task, dancers outperformed both musicians and controls (ps < 0.0001). Musicians also performed better than controls (p < 0.007). Analogously, on the most music-relevant task, the Melody Discrimination Task, musicians outperformed both dancers and controls (ps < 0.0001), whereas dancers' performances were comparable to those of controls (p = 1). Finally, on the Rhythm Synchronisation Task, musicians outperformed both dancers (p = 0.013) and controls (p < 0.0001) with no other significant differences between groups.

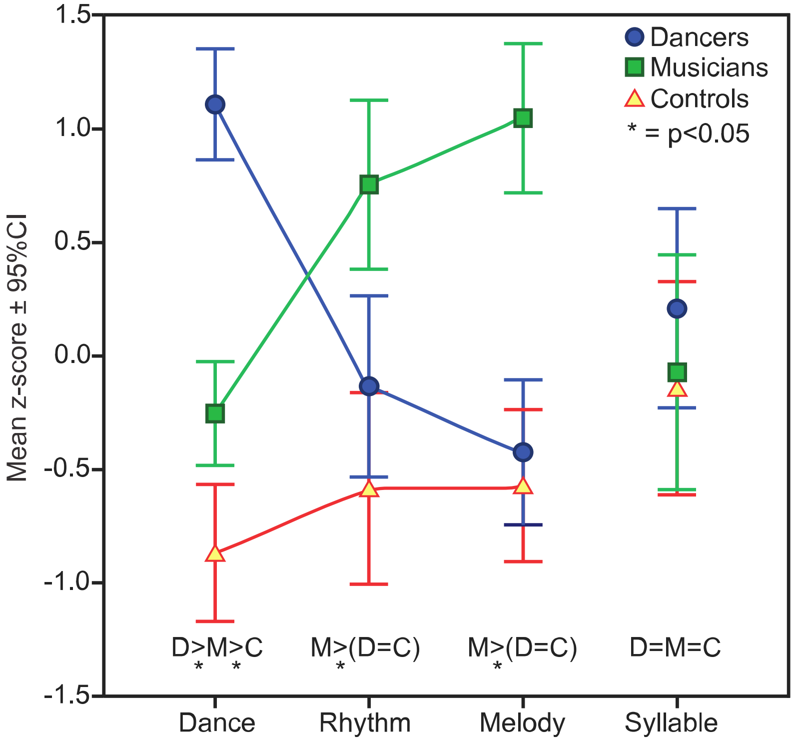


Figure 2.1 Behavioural results.

Performance on the behavioural tasks (z-scores) across the three groups (dancers = blue circles, musicians = green squares, and controls = red and yellow triangles).

Control tasks

In order to compare cognitive abilities between groups, one-way ANOVAs were performed for each control task separately with group as the between subject factor (See Table 2.2). Main effects of group were found for Letter Number Sequencing (F(2, 53) = 0.5, p = 0.007), where musicians outperformed both dancers (p = 0.019) and controls (p = 0.016), and Matrix Reasoning (F(2, 53) = 4.2, p = 0.019), where dancers (p = 0.044) and musicians (p = 0.045) both outperformed controls. No significant effect was found in either the Digit Span (F(2, 53) = 0.8, p = 0.463) or the Syllable Sequence Discrimination Task (F(2, 53) = 0.3, p = 0.729).

Univariate analyses including age and sex as covariates of no interest confirmed the ANOVAs results (Letter Number Sequencing: F(2, 51) = 3.675, p = 0.032; Matrix Reasoning: F(2, 51) = 4.076, p = 0.023; Digit Span: F(2, 51) = 0.879, p = 0.421; Syllable Sequence Discrimination Task: F(2, 51) = 0.333, p = 0.718).

Taken together, the groups performed relatively similarly on all tasks and all were in the normal range. This suggests that any differences on the experimental tasks or in brain structure are not likely to be related to differences in global cognitive function.

		Cognitive Tasks			
Group		**Letter Number Sequence**	**Matrix Reasoning**	**Digit Span**	**Syllable Sequence Discrimination**
Dancers	Mean ± SD (Range)	10.05 ±2.01 (8 – 15)	13.37 ±1.3 (11 – 16)	9.05 ±2.12 (7 – 13)	69.65 ±7.42 (53.33 – 86.67)
Musicians	Mean ± SD (Range)	12.50 ± 2.47 (7 – 17)	13.39 ±2.03 (10 – 16)	10.11 ±2.56 (5 – 14)	67.96 ±9.24 (43.33 – 81.67)
Controls	Mean ± SD (Range)	10.00 ±3.2 (5 – 18)	11.58 ±2.91 (2 – 15)	9.89 ±3.36 (5 – 18)	67.60 ±8.57 (51.67 – 83.33)
Total	Mean ± SD (Range)	10.82 ±2.82 (5 – 18)	12.77 ±2.31 (2 – 16)	9.68 ±2.72 (5 – 18)	68.41 ±8.32 (43.33 – 86.67)
Comparison between groups		M>D=C P < 0.05	D=M>C P < 0.05	D=M=C *ns*	D=M=C *ns*

Table 2.2 Cognitive results.

Mean values, standard deviations (SD) and ranges for each of the cognitive measures are shown for each group separately and for all groups together. P-values for the comparisons between groups are applicable only for significant differences.

2.4.2 Diffusion tensor imaging results

Group comparisons

In order to determine how dance training differently affects WM structure in comparison to music training, three group analyses were performed: dancers versus musicians, dancers versus controls and musicians versus controls. For each analysis, five non-directional (RD, AD, MD, FA and MO) and two directional (F1 and F2) diffusivity measures were compared between groups. All significant results have ps < 0.05, FWE corrected for multiple comparisons (see Table 2.3) for specific peak p-values and localisation and Supplementary table A.A1 for a summary).

TBSS voxelwise analysis of non-directional diffusivity measures

Over the whole WM skeleton and across all measures, dancers showed increased diffusivity relative to musicians predominantly in the right hemisphere (Fig. 2.2 A). More specifically, dancers had significantly higher RD values in bilateral projection fibres(corticospinal tract (CST), corona radiata (CR), internal (IC) and external (EC) capsules), association fibres (bilateral superior longitudinal fasciculus (SLF) and right cingulum), the body and splenium of the corpus callosum (CC) and in right ventral WM regions of the temporal and prefrontal lobes, including the inferior-fronto-occipital fasciculus (IFOF) and the inferior longitudinal fasciculus (ILF). Peaks of significance were reached for RD in most of the voxels of the right hemisphere ($p < 0.01$). Note that, except for the CC, all the above-mentioned regions are particularly rich in crossing fibres. For instance, the projection fibres of the CST are crossed by the association fibres of the SLF and the IFOF. AD was also increased in dancers, especially in the medial regions of the CC. MD values were increased in dancers compared to musicians in the same WM regions as RD, although with a more symmetrical involvement of the left CST, SLF and body of the CC. Conversely, FA and MO were lower in dancers compared to musicians in the main WM regions where RD and MD were higher in dancers. These findings are consistent since greater RD values reduce FA values. In particular, lower FA values were observed in similar regions of the right hemisphere, including projection fibres (CST, IC, and EC), association fibres (SLF) and, more ventrally, the crossing between the CST, the ILF and IFOF. MO differed in the same, although more extended, regions as FA, but involved also some homologous tracts in the left hemisphere (CST and SLF).

In the group comparison of dancers versus controls, the only significant differences were found for MO. Analogously to the comparison with musicians, dancers had reduced MO in both hemispheres, although predominantly in the right. More specifically, lower MO was found in dancers' projection fibres (especially the CST), association fibres (SLF), and some ventral prefrontal regions. Consistently, compared to controls, dancers also showed trends for higher values of RD ($p < 0.12$) and MD ($p < 0.1$) in the CST crossing the SLF, in the SLF more laterally, and in the CC, the same regions of the right hemisphere where dancers differed from musicians.

There were no significant differences in any non-directional diffusivity measures between musicians and controls.

Analysis of subjectwise averaged non-directional diffusivity measures

Univariate analyses were performed across all populations on the extracted values of RD, FA and MO over the whole WM skeleton and the 'Dancers versus Musicians' ROIs. Bonferroni-corrected between group post-hoc tests not including age and sex allowed for pair-wise comparisons between groups.

Consistent with the voxelwise analyses, over the whole WM skeleton, a main effect of group emerged for MO ($F(2,51) = 3.835$; $p = 0.028$). Furthermore, over the 'Dancers versus Musicians' ROIs, all measures showed significant group differences (FA: $F(2,51) = 10.49$, $p < 0.0005$; MO: $F(2,51)=24.91$, $p < 0.0001$; RD: $F(2,51) = 10.22$, $p < 0.0005$). Musicians had highest FA (musicians

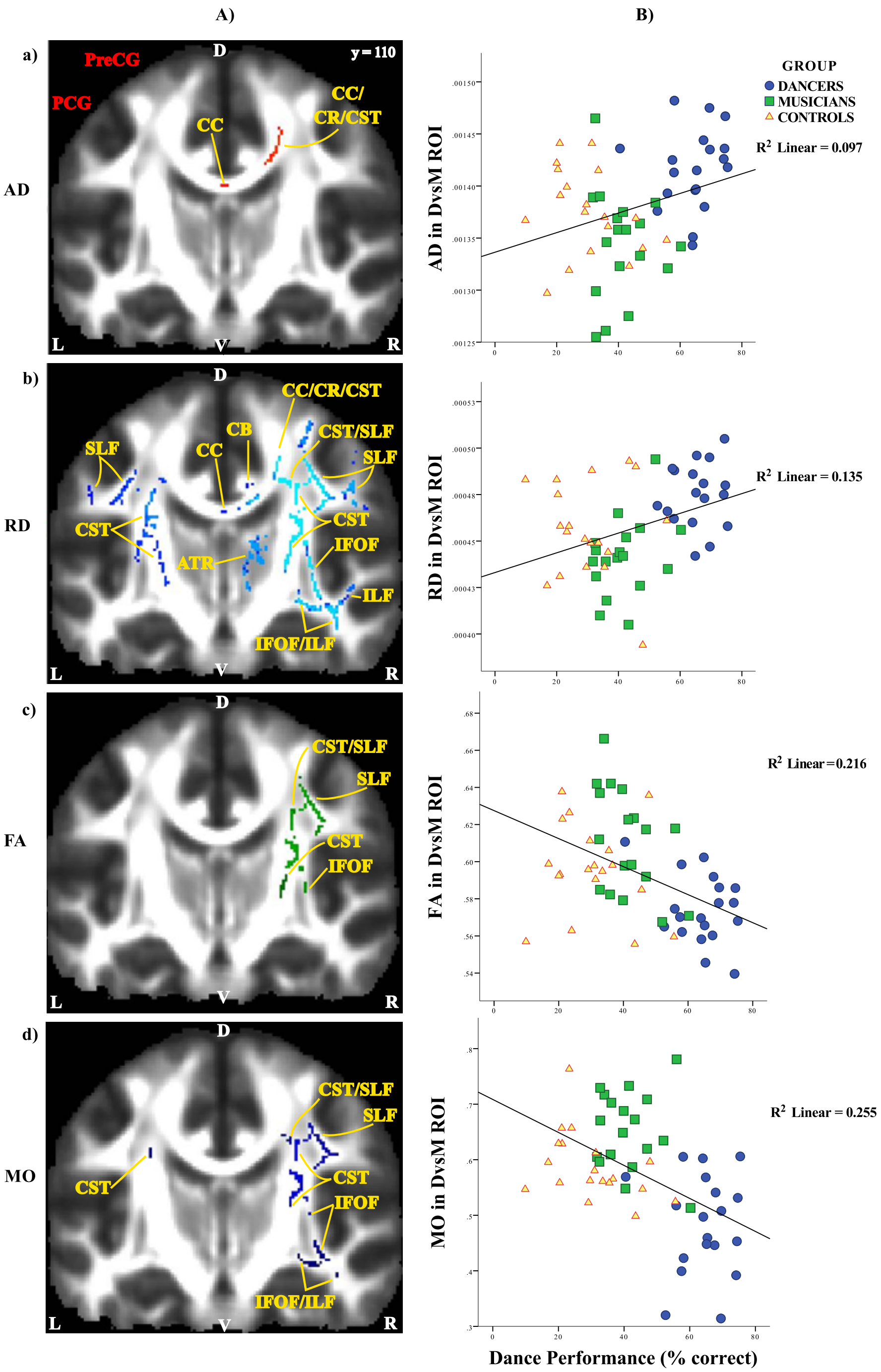


Figure 2.2 Dancers versus musicians group comparisons and brain-behaviour correlations

The left column (A) illustrates the regions of significant difference between dancers and musicians for axial (AD), radial diffusivities (RD), fractional anisotropy (FA) and mode of anisotropy (MO). The right column (B) illustrates the correlations between diffusivity measures and dance performance. **(Column A)** In comparison to musicians, dancers have higher AD and RD (rows 1 and 2) and lower FA and MO (rows 3 and 4). 1-p-values are presented over the FA mean image calculated for the present study sample. Images are presented in neurological view. All images were taken at the same slice level (MNI coordinates). Colours show the voxels where groups statistically differ ($p < 0.05$, FWE corrected). The colour scale in the RD map (Ab) shows significant voxels ranging from dark blue ($p<0.05$) to light blue (most significant). **(Column B)** The extracted values of AD and RD, averaged over the 'Dancers versus Musicians' ROIs are positively correlated with dance performance (rows 1 and 2); those of FA and MO are negatively correlated with dance performance (rows 3 and 4). L= left, R = right, D = dorsal, V = ventral.
ATR = anterior thalamic radiations, CC = corpus callosum, CB = cingulum bundle, CR = corona radiata, CST = corticospinal tract, EC = external capsule, IC = internal capsule, IFOF = inferior fronto-occipital fasciculus, ILF = inferior longitudinal fasciculus, SLF = superior longitudinal fasciculus.

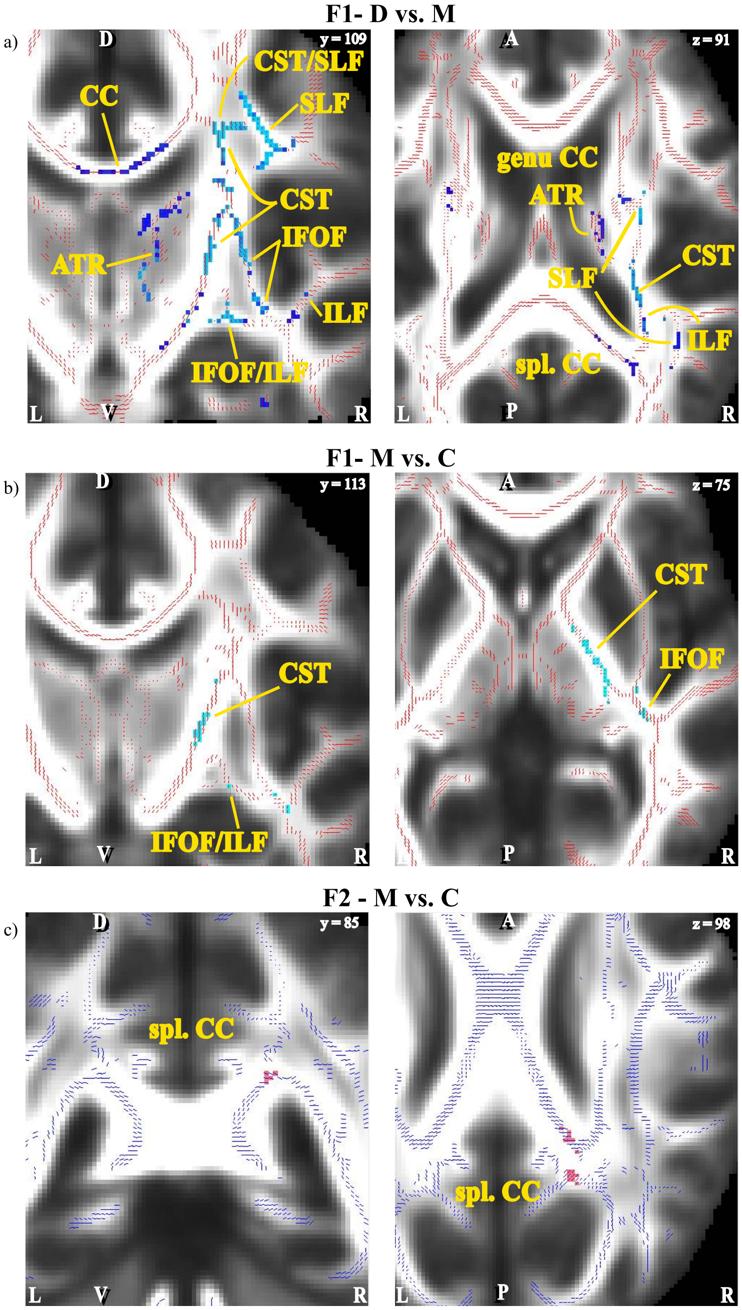


Figure 2.3 Comparison of directional measures.

The left panels illustrate the coronal view; the right panels show the axial view. Coordinates on the figures are in MNI space. **3a - Top row.** Dancers versus Musicians, F1 (red lines). Musicians have higher F1: significant voxels range from dark blue ($p<0.05$) to light blue (most significant). Red lines show the orientations associated with F1 at each voxel. Principal fibres follow the dorsal-ventral direction in the CST regions, and the anterior-posterior direction in the SLF. **3b - Middle row.** Musicians versus Controls, F1 (red lines). Musicians have higher F1 (significant voxels in light blue). Principal fibres follow the dorsal-ventral direction in the CST regions, and the anterior-posterior direction in the IFOF. **3c - Bottom row.** Musicians versus Controls, F2 (blue lines). Musicians have reduced F2 (pink, here thresholded at $p<0.06$) in the right splenium of CC. Orientations of F2 are shown with blue lines.
L = left; R = right; A= anterior; P = posterior; D = dorsal; V = ventral. ATR = anterior thalamic radiations; CC = corpus callosum; CST = corticospinal tract; IFOF = inferior fronto-occipital fasciculus; ILF = inferior longitudinal fasciculus; SLF = superior longitudinal fasciculus; spl. = splenium.

Contrast	ROI	Diffusivity measurement	WM region	# of voxels	Peak p-value	Peak t-value	Peak coordinates (mm)		
							X	Y	Z
Dancers > Musicians	**Whole WM skeleton**	RD	R SCR/CST	9661	0.003	5.26	27	-20	25
			L SCR/CST	2499	0.022	5.76	-25	-12	23
			R --/SLF	24	0.049	3.22	47	6	14
			R --/ATR-IFOF	19	0.050	2.52	28	30	20
		AD	R PCR/--	654	0.034	4.26	20	-33	36
			L --/SLF	425	0.041	3.68	-22	-41	42
			R spl.CC/FM	223	0.046	4.2	6	-38	14
			R body CC/ *ATR*	37	0.049	3.45	-6	-26	24
		MD	R SCR/--	18495	0.004	6.43	21	-12	35
			R --/--	336	0.048	4.21	13	-16	7
Dancers < Musicians	**Whole WM skeleton**	FA	R plIC/SLF-CST	1634	0.027	4.43	27	-9	18
		MO	R alIC/--	1892	0.009	4.68	22	-3	17
			R rlIC/ILF-IFOF	730	0.029	4.36	36	-32	8
			R ACR/ IFOF-UF	466	0.013	5.26	21	28	-7
			L PCR/CST	222	0.037	3.66	-27	-24	25
			L plIC/ATR	204	0.041	4.08	-19	-5	11
			L rlIC/--	77	0.047	3.34	-27	-31	12
			L alIC/ATR	68	0.045	3.45	-21	8	17
			L ILF-IFOF/=	38	0.049	2.46	42	-32	-12
		F1	R SCR/CST	5359	0.007	5.34	26	-19	34
			R body CC/ ATR	712	0.034	4.84	12	-26	27
			R --/SLF	35	0.048	4.02	46	7	11
			R CST/CST	28	0.049	3.52	11	-21	-25
			L EC/SLF	25	0.046	5.04	-29	-11	16
			R SCR/CST	10	0.050	2.87	-26	-11	22
Dancers < Controls	**Whole WM skeleton**	MO	R alIC/ATR	2093	0.014	4.52	23	6	18
			L alIC/ATR	790	0.023	4.34	-22	16	12
			R --/SLF	27	0.047	4.02	48	-11	25
Musicians > Controls	**Whole WM skeleton**	F1	R plIC/CST	193	0.045	3.21	20	-12	4
			R rlIC/IFOF	140	0.048	3.43	31	-29	5
			R --/--	78	0.046	3.96	29	-18	-8
			R --/SLF	57	0.049	2.97	53	-22	-14
			R --/ILF	15	0.050	2.84	41	-10	-18
			R plIC/CST	11	0.050	2.86	26	-18	13
Regressions with dance performance	**Whole WM skeleton**	MO	R plIC/CST	3047	0.002	-4.19	20	-8	6
			L alIC/ATR-IFOF-UF	1021	0.008	-4.6	-22	16	12
	DvsM ROIs	RD	R SLF/SLF	2935	0.002	5.1	31	-18	36
			L EC/CST	522	0.022	4.06	-28	-20	17
		MD	R --/SLF	2308	0.016	4.11	33	-15	38
		FA	R SLF/SLF	950	0.003	-4.3	32	-15	34
		MO	R plIC/CST	1168	0.007	-4.19	23	-12	9
		F1	R SCR/--	608	0.004	-4.06	26	0	34
			R SCR/SLF	80	0.031	-2.93	29	-9	22
			R EC/SLF	62	0.020	-3.23	30	-9	15
Regressions with melody performance	**DvsM ROIs**	AD	R SCR/--	14	0.045	-2.88	18	-7	39
			R PCR/--	11	0.041	-4.02	20	-34	38
		FA	R plIC/CST	434	0.008	3.92	26	-17	15
			R EC/IFOF	7	0.049	2.38	32	-18	5
		MO	R plIC/CST	511	0.004	4.57	21	-7	9
			R --/IFOF-ATR-UF	25	0.045	3.51	18	43	-8

Table 2.3 Localisation of TBSS results and statistical values.

Regions are labelled according to the JHU ICBM-DTI-81 White-Matter Labels / JHU White-Matter Tractography Atlas. WM = white matter; R = right; L = left. – = no labels provided with the first (–/) or the second (/–) atlas. alIC = anterior limb of internal capsule; ATR = anterior thalamic radiations; CC = corpus callosum; CST = corticospinal tract; EC = external capsule; FM = forceps major; IFOF = inferior fronto-occipital fasciculus; ILF = inferior longitudinal fasciculus; PCR = posterior corona radiata; plIC = posterior limb of internal capsule; rlIC = retro-lenticular part of internal capsule; SCR = superior corona radiata; SLF = superior longitudinal fasciculus; spl. = splenium; UF = uncinate fasciculus.

versus dancers: $p < 0.0001$; dancers versus controls: $p = 0.023$; musicians versus controls: $p = 0.2$) and MO (musicians versus dancers: $p < 0.0001$; dancers versus controls: $p < 0.0005$; musicians versus controls: $p=0.03$), and lowest RD (musicians versus dancers: $p < 0.0005$; dancers versus controls: $p=0.05$; musicians versus controls: $p = 0.154$), whereas dancers occupied the opposite extremes, with highest RD, and lowest FA and MO (see Supplementary table A.A2 for a summary).

TBSS voxelwise analysis of directional diffusivity measures

Consistent with the results of the non-directional measures, compared to musicians, dancers showed reduced F1 in right projection (CR, CST) and association (SLF) pathways, as well as bilateral commissural fibres (CC), the same WM regions where these two groups differed in non-directional measures. This suggests that musicians show greater coherence in these regions. In agreement with this finding, compared to controls, musicians had increased F1 ($p < 0.05$) in the inferior portions of the CST and in the ILF, where the two fibre bundles cross. These locations are included in the regions where diffusivity (especially RD and MD) was reduced and anisotropy (FA and MO) increased in musicians compared to dancers. The orientations associated with F1 correctly follow the anatomical orientation of projection and association fibres, as shown in Fig. 2.3 A and B. On the other hand, F2 was reduced in the musicians' right splenium of CC ($p < 0.05$). The orientations of F2 are shown in Fig. 2.3 C. No significant differences were found in F1 or F2 when comparing dancers to controls.

Brain-behaviour relations

To further establish the relationship between brain structure and dance or music expertise, voxelwise regressions were performed between all diffusivity measures and performance on behavioural tasks (Dance Imitation, Melody Discrimination and Rhythm Synchronisation). Moreover, correlations between the subjectwise averaged extracted values of diffusivity measures and behavioural performance were analysed. All analyses were accomplished over the 'Dancers versus Musicians' ROIs and over the whole WM skeleton, across all groups together and in each one separately.

Dance Imitation Task

Voxelwise regressions in the 'Dancers versus Musicians' ROIs revealed positive relations between dance performance and RD ($p < 0.01$) or MD ($p < 0.05$), and negative associations between dance task performance and FA, MO or F1 ($p < 0.01$) (Fig. 2.2 B). More precisely, better performance predicted higher RD and MD, as well as lower FA and MO, in the right projection (CR, CST) and association fibres (SLF). RD and MD values were also positively associated with dance performance in the right CC, whereas MO showed negative associations in some anterior projection and association tracts, including CR, anterior limb of IC and ATR. Similar trends were also observed over the whole WM skeleton, although significant associations were found only for MO.

Separate regressions within groups were not significant, indicating that the association is likely driven by group differences, especially between dancers and musicians.

Correlation analyses with the subjectwise averaged extracted values were consistent with the analyses of regression, showing positive relations between dance performance and diffusivity (RD, AD and MD) and negative ones with FA and MO. Significance was reached in the 'Dancers versus Musicians' ROIs for all measures.

Melody Discrimination Task

Regressions with the Melody Discrimination performance over the 'Dancers versus Musicians ROI' revealed opposite associations with diffusivity measures compared to dance performance. Better melody performance predicted lower values of RD, MD and AD, and higher values of FA and MO. More specifically, melody performance was negatively associated with RD in projection fibres, especially including the CST, and with AD and MD in small regions of the CR. Furthermore, melody performance was positively associated with both FA and MO in the right CST (with peaks of $p < 0.01$), also where it crosses the SLF, and, with MO only, in the anterior limb of IC. Results over the whole WM skeleton were not significant, nor were any of the individual group analyses.

Regression analyses were also conducted across all groups in the regions where musicians and controls differed. Over these 'Musicians versus Controls' ROIs, better melody performance predicted higher F1 values in the right posterior limb of IC and lower F2 in the right splenium of CC. This suggests that music training particularly enhances these WM structures (right IC and CC).

The correlations with the subjectwise averaged values were consistent with the voxelwise regressions. Melody performance was negatively correlated with diffusivity measures (RD, AD and MD) and positively with FA and MO in the 'Dancers versus Musicians' ROIs. Conversely, no trends were found over the whole WM skeleton.

Rhythm Synchronisation Task Regressions between diffusion measures and performance on the rhythm task in the 'Dancers versus Musicians' ROIs revealed that, in musicians, better performance predicted higher FA values in the right SLF. No significant results were obtained for the whole WM skeleton.

However, the correlations with the subjectwise ROI averaged diffusivity measures revealed significant negative associations between rhythm performance and FA or MO over the 'Dancers versus Musicians' ROIs; these results persisted for MO in the whole WM skeleton.

2.5 Discussion

2.5.1 Summary of main findings

This study is the first to examine the differential effects of long-term dance and music training on white matter (WM) structure. Our findings show that dancers have increased diffusivity and reduced anisotropy in WM regions, including the CST, the SLF and the CC. In contrast, musicians showed reduced diffusivity and a greater proportion of primary fibres in similar regions, particularly in the right hemisphere. Crucially, diffusivity measures were related to performance on dance and music tasks that differentiated the groups. Groups were well matched for age, sex, and body-mass index. Further, dancers and musicians had equal years of experience in their respective disciplines. To better understand the physiological underpinnings of the observed decreases in FA, we examined multiple concurrent diffusivity measures. Based on these findings, we hypothesize that increased diffusivity in dancers may be either related to greater heterogeneity of fibre orientation within these tracts, or enhanced coherence of specific tracts in crossing pathways. It is also possible that our findings result from the combined effects of enhanced and reduced diffusivity in overlapping pathways that are each related to specific aspects of dance training. For musicians, reduced diffusivity is more likely due to increased coherence of effector-specific fibre pathways. This suggests that dance and music training may produce opposite effects on WM structure. Whole-body dance training may result in greater fanning of fibres connecting different brain regions and/or an increase in crossing fibres. In contrast, musical training may result in more focussed enhancements of effector-specific pathways.

2.5.2 The direction of diffusivity and anisotropy in dancers

In the present study, we found reduced anisotropy (FA, MO) and increased diffusivity (RD, AD and MD) in widespread WM regions of dancers in comparison to musicians with similar trends in comparison to controls. While most research in musicians has reported FA increases (Bengtsson et al., 2005; Han et al., 2009; Halwani et al., 2011; Rüber et al., 2013; Steele et al., 2013), studies in dance and other whole-body motor activities, such as gymnastics, have found reduced FA values (Hänggi et al., 2010; Huang et al., 2013; Hummel et al., 2014).

Decreases in FA, particularly in clinical studies, have been interpreted as indicating disruption of the organization and integrity of fibres, or damage to myelin sheaths (Werring et al., 1999; Filippi et al., 2001; Concha et al., 2006; Han et al., 2009). However, in the context of learning and expertise, other interpretations may be more relevant, such as changes in axon diameter, in the fanning of primary fibres, or in the density and coherence of secondary fibres in crossing fibre regions (Beaulieu, 2002; Mori and Zhang, 2006; Douaud et al., 2009, 2011; Zatorre et al., 2012). Large axon diameters have been associated with increased RD (Barazany et al., 2009), which studies in phantoms have shown can lead to reduced FA (Fieremans et al., 2008). Indeed, large axons are usually less densely packed than smaller axons (LaMantia and Rakic, 1990; Alexander et al., 2010), leaving more extracellular space between them, which could also contribute to increased RD (Barazany et al., 2009; Beaulieu, 2009). Similarly, highly fanning tracts that make connections with broader, or even divergent (Kalil and Dent, 2014), cortical regions would have a less coherent orientation than more coherent tracts connecting narrower regions, potentially leading to lower FA and higher

RD values (Budde and Annese, 2013; Chiang et al., 2014; Pasternak et al., 2014; Teipel et al., 2014; Canese et al., 2015). Consistent with this idea, Taubert et al. (2010) attributed reductions in FA related to learning of a whole-body balance task to possible increases in crossing fibre. It might also be possible that increased connections with broader cortical regions are physiologically underpinned by increased axonal branching. During development more frequent and intense activity between neurons guides the axons to expand and intensify connections by sprouting and extending collateral branches (Cantallops and Routtenberg, 1999), especially in the CST (Carmel and Martin, 2014). Thus, it is possible that long-term intense training might create similar conditions, especially when training starts at young age.

Another reason why diffusivity might be greater in dancers compared to musicians is that many of the regions that differed between the groups are rich in crossing fibres, particularly between the CST and SLF. The FA reductions associated with dance training were accompanied by increases in RD and MD, with only limited changes in AD. This indicates that the observed increases in FA are not due to a decrease along the principal axis of diffusion (AD), but rather to an increase along the transverse axis (RD). Because RD is a combined measure of diffusivity in the two orthogonal directions, it is impossible to know whether diffusion is increased in one or both, without looking at the eigenvalues from which this metric is derived. In regions where many fibres cross each other, MO can be used to discriminate between an effect involving multiple fibres lying on the same plane, and one occurring along a specific direction (Douaud et al., 2011). In our study, we observed concurrent decreases in MO and FA, suggesting that there is a preferential plane of diffusivity (Ennis and Kindlmann, 2006). Therefore, the FA decreases observed in dancers are unlikely to be due to general changes in myelinisation of axons, which would have symmetrical effects around the principal axis of diffusion, and may rather be attributed to the proliferation of secondary fibres.

2.5.3 Region specific findings

Corticospinal tract

In this study, two of the WM regions where groups diverged most significantly included the corticospinal tract (CST) and the superior longitudinal fasciculus (SLF) where dancers showed increased diffusivity compared to musicians. Both of these tracts are part of the sensorimotor system. The fibres of the CST project from the sensorimotor and premotor cortices to the motor-neurons in the spinal cord, and this pathway plays a key role in the control of voluntary movement (Wakana et al., 2004). The SLF connects posterior sensory to frontal regions, and is thought to be involved in the integration of sensory and motor information for action (Ptak, 2012; Hecht et al., 2013a; Rodriguez-Herreros et al., 2015).

The finding of reduced anisotropy in the CST is consistent with the only previous study in dancers (Hänggi et al., 2010) and with one in gymnasts (Huang et al., 2013). Both dance and gymnastics require the ability to execute rapid and precise whole-body movements, and to rapidly integrate proprioceptive information, crucially transmitted via the CST. We hypothesize that whole-body dance or gymnastics training could generate intensified connections between widespread sensorimotor areas resulting in increased fibre branching and fanning, and thus higher RD and lower FA values. In contrast, music requires intensive training of specific body parts which would be more likely to lead to focal changes in WM structure that appear as local decreases in diffusivity. Long-term dance training might result in increased diffusivity in the CST because of the proliferation of crossing fibres. Studies of expert gymnasts showed that FA was lower in part of the CST (Huang et al., 2013). It is possible that greater diffusivity in this region of the CST was due to fibre bundles crossing this region, such as the SLF. Supporting this hypothesis, we also observed reduced MO in the region of the CST, which suggests that the increased diffusivity lies on the same plane, such as the SLF (Douaud et al., 2011). While dance training might enhance crossing connections between widespread cortical regions, music training might reinforce the coherence of CST principal fibres. Higher FA values have been reported in the CST of expert musicians which have been shown to be related to childhood piano practice and finger tapping performance (Bengtsson et al., 2005; Han et al., 2009; Rüber et al., 2013).

Thus, music and dance expertise might affect WM in two opposite directions. Indeed, performance on the dance and melody tasks, reflecting expertise, showed opposite relationships with diffusivity measures: while dance performance was positively associated with diffusivity, and negatively with anisotropy and F1 (Fig. 2.2 B); melody performance was negatively associated with diffusivity and positively with anisotropy.

Superior longitudinal fasciculus

The SLF is an associative fibre bundle that crosses the CST, travelling perpendicularly to it for the majority of its length (Wakana et al., 2004). The SLF is made up of short- and long-range bi-directional fibre bundles, linking the posterior sensory regions to parietal and frontal areas (Catani et al., 2002; Makris et al., 2005; Martino et al., 2013; Kamali et al., 2014). In particular, three fibre bundles connect the occipital and parietal lobes to the motor and prefrontal cortices; in addition the arcuate fasciculus makes connections between the superior temporal and prefrontal cortices (Makris et al., 2005). The first three bundles are implicated in the regulation of higher aspects of motor behaviour (Makris et al., 2005; Koch et al., 2010), as well as the visuo-spatial aspects of working memory (Olesen et al., 2003; Nagy et al., 2004; Klingberg, 2006; Vestergaard et al., 2011) and visuo-spatial attention (Hoeft et al., 2007; Chechlacz et al., 2012, 2013; Vallar et al., 2014; Cerami et al., 2015). The arcuate fasciculus is particularly relevant for auditory-motor integration necessary for perception and production of speech and music (Catani et al., 2005; Oechslin et al., 2009; Lopez-Barroso et al., 2013). In the current study, several components of the SLF differed between dancers and musicians, especially the long-range fronto-parietal connections (Hua et al.,

2008) and short-range fibres within the frontal lobe.

Similar to our findings in dancers, gymnasts showed reduced FA values in the SLF compared with non-athletes (Huang et al., 2013). The authors attributed these FA changes to greater axonal diameter in SLF fibres. These changes in the SLF may be related to enhanced visuo-motor integration skills developed with dance training. In support of this interpretation, FA in the SLF has been linked to visuo-motor sequence learning (Tomassini et al., 2011; Steele et al., 2012).

Part of the SLF that connects posterior with frontal GM regions has been shown to be involved in the action observation-execution matching, or "mirror neuron", system in humans (Makris et al., 2005; Hecht et al., 2013a; Kamali et al., 2014), which is part of the action observation network. This network is composed of sensorimotor regions of the occipital, temporal, parietal, as well as frontal lobes that respond to the observation of others' actions (Buccino et al., 2001; Cross et al., 2009b; Grafton, 2009; Caspers et al., 2010). This system has been hypothesized to be critical for dance learning because dancers typically observe and imitate others in order to learn new movements (Cross et al., 2006). Therefore, greater efficiency of this network in dancers might partially explain the reduction of FA that we observed in the SLF. Indeed, the conduction velocity of fibres is facilitated by larger axon calibres (Horowitz et al., 2015) that are detectable with DTI by lower values of FA (Fieremans et al., 2008).

Another part of the SLF might convey vestibular responses (Spena et al., 2006), which are inhibited in dancers and other balance-trained individuals (Keller et al., 2012) to reduce destabilizing compensatory movements in favour of increased visual (Hugel et al., 1999; Hüfner et al., 2011; Costa et al., 2013) and proprioceptive information (Jola et al., 2011; Hutt and Redding, 2014). The attenuation of the vertigo reflex in dancers has been explained in terms of the uncoupling between vestibular perception and reflex involving an extended network, centred around the SLF and temporo-parietal WM (Nigmatullina et al., 2015).

One possible explanation for these contrasting results of the FA direction in the SLF is that this fibre bundle contains various subcomponents that convey specific information (visuo-spatial, vestibular, audio-motor) between different cortical regions (Martino et al., 2013). Each subcomponent may therefore be differently affected by the various aspects of dance and, more generally, motor training. Future studies with tractography may investigate this hypothesis, by subdividing the SLF into its subcomponents and linking them to specific behavioural aspects of dance training.

Corpus callosum

Dancers and musicians also differed in lateral and medial portions of the corpus callosum (CC), including the posterior body and splenium, which connect primary sensory and motor cortices (Hofer and Frahm, 2006; Wahl et al., 2007). The body of the CC links premotor and sensorimotor cortices, whereas the splenium links the visual, parietal and auditory cortices (Hofer and Frahm, 2006; Knyazeva, 2013). The lateral portions of the CC are crossed by other fibre tracts, including the SLF and the CST. Increased connectivity of these crossing fibres might reduce the density of fibres in the lateral CC, explaining the reduced FA and augmented RD observed in dancers (Budde and Annese, 2013). Importantly, for dancers, in the lateral portions of the CC RD was increased, whereas in the medial CC both RD and AD were increased. Because the lateral portions of CC connect many different cortical areas, fibres in this region may tend to fan and be less coherent than fibres in the medial CC. Therefore, the higher RD values observed in dancers may be explained in terms of increased connections between sensorimotor regions. Dance and music training differ crucially in the involvement of whole-body movements as opposed to effector-specific movements, respectively. Given the somatotopic organisation of sensorimotor cortices, it is possible that dance training enhances connections between widespread cortical regions that involve the representation of the whole body. Conversely, music training may increase the density and coherence of the fibres that link more limited regions representing the trained effectors. Indeed, F1 was increased in our sample of musicians, indicating increased coherence of fibres CC. This interpretation is further supported by previous studies where musicians showed higher FA in the genu (Schmithorst and Wilke, 2002), body and splenium (Bengtsson et al., 2005; Steele et al., 2013) of CC.

The interpretation of our concomitant findings for increased RD and AD in the medial CC is more complex. The fact that FA did not differ between groups means that the ratio between diffusivities along the longitudinal direction (AD) and perpendicular to it (RD) is constant. It has been shown that anisotropy varies along the midsagittal course of the CC (Hofer and Frahm, 2006). Nonetheless, the medial fibres of CC are extremely packed and parallel to each other, thus constituting one of the most coherent fibre bundles of the brain (Johansen-Berg et al., 2007). Therefore, while higher values of AD in experts are easily attributable to increased myelination, coherence or packaging of fibres, the concomitant findings for greater RD in dancers are less clear. One possibility might be that the enhanced connections between whole-body cortical representations developed with dance training result in greater heterogeneity of fibre orientation, and thus less coherent, and less densely packed, fibres. This would explain the global increase of the amount of diffusion (MD) that we observed in dancers, irrespective of the direction of motion.

2.5.4 Limitations and future directions

In this paper, we attributed the WM differences observed between groups to brain plasticity related to their specific training. However, with a cross-sectional design we cannot exclude the possibility that there were pre-existing differences in structure between groups that might underlie dance skills and the propensity to undertake training. Longitudinal studies of dance training could allow us to verify whether WM changes were due to training or pre-existing differences; although expertise is likely to result from the combination of both environmental and genetic factors.

DTI findings must be interpreted with care due to the intrinsic limitations of this technique, especially in regions rich in overlapping pathways (e.g., the multiple components of the SLF) or crossing fibres (e.g., CST and SLF). We have proposed several plausible macrostructural fibre configurations that may explain the observed lower FA values in dancers, such as reduced coherence due to fanning, crossing or increased axonal diameter. Additional analyses may help to specify our results and future studies using techniques, such as tractography (Tournier et al., 2004; Tuch, 2004), and the estimation of the axon diameter (Assaf et al., 2008), may be useful next steps to validate the interpretation of our findings. Furthermore, novel methodologies of investigation might explore alternative physiological explanations, such as modifications of the axonal membrane permeability or of the myelin thickness, that cannot be excluded neither with DTI nor tractography.

The present study revealed the most significant results in the contrast between dancers and musicians rather than in comparison with untrained subjects. This may be the result of the fact that the highly selected dancer and musician groups may be more homogeneous than the control group, merely selected to have negligible training in both dance and music. Pure and uniform groups of experts, like our samples of dancers and musicians, may have more extreme and localised values, which are more easily discernible than dispersed ones. In support of this interpretation, comparisons between specific groups of musicians revealed more evident differences than contrasts with controls (Steele et al., 2013; Bailey et al., 2014; Vollmann et al., 2014).

2.6 Conclusions

This study is the first to examine the differential effects of long-term dance and music training on WM structure. Dancers showed increased diffusivity in sensorimotor pathways in comparison to musicians who showed greater coherence in the same regions. We propose that intensive whole-body dance training may result in greater heterogeneity of fibre orientation connecting various brain regions, an increase in crossing fibres, or larger axon diameter. In contrast, musical training may result in more focussed enhancements of effector-specific pathways. These findings expand our understanding of brain plasticity literature by emphasizing that different types of training can have different long-term effects on the brain.

CHAPTER 3

The descending motor tracts are different in dancers and musicians

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3.1 Abstract

Long-term motor training, such as dance or gymnastics, has been associated with increased diffusivity and reduced fiber coherence in regions including the corticospinal tract. Comparisons between different types of motor experts suggest that experience might result in specific structural changes related to the trained effectors (e.g., hands or feet). However, previous studies have not segregated the descending motor pathways from different body-part representations in motor cortex (M1). Further, most previous diffusion tensor imaging (DTI) studies used whole brain analyses based on a single tensor, which provide poor information about regions where multiple white matter (WM) tracts cross.

Here, we used multi-tensor probabilistic tractography to investigate the specific components of the descending motor pathways in well matched groups of dancers, musicians and controls. To this aim we developed a procedure to identify the WM regions below the motor representations of the head, hand, trunk and leg that served as seeds for tractography.

Dancers showed increased radial diffusivity (RD) in comparison to musicians, in descending motor pathways from all the regions, particularly in the right hemisphere, whereas musicians had increased fractional anisotropy (FA) in the hand and the trunk/arm motor tracts. Further, dancers showed larger volumes compared to both other groups. Finally we found negative correlations between RD and FA with the age of start of dance or music training, respectively, and between RD and performance on a melody task, and positive correlations between RD and volume with performance on a whole body dance task.

These findings suggest that different types of training might have different effects on brain structure, likely because dancers must coordinate movements of the entire body whereas musicians focus on fewer effectors.

3.2 Introduction

Studies with dancers and athletes, using diffusion weighted imaging (DWI), point toward an association between expertise and changes in white matter (WM) architecture. In particular, in a recent paper we showed that highly trained dancers have increased diffusivity and reduced fiber coherence in the corticospinal tract, superior longitudinal fasciculus and the corpus callosum in comparison to musicians (Giacosa et al., 2016). Similar findings have been reported in other studies of dancers and athletes (Jäncke et al., 2009; Hänggi et al., 2010; Huang et al., 2013; Meier et al., 2016; Burzynska et al., 2017). In comparison, studies in trained musicians have generally reported focal increases in measures of fiber coherence (Han et al., 2009; Halwani et al., 2011; Rüber et al., 2013; Acer et al., 2018). Reduced measures of WM coherence in dancers and athletes have been interpreted as an increase in crossing or fanning of fibers and attributed to enhanced connectivity between sensorimotor regions representing different body parts. In contrast, the focal increases observed in musicians may represent increased coherence resulting from intensive training of specific effectors (e.g. hands). In the current study we test these hypotheses in a sample of highly trained musicians and dancers using probabilistic tractography to examine the connectivity of different body part representations in the motor cortex (M1). To do this, we developed a novel procedure to identify the seed regions for the hand, trunk/arm, leg and head in M1. Those regions were then used as seeds to track sub-divisions of the descending primary motor pathways and compare diffusion parameters and volumes between dancers and musicians.

Most of the previous research (Hänggi et al., 2010; Giacosa et al., 2016; Burzynska et al., 2017) is based on whole brain analyses, which provide global information about the location of WM changes, but cannot tell us about the specific connections from individual regions. Moreover, the most common diffusion tensor imaging (DTI) model assumes that all fibers in each voxel follow the same direction (Basser et al., 1994), which is less accurate in regions with many crossing fibers. In contrast, probabilistic tractography based on a multi-tensor model allows the reconstruction of individual fiber tracts (Behrens et al., 2007).

There is a large body of evidence showing neural plasticity of grey (GM) and white matter in sensorimotor regions of novices who undergo short-term training (Draganski et al., 2004; Scholz et al., 2009; Taubert et al., 2010, 2016; Bezzola et al., 2011; Sampaio-Baptista et al., 2013), as well as of trained dancers, musicians, and athletes (Schlaug et al., 1995a; Gaser and Schlaug, 2003; Jäncke et al., 2009; Hänggi et al., 2010; Wang et al., 2013; Steele et al., 2013; Schlaffke et al., 2014; Bailey et al., 2014; Huang et al., 2013; Burzynska et al., 2017; Karpati et al., 2017). Training studies in both animals and humans show local reorganization of the specific representations of the trained effectors (e.g., Karni et al., 1995; Kleim et al., 2002, 1998; Morgen et al., 2004; Nudo et al., 1996; Taubert et al., 2016. Similarly, most studies with trained musicians, dancers or other athletes found enlargements in the motor representation of the trained effectors (Elbert et al., 1995; Pantev et al., 2001; Tyč et al., 2005; Vaalto et al., 2013; Choi et al., 2015; Meier et al., 2016), and/or changes in WM motor pathways (Bengtsson et al., 2005; Han et al., 2009; Imfeld et al., 2009; Wang et al., 2013; Rüber et al., 2015; Giacosa et al., 2016; Acer et al., 2018), linked to the effector used (Meier et al., 2016). In particular, professional dancers and gymnasts, whose training involves comparably complex whole-body movements, had lower fractional anisotropy (FA) in sensorimotor and interhemispheric motor pathways which was attributed to greater axon diameter, increased crossing or fanning of fibers, or more wide-spread connectivity (Hänggi et al., 2010; Huang et al., 2013; Giacosa et al., 2016; Burzynska et al., 2017). Conversely, long-term music training has frequently been associated with increased FA in the corticospinal tract (CST) (Bengtsson et al., 2005; Han et al., 2009; Rüber et al., 2015, but see Imfeld et al., 2009; Schmithorst and Wilke, 2002), and in the arcuate fasciculus (Halwani et al., 2011). In a previous study (Giacosa et al., 2016), using tract-based spatial statistics (TBSS), we showed that dancers had higher radial diffusivity (RD) values, while musicians had higher FA, in a variety of regions, including the CST. Interestingly, controls' RD and FA values fell between the two expert groups, suggesting opposite associations between dance or music training and WM microstructure. Consistent with these findings, Meier et al. (2016) observed lower FA and higher RD values in ballet dancers in comparison to handball players, especially in the tract seeded in the motor cortex region that included the representation of the leg/foot. Lower FA and higher RD might indicate greater fiber crossing or increased axon diameter within this tract. Together with our own results, this points to enhanced connectivity among a broader selection of brain regions for dancers, in contrast to enhanced connectivity in more focal sets of connections for musicians.

To test this hypothesis, in the current study we used a multi-tensor probabilistic tractography approach to compare the primary motor pathways in professional dancers and musicians with a similar amount of training. The TBSS approach that we previously used is based on the whole brain diffusion single-tensor model (Basser et al., 1994), which only represents one fiber direction. Conversely, the multi-tensor probabilistic tractography (Behrens et al., 2003) can model more than one possible fiber direction, allowing for a better assessment of tracts in regions with multiple crossing fibers, such as certain portions of the CST. We therefore used two-fiber probabilistic tractography to identify the motor pathways descending from the head, hand, trunk/arm and leg/foot motor regions. To do this, we first identified the motor hand areas in each participant based on gross anatomical landmarks (Yousry et al., 1997; Caulo et al., 2007). The ROIs for the trunk/arm, leg and head areas were created relative to this location. Seed masks based on these ROIs were placed in the subjacent WM because tracking from WM is more reliable than from GM, where the orientation of fibers is neither coherent nor clearly detectable. We then tracked the fiber bundles connecting these regions to the cerebral peduncles, and extracted diffusivity and volumetric measures across the entire tracts, as well as in the WM seed masks and the posterior limb of internal capsules (plIC). This allowed us to test the hypothesis that dancers might have increased connectivity across all the body part representations, whereas musicians might have more focused connectivity with the hand region.

3.3 Materials and Methods

3.3.1 Participants

Three groups of participants (age 18-40) were recruited for this study: trained dancers (N=20), trained musicians (N=19) and a control group of non-musician/non-dancers (N=20). This is the same sample used in our previous studies examining WM and GM structure in dancers and musicians using whole-brain approaches (Giacosa et al., 2016; Karpati et al., 2016, 2017, 2018). Groups did not differ in age, sex distribution, body-mass index (BMI) or years of education (Table3.1). Participants had no past or current developmental, neurological or psychiatric disorder, nor reported any alcohol or substance abuse. Dancers and musicians were either currently practicing as professionals, or students involved in professional training. Their training was assessed via a detailed questionnaire developed in our lab: the Montreal Dance and Music History Questionnaire (MDMHQ) (Karpati et al., 2016), based on (Bailey and Penhune, 2010; Coffey et al., 2011). Dancers and musicians had, on average, approximately 15 years of training in their respective disciplines, with a variety of training backgrounds. Controls had, on average, less than one year in dance, music, figure skating, or aerobics experience (See Table 3.1). All participants were physically active (biking, running or practicing other physical exercises) and none had absolute pitch. Since the dance task was based on a video-game, participants were excluded if they had more than 2 years of experience with dance video-games.

One participant in each group was excluded due to artefacts in the DTI data (see Giacosa et al., 2016 for more details). The experimental protocol was approved by the Research Ethics Board at the Montreal Neurological Institute and Hospital, and a written informed consent was obtained from all participants. All participants were compensated for their participation.

3.3.2 General procedures

Participants took part in two testing sessions distributed over two non-consecutive days: one for behavioral testing and the other for MRI acquisition, including DTI images. The behavioral battery included dance- and music-related tasks as well as tests of global cognitive and memory function (described in more detail in Karpati et al., 2016. The Dance Imitation Task was developed in our laboratory based on the video game Dance Central 1 for the console Xbox Kinect 360 (Harmonix, http://www.harmonixmusic.com) to assess the ability to observe and imitate in real time whole-body dance movements synchronised with music (Karpati et al., 2016). The Melody Discrimination Task (Foster and Zatorre, 2010a) assesses auditory processing and pitch discrimination. Furthermore, a language task and three standardized cognitive tests were given to all participants to examine any possible group differences in global cognitive or memory function (Karpati et al., 2016).

3.3.3 Brain imaging and analysis

Diffusion data acquisition

Diffusion-weighted images (DWI) were acquired for all participants at the Montreal Neurological Institute (MNI) on a 3T Siemens Trio MR scanner with a 32-channel head coil. The following parameters were applied: 99 diffusion-weighted gradient directions with a b-value of 1000 s/mm2, 10 b0 non-weighted images, TE of 88 ms, TR of 9340 ms, EPI factor 128, isotropic voxels of 2 x 2 x 2 mm3, 72 slices, FOV of 256 mm. Ear plugs and headphones, as well as foam pads were used to reduce noise perception and head motion, respectively.

Tractography procedure

We developed a procedure, combining FSL and Freesurfer tools, to separately track the motor pathways connecting the head, hand, trunk or leg regions. These tracts comprise the fibers that descend from the primary motor and premotor cortices to the brainstem (Fig. 3.1). In the current study, only the fibers originating in the WM subjacent M1 were tracked; in addition, the leg tracts included the fibers originating in the WM below both pre- and post-central cortices (M1 and S1 respectively) because the available parcellation of the paracentral cortices, provided by the Desikan-Killiany Atlas (Desikan et al., 2006), does not allow us to distinguish between them. To analyze diffusion and volumetric measures in the four bilateral distinct components of the primary motor pathways, we defined four seed masks per hemisphere, located in the WM immediately subjacent the M1 head, hand, trunk/arm, leg/foot representations, and the cerebral peduncles (see below and the Supplementary Material for a detailed description on how these masks were identified). It is worth noting that separately tracking the descending tract components from each seed mask is more precise than tracking from the entire motor cortex and then dividing the whole tract into portions. Indeed, it would be impossible to identify the borders of the tract components along their length because they overlap. Moreover, tract shapes or sizes might differ between groups and along each tract component.

DWI pre-processing

The first steps of the DWI image pre-processing were previously explained (Giacosa et al., 2016). Briefly, individual raw data were corrected for eddy current distortions and head motion using the FMRIB's Diffusion Toolbox (FDT); then, non-brain voxels were excluded with the Brain Extraction Toolbox (BET) (Smith, 2002), and the diffusion tensor model was applied (FDT) to estimate the diffusivity measures in each voxel. From the three eigenvalues, fractional anisotropy (FA) and radial (RD) diffusivities were calculated as the eccentricity of anisotropy and the average between the two lowest eigenvalues (RD), respectively. One subject per group was excluded from the analyses due to artefacts or outlier values. After correction, all subjects had between 70 and 99 gradient directed

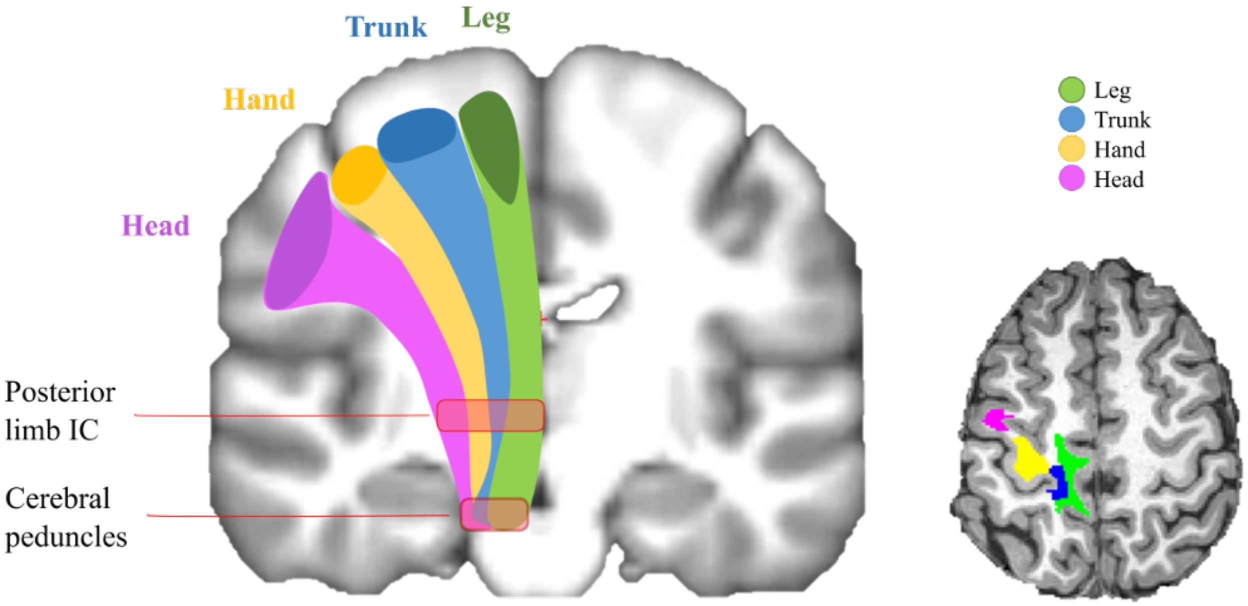

Figure 3.1 Reconstruction of the primary motor tracts for one hemisphere (left).

The four seed masks are indicated in darker color in the WM below the motor cortex. The approximate location of the cerebral peduncles and of the posterior limb of the internal capsule (IC) is also shown with red boxes. Axial view of the WM seed masks in one subject's structural T1 image (right).

frames of good quality, which allowed full analyses for the entire sample. An average of all subjects' FA images was created in the 1 x 1 x 1 mm3 MNI152 space, after linear (FLIRT) (Jenkinson and Smith, 2001; Jenkinson et al., 2002) and non-linear (FNIRT) transformations (Andersson et al., 2007) were applied to the individual FA images.

Probabilistic tractography

After modelling crossing fibers within each voxel of the brain with BedpostX (Behrens et al., 2007), a probabilistic two-fiber tractography approach was run with FSL ProbtrackX Tool (Behrens et al., 2003, 2007) to create connectivity distribution maps of the primary motor pathways in each subject. A connectivity distribution map indicates, at each voxel, how many streamline samples, originating from the seed mask, pass through that particular voxel and reach the target mask, avoiding the exclusion masks. Two fiber tracking procedures were executed for each tract: one to estimate the connectivity map (i.e, probability tractogram) originating in the seed mask and directed to the target, and the other reconstructed in the opposite direction, from the target to the seed. The probability tractograms were normalized by dividing the number of streamline samples at each voxel by the total number of samples that reached the target (waytotal) and then combined to obtain a defined tract, i.e. the probability of the union of the tractograms (P_{un}) (Andoh et al., 2015; Oechslin et al., 2017). Thus, a union tract (P_{un}) indicates the probability of tracking in both directions and was calculated according to the probability rules:

$$P_{un} = P_{A \to B} \cup P_{B \to A} = P_{A \to B} + P_{B \to A} - (P_{A \to B} \cap P_{B \to A}),$$

where

$$P_{A \to B} \cap P_{B \to A} = P_{A \to B} \times P_{B \to A}.$$

Individual P_{un} maps were then thresholded at 5% of the robust range of non-zero voxels (thrp = 0.05, multiplied by 100) and projected onto the standard FMRIB58_FA template. The volume (V_{un}) of the thresholded P_{un} map was calculated as the number of the voxels in the FMRIB58_FA space (which corresponds to the MNI_1mm space).

In order to extract quantitative data from the tracts, the individual thresholded P_{un} were multiplied by each DTI measure (FA and RD) in the individual FA space and then projected on the common FMRIB58_FA template to allow for group comparisons. The DTI measures were then averaged across the entire tract, or across the extraction masks. To further investigate the volumetric properties of the tracts, two parts of each tract were identified: the core tract (T_{core}) and the dispersion tract (T_{disp}) (Oechslin2017). T_{core} is the part of the tract with the most consistent fiber bundle of the pathway and corresponds to the combined probability of both tracking directions; it was therefore calculated as the binarized intersection of the tractograms created in the opposite direction, which, in practical, means: $T_{core} = P_{A \to B} \times P_{B \to A}$. In contrast, T_{disp} points to the more peripheral part of the fiber bundle, which is less consistent between the two tracking directions; to calculate it, the binarized T_{core} images were subtracted from the binarized unthresholded P_{un}: $T_{disp,bin} = P_{un,bin}$ - $T_{core,bin}$. As before, T_{core} and T_{disp} were then transformed into the FMRIB58_FA space.

Tract identification

To examine the structure of the tracts connected to different body part representations, we created four seed ROIs in the WM underlying the motor cortex in both hemispheres. To do this, we first created a mask for the hand area based on anatomical landmarks (Yousry et al., 1997; Caulo et al., 2007) and then identified the trunk/arm, head and leg ROIs relative to that. These anatomically based ROIs likely contain multiple body part representations: the hand ROI would also contain the fingers and wrist, the trunk/arm ROI would contain the representations of the trunk, shoulders and arm, the head ROI would contain the throat, face and neck representations, and the leg ROI would contain the leg, knee and foot representations. These WM ROIs were used as seed masks to track the portions of the primary motor pathways that connect each region to the ipsilateral cerebral peduncles (see3.1). We remind that tractography between the cortical and brainstem ROIs was run bidirectionally, so that each ROI served once as target and once as seed mask. A three-voxel-thick slice, centered at x = 0 of the MNI space, was used as exclusion mask to avoid the confounding fibers of the corpus callosum.

Definition of the seed and extraction masks

To create the seed masks for the four body-part regions in each hemisphere, we developed a procedure that included five main steps (see the diagram in the Supplementary Material B.A2): 1) the localization of the hand regions, based on individual anatomical landmarks; 2) averaging of the individual hand maps to create a sphere based on the center of gravity for each hemisphere; 3) localization and creation of the spheres for the other body parts, relative to the hand regions, on a template M1; 4) projection of the spheres on each individual space; 5) masking of the spheres with the individual parcellation of the WM subjacent M1 (Salat et al., 2009). This procedure is intended to be a good compromise between specificity and standardization across subjects.

As first step, the Freesurfer Recon-all Tool was applied to each subject's structural T1 image to calculate the individual parcellation of GM and WM, given in the individual Freesurfer conformed space. The obtained label of the precentral cortex (M1) served as visual guidance to manually draw each subject's hand region (Fig. 3.2 a), according to the well-established landmarks of the hand knob (Yousry et al., 1997; Caulo et al., 2007). Individual T1 images were coregistered to the standard MNI152 (2mm) space via linear (FLIRT) and non-linear (FNIRT) transformations and averaged across the entire sample to create a customized template. The Freesurfer Recon-all Tool was then applied to the template to calculate its GM-WM parcellation that served as a further guidance in the determination of the masks. The manually-drawn masks of the hand regions were non-linearly projected onto the template, averaged and thresholded at 30% (Fig. 3.2 b and c), to calculate their center of gravity (COG) in each hemisphere. Two spheres of 15 voxels (voxel size = 1mm3) were centered around these COGs (x = 37 mm, y = -19 mm, z = 60 mm in the right hemisphere; x = -35 mm, y = -21 mm, z = 61 mm in the left) to completely include the hand regions of the precentral cortex. These were then projected back to the individual structural T1 space from the template conformed space. Our sample-specific COGs were consistent with the centers of the spheres previously used for defining the hand and leg regions (Meier et al., 2016; Sehm et al., 2016). The hand spheres were appropriately shifted along M1 to create the head, trunk/arm and leg spheres. Since the regions containing the representations of the head and leg are more extended in the dorso-ventral direction, the radii of their spheres were adjusted accordingly (head radius: 24 mm; leg radius: 21mm). The COG coordinates for the spheres were: x = 14 mm, y = -25 mm, z = 66 mm in the right hemisphere, and at x = -13 mm, y = -25 mm, z = 66 mm in the left, for the trunk spheres; x = 49 mm, y = 3 mm, z = 25 mm in the right hemisphere, x = -46 mm, y = 3 mm, z = 25 mm in the left, for the head spheres; x = 13 mm, y = -25 mm, z = 54 mm in the right hemisphere, x = -13 mm, y = -25 mm, z = 54 mm in the left, for the leg spheres. All spheres were then masked, in the individual T1 space, with the individual WM regions underlying M1, also transformed in the same space (Fig. 3.2 d). To avoid overlapping, the trunk WM masks were subtracted from the hand WM masks. Finally, all WM masks were transformed into the individual diffusion space (FA) and used as seeds for tractography (Fig. 3.2 e). The combined use of non-linear transformations, employed to project the spheres onto the individual space, and of the automatized subcortical WM parcellation, used for masking the spheres, ensured that the selection of regions was subject-specific and consistent across subjects. More details on the procedure are reported in the Supplementary Material B.B.

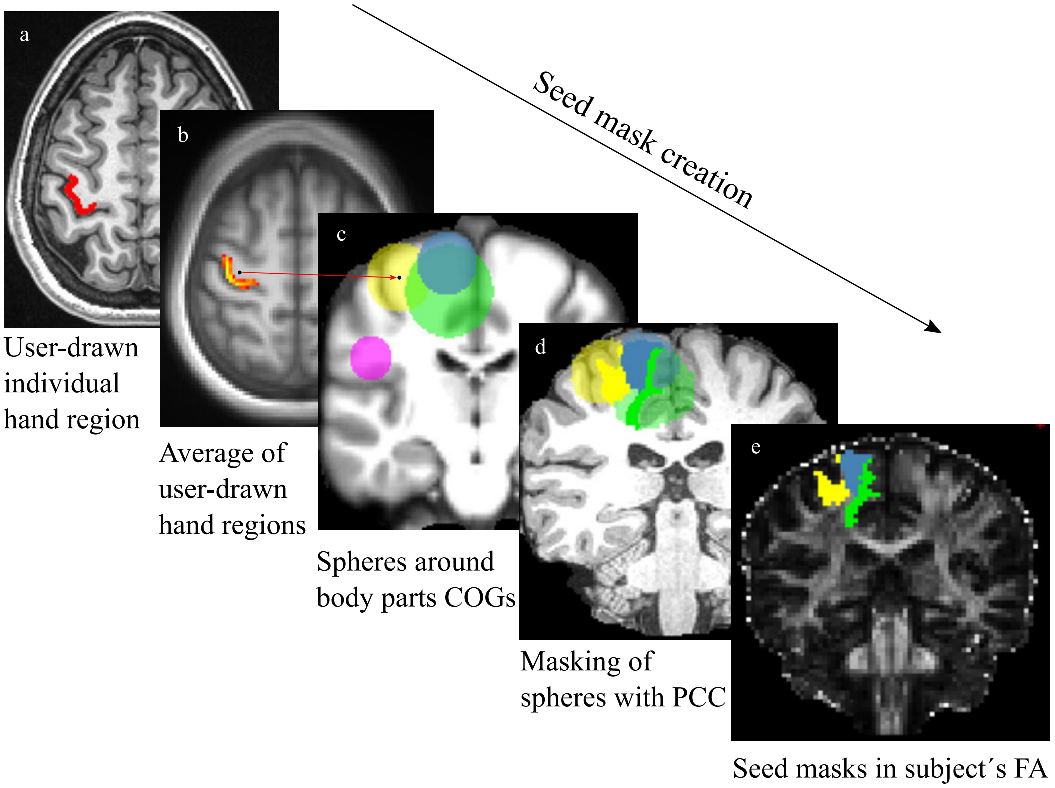

Figure 3.2 General steps followed to create the seed masks in one hemisphere.

(a) User-drawn hand region (red) in one subject, axial view. (b) Average of user-drawn hand regions with center of gravity (COG) indicated as a black dot. (c) Spheres created from the COG of each body part, coronal view: hand sphere (yellow), trunk sphere (blue), leg sphere (green), head sphere (pink). The black dot is only an approximation of a COG with the red arrow showing the correspondence between the axial and coronal views. (d) The spheres (transparent colors) are overlapped with (opaque) masking of the WM regions subjacent the precentral cortex (PCC). (e) Final seed masks in one subject, diffusion FA space.

Based on previous work (Giorgio et al., 2010), the cerebral peduncle seed masks were created by taking two symmetrical three-voxel-thick slices centered around z = -22 mm in the MNI152 1mm space and limited to the area around the peduncles (x range: 0, -15; y range: -14, -46, z range: -21, -23). This binarized mask was then projected onto each subject's individual FA space and thresholded at the individual FA maps where FA $>$ 0.2.

The masks described above were used to identify the primary motor tracts connecting specific body-parts. Since the fiber bundle architecture might change along the tract, we aimed at analyzing these tracts at different levels: not only in its entirety (whole tract), but also in the WM seeds underlying the motor cortex and in the plIC. The latter is a key region along the descending motor tracts, being the bottleneck where all fibers gather parallel and packed; thus, the plIC is often examined as indicative of the entire CST. The plIC ROIs were designed in the FMRIB_FA space as WM 3D boxes (xright range: [20 mm, 28 mm], xleft range: [-19 mm, -27 mm], y range: [-13 mm, -26 mm], z range: [9 mm, 17 mm]) around the area labelled as 'posterior limb of internal capsule' by the JHU ICBM-DTI-81 White-Matter Labels atlas (Mori and Crain, 2005).

Group comparisons

Once tractography was completed, all the quantitative measures were extracted from the whole probabilistic tracts and from the seed and plIC ROIs described above. For the DTI measures (FA, and RD), the values of these measures, contained in each voxel, were averaged across the voxels of the ROIs used as extraction masks for each subject; for the volumetric measures (volume of the P_{un} tract = V_{un}, volume of $T_{core} = V_{core}$ and volume of $T_{disp} = V_{disp}$), the number of the voxels of the relevant extraction masks constituted the individual values to use for the statistical analyses. The quantitative measures were compared between groups with ANCOVA analyses, in R; age and sex were included as nuisance variables. Because no interaction effects were observed in the analyses where the main effects of group were significant, we calculated type II sums of squares for the ANCOVAs. To calculate pairwise group comparisons, adjusted for multiple comparisons, post-hoc Tukey HSD tests were also performed.

Correlations with demographic and behavioral data

In order to estimate the associations between the brain data extracted from the hand, trunk and leg whole tracts and dance or music training, partial correlations were performed, within the groups of dancers or musicians separately, between the abovementioned extracted values and: (1) dance or music training duration (calculated in number of years of training), or (2) age of start of dance or music training. Partial correlations were executed using the ppcor R package, following the Pearson correlation method and correcting for age and sex. The same partial correlation analyses were also performed between the brain data extracted from the whole tracts and performance on the dance and melody tasks.

3.4 Results

3.4.1 Group Characteristics

As reported in previous papers, the groups did not differ in age, sex distribution, body-mass index (BMI) or years of education, and dancers and musicians had a similar amount of training in their respective disciplines (see Table 3.1 and Giacosa et al., 2016; Karpati et al., 2016). These studies also showed that dancers outperformed musicians and controls on the dance task and that musicians performed better than dancers and controls on a melody discrimination task. Thus the groups were well matched and demonstrated domain-specific expertise.

Group	**N**	**Age (yrs ± SD)**	**Sex**	**BMI (±SD)**	**Years of dance training (±SD)**	**Years of music training (±SD)**	**Level of education (±SD)**
Dancers	19	25.1 ± 3.9	13F, 6M	21.6 ± 2.3	15.5 ± 5.2	1.7 ± 1.9	2.37 ± 0.6
Musicians	18	22.9 ± 3.4	12F, 6M	22.5 ± 3.2	1.04 ± 1.8	15 ± 3.6	2.39 ± 0.98
Controls	19	25.4 ± 5.1	12F, 7M	22.1 ± 3.1	0.4 ± 0.9	0.4 ± 1.0	2.58 ± 1.12
Comparison between groups	56	D=M=C *ns*		D=M=C *ns*	D>M=C P < 0.0001	M>D=C P < 0.0001	D=M=C *ns*

Table 3.1 Participant characteristics.

F= females, M= males, SD = standard deviation, BMI = Body Mass Index. Education levels for each group are calculated on a scale 1-5, where 1 is the lowest (completed high school) and 5 is the highest (completed PhD).

3.4.2 Tractography analyses

General information

Statistical analyses were conducted on the mean values extracted from the entire pyramidal tracts, the plICs, as well as from the seed ROIs. For each analysis, DTI measures (fractional anisotropy (FA) and radial diffusivity (RD)) and volumetric measures (volume of the probability of the union of bidirectional streamlines (V_{un}), tract core volume (V_{core}), tract dispersion volume (V_{disp}) were analyzed. All reported results are significant at p-values $< .05$, except where otherwise specified. Sex and age were included as covariates in all analyses.

Group differences

To assess effector-specific differences in the descending motor tracts, the DTI (FA and RD) and the volumetric measures (V_{un}, V_{core}, V_{disp}) were compared between groups for the whole tracts, the plIC ROIs, often used as indicator for the entire CST, and the seed masks, where most group differences in crossing fibers might be expected. The tracts that significantly differed between groups are shown in Fig. 3.3; the statistical values are reported in Table 2. In general, RD values were higher in dancers and FA values were higher in musicians and the majority of significant effects were found in the right hemisphere.

In the primary motor pathways seeded in the right hand region, across the entire tract, FA was higher in musicians in comparison to dancers, while V_{un} was bigger in dancers, with controls' values falling in between. In the plIC, RD and V_{un} were both higher in dancers in comparison to musicians and, in the hand ROI, RD and V_{disp} were higher. Control values fell between the two groups. For the primary motor pathways seeded in the right trunk/arm ROI, FA was higher in musicians compared to the other groups, whereas RD was higher in dancers versus musicians, and V_{un} was bigger in dancers compared to both other groups. For the plIC, RD and V_{un} were lower in musicians in comparison to both controls and dancers. Finally, in the seed ROI, only V_{disp} was significantly larger in dancers in comparison to musicians. For the tract seeded in the leg region of the right hemisphere, RD was higher in dancers compared to musicians across the whole tract and in particular in the plIC. No volumetric differences were found between groups. For the tracts seeded in the right head region, RD was higher in dancers. Consistent with this, in the plIC of this tract, RD was higher and V_{un} was bigger in dancers compared to musicians. Similarly, in the head seed ROI, RD was higher in dancers compared to the other groups. No difference was found for V_{core} in any tract. Taken together, these results show that, for the tracts seeded in the right hand and trunk/arm regions, musicians have increased coherence and packing of fibers, across the entire bundles and particularly at the level of the plIC of the trunk/arm tract. In contrast, dancers have increased dispersion of fiber orientation across the entire bundles. For the leg and head right motor pathways, dancers show greater diffusivity in every direction, likely suggesting an increase in the fiber orientation dispersion, especially below the cortex, and/or in the size of the axon diameter.

Left-hemisphere findings were more limited and largely consistent with those in the right hemisphere. In the left hand seed ROI, RD was higher and V_{disp} was bigger in dancers, whereas only a trend for smaller V_{un} was found in musicians in comparison to dancers. In the whole tract seeded in the left trunk, RD and V_{un} values were both higher in dancers in comparison to musicians. In the seed region of the same tract, no significant difference between groups was found neither in the V_{core} nor in the V_{disp}. No significant differences were found for either the head or leg regions. Together, these results are consistent with those of the right hemisphere, showing increased RD in the hand and trunk tracts of dancers, likely suggesting their reduced coherence and increased fiber orientation dispersion and/or augmented axon diameter.

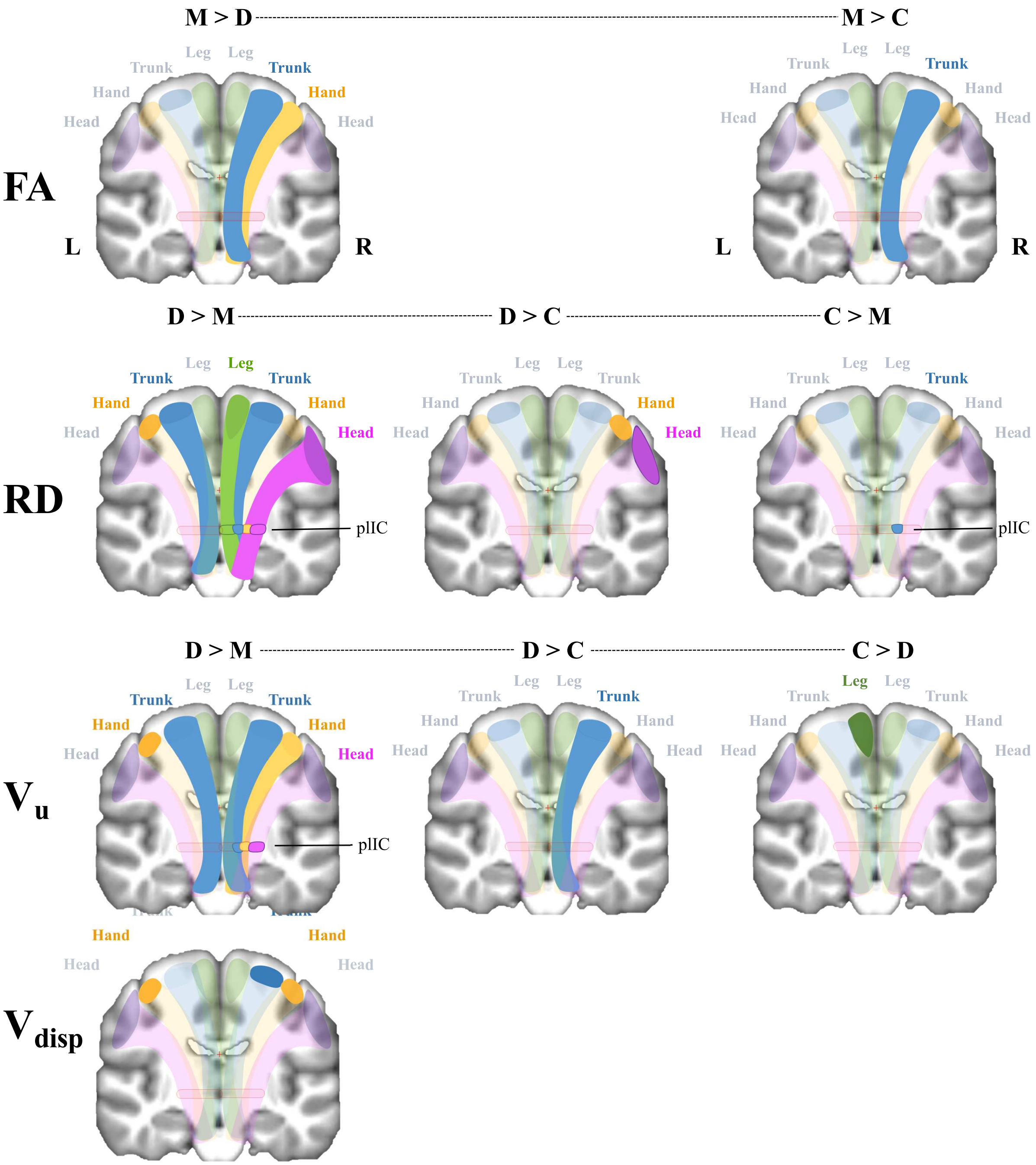

Figure 3.3 Group comparison results.

The opaque colors illustrate the portions of the tracts that differ between groups. The right hemisphere is shown on the right. R = right; L = left; D = dancers; M = musicians; C = controls; RD = radial diffusivity; FA = fractional anisotropy; V_u = volume of the union tract; V_{disp} = volume of the tract dispersion; plIC = posterior limb of internal capsule.

			RD				FA				V_{un}				V_{disp}			
	Seed	**Mask**	$F_{2,50}$	**P**	**Part η^2**	**Tukey**	$F_{2,50}$	**P**	**Part η^2**	**Tukey**	$F_{2,50}$	**p**	**Part η^2**	**Tukey**	$F_{2,50}$	**P**	**Part η^2**	**Tukey**
Right	**Trunk**	**Whole**	3.817	0.029	0.132	D>M: 0.048	4.278	0.019	0.146	M>D: 0.002 M>C: 0.02	5.869	0.005	0.19	D>M: 0.006 D>C: 0.039				
		Seed													3.416	0.041	0.12	D>M: 0.018
		plIC	9.858	0.0002	0.283	D>M : 0.001 C>M: 0.028					6.072	0.004	0.195	D>M: 0.005 C>M: 0.005				
	Hand	**Whole**					3.116	0.053	0.111	M>D: 0.014	3.314	0.045	0.117	D>M: 0.033				
		Seed	4.259	0.02	0.146	D>C: 0.024 *D>M: 0.075*									3.76	0.03	0.131	D>M: 0.008
		plIC	4.189	0.021	0.144	D>M: 0.006					3.685	0.032	0.128	D>M: 0.006				
	Head	**Whole**	5.447	0.007	0.179	D>M: 0.006 *D>C: 0.081*												
		Seed	5.441	0.007	0.179	D>M: 0.024 D>C: 0.017												
		plIC	4.384	0.018	0.149	D>M: 0.009												
	Leg	**Whole**	4.692	0.014	0.158	D>M: 0.045												
		plIC	3.813	0.029	0.132	D>M: 0.032												
Left	**Trunk**	**Whole**	3.796	0.029	0.132	D>M: 0.022												
	Hand	**Seed**	4.246	0.02	0.145	D>M: 0.008	3.101	0.054	0.11	M>D: 0.052	3.65	0.033	0.127	*D>M: 0.059*	3.76	0.03	0.131	D>M: 0.006
	Leg	**Seed**									3.311	0.045	0.117	C>D: 0.041				

Table 3.2 Statistical results of the group contrasts with age and sex included.

F-values, p-values and partial eta squared (Partη^2) and the Tukey adjusted p-values are reported in the appropriate column. P-values slightly above the significant threshold of 0.05 are reported in italics. The columns F, p and Partη^2 indicate the values of the type II ANCOVAs with dancers (D), musicians (M) and controls (C) as levels for the factor GROUP, and age and sex included as covariates; the columns Tukey indicate the p-values of the post-hoc Tukey tests in addition to the directionality of group difference (e.g., D>M meaning dancers greater than musicians).
ROI = region of interest; Whole = whole tract (seeded in the corresponding Seed column); Seed = white matter seed ROI; plIC = posterior limb of internal capsule. FA = fractional anisotropy; RD = radial diffusivity; V_{un} = volume of the union tract; V_{disp} = volume of the tract dispersion.

Correlations with dance or music training

For the whole tracts of the hand, trunk and leg regions, where the groups differed, we examined the correlations of training variables with DTI and volume measures. Younger age of start for dancers was correlated with increased RD in the whole right trunk/arm tract, while younger age of start for musicians was associated with higher FA. No volumetric measures correlated with age of start of dance or music training. Of note, DTI measures were related to age of training start but not with years of training, despite age of start and years of training were correlated for both dancers ($r = -.59$, $p = .013$) and musicians ($r = -.863$, $p < .0001$). In summary, consistent with the group differences, these results suggest that early start of dance training is associated with increased RD, whereas early start of music training is associated with increased FA.

Correlations with dance or musical task performance

In order to confirm that the most relevant WM differences were related to dance and musical abilities, we calculated the partial correlations between quantitative measures, extracted from the entire hand, trunk and leg tracts in the right hemisphere, and performance on the dance and melody tasks (Karpati et al., 2016). Age and sex were included in the model as variables of no interest. As shown in Table 3 and Fig. 4, RD and the volume were positively correlated with performance on the dance task and negatively correlated with performance on the melody task, whereas FA did not correlate with any measure of task performance. In particular, in the entire right trunk tract, V_{un} was positively correlated with dance performance, while RD was negatively correlated with melody performance. Moreover, in the right leg tract, dance performance was positively correlated with RD across the whole tract.

Right Tract	**Age of dance training start**		**Age of music training start**		**Dance performance (% correct)**				**Melody performance (% correct)**	
	RD		**FA**		**RD**		**V_{un}**		**RD**	
	r	**p**	**r**	**P**	**r**	**p**	**r**	**P**	**R**	**P**
Trunk	-0.51	0.034	-0.52	0.037			0.33	0.015	-0.27	0.048
Leg					0.32	0.019				

Table 3.3 Significant brain- behavioral correlations for the tracts seeded in the right trunk and leg.

RD = Radial diffusivity; FA = fractional anisotropy; V_{un} = volume of the tract union; r = Pearson's correlation coefficient; p = p-value; % correct = percent correct.

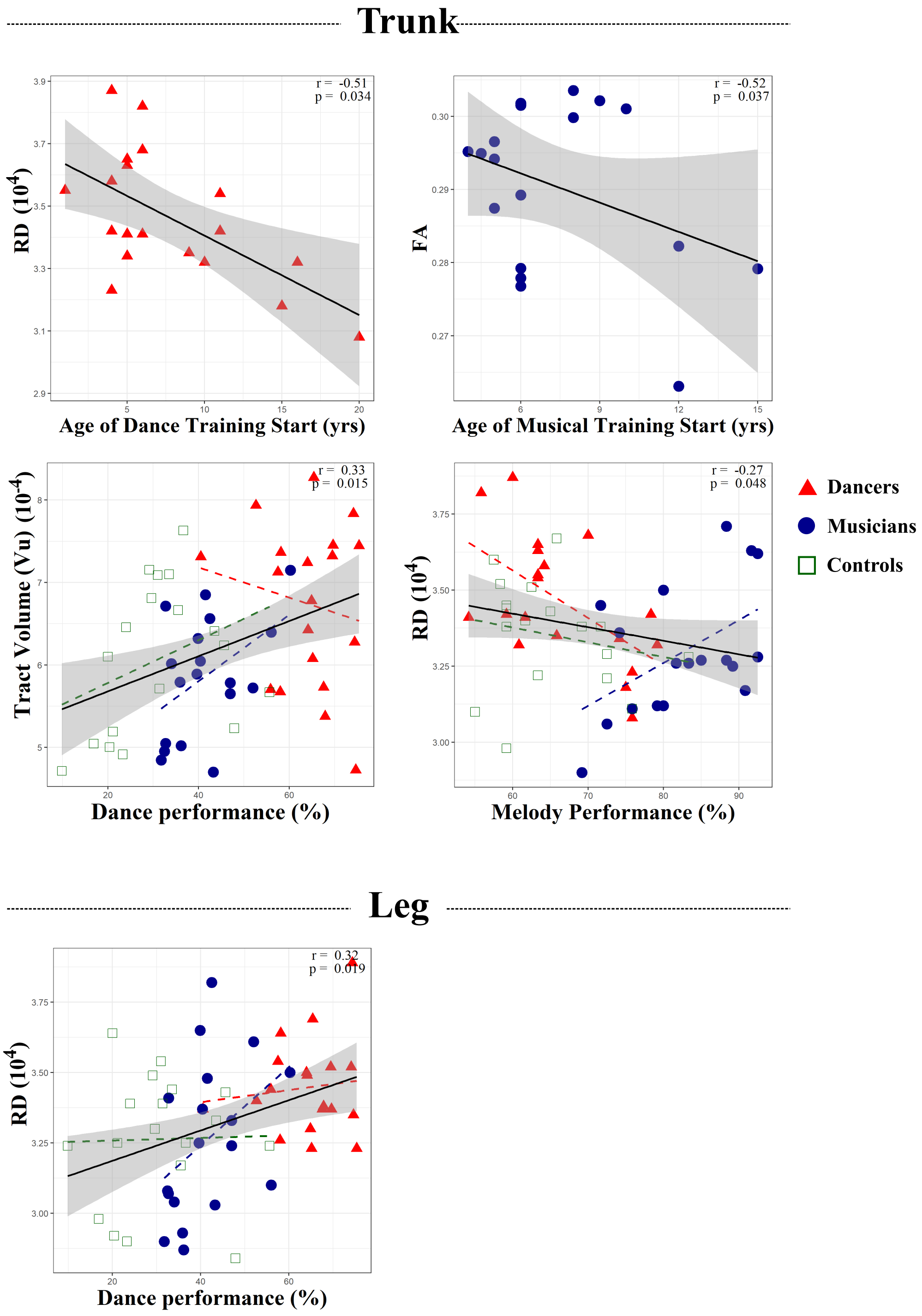

Figure 3.4 Correlations between WM and behavioral measures for the tracts seeded in the right trunk and leg.

The dance-related measures are shown on the left column; the music-related measures are on the right. Shadows show the standard errors. RD = radial diffusivity; FA = fractional anisotropy; V_{un} = volume of the union tract; r = Pearson's correlation coefficient; p = p-value; % = percent correct.

3.5 Discussion

Using probabilistic two-fiber tractography, we showed that dancers had greater diffusivity (especially RD) in the primary motor pathways for all body regions in comparison to musicians, particularly in the right hemisphere. In contrast, musicians had greater anisotropy (FA) in the right hand and the trunk/arm tracts. Further, dancers had greater tract and dispersion volumes in these regions compared to both the other groups. The greater diffusivity and larger volumes observed in dancers might reflect increased fiber orientation dispersion, especially in proximity to the cortex, or increased axon diameter. In contrast, the higher FA values in musicians suggest increased coherence and packing of the fibers connecting the hand and arm motor representations. This confirms our hypothesis that dancers have broader connectivity in a larger number of regions, while musicians have more focused connections (Giacosa et al., 2016). Importantly, the observed differences in RD and FA were negatively correlated with the age of start of dance or music training, respectively. Finally, better dance performance was associated with increased diffusivity and volumetric measures, while better melody performance was associated with reduced RD.

Consistent with our previous study (Giacosa et al., 2016), we show that mean RD for dancers was higher in most of the primary motor pathways, particularly on the right. Increased RD in dancers might indicate enlarged axon diameter or enhanced fanning of the fiber bundles and is compatible with a previous study comparing ballet dancers with handball players (Meier et al., 2016). Greater RD might result from use-dependent enlargement of axon diameter (Chéreau et al., 2017), and fibers with larger axon diameters are less packed, which would also contribute to increased RD. Higher RD is also compatible with greater fiber bundle branching or dispersion of fiber orientation. Greater branching in dancers might result from broader connectivity among representations of different body parts. Co-occurring movements are represented together in the primary motor cortex (Nudo et al., 1996); moreover, in the corticospinal tract, neurons originating in distinct, even non-contiguous, portions of M1 can converge, projecting to the same motor-neuron in the spinal cord (Hammond, 2002). Therefore, the extraordinary variety of movement combinations learnt by dancers might lead to the encoding of a larger number of co-occuring movements and greater complexity of motor connections that would contribute to increasing the fanning of fibers. We observed higher RD in most tracts of dancers, in particular in the right leg. The leg tract is of peculiar relevance, given its fundamental involvement in dance training. This is consistent with Meier's and colleagues work (Meier et al., 2016), showing higher RD in the leg/foot component of ballet dancers' CST in comparison to handball players. Similar results were observed in the right head tract, where dancers showed increased RD, compared to both other groups. However, given the inherent non-specificity of diffusion measures (O'Donnell and Pasternak, 2015), we cannot exclude other possible explanations for higher RD, such as: decreased myelin thickness, changes in the axonal membrane permeability and internode distance (Sampaio-Baptista and Johansen-Berg, 2017).

In comparison to dancers, musicians had higher FA values in the right hand and trunk/arm tracts. The result of concurrent higher FA in musicians and higher RD in dancers is consistent with previous findings in the CST when comparing dancers to musicians and other athletes (Giacosa et al., 2016; Meier et al., 2016). Importantly, musicians' FA values were also higher than controls in the trunk/arm tract, indicating that these changes were specific to musicians, and not just relative to the RD increases in dancers. Higher FA in the right CST (or plIC) has been previously shown in musicians in comparison to controls (Acer et al., 2018; Han et al., 2009; Rüber et al., 2015, but see: Imfeld et al., 2009; Schmithorst and Wilke, 2002), and it was associated with music training in childhood (Bengtsson et al., 2005). Here, the combination of higher FA and similar tract volume in musicians might be explained with increased coherence and packing of fibers (Wan and Schlaug, 2010; Zatorre et al., 2012; Sampaio-Baptista and Johansen-Berg, 2017). Indeed, musicians' specific training might increase the variety of movement representations within a single effector representation (e.g., hand), thus strengthening only those specific connections. The same findings can also be considered from the prospective that dancers, in both these tracts, showed lower FA and larger volume in comparison to musicians. Lower FA was previously observed in dancers and gymnasts (Hänggi et al., 2010; Huang et al., 2013; Giacosa et al., 2016; Meier et al., 2016; Burzynska et al., 2017) in comparison with non-dancers. The combination of bigger volume and lower FA in dancers supports the hypothesis of axon diameter augmentation with reduced packing of fibers, perhaps in combination with broader bundle fanning (see the concept of M1 fiber convergence in Hammond, 2002). Taken together, our results demonstrate different types of plastic changes in the white matter of musicians and dancers: music training is associated with higher FA which can be interpreted as stronger connectivity related to the specific effector trained, whereas dance training is associated with higher RD which can be interpreted as enhanced connectivity across many effectors.

The finding that WM differences between dancers and musicians are predominantly right sided is consistent with the whole brain findings of our previous study (Giacosa et al., 2016). While structural changes have also been observed in the left hemisphere both in our study and others, (Hänggi et al., 2010; Meier et al., 2016; Burzynska et al., 2017), we hypothesize that greater changes on the right are the result of greater training of the non-dominant left hand (Rüber et al., 2013), and the complexity and bilateral coordination of movements learned. For example, increased movement coordination and complexity likely require broader functional bilateral activity (Horenstein et al., 2009; Noble et al., 2014), and increasing complexity of finger tapping sequences was correlated with increased ipsilateral activation of motor regions (Harrington and Alan Fine, 2000; Verstynen et al., 2005).

Importantly, correlations with age of training start give support to our findings. Younger age of start of dance training was negatively correlated with RD values in the entire right trunk tract, indicating that the earlier dance training started, the greater was the fiber orientation dispersion. In the same tract, age of start of music training was negatively correlated with FA, indicating that the earlier music training started, the more coherent were the fibers. Further, larger tract volumes were associated with better performance in the dance task. These correlations validate a stronger association between dance training and fiber orientation dispersion and axonal enlargement, in contrast to an association between music training and changes in fiber coherence and packing.

Considering that the same tract may present different fiber bundle configurations at different levels, one of the goals of the present study was to examine the primary motor pathways both where the tracts enter the cortex (seed ROIs) and at the level of the plIC. Thinking of the fiber bundle as tree-shaped, in the plIC, all fibers converge and run parallel to each other, like in the tree trunk; in contrast, in the seed regions, the multiplicity of neurons leaving the cortex constitutes the broad branching foliage of the fiber bundles (Fig. 4.4.1). In the present study, in the right plIC of the head and hand tracts, dancers had higher RD and V_{un} in comparison to musicians. Dancers' larger motor axons, although more packed in the lower tract portions of the plIC compared to the seed regions, might be less organized than the highly packed fibers of musicians, resulting in increased RD and larger volume. In addition, their more extensive combination of co-executed movements might require several M1 fibers to connect to the same motor-neurons, possibly explaining the "thicker tree-trunk", or bigger plIC volume. In contrast, musicians' trunk/arm plIC had lower RD values and smaller volume compared to both dancers and controls. This could reflect particularly myelinated, coherent and packed fibers, supporting the hypothesis of a more sharply defined tract morphology in the CST of musicians, as suggested by Oechslin et al. (2017).

Another interesting finding is that dancers showed higher RD and V_{disp} in the hand and trunk seed ROIs bilaterally. It is worth reminding that each fiber tract was tracked bi-directionally, from the seed to the target and vice versa. Thus, the V_{disp} included only the voxels that contained the non-overlapping streamlines obtained from tracking in only one of the two directions, i.e. from seed to target or the opposite (dispersion tract, T_{disp}). The increased dispersion of fiber orientation is likely the consequence of microstructural properties, such as greater incoherence of fibers in dancers. This might be particularly true in the seed regions, not only because these are larger ROIs than the cerebral peduncles, but also because they lie right below the cortex, where is the maximal incoherence of fibers. Furthermore, the greater V_{disp} observed in dancers might reflect their increased fiber orientation dispersion, or the fact that the tracts might be more easily identified in one direction or the other (from the cortex to the cerebral peduncles or the opposite).

Training effects or pre-existing differences?

Differences in brain structure between dancers and musicians have generally been attributed to long and intensive training. However, it is more likely that they result from an interaction between training-induced plasticity and pre-existing differences in physical characteristics, brain structure or personality traits that predispose certain people to engage in one or the other discipline (see (Penhune, 2019). However, while comparisons between trained and non-trained groups might be confounded by differences in environmental factors such as motivation, familiarity, or personality traits like perseverance, given the similar intensity of training required by both disciplines, it is highly plausible that such factors are similar in dancers and musicians. Therefore, the brain differences observed between these groups are more likely attributable to the specific training. Future longitudinal or targeted cross-sectional studies may more directly address the issue of distinguishing between the training-induced changes versus predispositions.

Advantages of our methodological procedure

The procedure we developed to identify the sub-regions of M1 has several advantages. First, the identification of ROIs was both individual specific and consistent across groups. Another advantage is that placing these ROIs in the WM ensures more reliable tracking because the principal diffusion directions are more certain in WM than in the cortex. Most importantly, these ROIs allowed us to separately track each pathway from the specific region of M1. Finally, analyzing diffusion measures at the level of both the IC and cortex provided us with additional information about the tract structure. Of course, our sub-division of M1 is a simplified model because the descending motor pathways actually originate in overlapping body part representations, located not only in M1, but also in the premotor, supplementary motor and somatosensory (post-central) regions (Murray and Coulter, 1981; Nudo and Masterton, 1990; Dum and Strick, 1991, 2005; Porter and Lemon, 1995). Nonetheless, this approach could still be useful for other experimental or clinical studies that aim to identify specific components of the descending motor pathways, for example to examine effector-specific outcomes of rehabilitation. In the future, functional data could be used to identify the location and extent of each body part representation.

3.6 Conclusions

In this paper, we developed a novel approach to compare descending motor pathways in dancers and musicians. We found that dancers have higher diffusivity values and larger tract volume across most regions, with evidence for increased fiber bundle fanning at the level of the cortex, and larger axon diameter at the level of the internal capsule. Conversely, musicians showed increased FA in the hand and trunk/arm tracts, indicating that they have increased coherence and packing of the fibers that specifically connect the effectors they trained over time. Correlations with age-of-start of training and performance on dance and music tasks indicate that these structural changes are directly linked to specialized training of dancers and musicians. Taken together, our findings support the hypothesis that different types of training have different effects on brain structure.

CHAPTER 4

General Discussion

4.1 Overview

The purpose of this dissertation is to compare the WM structure of dancers and musicians and relate it to their specific training and acquired skills. In Study 1, a variety of DTI metrics were examined together, at a whole-brain level, in dancers, musicians and controls, and related to performance on a dance and a melody task. In Study 2, the descending primary motor pathways from the hand, trunk/arm, leg and head regions were examined. These analyses were performed on selected DTI and volume metrics in both hemispheres. WM metrics were also correlated with task performance and age of start of training.

4.2 Summary of our findings

Across the whole brain, dancers showed increased diffusivity (especially RD) and reduced anisotropy (FA, MO) in comparison to musicians in a variety of WM regions, including projection (such as the CST or, more generally, the descending motor pathways), associative (SLF) or interhemispheric (CC) fibers that constitute sensorimotor networks. The extracted mean analyses revealed that most of the structural modifications occurred in dancers. In comparison, musicians had higher FA and lower RD in the same regions, suggesting increased coherence and packing of fibers. Further, in regions where multiple fiber bundles cross, musicians had an increased proportion of primary fibers (F1), indicates that these structural alterations might concern a particular fiber bundle, leaving the others unchanged. Consistent with these results, the analyses of the descending motor pathways in Study 2 showed that dancers had increased RD compared to musicians and, in some portions, to controls too. FA increases in musicians were localized to the right hand and trunk/arm tracts, particularly relevant to their specific training. Further, dancers had greater tract and dispersion volumes compared to the other groups. The combination of dancers' greater volumes and higher RD points toward their greater dispersion of fiber orientations or larger axonal diameter. In both studies, group differences were especially evident in the right hemisphere, ranging from completely lateralized changes for FA to more symmetrical ones for RD and MD.

It is crucial to remember that in our sample, dancers and musicians were well matched in years of training and hours of current practice. Therefore, the structural changes observed can be more directly linked to specific training. Importantly, for the first time in studies of dancers, DTI and volume metrics were related to performance on tasks that characterized the groups. Across both studies, performance on the dance task showed an opposite direction of correlation with DTI metrics compared to melody performance. This suggests that acquisition of dance and music skills has a differential impact on WM structure. Moreover, in the trunk motor tract, age of training start was negatively related to RD in dancers and to FA in musicians, which indicates a direct relation between the structural changes observed and training.

4.3 Interpretations

4.3.1 Comparison with previous literature

The most general finding of the present dissertation is that dancers showed reduced anisotropy (FA and MO) and increased diffusivity metrics (RD, AD and MD) in comparison to musicians, and at a lower threshold, with controls. We hypothesize that these findings might reflect an enhanced connectivity with enlarged axons and increased heterogeneity of fiber orientation across broader regions in dancers, in contrast to more focused enhancements related to the trained effectors in musicians. Our findings are consistent with other studies that showed reduced FA in subjects with long-term motor training of the whole-body (Jäncke et al., 2009; Hänggi et al., 2010; Burzynska et al., 2017; Meier et al., 2016; Huang et al., 2013, but see Hänggi et al., 2015 for different direction of FA changes). In contrast, subjects with short-term motor training of specific effectors showed increased FA (Scholz et al., 2009; Palmer et al., 2013; Wang et al., 2014), with the only exception for short-term whole-body balance training (Taubert et al., 2010). On the other hand, the finding of increased FA in musicians in comparison to dancers is consistent with other research (Rüber et al., 2013; Steele et al., 2013; Halwani et al., 2011; Han et al., 2009). These WM findings are not as straightforward as GM, where training more consistently results in increased volume or cortical thickness. This may be due to the effects of intensive whole-body training on a broad range of WM pathways that result in structural changes, including greater heterogeneity of fiber orientation and larger calibre fibres. It may also be due to multiple physiological properties of WM, which may be affected by training and reflected in DTI metrics (see discussion below), and to different fiber bundles involved (Schmithorst and Wilke, 2002; Steele et al., 2012; Acer et al., 2018).

In our studies, the FA decreases observed in dancers were mostly driven by RD increases. FA is typically inversely correlated with RD and such a relationship in training-related studies has been observed in musicians (Steele et al., 2012; Vollmann et al., 2014) and after a short-term training of finger-thumb movements (Reid et al., 2017). However, the only other study reporting multiple DTI metrics did not show any global differences in RD when comparing dancers to controls and handball players (Meier et al., 2016). Nonetheless, more specific analyses revealed higher RD values in the foot CST tract of dancers, in comparison to the higher RD values in the hand tract of handball players. These relations were reversed for FA in the same tracts. Meier et al. (2016) regarded this result as evidence for a direct relation between the type of training and changes in DTI metrics. We attempted to replicate this interesting finding by comparing the hand and leg tracts of the CST in dancers and musicians but did not find consistent results. There might be multiple reasons contributing to such lack of compatibility between Meier's and our studies. First, the comparison between dancers and handball players is between two groups of athletes who train their whole-body, with a particular focus on a specific effector (feet and hands respectively). In our study, instead, the primary goal was to compare dancers with musicians, whose main distinction in motor training depends on the engagement of the whole body *versus* a specific effector. Secondly, while our tractography analyses were seeded in WM regions, Meier's were started in regions that included GM, which leads to less reliable tracking. Importantly, the pathways tracked in Meier's study included tracts seeded in both in the primary motor precentral regions (M1) and the sensory postcentral cortex (S1). On the contrary, our focus was on the motor pathways descending from M1 to the brainstem. If the aim was to include all the motor fibers, we should have included also fibers seeded in premotor and supplementary motor regions, beyond those coming from S1. However, most of the fibers seeded in S1 come from the thalamus, therefore, without specific functional data, including such pathways would have reduced the specificity and reliability of our study. Finally, on a more technical perspective, while Meier et al. excluded overlapping voxels in order to compare "pure" tract portions, our first goal was to compare the entire tract portions between groups, therefore in our approach we didn't distinguish overlapping from unique sub-portions of each tract component.

Among the various tracts that differed between dancers and musicians in Study 1, of particular relevance are: the descending primary motor pathways (including the CST), the SLF and the CC. All of these bundles cross each other in multiple locations, making it difficult to attribute changes to a single tract (see Steele et al., 2012). In the primary motor pathways, dancers showed increased RD in Study 1, and greater volumes for all tract portions in comparison to musicians in Study 2. Specific increases of FA in musicians were observed in the right hand and trunk/arm tracts. This is consistent with previous work on dancers and subjects who followed a short-term motor training, showing an effect of training on the specific trained-related structures (Meier et al., 2016; Taubert et al., 2016; Landi et al., 2011; Bangert and Schlaug, 2006; Elbert et al., 1995) and functional representations (Pascual-Leone and Torres, 1993; Pascual-Leone et al., 1995; Svensson et al., 2003; Adkins et al., 2006).

We also found decreased FA in the SLF of dancers relative to musicians, which is consistent with findings observed in gymnasts (Huang et al., 2013). The SLF is an associative fiber bundle that connects frontal and temporo-parietal regions that is composed of multiple bundles belonging to the action-observation network (AON), the vestibular network and the arcuate fasciculus. Given its structural and functional heterogeneousness, the changes that we observe at a global level of the entire fasciculus may result from the combination of distinct effects on each portion. In particular, the SLF bundles, part of the AON, might develop, with training, greater efficiency, possibly conveyed by fibers with larger axon diameter. In fact, the AON is a network of neurons that fire during observation and execution of actions or movements (Buccino et al., 2001; Calvo-Merino et al., 2005; Cross et al., 2009b; Grafton, 2009; Caspers et al., 2010; Cross et al., 2006) as well as their mental visualization (or imagery) (Grèzes and Decety, 2001; Cross et al., 2006). This network is crucial for dance learning, which is largely based on imitation and motor rehearsal (Cross et al., 2006). Interestingly, Bar and DeSouza (2016) recently investigated the changes in brain activity as dancers learned to perform a new choreography. They found that neural activity was increased in the supplementary motor area (SMA, part of the AON) and auditory regions during the early "rehearsal" phase of training, but decreased in the long-term "performing" phase, following the typical inverted-U-shaped learning curve. This suggests that the cortical network engaged during motor learning – which includes the SMA and auditory regions, as well as the SLF – might become more efficient with long-term training, possibly through changes in the combination or weight of connections (Bar and DeSouza, 2016). Therefore, the FA decreases and RD increases that we observed in dancers might reflect such connectivity changes related to long-term plasticity.

In Study 1, we also showed that AD and RD were higher, while MO and F1 were lower, in the CC of dancers compared to musicians. The CC, connecting homologous regions of the two hemispheres, is responsible for the motor coordination between the two sides of the body (Steele et al., 2013; Schmithorst and Wilke, 2002; Johansen-Berg et al., 2007; Gerloff and Andres, 2002; Gooijers and Swinnen, 2014). Interhemispheric connectivity plays a crucial role in bilateral coordination abilities, fundamental for both dance and music performance. Therefore, dancers might have broadened connectivity among all the body part representations, possibly inducing increased fiber fanning, in contrast to the greater fiber coherence of musicians. To further investigate whether dancers had enhanced interhemispheric connections between cortical representations of all body parts, we performed additional tractography analyses not included in Study 2. There, we used tractography to examine the CC bundles connecting all contralateral body part motor representation in dancers and musicians. Our hypothesis was that dancers whole-body training would strengthen the connections among all different body parts, whereas musicians bimanual motor training would enhance connectivity between the hand representations, maybe extending to the trunk/arm. We tested this hypothesis with two approaches: 1) tracking from each joint seed ROI through the mid-body of the CC, 2) and specifically tracking from each joint seed ROI toward each contralateral joint representation; in both approaches DTI and volumetric values were then extracted from relevant ROIs located at the seed, target and regions of crossing with the descending motor pathways. Unfortunately, the results did not provide any support for this hypothesis, showing unclear patterns of group differences, that were inconsistent between the two approaches. Nonetheless, similarly to Study 1 and 2, diffusivity was generally increased in dancers and reduced in musicians while FA had the opposite trend. This corroborates the idea that dance training may contribute to develop broader general connectivity between motor regions.

4.3.2 Dance and music training have different structural WM correlates

One of the main findings of the present work is that multiple WM structures, including the primary motor pathways (Study 2), differ between dancers and musicians and performance on dance and melody tasks had opposite relationships with DTI metrics. Given that, in our sample, dancers and musicians had a comparable amount of training, the observed WM differences can more confidently be attributed to the type of training. There are a few possible explanations for these opposite results: either dance and music training have the same effect on specific portions of the same structures, or they have different effects on the same structures.

Under the first hypothesis, given the similar but specific engagement of the sensorimotor network in dance and music training, it would be reasonable to expect that the connections of the body parts trained in each discipline would be particularly strengthened. Sustained activity is known to reinforce the solicited connections by increasing the speed of information processing (Chéreau et al., 2017), which is frequently underpinned by increased myelination (Waxman, 1980; Hartline and Colman, 2007; Saab and Nave, 2017; Nave, 2010; Fields, 2015; McDougall et al., 2018) . For musicians, the body parts and muscles recruited to play an instrument are usually small and represented contiguously along the motor cortex. Further, the fast and fine movements learnt by musicians require the ability to segregate muscles, represented in adjacent regions on the motor cortex (e.g., fingers), and activate them separately. Such training would mainly strengthen the adjacent fibers of the trained tract (e.g., hand), increasing both myelination and orientation coherence. In contrast, dancers showed opposite FA changes. If a similar reinforcement process occurred in dancers as in musicians, the observed higher RD and lower FA could be attributed to the strengthening of broader connections between more extended cortical body part representations. Many of the complex movements learnt by dancers simultaneously involve body parts with more distant representations along the motor cortex. Each rehearsed movement would therefore reinforce the links between the body parts engaged, broadening the tract connectivity and making the fibers from each region more intertwined with each other and less coherent.

It has also been proposed that the motor cortex does not represent each separate muscle but might represent complex actions, or muscles recruited together (Nudo et al., 1996; Makino et al., 2016). The extraordinary amount of complex whole-body movements learnt by dancers would therefore be underpinned by an increased variety of motor cortical representation of coactive muscles. The motor pathways connecting these amplified motor representations might explain their broadened and intricate motor connections.

Alternatively, it is possible that different types of training affected the same structures in different ways, as suggested by the opposite correlations between DTI metrics and dance or melody performance. Beyond increased myelination, trained connections can also be reinforced by increased axon diameter and axonal branching or sprouting (Zatorre et al., 2012). While increases in fiber coherence and myelination induce an augmentation of FA, larger axon diameter or augmented branching could lead to increases in RD and, consequently, decreases in FA, as we observed in dancers. Hence, whole-body dance training might induce, not only greater heterogeneity of fiber orientation, but also larger axon diameter or axonal branching, in contrast to musicians' more coherent and packed fibers.

Other physiological changes might occur during training that are related to speed and synchronization of neuronal firing. While conduction velocity of single fibres might contribute to the efficiency of pathways, the precise timing of action potentials among fibers of the same network is even more crucial in improving synaptic transmission and information processing (Ford et al., 2015; Fields, 2015). Physiological processes that might adjust the timing of spike arrival between fibers include alterations of node and internode length, number of nodes of Ranvier and local modifications of axonal diameter at the node or of membrane permeability (Ford et al., 2015; Sampaio-Baptista and Johansen-Berg, 2017; Zatorre et al., 2012). For instance, larger diameter and shorter internode distance was observed in the auditory brainstem axons of rodents to precisely tune their conduction velocity and spike timing (Ford et al., 2015). Changes in the node of Ranvier lengths have been proven to affect conduction velocity of 20%, comparable to the amount of change achievable with changes in myelination or internode distance (Arancibia-Cárcamo et al., 2017). Further, changes in nodal length are more energy efficient than changes in myelination thickness or length (Kaller et al., 2017). Therefore, it is possible that distinct optimisations are also needed by different types of training, such as dance and music, because of the different body parts and types of movements involved. The activity of long and short axons of large and distant body parts, like limbs, recruited during dance training, must be precisely synchronized to each other despite their different lengths. In contrast, the signals arriving from the axons of the effectors trained by musicians, such as fingers, must be coordinated to adjacent axons of similar lengths. Further, the fine movements that musicians accomplish with their fingers can become much faster than dancers' limb gross movements. Thus, the diverse synchronization processes needed in dance and music may lead to diverse morphological properties that could vary among similar, or even along the same, axons (Ford et al., 2015; Arancibia-Cárcamo et al., 2017). Moreover, across a life-time training, distinct mechanisms of plasticity might predominate at different ages. While myelination processes are particularly sensitive during childhood, growing of glial cells and branching of unmyelinated axons seem to be the advantaged plastic responses during adulthood (Markham et al., 2010; Zatorre et al., 2012). To study such microscopic scale features, combinations of electron microscopy, immunohistochemistry and electrophysiological analyses have been conducted in animals. In humans, techniques, such as neurite orientation dispersion and density imaging (NODDI) or AxCaliber, are able to measure the myelin thickness (g-ratio) or the axonal diameter (Ellerbrock and Mohammadi, 2018; Zhang et al., 2012; Assaf et al., 2008). Promising models that map MRI signals to microscopy (Stüber et al., 2014; Chen et al., 2017) might be used in the future to deepen the understanding of the dynamic myelination processes undergoing late phases of training.

It is also important to remember that DTI metrics reflect an average measure of the properties of a large number of neurons in any given voxel. This suggests that the differences observed in the descending motor pathways might also be due to changes in the bundles crossing them, such as the interhemispheric fibers of the corpus callosum and the anterior-posterior connections of the superior longitudinal fasciculus. In Study 1, the structural differences between dancers and musicians included association fibers of the SLF that connect posterior sensory to frontal cognitive regions. As described above, the SLF connects sensory and motor regions, as well as the AON, to prefrontal areas that are implicated in memory and other executive functions. Thus the observed differences between dancers and musicians might reflect plasticity in pathways that regulate higher levels of cognitive processing, and are not limited to the sensorimotor systems. The SLF also includes fibers of the arcuate fasciculus, which connects temporal, parietal and frontal regions. The arcuate fasciculus has been related to visuospatial abilities and pitch-based grammar learning (Doricchi et al., 2008; Loui et al., 2011), and structural modifications have been already observed in musicians compared to non-musicians (Halwani et al., 2011).

4.3.3 Further physiological interpretations enriched by the analysis of multiple metrics

In Study 1 and 2, dancers consistently showed lower values of FA in comparison to musicians. This result is consistent with other studies showing reduced FA in dancers or gymnasts compared to laymen or other athlete controls (Meier et al., 2016; Hänggi et al., 2010; Burzynska et al., 2017; Huang et al., 2013). However, as discussed in the Introduction 1.1.4, FA alone is not sufficient to make inferences about the morphological or physiological underpinnings of such differences, since it is influenced by a variety of factors (e.g., axon size, myelin sheath thickness and length, and node of Ranvier characteristics) (Zatorre et al., 2012; Sampaio-Baptista and Johansen-Berg, 2017). Because FA is a composite measure proportional to AD and inversely related to RD, the joint examination of these two metrics can allow a more detailed interpretation of our data. In our sample, in the regions where FA was lower in dancers, RD, and in some cases also AD, was higher. Although AD co-occurred with RD changes in some regions, RD changes were larger than AD ones and therefore have a stronger impact on FA This suggests that FA increases were mostly led by the increases in RD rather than in AD. Physical activity and sensory enrichment are known to boost conduction velocity and myelination (Zatorre et al., 2012; Canu et al., 2009; Ruegg et al., 2003; Hughes et al., 2018), and active neurons will preferentially be selected for myelination (Hines et al., 2015).

Another measure that could be analyzed is MO which was the only metric that differed between dancers and controls in Study 1, showing that it is complementary to FA and is sensitive to changes that other metrics are not able to detect. Despite being rarely reported in literature, MO can be used in combination with MD and FA (see Introduction 1.1.4) to fully represent the ellipsoidal shape of diffusion (Ennis and Kindlmann, 2006). For example, for a constant value of MD, concurrent reductions of FA and MO indicate a more planar (pancake) shape of the ellipsoid (see Fig. 1.1.4), which means that structural changes occur in fiber bundles that lay on a plane. However, it is crucial to remember that the ellipsoid describes diffusion within a single voxel, whereas group contrasts refer to the metric averaged across subjects and across voxels. Therefore, it could be interesting to reconstruct voxelwise glyphs representing the relations between FA, MD and MO (Ennis et al., 2005). Following the glyph orientations across voxels, it is possible to identify the other tracts that differ between groups and this could drive further tractography analyses.

Distinct structural organizations might occur at different tract levels

Another hypothesis to keep in consideration is that microstructural properties, such as axon diameter and internode distance, are not as constant as previously theorized but may vary significantly along the same axon or among similar axons (Ford et al., 2015; Arancibia-Cárcamo et al., 2017). This implies that distinct structural organizations might occur at different levels or portions of the tracts, even in presence of the same metric changes. For instance, increased RD in dancers might be due to the axons with larger diameters at the level of plIC that then branch and thin as they approach their terminals (Fig. 4.1). In contrast, at the seed and whole tract levels, higher RD might be due to greater connectivity among multiple regions. To test this hypothesis, we looked

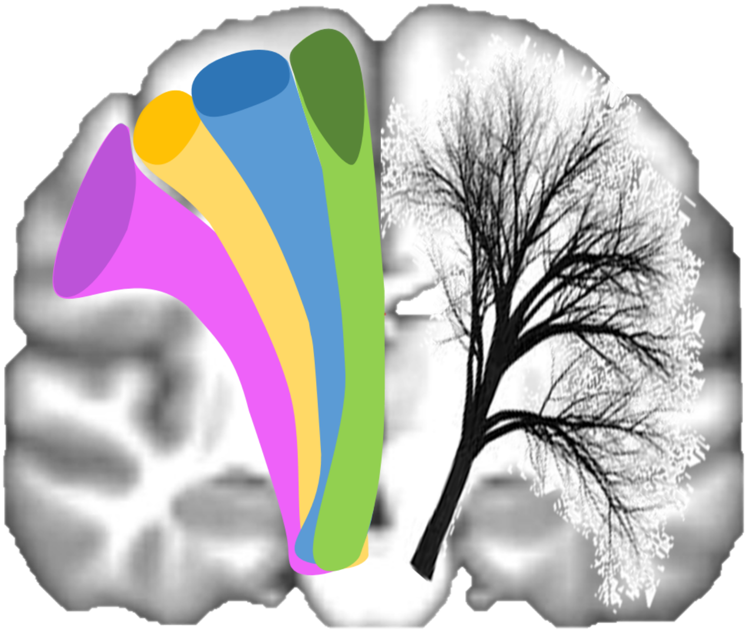

Figure 4.1 Enhanced tree-shape structure of descending motor pathways.

at the measures within the seed regions to see if there is such evidence. We would have predicted that dancers would show greater fanning or complexity of fiber organization. However, no relevant differences between groups were observed in the seed regions. Since the tractography analysis was restricted to the descending motor pathways, the hypothesis of increased branching in dancers should be carefully pondered. The neurons that belong to the motor pathways are divergent fibers that descend from the cortex and target the brainstem or the spinal cord. Therefore, axonal branching would mostly occur at the brainstem or spinal cord level, although we cannot exclude that some branches are formed long before reaching their targets. What could happen in the cerebral white matter is that synergic fibers might communicate via axonal collaterals.

The plIC is a region where there is a lot of overlap between the distinct portions of the descending motor tracts due to its bottleneck shape. This might explain the high consistency of findings, showing dancers higher RD in this ROI, across tract portions. However, despite such overlap, musicians showed different changes in the plIC of the fibers seeded in the trunk/arm, with reduced RD and volume in comparison with both other groups; further, these values correlated with melody performance. This suggests a peculiar relation between music training and the extremely packed and myelinated trunk/arm fibers at the level of the plIC, which might indicate more efficient connections to control arm movements, fundamental for most instrumental players.

4.3.4 Asymmetry

In both our studies, the group differences between dancers and musicians were more prominent in the right hemisphere. More changes in the right hemisphere have been previously observed in musicians compared to non-musicians (Bengtsson et al., 2005; Han et al., 2009; Rüber et al., 2013; Imfeld et al., 2009). To further explore this asymmetry, we performed supplemental analyses comparing FA between hemispheres, at the whole brain level and in an atlas-based extraction of the CST. For both dancers and musicians, we observed a left-greater-than-right asymmetry for FA across hemispheres and in most descending pathways, both at the whole tract and plIC level. A previous study examining the CST also observed this L>R asymmetry, and showed that it was not related to handedness, suggesting that it might be an intrinsic or more genetically determined feature of this pathway (Westerhausen et al., 2007). This raises the possibility that the right hemisphere may be more susceptible to plastic changes driven by experience. This, combined with the fact that both dance and music require extensive training of the non-dominant side of the body might explain why greater differences were observed in the right hemisphere. Further, we observed that the L>R asymmetry of FA was greater in dancers than musicians, both across the whole WM and in the CST. Dance and music performers need to enhance the abilities with their non-dominant body sides and efficiently coordinate their bilateral motor activity (see Schlaug, 2015). Given that the right hemisphere mostly controls the contralateral body side, greater modifications of the right WM in dancers and musicians might be due to a stronger effect of training on the left, non-dominant body side. Despite reporting opposite trends for asymmetry values in musicians and controls, which is consistent with their opposite findings for FA, Imfeld et al. (2009) came to the same conclusion of greater structural changes in one hemisphere related to training. Moreover, increasing movement complexity and coordination is thought to enhance bilateral activity (Horenstein et al., 2009; Noble et al., 2014). Bilateral, in addition to unilateral, training could further stimulate the non-dominant right hemisphere and enhance its structural modifications.

4.3.5 Integration of GM and WM findings

The WM studies reported in this thesis were part of a larger project which also examined GM measures in the same sample (Karpati et al., 2017). The main finding from the GM study was that both dancers and musicians had greater cortical thickness in the right superior and middle temporal gyri in comparison to controls, and that these increases were positively correlated with performance on both the dance and melody tasks across all participants. The superior temporal cortex is involved in multiple functions relevant to both music and dance, from auditory processing and integration with the motor network, to temporal control of movements, action imitation and balance (Mendoza, 2011; Bengtsson and Ullén, 2006; Bangert et al., 2006; Hickok et al., 2003; Bengtsson et al., 2004; Zatorre et al., 2007; Jola et al., 2011; Lappe et al., 2016; Karim et al., 2012; Iacoboni et al., 2001; Tachibana et al., 2011; Molenberghs et al., 2010; Karpati et al., 2017). The WM results of Study 1 did not mirror the GM findings when dancers and musicians differed from controls. However, voxelwise comparison of the two trained groups revealed higher RD and MD for dancers in two clusters subjacent to the right superior temporal gyrus in a region close to the location of the GM findings. These WM clusters comprise the acoustic radiations, according to the Jülich Histological Atlas (Bürgel et al., 2006), which connect the thalamus to the primary auditory cortex (Lee, 2013). Together, these analyses show that dancers and musicians have similar GM modifications compared to untrained subjects, but they differ in WM structures. While the auditory cortex is similarly engaged in the auditory (musical) and multisensory processing of dance and music, the somatotopic organization of the motor cortex (and connected fiber bundles) might accentuate the differences between the effectors used in each discipline. The combination of increased diffusivity in dancers *versus* musicians with increased cortical thickness in both groups compared to controls supports our interpretation that increased RD in dancers is the result of the modification of fiber organization rather than reduced myelination.

While the overlapping changes in auditory regions are interesting, we might have expected GM differences in motor regions corresponding to the observed WM changes. The lack of such finding might be due to the fact that the structural differences in the motor cortex are too subtle to be detected at the whole-brain level. It has been observed that training-related changes in the sensorimotor cortex are locally reorganized within M1 (Kleim et al., 2002), which means that they might not be visible at the scale of the whole brain.

Moreover, the temporal dynamic of changes has not been clearly investigated. In the timescale of days to months, learning induces functional and structural transient changes, which are characterized by an inverted-u-shape pattern (Classen et al., 1998; Pascual-Leone et al., 1995; Bar and DeSouza, 2016; Scholz et al., 2009; Draganski et al., 2004; Makino et al., 2016; Wenger et al., 2017; Chen et al., 2015; Nudo et al., 1996). However, the modifications occurring in the first phases of training might predominantly impact the networks related to learning of novel movements (Conner et al., 2003; Kleim et al., 2004; Taubert et al., 2010; Kaminski et al., 2013) , which do not coincide with those engaged during the execution of well-learnt or repetitive motor tasks (Chen et al., 2012; Taubert et al., 2016; Plautz et al., 2000; Doyon et al., 2009, see Monfils et al., 2005 and Adkins et al., 2006 for reviews) and in later phases of training (Floyer-Lea and Matthews, 2004; Yin et al., 2009; Howe et al., 2011; Kawai et al., 2015). Conversely, the WM connections, established at the beginning of training, might be continuously reinforced with regular stimulation. ROI approaches could be used to verify whether the WM differences observed in Study 2 correspond to local GM or functional changes in the motor representations.

Few studies have shown simultaneous changes in GM and related WM tracts in relation to learning or training. Few weeks of complex visuo-motor training induced changes in GM density and FA in contiguous sensorimotor regions (Scholz et al., 2009; Landi et al., 2011; Taubert et al., 2010), although the magnitude and time courses of GM and WM increases did not correlate (Scholz et al., 2009), nor the direction of changes was coherent between GM and WM in (Taubert et al., 2010). Highly trained dancers showed consistent decreases in GM and WM densities, as well as in FA, in contiguous premotor or parietal regions (Hänggi et al., 2010). However, this finding was not replicated in subsequent studies with dancers, gymnasts and musicians (Huang et al., 2013; Burzynska et al., 2017; Acer et al., 2018), where GM increases were accompanied by FA decreases in not always related regions (Huang et al., 2013; Acer et al., 2018). In musicians, GM changes in comparison to non-musicians seem to be more consistent, showing increased gyrification, cortical thickness, GM volume in auditory, motor, subcortical and cerebellar regions (Schneider et al., 2002, 2005; Bermudez et al., 2009; Foster and Zatorre, 2010b; Gaser and Schlaug, 2003; Vaquero et al., 2016; Hutchinson et al., 2003; Penhune, 2019). However, also in musicians, the direction of WM changes is less coherent (Acer et al., 2018; Rüber et al., 2013; Steele et al., 2013; Halwani et al., 2011; Imfeld et al., 2009; Han et al., 2009; Schmithorst and Wilke, 2002, see Moore et al., 2014 for a review) probably because it incorporates changes of multiple bundles coexisting in a voxel and depends on a variety of concurring microstructural factors (see section 4.3.3 above).

4.3.6 Training effects or pre-existing predispositions?

Across this dissertation, we interpreted the differences between dancers and musicians as related to their training. However, like all other studies in the field, participants self-select into dance and music training, meaning that it is impossible to discern whether the structural differences observed between groups are the cause or the consequence of training. The relative contributions of nature and nurture to expertise has been extensively debated. Studies showing structural changes associated with learning of a new skill support the existence of training-induced plasticity (Draganski et al., 2004; Scholz et al., 2009; Taubert et al., 2010, 2016; Tomassini et al., 2011; Kodama et al., 2018). Specifically, in Study 2, the inverse correlations found between DTI metrics and age of training beginning play in favor of training-induced plasticity. On the other hand, genetic or environmental pre-existing factors may influence training commencement and continuation (Theorell et al., 2015). Evidence for pre-existing neuroanatomical characteristics linked to musical aptitude were reported in a longitudinal study with school-age children, where the volume of Heschl's Gyrus was a stronger predictor of musical aptitude than musical practice (Seither-Preisler et al., 2014). Personality traits such as motivation, openness to experience and psychological flow – the ability to reach a state of highly focussed concentration and absorption in an activity (Nakamura and Csikszentmihalyi, 2002) – have been associated with music practice (Butkovic et al., 2015). Moreover, some aspects of musical aptitude and creativity, as well as musicality, have been linked to genetic components (Ukkola et al., 2009; Ukkola-Vuoti et al., 2013; Mariath et al., 2017; Oikkonen et al., 2016). In studies with twins, Mosing and Ullén have found evidence supporting the influence of genetic predispositions on musical genre, ability, practice and instrument preference (Mosing et al., 2014; Mosing and Ullén, 2018; Ullén et al., 2016), as well as the independence of IQ and basic motor timing from musical practice (Mosing et al., 2016; Ullén et al., 2016). However, a recent study from the same group provided the first and strongest evidence for a causal impact of musical training on brain structure, showing greater cortical thickness and higher FA in keyboard players compared to their non-musician twins (de Manzano and Ullén, 2018). Taken together, this literature indicates that it is likely that both genes and practice contribute to the neuroanatomical differences observed between highly trained and untrained subjects (de Manzano and Ullén, 2018). It is reasonable to conclude that physical and cognitive predispositions are likely to drive children toward the type of training (music, dance, etc.) that is more compatible with their genetic predispositions, and such experience will amplify the pre-existing individual differences (Schellenberg, 2015). Further, gene-environment interaction effects – the modulatory effects of genes in response to the changing environment – are likely also relevant. Indeed, both genetic and shared environmental factors have increasing influence on cognition across the lifespan (Tucker-Drob and Briley, 2014). Thus, a musically enriched environment during childhood has the potential to exaggerate the individual differences in musical achievement (Wesseldijk et al., 2019).

4.3.7 Methodological considerations and future directions

The research project here presented was the first one to compare dance to another type of intensive training with differential involvement and integration of the visual, auditory and motor systems. In addition, a novel combination of multiple approaches was developed, in Study 2, to track the portions of the motor pathways from the head, hand trunk and leg. Other scholars have previously analyzed ROIs within a tract or portions of tracts using coordinates from other functional studies (e.g. Sehm et al., 2016; Meier et al., 2016). However, this is the first time that the entire motor cortex has been segregated into regions corresponding to the main body parts, according to the topographical organization of the homunculus, without functional data. Moreover, portions of the descending motor pathways have been separately tracked from each WM seed region subjacent to the GM motor parcellation, allowing for the independent analysis of the motor tract components that control each specific body part. It's worth noting that tracking from the WM below the motor cortex gives more reliable results than tracking from a cortical region, because the low values of FA within GM are hardly interpretable in terms of fiber orientations.

Nonetheless, both studies present some methodological limitations. Given the predominance of women in the dancer population, a big challenge in this project was to include an adequate number of men dancers in our sample. Since it is well-known that sex differences may influence brain structure (Ritchie et al., 2018; Ingalhalikar et al., 2014; Sowell et al., 2007; Ruigrok et al., 2014), to avoid the confounding effects of sex we matched the male/female ratio across groups and controlled for sex in all analyses.

In Study 1, the DTI-based TBSS approach used has the intrinsic drawbacks of not being sensitive to multiple fiber bundle orientations co-existing in a voxel and of not being able to discriminate the specific tracts affected by group modifications. Although, with tractography, in Study 2 it was possible to select the voxels through which the tracts of interest pass, we cannot exclude that other fiber bundles traverse some of the same voxels. Therefore, although tractography allows better tract identification, crossing fibers can still have potential confounding effects one the DTI metrics calculated across voxels. To overcome such issues, more advanced techniques should be used. Of particular interest, a recent combination of neurite orientation dispersion and density imaging (NODDI) with myelin water imaging (MWI) allowed for the *in vivo* mapping of the whole human brain g-ratio, which is a voxelwise index of the ratio between the axon and myelin volume fractions respectively (Jung et al., 2018). Other methods, such as AxCaliber, permit to measure the axon diameter distribution (without myelin sheaths) (Assaf et al., 2008), whereas magnetization transfer (MT) provides an index of the myelin content (Schmierer et al., 2004) within each voxel of the entire brain. Another novel promising technique, called Spectral Confocal Reflectance Microscopy, uses the spectral reflectance from the myelin multilayered sheaths wrapped around axons, to visualize 3D *in vivo* maps of axons, myelin sheaths and even nodes of Ranvier at a nanoscale (Schain et al., 2014; Kwon et al., 2017). Such method should be applicable to the human cerebral cortex (Schain et al., 2014).

Another limitation of the tractography approach in Study 2 is that the tracts from each body part partially overlap, notably in the plIC. One possibility to overcome this issue would be to segregate the overlapping portions and analyze them separately. However, the fact that we obtained differences at the whole tract level between the different body parts suggests that such overlaps did not strongly affect our results. Conversely, the hand and trunk tracts showed more similar results and could thus be interpreted together. Such clustering would still be coherent with our interpretations, since the trunk might include the arm representation.

One of the main questions that this dissertation, and most of the literature about training-related brain changes, aims to answer is whether and to what extent training causes changes in the brain. Traditional approaches try to investigate this question by examining associative relationships, which should not be mistaken for causal relationships. Statistics alone cannot answer causal questions. Recently, causal inference methods have gained in popularity to disentangle spurious associations and to estimate the true causal effects. The starting point of a causal analysis is a graphical model, called causal model, that represents the causal relationships assumed by the researcher. Causal models may be tested against experimental data to validate the assumptions. Once a causal model has been adopted, mathematical rules can be used to compute the causal effects. However, depending on the particular configuration of the causal model and the available data, not all the causal relationships of the model might be solvable. It would be interesting to apply this approach to this project to assess the causal relationships between training and brain structure (Pearl, 2009).

4.4 Conclusions

This is the first research project that compared the brain structure between highly trained dancers and musicians and linked the observed structural changes to specific measures of the acquired abilities and age of training start. Comparing brain structure in such similar but unique domains of training contributes to deepening our knowledge about experience-related plasticity. In Study 1, the concurrent analysis of a complementary set of DTI metrics has provided a more thorough understanding of the complex neuroanatomical configurations that differ between groups. In Study 2, the novel approach developed to segregate M1 and the subjacent WM allowed us to examine effector-specific components of the primary motor tracts. Together, our results showed that different types of training may result in distinct structural modifications. In particular, dance training seems to increase the heterogeneity of fiber orientation and axonal diameter, while music training seems to reinforce more coherent fibers connecting the trained effectors, such as the descending motor tracts linked to the hand. Importantly, this demonstrates that training does not necessarily induce increases in WM structures. On the contrary, training-related structural changes are more complex and need to be carefully evaluated. Crucially, the observed correlations between DTI metrics and measures of dance and music skills support our interpretation that these WM differences are related to specific training. Finally, this work is consistent with literature showing the influence of training experience on brain plasticity, but does not exclude potential interactions of training experience with pre-existing factors.

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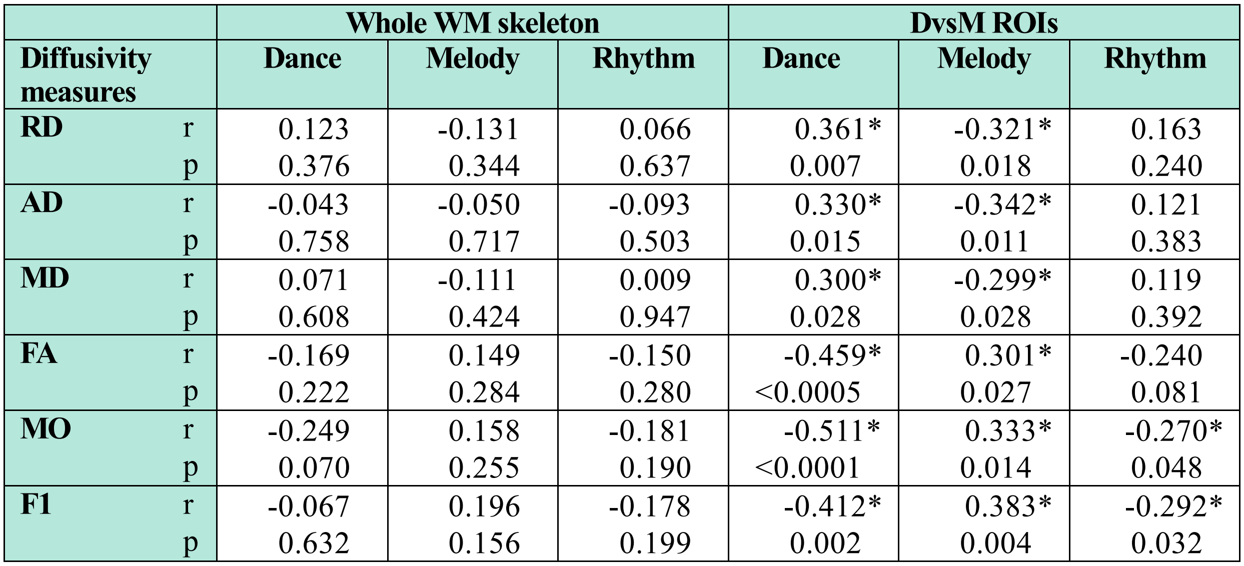
APPENDIX A

Supplementary Material for Study 1

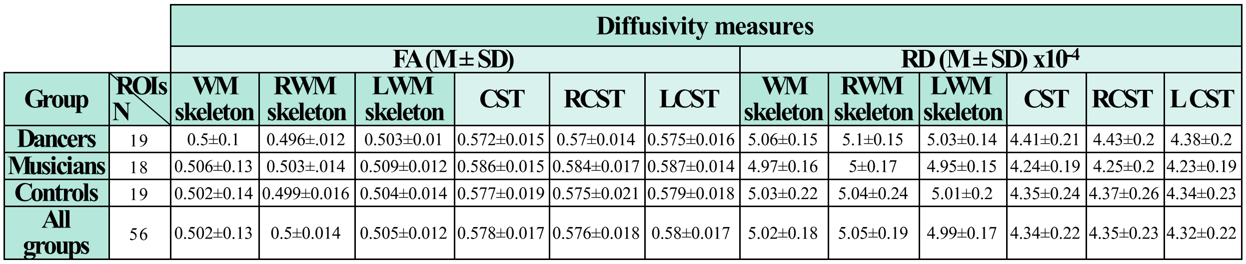
Supplementary Tables



Diffusivity measures		Whole WM skeleton			DvsM ROIs		
		Dance	Melody	Rhythm	Dance	Melody	Rhythm
RD	r	0.123	-0.131	0.066	0.361*	-0.321*	0.163
	p	0.376	0.344	0.637	0.007	0.018	0.240
AD	r	-0.043	-0.050	-0.093	0.330*	-0.342*	0.121
	p	0.758	0.717	0.503	0.015	0.011	0.383
MD	r	0.071	-0.111	0.009	0.300*	-0.299*	0.119
	p	0.608	0.424	0.947	0.028	0.028	0.392
FA	r	-0.169	0.149	-0.150	-0.459*	0.301*	-0.240
	p	0.222	0.284	0.280	<0.0005	0.027	0.081
MO	r	-0.249	0.158	-0.181	-0.511*	0.333*	-0.270*
	p	0.070	0.255	0.190	<0.0001	0.014	0.048
F1	r	-0.067	0.196	-0.178	-0.412*	0.383*	-0.292*
	p	0.632	0.156	0.199	0.002	0.004	0.032

Table A1 Partial correlations between diffusivity measures and task performance.

Age and sex are included as covariates of no interest. Significant values are marked with . r = Pearson's correlations; WM = white matter; DvsM ROIs = 'Dancers versus Musicians' regions of interest.



		Diffusivity measures											
		FA (M ± SD)						RD (M ± SD) x10^{-4}					
Group	**ROIs N**	**WM skeleton**	**RWM skeleton**	**LWM skeleton**	**CST**	**RCST**	**LCST**	**WM skeleton**	**RWM skeleton**	**LWM skeleton**	**CST**	**RCST**	**L CST**
Dancers	19	0.5±0.1	0.496±.012	0.503±0.01	0.572±0.015	0.57±0.014	0.575±0.016	5.06±0.15	5.1±0.15	5.03±0.14	4.41±0.21	4.43±0.2	4.38±0.2
Musicians	18	0.506±0.13	0.503±.014	0.509±0.012	0.586±0.015	0.584±0.017	0.587±0.014	4.97±0.16	5±0.17	4.95±0.15	4.24±0.19	4.25±0.2	4.23±0.19
Controls	19	0.502±0.14	0.499±0.016	0.504±0.014	0.577±0.019	0.575±0.021	0.579±0.018	5.03±0.22	5.04±0.24	5.01±0.2	4.35±0.24	4.37±0.26	4.34±0.23
All groups	56	0.502±0.13	0.5±0.014	0.505±0.012	0.578±0.017	0.576±0.018	0.58±0.017	5.02±0.18	5.05±0.19	4.99±0.17	4.34±0.22	4.35±0.23	4.32±0.22

Table A2 Subject-wise extracted mean values

Over the whole WM skeleton and in the CST, in both hemispheres together and separately in each hemisphere, for FA and RD. RWM = right white matter; LWM = left white matter.

APPENDIX B

Supplementary Material for Study 2

Sample-specific template

A sample-specific template with its parcellation of GM and WM regions was created from the raw images in order to define the center of gravity (COG) of the hand motor regions and standardize some operations across the sample. For instance, a sample-specific parcellation of GM and WM, implemented with the Freesurfer's Desikan-Killiany Atlas, was automatically calculated on the sample-specific template to localize the precentral motor cortices to guide the regions of interests (ROIs) localization. To make the template, all individual raw brain images were first projected to Freesurfer's operational space, named conformed space, applying the Freesurfer's tool recon_all. With this command, the individual labels of the GM and WM parcellated regions, necessary at different steps of the seed mask creation, were also produced. With a combination of Freesurfer's and FSL's tools, the structural brain images were transformed into the MNI152 standard space and averaged to constitute the sample-specific template in the MNI space.

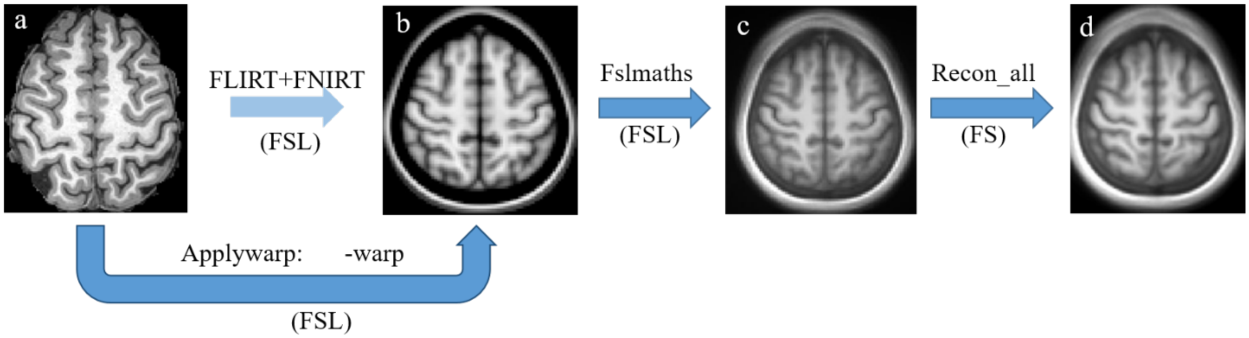


Figure A1 Template creation.

a) Individual structural brain image. b) Individual brain image in MNI space. c) Averaged brain image in MNI space. d) Averaged brain image in conformed space, i.e. template.

More specifically, the brain structural images were transformed from the structural space (A1 a) to the MNI space (A1 b) with linear and non-linear transformations, using FSL's FLIRT and FNIRT tools. They were then averaged, with FSL's Fslmaths tool, in the MNI space (A1 c) and transformed into the conformed space (A1 d) with recon-all, which also created the GM and WM parcellations of the template.

Seed mask creation

In order to separately track the primary motor pathways connecting the head, hand, trunk or leg representations, we defined, in each hemisphere, the four WM regions subjacent the motor cortex that topographically correspond to the head, hand, trunk/arm or leg/foot representations. To do this, we developed a procedure that permits to define the seed masks for tractography, using an approach that is at the same time sample-specific and reproducible across subjects.

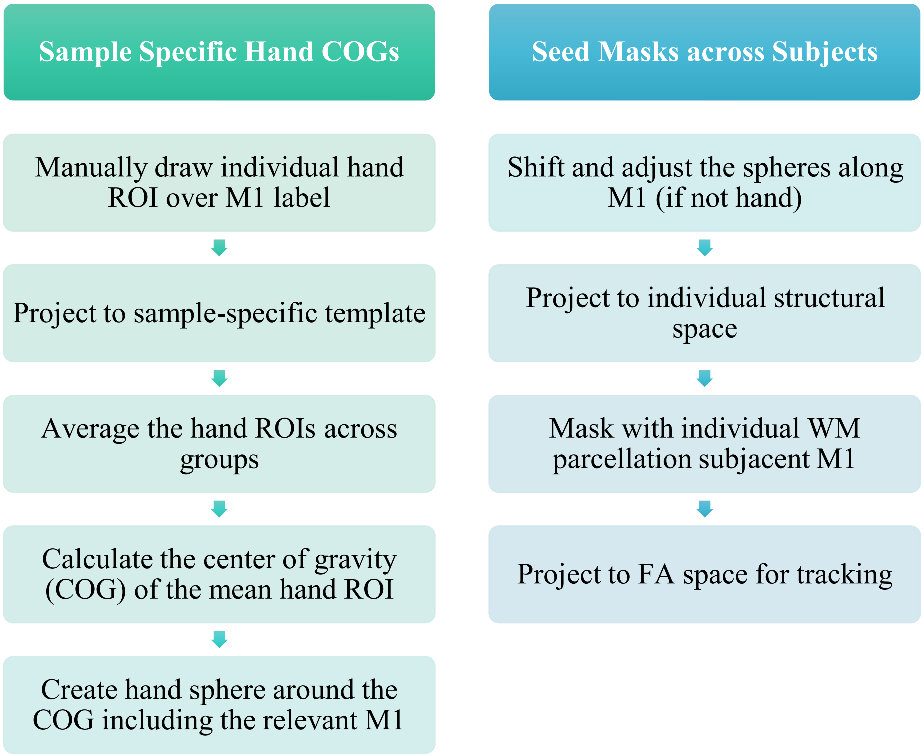


Figure A2 Diagram of the steps followed to create the seed masks.

The yellow windows indicate the user-defined steps; the light orange windows indicate the steps that were standardized across subjects.

Creation of sample-specific hand centers of gravity (COGs)

The hand is the only body part whose topographical location within the motor cortex that can be identified using well-established gross anatomical landmarks (Yousry et al., 1997; Caulo et al., 2007). Therefore, the first step was to identify the hand motor region individually, created a sphere based on its center of gravity (COG) and then to locate the other body parts along M1 relative to its position. Hand motor regions for each individual were manually labeled in three dimensions for both hemispheres in Freesurfer's conformed space (A3 a). To do this we overlaid the GM label of the precentral cortex provided by the Desikan-Killiany Atlas on each individual structural brain.

To create the hand masks, we identified the hand regions defined by the hand landmarks, previously described as an omega or epsilon shaped portion of the cortex, with their variants (Yousry et al., 1997; Caulo et al., 2007). The user-drawn hand regions were then non-linearly projected onto the MNI152 standard space with the FSL's tool applywarp (A3 b). The hand masks were then averaged (A3 c), with the FSL's tool Fslmaths, and projected again onto the sample-specific template space (A3 d), using the Freesurfer's tool mri_vol2vol. Finally, the COGs of the average hand masks were calculated, in the template conformed space, using the FSL's tool Fslstats.

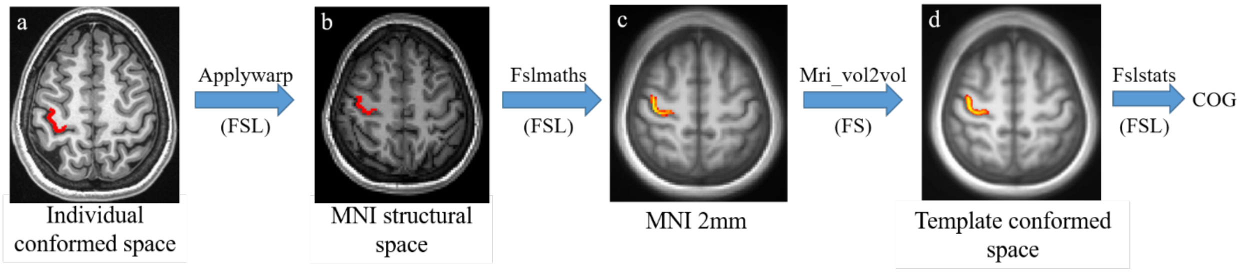


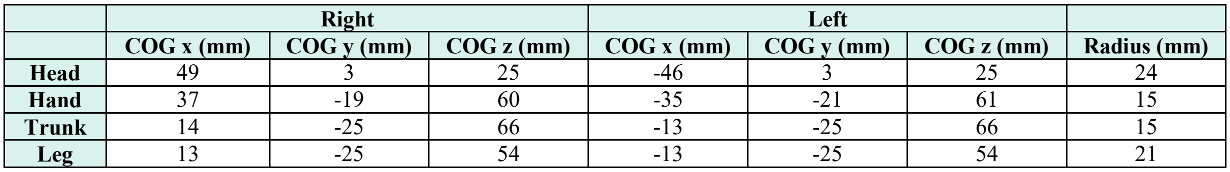
Figure A3 Calculation of the hand center of gravity (COG) for the right hemisphere, from manually-drawn hand ROIs.

(a) Individual manually-drawn hand ROI in the subject Freesurfer's conformed space. (b) Individual manually-drawn hand ROI in the MNI structural space. (c) Average of all subjects manually-drawn hand ROIs in MNI 2mm space. (d) Average of manually-drawn hand ROIs in template conformed space (thresholded at 30%).

Creation of seed masks from COGs across subjects

Once the hand COGs were calculated, the appropriate radii were estimated to draw the hand spheres around them. These parcellations were critical as visual checks for the determination of the radii of the spheres, allowing us to ensure that the spheres included all the relevant portions of the precentral cortex parcellation (Desikan-Killiany Atlas). The trunk, leg and hand spheres were created relative to the hand sphere positions by shifting the hand COGs along the precentral cortex (Table A1). In particular, the trunk sphere was entirely shifted along the x direction medially, so that the sphere included a similar portion of the cortex with minimal overlapping. For the leg and head, the spheres were first shifted along the x direction - medially and laterally respectively -, and then along the z (both spheres) and the y (head sphere only) directions, in order to include all the cortex.

The radii were also adjusted to include all the relevant portion of the precentral motor cortex. In the end, the hand and trunk spheres had the same radii, whereas the leg and the head regions, being more elongated, had bigger radii. Because there was some overlap between the hand and the trunk spheres, the trunk spheres were subtracted from the hand spheres; this was not necessary for the other spheres. While the hand, head and trunk spheres were masked with the precentral



	Right			Left			
	COG x (mm)	**COG y (mm)**	**COG z (mm)**	**COG x (mm)**	**COG y (mm)**	**COG z (mm)**	**Radius (mm)**
Head	49	3	25	-46	3	25	24
Hand	37	-19	60	-35	-21	61	15
Trunk	14	-25	66	-13	-25	66	15
Leg	13	-25	54	-13	-25	54	21

Table A1 Coordinates of the centers of gravity (COGs) in the MNI space (mm) for the four motor regions.

WM parcellation (see below), the leg spheres were masked with the paracentral WM parcellation; therefore there was no problematic overlapping with the trunk regions. It is worth noting that the paracentral WM underlies both the pre- and post-central cortices, therefore the leg tracts were not restricted to the descending primary motor fibers, but included also the ascending sensorimotor fibers.

Once obtained the bilateral COGs and spheres, we projected the spheres onto the structural subject space and masked them with the individual precentral WM masks. The choice of masking the spheres with the individual WM masks was done to take advantage of the more precise individual parcellations compared to the template parcellation. In detail, the spheres were projected from the template conformed space (Fig. A3 a) into the standard MNI152 space (Fig. A3 b) applying the mri_vol2vol tool by Freesurfer. In this passage, the transformation matrix came from the previously calculated projection of the MNI space to the template conformed space, performed with tkregister, and was here inverted with the -inv option. A non-linear warping procedure was then applied to project the spheres from the MNI space (Fig. 3 b) to the individual structural space (Fig. A3 c), using applywarp fed with linear and non-linear warping, previously calculated with FLIRT and FNIRT. Then, by means of Fslmaths (‘–mas’ option), the spheres were masked with the WM individual parcellation in the structural space, previously transformed from the individual conformed space with FLIRT. Finally, the selected WM ROIs were projected onto the diffusion FA space with a linear transformation (FLIRT). The WM ROIs in FA space were now ready to be used as seed masks for tractography.

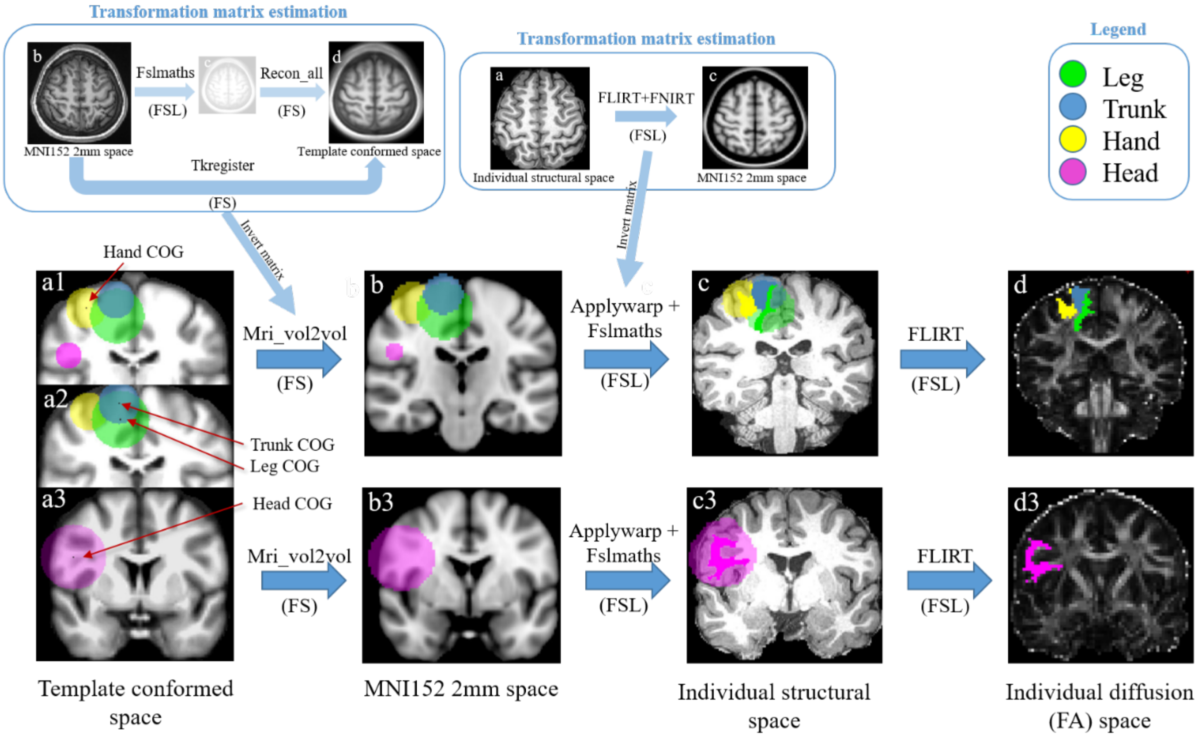


Figure A4 Seed mask creation from spheres to final masks in the right hemisphere.

(a) Spheres and COGs are shown in the template conformed space for the hand (yellow sphere, COG indicated by red arrow in a1), trunk (light blue sphere, COG in a2), leg (green sphere, COG in a2) and head (fuchsia sphere, COG in a3). (b) Spheres in MNI152 space. (c) Spheres in one subject individual structural space overlapping with the precentral/paracentral cortex; bottom raw shows the head transformation not visible in the same slice as the other body part regions. (d) Individual final seed masks in one subject FA diffusion space.

The light blue arrows between images indicate the transformations between images, the commands used, above the arrow, and the Software, below the arrows (FSL and Freesurfer, FS). Above the main images transformations, the transformation matrix estimations are shown to indicate where the transformation matrices come from. For instance, to project the spheres from the template space to the MNI space, it was applied the inverted matrix created with the command tkregister from the MNI space to the template conformed space (See Supplementary Material Fig. A1 b)→ d).

APPENDIX C

Sensorimotor integration is enhanced in dancers and musicians

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RESEARCH ARTICLE

Sensorimotor integration is enhanced in dancers and musicians

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Abstract Studying individuals with specialized training, such as dancers and musicians, provides an opportunity to investigate how intensive practice of sensorimotor skills affects behavioural performance across various domains. While several studies have found that musicians have improved motor, perceptual and sensorimotor integration skills compared to untrained controls, fewer studies have examined the effect of dance training on such skills. Moreover, no study has specifically compared the effects of dance versus music training on perceptual or sensorimotor performance. To this aim, in the present study, expert dancers, expert musicians and untrained controls were tested on a range of perceptual and sensorimotor tasks designed to discriminate performance profiles across groups. Dancers performed better than musicians and controls on a dance imitation task (involving whole-body movement), but musicians performed better than dancers and controls on a musical melody discrimination task as well as on a rhythm synchronization task (involving finger tapping). These results indicate that long-term intensive dance and music training are associated with distinct enhancements in sensorimotor skills. This novel work advances knowledge of the effects of long-term dance versus music training and has potential applications in therapies for motor disorders.

Keywords Dancers · Musicians · Sensorimotor integration · Dance video game · Rhythm · Melody

Introduction

Dance and music involve concentrated training of specific perceptual and sensorimotor skills that are typically initiated at a young age, are long term and can be quantified. As such, expert dancers and musicians are an ideal population in which to investigate the behavioural effects of intensive sensorimotor training. The behavioural correlates of music training have been well studied (for a review, see Herholz and Zatorre 2012), and there has been growing interest to study dance as well (for a review, see Bläsing et al. 2012 or Karpati et al. 2015). Both dance and music training have similarities, such as the importance of sensorimotor integration, as well as their artistic components and the easily quantifiable nature of the training process. However, music training generally focuses on *producing* sound using *effector-specific* movements, while dance training commonly focuses on *following* sound using *whole-body* movements. To date, no studies have directly compared the behavioural correlates of dance and music training. Comparing both forms of training is important to better understand how intensive sensorimotor training affects performance across a variety of tasks, and what effects might be specific to each form of training. Such knowledge may then be used to guide future research in clinical practice such as the development of dance- and music-based therapies for a variety of conditions such as Parkinson's disease (Mandelbaum and Lo 2014; Duncan and Earhart 2012) and stroke

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(Schneider et al. 2007). To these aims, in the present study, the behavioural correlates of long-term dance and music training were compared.

Behavioural differences between dancers and non-dancers as well as between musicians and non-musicians have been found using tasks in a variety of domains including motor control, perception and sensorimotor integration. In terms of motor control, both dancers and musicians have shown enhanced performance relative to their untrained counterparts. Dancers have improved balance (Crotts et al. 1996) and postural control (Rein et al. 2011) compared to non-dancers. Musicians show advantages in hand and finger movements compared to non-musicians (Fernandes and de Barros 2012; Verheul and Geuze 2004). These results may be related to the finding that both dancers (Thullier and Moufti 2004) and musicians (Inui and Ichihara 2001) can better optimize and combine movements than untrained controls.

In addition to motor tasks, the correlates of long-term dance and music training have been examined using perceptual tasks. Perceptual studies in dancers have focused on the visual domain using dance-related stimuli. Relative to non-dancers, dancers can better detect differences in moving point-light displays (Calvo-Merino et al. 2010) and show faster eye movements when viewing a dance film (Stevens et al. 2010). In contrast, perceptual studies in musicians have focused on the auditory domain (for a review, see Herholz and Zatorre 2012); especially relevant to the present study are findings that musicians can better detect differences in rhythmic and melodic stimuli than non-musicians (Foster and Zatorre 2010; Fujioka et al. 2004; Rammsayer and Altenmuller 2006).

Sensorimotor integration is a crucial aspect of both dance and music training. Dancers combine auditory information from music, along with visual information from observing their own and others' movements, with their motor output during performance. Musicians combine visual information from reading music or following a conductor, as well as auditory information from the output of their own and others' instruments, with the movements required to produce the desired sound. The forms of sensorimotor integration most relevant to dance and music include audiomotor and visuomotor integration. In the audiomotor domain, dancers more accurately synchronize knee bending to an auditory beat than non-dancers (Miura et al. 2011, 2013), and musicians more accurately synchronize hand/finger tapping to an auditory stimulus than non-musicians (Repp 2010; Chen et al. 2008; Bailey et al. 2014). In the visuomotor domain, dancers show increased ability compared to non-dancers in synchronizing with observed dance movements in the absence of auditory cues (Washburn et al. 2014). Musicians have better visuomotor integration compared to non-musicians, for example, in terms of motor reproduction of visually presented temporal intervals (Aagten-Murphy et al. 2014).

Some studies in dancers and musicians have also examined performance on multi-modal tasks across the auditory, visual and motor domains. These studies are especially informative since dance performance and music performance involve the integration of all three of these domains. Sofianidis et al. (2012) observed that dancers were more stable and coordinated than non-dancers in a dance synchronization task with visual and auditory cues. In musicians, audio-visuomotor performance has been mainly studied using interference paradigms (Drost et al. 2005; Keller and Koch 2008; Taylor and Witt 2015), such as playing chords in response to visual cues while hearing irrelevant auditory stimuli (Drost et al. 2005). Musicians show a greater interference effect of incongruent auditory and visual information relative to non-musicians, signalling that this action-effect representation in multi-modal integration is affected by training (Drost et al. 2005).

Taken together, this literature suggests that both dancers and musicians show enhancements in a range of sensorimotor skills compared to their untrained counterparts. However, it is not yet known whether the sensorimotor enhancements associated with long-term dance training are similar to or distinct from those associated with long-term music training. To this aim, the main objective of the present study was to investigate the behavioural correlates of long-term dance versus music training by examining sensorimotor integration in expert dancers, expert musicians and untrained controls.

In the present study, all participants were tested on a battery of behavioural tasks ranging from more dance-relevant to more music-relevant tasks. This type of behavioural battery provides the opportunity to investigate performance that is directly relevant to the trained skill (e.g. dancers performing a dance-related task), as well as transfer effects to the other skill (e.g. dancers performing a music-related task). A dance imitation task was the most dance relevant, in which participants executed whole-body dance movements simultaneously with visual and auditory stimuli. The synchronization of whole-body movements to sensory stimuli is a main component of dance training, while music training generally relies less on whole-body movements and more on effector-specific movements. Compared to dance-related tasks used in previous studies (Cross et al. 2009; Tachibana et al. 2011; Ono et al. 2014), this task includes more ecologically valid dance movements since they require use of the whole-body rather than only the lower limbs. A rhythm synchronization task, in which participants tapped a finger in synchrony with auditory stimuli, was relevant to both dance and music since rhythm is a crucial aspect of both types of training. Dancers often synchronize their movements with the rhythmic aspect of auditory

Table 1 Participant characteristics

Group	*N*	Age (years ± SD)	Sex	Body mass index (BMI) (±SD)	Years of dance training (±SD)	Years of music training (±SD)	Level of education (±SD)
Dancers	20	25.1 ± 3.9	14F, 6M	21.7 ± 2.2	15.3 ± 5.2	1.8 ± 1.9	2.35 ± 0.6
Musicians	19	23.7 ± 3.6	12F, 7M	22.5 ± 3.2	1.1 ± 1.7	16.1 ± 3.4	2.32 ± 1.0
Controls	20	25.8 ± 5.1	13F, 7M	21.8 ± 3.2	0.4 ± 0.8	0.5 ± 1.0	2.6 ± 1.1
Comparison between groups		D = M = C $F(2,56) = 1.32$ $p = 0.28$		D = M = C $F(2,55) = 0.38$ $p = 0.68$	D > M ($p < 0.0001$) D > C ($p < 0.0001$) M = C ($p = 1$)	M > D ($p < 0.0001$) M > C ($p < 0.0001$) D = C ($p = 0.27$)	D = M = C $F(2,56) = 56$ $p = 0.57$

Education levels for each participant are calculated on a scale of 1–5, where 1 is the lowest (completed high school) and 5 is the highest (completed doctorate degree)

F females, *M* males, *SD* standard deviation

and visual stimuli, while musicians produce sound in accordance with perceived rhythmic stimuli. A melody discrimination task was the most music-relevant task, which required participants to determine whether pairs of melodies were the same or different. Musicians are often trained to distinguish between pitches and melodies in order to be able to analyse performed or heard music in a critical manner, while this is less relevant to dance training as dancers generally follow rather than produce sound. In addition, cognitive tasks (Digit Span, Letter-Number Sequencing and syllable sequence discrimination) were administered in order to test for group differences in auditory working memory (Wechsler 1997; Foster and Zatorre 2010).

On the dance imitation task, dancers were expected to outperform both musicians and controls since dance training focuses on performing whole-body movements often in synchrony with auditory and visual stimuli. This is supported by the finding that dancers perform better than non-dancers on a visuomotor dance imitation task (Washburn et al. 2014). On the rhythm synchronization task, both musicians and dancers were expected to outperform controls. Musicians have previously shown enhanced performance relative to non-musicians on the same rhythm synchronization task used here (Chen et al. 2008; Bailey et al. 2014), while dancers have shown better audiomotor integration in a rhythmic context than non-dancers (Miura et al. 2011, 2013). Since both dancers and musicians have demonstrated enhanced rhythmic abilities versus untrained controls, it was expected that they would perform similarly on the rhythm synchronization task. On the melody discrimination task, musicians were expected to outperform both dancers and controls. Music training often involves learning to distinguish between melodies, such as identifying whether a produced sound was correct or incorrect, and has been previously shown to provide advantages relative to non-musicians on the same melody task used here (Foster and Zatorre 2010).

Methods

Participants

Three groups of participants (aged 18–40 years) were recruited for this study: expert dancers ($N = 20$), expert musicians ($N = 19$) and a control group of non-musicians/non-dancers ($N = 20$) (Table 1). Dancers and musicians were either currently practicing as professionals or students involved in professional training programs. Their training was assessed via a detailed questionnaire developed in our laboratories (Coffey et al. 2011; Bailey and Penhune 2010). Dancers and musicians had on average approximately 15 years of experience in their respective disciplines, and controls had on average <1 year of experience in dance, music, figure skating and aerobics. All participants were physically active (i.e. biking, running or practicing other physical exercises). Dancers were currently practicing contemporary dance as their principal style, but had a variety of training backgrounds including ballet, tap, jazz, swing and ballroom. Dancers whose main style was too similar to the dance task used here (i.e. urban, street or hip hop) were excluded. Musicians had various instrumental backgrounds, including keyboard instruments, strings, woodwinds, brass and percussion. None of the musicians had absolute pitch. Since the dance task was based on a video game, participants were screened for experience with dance video games; 56 out of 59 participants reported that they never or rarely (up to three times per year) played dance video games. The remaining three participants (one dancer and two musicians) reported a maximum 4 months of experience with dance video games. The groups did not differ in age, sex distribution, body mass index (BMI) or level of education (Table 1). Participants had no past or current learning or developmental disorder, neurological or psychiatric condition, or alcohol or substance abuse. This study was approved by the Research Ethics Board at the Montreal

Fig. 1 Dance imitation task. The participants stand facing the television screen where they view an avatar dancing using whole-body movements, and are asked to mirror the avatar's movements in real time. Participants' movements are registered by the Kinect sensor

Neurological Institute and Hospital, and written informed consent was obtained from all participants.

Tasks

Dance imitation

The whole-body dance imitation task (Fig. 1) consisted of performing sequences of dance movements from a video game, Dance Central for Xbox Kinect version 1 (Harmonix, http://www.harmonixmusic.com). Participants viewed an avatar performing dance movements to music on a large television screen directly in front of them, and were asked to mirror the avatar's movements in real time. A rectangular area corresponding to the field of view of the Kinect sensor was marked on the floor, and participants were instructed to keep their movements within this area. Music was presented through speakers on each side of the television. Movements were recorded by the Kinect infrared light sensor (http://www.xbox.com/en-ca/Kinect; US Patent No. 20100197399), which has been shown to validly represent movement and posture (Clark et al. 2012, 2013).

Prior to performing the test sequences, participants were required to achieve at least 60 % correct moves on a familiarization dance sequence in order to be sure that they could perform the task. One control participant did not reach this threshold and was thus excluded from the sample.

Participants performed seven test dance sequences covering a range of difficulty levels (labelled as sequences 1–7, with 1 being the easiest and 7 being the most difficult). These dance sequences were chosen from the game through pilot testing in order to minimize floor effects in the non-dancers and ceiling effects in the dancers. Level of difficulty was rated within the game and depended on the number of different moves, rate of change and complexity (e.g. speed and number of body parts required). The dance task was divided into two blocks: (1) the familiarization sequence followed by sequences 1–4 and (2) a warm-up sequence (repeat of sequence 3) followed by sequences 5–7. Familiarization and warm-up sequences were not included in the analyses. The Kinect system provided a score of the per cent of correct moves made by each participant for each sequence. This score was based on the movement of the correct body parts in the correct direction within a restricted time window. The manufacturer does not disclose additional details about how scores are calculated.

Rhythm synchronization

In the rhythm synchronization task (Fig. 2), as used by Bailey and Penhune (2010), participants were asked to listen to and tap in synchrony with auditory rhythms at three levels of metrical complexity. Each trial consisted of two presentations of the same stimulus. Participants were instructed to listen to the first presentation and tap in synchrony with the second on a computer mouse button. Participants completed two blocks of 36 trials each. Stimuli were 6 s in duration and included 11 woodblock sounds of 200 ms each. Each stimulus included five onset-to-onset intervals of 250 ms, three 500-ms intervals, and one interval of each of 750, 1000 and 1500 ms. The order of these intervals differed in each stimulus to create three levels of increasing rhythmic complexity corresponding to decreasing metrical structure: metric simple (MS), metric complex (MC) and non-metric (NM). Two rhythms of each complexity were used. The six rhythms were randomly ordered, and each was presented six times per block. The task was scored using the absolute value inter-tap interval (ITI) deviation, which is the ratio of the time between two taps (ITI) to the time between the two corresponding sounds in the stimulus (inter-stimulus interval) and measures the accuracy in reproducing the temporal intervals between sounds in the stimulus. Lower ITI values indicate higher interval reproduction accuracy and therefore better performance. For more details about the stimuli and scoring of this task, please see Bailey and Penhune (2010).

Melody and syllable sequence discrimination

The melody discrimination task (Fig. 3), designed by Foster and Zatorre (2010), required participants to determine whether two melodic stimuli were the same or different. It consisted of two sub-tasks, simple and transposed melody discrimination, each consisting of two blocks of 30 trials each. The simple task was always performed before the transposed task. In the simple task, two melodies

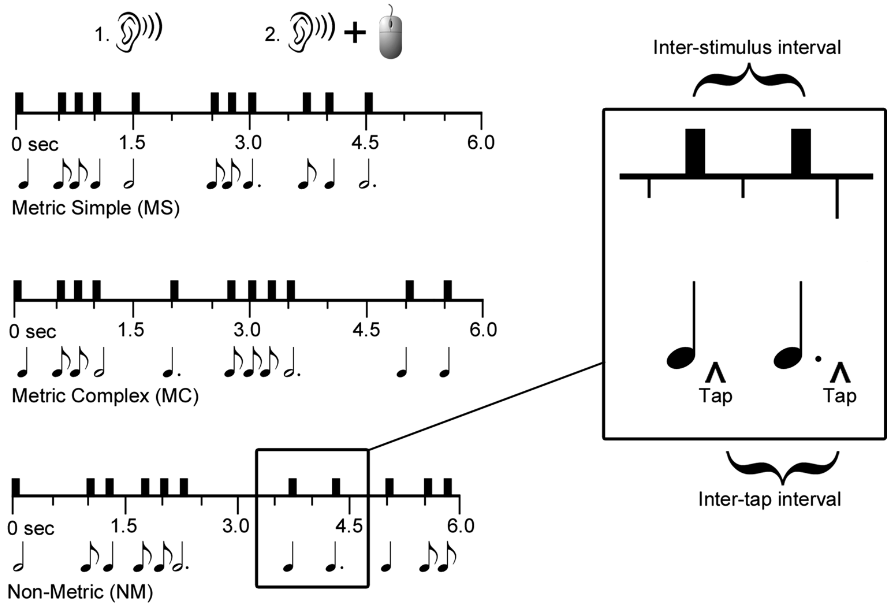

Fig. 2 Examples of stimuli and scoring of the rhythm synchronization task. Participants listen to and tap in synchrony with stimuli of three rhythmic complexities. Inter-tap interval (ITI) deviation is calculated as the ratio of the ITI to the corresponding inter-stimulus interval (figure adapted from Bailey and Penhune 2010)

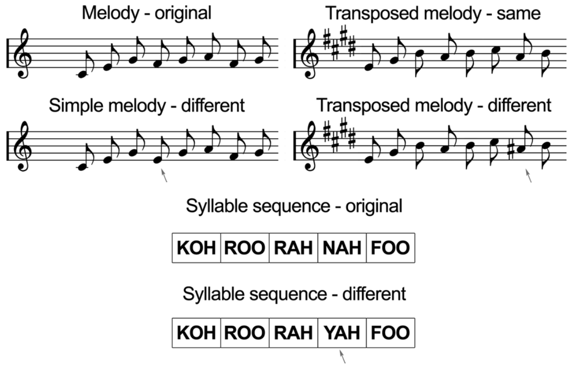

Fig. 3 Examples of stimuli from the melody and syllable sequence discrimination tasks, in which participants hear pairs of melodies or syllable sequences and are asked to determine whether they are the same or different. *Arrows* show alterations in the "different" stimuli (figure adapted from Foster and Zatorre 2010)

containing 5–13 low-pass-filtered harmonic tones were presented. Tones were 320 ms in duration and included notes in the Western major scale ranging in pitch from C4 to E6. In half the trials, these melodies were identical ("same" trials). In the other half, one tone in the second melody was altered in pitch by up to five semitones ("different" trials). Key and melodic contour were not affected by this alteration. Following presentation of each melody pair, participants were asked whether the presented melodies were the same or different. The transposed task was similar to the simple task, except that all second melodies were transposed four semitones higher in pitch than the first melodies and the pitch alterations in the "different" trials had a magnitude of one semitone, which produced a note outside of the melody's key. This task was scored using per cent of trials correct.

The syllable sequence discrimination task (Fig. 3), also designed by Foster and Zatorre (2010), is a control task for the melody discrimination task described above. By comparing performance on this task to that of the melody discrimination task, it can be determined whether group differences on the melody task represent music-specific skills or may be due to group differences in working memory. On each trial, participants heard two syllable sequences and were asked to determine whether they were the same or different. Syllables consisted of one consonant with one vowel and were recorded in monotone from one speaker. Sequences had no meaning in English and contained 5–13 syllables of 320 ms each. On half the trials, the two sequences were identical. On the other half, one syllable was changed to a different syllable in the second sequence. Participants completed two blocks of 30 trials each. This task was scored using per cent of trials correct.

Cognitive tasks

To test for group differences in auditory working memory, participants completed two subtasks of the Weschler Adult Intelligence Scale (WAIS) III: Digit Span and Letter-Number Sequencing (Wechsler 1997). Scores on each task were converted to scaled scores using standard protocols.

Procedure

Each participant completed all tasks in one or two sessions. The rhythm, melody and syllable tasks were administered using Presentation software (Neurobehavioural Systems, http://www.neurobs.com), and auditory stimuli for these tasks were delivered using Sennheiser HD 25-1 II headphones at a comfortable volume. Participants were randomly assigned to one of four task orders, and the task order distribution was matched between groups. The non-dance tasks were performed between the dance task blocks to minimize the effect of fatigue on dance task performance.

Analyses

Group characteristics

Age, BMI, level of education and years of dance and music training were compared between groups (dancer, musician or control) using one-factor ANOVAs with group as the between-subjects factor. Post hoc pairwise comparisons were conducted where appropriate and corrected for multiple comparisons using the Bonferroni method.

Within-task analyses

Linear fixed-effects models with repeated measures were used to analyse each task using its respective score. This technique uses a restricted maximum likelihood estimation method, which provides identical estimates to ANOVA when applied to balanced data (IBM Corporation 2012), but has important differences: it allows the specification of the relationship between repeated measures (i.e. covariance structure) so that the sphericity assumption does not have to be satisfied, and it allows the inclusion of subjects with missing data. These models included group as a between-subjects factor and task-specific within-subject repeated measures using a compound symmetry covariance structure. Task-specific repeated measures included sequence difficulty in the dance task, rhythm complexity in the rhythm task, simple versus transposed melody discrimination subtasks, and syllable sequence versus melody discrimination tasks. Group comparisons in the cognitive tasks were analysed using univariate ANCOVAs. Post hoc pairwise comparisons were conducted where appropriate and were corrected for multiple comparisons using the Bonferroni method. To control for effects of age and sex on task performance, these variables were included as covariates of no interest in all analyses.

Between-task analyses

To allow for between-task comparisons, overall scores for the dance, rhythm and melody tasks were converted to z-scores (i.e. standardized scores). Since lower scores on the rhythm task correspond to better performance, z-scores for this task were multiplied by -1 so that higher z-scores corresponded to higher performance, which was consistent with the directionality of the other task scores. A linear fixed-effects model was conducted on these data, with group as a between-subjects fixed factor and task as a within-subjects repeated measure using an unstructured covariance matrix. To control for effects of age and sex on task performance, these variables were included as covariates of no interest.

Results

Group characteristics

One-factor ANOVAs conducted on age, BMI and level of education with group (dancer, musician or control) as the between-subjects factor revealed no significant differences between groups [BMI: $F(2,55) = 0.4$, $p = 0.68$; age: $F(2,56) = 1$, $p = 0.28$; education: $F(2,56) = 0.6$, $p = 0.57$]. One-factor ANOVAs conducted on years of dance and music training with group as the between-subjects factor revealed significant differences for both training types [music: $F(2,55) = 271$ $p < 0.0001$; dance: $F(2,56) = 135$ $p < 0.0001$]. Post hoc pairwise comparisons confirmed that musicians and controls did not differ in years of dance training ($p = 1$) and dancers and controls did not differ in years of music training ($p = 0.27$).

Dance imitation

Linear fixed-effects analysis using group as a between-subjects factor and sequence difficulty as a within-subjects repeated measure showed significant main effects of group [$F(2,54) = 85$, $p < 0.0001$] and sequence difficulty [$F(6,334) = 154$, $p < 0.0001$] as well as an interaction between group and difficulty [$F(12,334) = 6$, $p < 0.0001$]. Post hoc pairwise comparisons suggest that overall, dancers had the highest per cent moves correct, followed by musicians, and controls had the lowest per cent moves correct ($p \leq 0.003$). Decomposition of the interaction suggests that on the easiest and three most difficult sequences, dancers performed better than both musicians and controls ($p < 0.0001$) with no difference between musicians and controls ($p > 0.18$). On the remaining three intermediate sequences, dancers performed better than both other groups, and musicians performed better than controls ($p \leq 0.01$).

Rhythm synchronization

Linear fixed-effects analysis using group as a between-subjects factor and stimulus complexity (MS, MC or NM) as a within-subjects repeated measure revealed significant main effects of group [$F(2,54) = 13$, $p < 0.0001$] and stimulus complexity [$F(2,112) = 42$, $p < 0.0001$], with no significant group by complexity interaction [$F(4,112) = 0.4$, $p > 0.8$]. Musicians showed lower ITI deviation (better performance) than both dancers and controls ($p \leq 0.007$), and no difference was observed between dancers and controls ($p = 0.19$). Across groups, the lowest ITI deviations were observed for MS rhythms, followed by MC rhythms, and highest ITI deviations were observed in the NM condition ($p < 0.0001$). In six participants (4 dancers, 1 musician, 1 control), one block of this task was discarded due to at least ten instances where the participant tapped during the listening stimulus instead of the tapping stimulus. Since there was an overall learning effect between the two blocks on this task (paired t test comparing block 1 and block 2: $t = 6.28$, $p < 0.0001$), the scores of these six participants were calculated using their single block score and an adjustment to compensate for the learning effect (estimated by regression analysis of the remaining participants).

Melody and syllable sequence discrimination

Linear fixed-effects analysis using group as a between-subjects factor and melody versus syllable discrimination tasks as a within-subjects repeated measure revealed significant main effects of group [$F(2,54) = 9$, $p < 0.0001$] and task [$F(1,56) = 7$, $p = 0.014$], as well as a significant interaction between group and task [$F(2,56) = 29$, $p < 0.0001$]. Post hoc pairwise comparisons on the interaction showed that musicians performed better than both other groups ($p < 0.0001$) with no difference between dancers and controls ($p = 1$) in the melody task, but no group differences were found in the syllable task ($p > 0.7$).

Linear fixed-effects analysis using group as a between-subjects factor and simple versus transposed melody discrimination tasks as a within-subjects repeated measure showed significant main effects of group [$F(2,54) = 28$, $p < 0.0001$] and task [$F(1,56) = 38$, $p < 0.0001$], and a significant interaction between group and task [$F(2,56) = 4$, $p = 0.017$]. Decomposition of the interaction revealed that musicians performed better than both dancers and controls ($p < 0.0001$), with no difference between dancers and controls ($p \geq 0.14$), on both simple and transposed tasks. Both dancers and musicians performed significantly better on the simple compared to the transposed task ($p \leq 0.003$), while controls did not show this difference ($p = 0.095$).

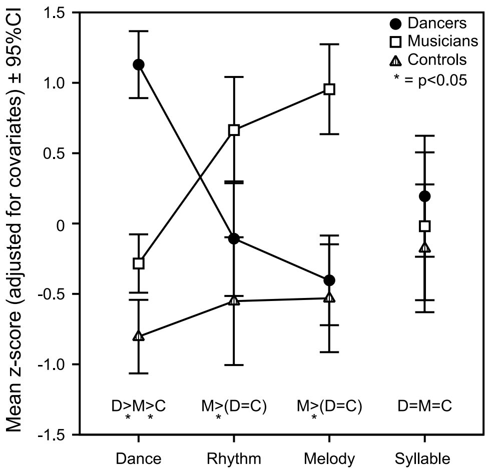

Fig. 4 Performance across the three groups (dancers are shown as *filled circles*, musicians as *unfilled squares* and controls as *striped triangles*) as measured by z-scores (adjusted for the covariates of age and sex) are shown across tasks from the most dance-related task (dance imitation), the rhythm synchronization, to the most music-related task (melody discrimination) as well as the syllable control task. As shown, dancers perform best on the dance task, and musicians perform best on the melody task

Z-score analysis (Fig. 4)

Linear fixed-effects analysis on the z-scores of the dance, rhythm and melody tasks (Fig. 4) with group as a between-subjects factor and task as a within-subjects repeated measure revealed a significant main effect of group [$F(2,51) = 26$, $p < 0.0001$] and an interaction between group and task [$F(4,56) = 30$, $p < 0.0001$]. No main effect of task was found [$F(2,56) = 0.001$, $p = 0.99$].

Post hoc comparisons revealed that across tasks, dancers and musicians showed similar z-scores ($p = 0.24$), and both groups showed higher z-scores than controls ($p < 0.0001$). Decomposition of the group by task interaction showed identical group differences as found in the individual task analyses. Post hoc analyses on the task by group interaction showed that dancers had higher z-scores on the dance task than both other tasks ($p < 0.0001$), and scored similarly on the rhythm and melody tasks ($p = 0.4$). Musicians had similar z-scores on the melody and rhythm tasks ($p = 0.49$), both of which were higher than their z-scores on the dance task ($p < 0.0001$). Controls scored similarly on all three tasks ($p > 0.4$).

Cognitive tasks

Univariate ANCOVAs revealed no differences between groups in the Digit Span task [$F(2,54) = 1$, $p = 0.41$]. A significant effect of group was found for the Letter-Number Sequencing task [$F(2,54) = 5$, $p = 0.013$), and post hoc pairwise comparisons showed that musicians performed better than both dancers and controls ($p < 0.03$) and no difference was observed between dancers and controls ($p = 1$).

Discussion

In the present study, performance on a battery of sensorimotor tasks ranging from more dance-related to more music-related as well as cognitive tasks was compared between expert dancers, expert musicians and untrained controls. On the dance imitation task, dancers performed best, followed by musicians, whereas controls scored the lowest. On the rhythm synchronization and melody discrimination tasks, musicians performed best, while dancers and controls performed similarly. This work investigates the behavioural profiles of expert dancers and musicians and thereby increases understanding of the specificity of the effects of long-term dance versus music training.

Dance imitation

The dance-related task used in this study was a whole-body dance video game imitation task that required audio-visuomotor integration. Participants viewed an avatar dancing to music and were asked to imitate the avatar's movement in real time. As expected, dancers performed better than both controls and musicians on the dance task. This result indicates that dancers have increased audio-visuomotor integration abilities involving whole-body movements relative to non-dancers. These findings are consistent with previous results from a study by Washburn et al. (2014) in which dancers performed better than non-dancers in a visuomotor interpersonal dance imitation task. These findings also support the work of Sofianidis et al. (2012) in which dancers were more stable and coordinated than non-dancers in a dance-related task involving the auditory, visual and motor domains. These results are likely explained by the fact that dance training involves performing whole-body movements in synchrony with auditory stimuli as well as other dancers. Dancers are trained to integrate the movements of multiple body parts (Thullier and Moufti 2004), and often learn choreography by observing and imitating movements. The advantage for dancers in this task may have been associated with an enhanced ability to engage the action observation network based on previous experience. This network of brain regions is implicated in action observation, understanding and imitation (Rizzolatti and Craighero 2004; Iacoboni 2005; Caspers et al. 2010). Consistent with these functions, dancers showed increasing engagement of this system as they learned a new dance sequence (Cross et al. 2006).

Musicians also performed better than untrained controls on the dance task, but only at the intermediate difficulty level. This indicates that music training showed some transfer to the dance imitation task. This finding supports previous work showing that musicians perform better than non-musicians in tasks involving sensorimotor integration, specifically the synchronization of finger or hand/arm movements to auditory (Chen et al. 2008; Repp 2010; Bailey et al. 2014) or visual (Spilka et al. 2010) stimuli. Even though the specific types of movements (i.e. whole-body vs. effector-specific) and stimuli may differ between music and dance contexts, the overlap may be enough to provide musicians with an advantage in dance. It is also possible that musical training allows musicians to make better temporal predictions from the music used in the dance task, allowing them to make more synchronized movements. Finally, as for the dancers, musicians may have enhanced abilities to engage the action observation network during this task which may facilitate their ability to imitate and synchronize movements with the avatar. This is supported by findings of enhancements in the mirror neuron system in musicians compared to non-musicians (Bangert et al. 2006; Pau et al. 2013; Proverbio et al. 2014).

Rhythm synchronization

The rhythm synchronization task lies between the dance imitation and melody discrimination tasks on the continuum from more dance related to more music related, since rhythm is a crucial component of both dance and music training. Participants were asked to synchronize finger taps to auditory rhythmic stimuli of varying metrical complexities. Across all participants, performance decreased with increasing metrical complexity, consistent with previous studies using the same task (Chen et al. 2008; Bailey and Penhune 2010) and other similar paradigms (Grahn and Brett 2007). As expected, musicians performed better than untrained controls on the rhythm synchronization task, consistent with previous reports of enhanced rhythm synchronization in musicians versus non-musicians on this same task (Chen et al. 2008; Bailey et al. 2014) as well as other work showing that musicians are less variable than non-musicians when tapping in synchrony with a changing auditory stimulus (Repp 2010). Musicians also performed better than dancers on the rhythm synchronization task, but dancers did not perform better than untrained controls. This may be due to the fact the rhythm task relied on finger tapping rather than whole-body movements and that finger movements are more prevalent in music than dance training.

Melody and syllable sequence discrimination

In the most music-related task, melody discrimination, participants were asked to determine whether pairs of melodies were the same or different. As expected, musicians performed better than both dancers and controls on this task. The syllable sequence discrimination task consisted of the same design except using non-musical syllable sequences instead of melodies, and was administered as a control for the melody discrimination task. No group differences were found in the syllable task. These results are consistent with those of Foster and Zatorre (2010), who found that musicians performed better than non-musicians on the same melody discrimination task used here, and both groups performed similarly on the syllable sequence discrimination task. The lack of group differences on the syllable task suggests that the differences observed in the melody task are related to music-specific advantages in the musician group and not to auditory working memory differences between groups. These advantages are likely due to the fact that melody discrimination is a crucial aspect of music training. Musicians must be able to hear pitch differences between melodies in order to determine whether they have correctly performed a musical sequence.

Overall, dancers performed similar to controls on the melody task. However, like musicians but unlike controls, they performed significantly better on the simple compared to the transposed condition of the task. This suggests that dancers' exposure to music during training may have some effect on their ability to process melodic information.

Cognitive tasks

Cognitive tasks (Digit Span and Letter-Number Sequencing) were administered to test for group differences in auditory working memory. No performance differences were found between dancers, musicians and controls on the Digit Span task; however, musicians performed better than both dancers and controls on the Letter-Number Sequencing task. These results are consistent with previous findings in musicians that years of music training was positively correlated with performance on the Letter-Number Sequencing task, which places greater demands on auditory working memory (Bailey and Penhune 2010) relative to the other tasks used. Potential explanations include training-associated enhanced working memory ability in musicians, or that individuals who pursued music training may have pre-existing enhancements in such cognitive skills.

Overall results

This study is the first to compare the behavioural correlates of dance versus music training and compare task performance between expert dancers and musicians. It expands on work comparing each of these groups to their untrained counterparts by demonstrating that dancers and musicians have distinct behavioural profiles relative to untrained controls as well as to each other. It also builds on the literature by applying tasks across the continuum from dance relevant to music relevant in the same sample. Individual dance- or music-relevant tasks have been used independently (e.g. Washburn et al. 2014; Bailey and Penhune 2010; Foster and Zatorre 2010); however, combining them allows for the investigation of a larger range of sensorimotor abilities.

Taken together, the results of the present study suggest that dancers and musicians have distinct sensorimotor enhancements relative to untrained controls. Dancers showed enhanced sensorimotor integration involving whole-body movements compared to both musicians and controls as demonstrated by their higher scores on the dance imitation task. Dancers performed similarly to controls on the rhythm synchronization task, but performed better on the simple than transposed melody discrimination (as observed in musicians but not controls), suggesting the possibility of some effect of dance training on melodic processing. As expected, musicians showed enhancements in melody discrimination and rhythm synchronization, but they also performed better than untrained controls on the dance imitation task, suggesting that music training may show some transfer to whole-body movement.

These findings have implications for sensorimotor training in general. They suggest that learning a specific skill is associated with improvements in tasks with a strong relation to that skill and that transference to less-related tasks may occur.

Future directions

Further work on the topic of the behavioural correlates of dance and music training will continue to advance knowledge on the specificity of these skills. To build on the present study, longitudinal work comparing task performance before and after dance and music training would be especially informative as this would distinguish skill enhancement caused by training from that which may have been present before training and predisposed certain individuals to pursue training. Another important avenue for further study is the investigation of a sensitive period in the context of dance. Sensitive periods have been demonstrated for music (for a review, see Penhune 2011), but have not yet been investigated for dance. This topic could be examined by comparing task performance between groups of early- and late-trained dancers, and would provide insight into the interaction between development and learning dance-related skills such as sensorimotor integration involving whole-body movement. In addition to studying the behavioural correlates of dance versus music training, comparing the brain structural and functional correlates of these two types of training can further our understanding of their effects and provide support and explanations for the observed behavioural correlates. Our laboratory is currently investigating the grey matter (Karpati et al. 2014) and white matter (Giacosa et al. 2014) structural correlates of dance versus music training. A clinical avenue for future work is the development of dance- and music-based therapies for a variety of conditions including Parkinson's disease (Mandelbaum and Lo 2014; Duncan and Earhart 2012) and stroke (Schneider et al. 2007). Evidence to date has demonstrated the efficacy of dance- and music-related interventions separately, and understanding how each may target specific skills may assist in designing protocols for specific symptoms or populations.

Conclusions

This study demonstrates that both dance and music training provide advantages in sensorimotor tasks, and each is associated with a unique behavioural profile. Dancers and musicians both showed a large advantage in tasks related to their trained skill, and some transference between skills was observed. This study expands on previous work that investigated the behavioural correlates of dance or music training separately, and is the first study to directly compare these two types of training. This work advances the knowledge of the specificity of dance versus music training on sensorimotor skills and can be applied to the development of arts-based therapies for motor disorders. By understanding the similar and different effects of dance versus music training, one could more accurately design a therapy protocol using one or both of these types of training to target specific skills.

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Compliance with ethical standards

The authors declare that they have no conflict of interest. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study. Additional informed consent was obtained from all individual participants for whom identifying information is included in this article.

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