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

Chiara Giacosa [a,b,*], Falisha J. Karpati [a,c], Nicholas E.V. Foster [a,d], Virginia B. Penhune [a,b], Krista L. Hyde [a,c,d]

[a] International Laboratory for Brain, Music and Sound Research (BRAMS), Pavillon 1420 Mont Royal, FAS, Département de psychologie, CP 6128 Succ. Centre Ville, Montreal, QC H3C 3J7, Canada
[b] Department of Psychology, Concordia University, 7141 Sherbrooke Street West, Montreal, Quebec H4B 1R6, Canada
[c] Faculty of Medicine, McGill University, 3655 Sir William Osler, Montreal, Quebec H3G 1Y6, Canada
[d] Department of Psychology, University of Montreal, Pavillon Marie-Victorin, 90 avenue Vincent d'Indy, Montreal, Quebec H2V 2S9, Canada

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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 (WM) 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 (Takeuchi et al., 2011; Baer et al., 2015).

1. 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 (WM) 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, 2009b, 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 works 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

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* Corresponding author.
E-mail address: chiagiarasa@gmail.com (C. Giacosa).

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expert dancers with equally well-trained musicians and untrained controls using both behavioural and a range of DTI measures.

1.1. Previous work on dance and music

The study of specialized training such as dance and music offers a unique way to investigate 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., 2015a) for review). A large part of this literature has focussed 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; Cross et al., 2009b; Gardner et al., 2015). In both animal and human studies (Grèzes and Decety, 2001; Rizzolatti and Craighero, 2004; Hecht et al., 2013), 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; Rizzolatti et al., 1996b; 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; Cross et al., 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 tested participants 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 hypothesised 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., 1995; 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., 1995; Steele et al., 2013).

1.2. 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 and Pasternak, 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 of diffusion along the principal axis; radial diffusivity (RD) which measures the diffusion on the plane 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 and Pasternak, 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.

1.3. 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. Materials and methods

2.1. 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 practising 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., 2015b), 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 practising other physical exercises). Dancers were currently practising 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 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). 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.

2.2. 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, 2010b) 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, 2010a, 2010b), 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, 1997) and the Matrix Reasoning subtask from the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999). Full behavioural results for these groups are reported in a previous paper (Karpati et al., 2015b). 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. Diffusion tensor imaging and analysis

2.3.1. 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/mm^2, 10 b_0 non-weighted images, TE of 88 ms, TR of 9340 ms, EPI factor 128, isotropic voxels of 2 × 2 × 2 mm^3, 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.

Table 1
Participant characteristics.

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, 6 M	21.6 ± 2.3	15.5 ± 5.2	1.7 ± 1.9	2.37 ± 0.6
Musicians	18	22.9 ± 3.4	12F, 6 M	22.5 ± 3.2	1.04 ± 1.8	15 ± 3.6	2.39 ± 0.98
Controls	19	25.4 ± 5.1	12F, 7 M	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*

F = females, M = males, SD = standard deviation, and 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).

2.3.2. Behavioural analysis

Behavioural analyses for the full sample are reported in detail in Karpati et al. (2015b). 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.

2.3.3. 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.

2.3.3.1. 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).

2.3.3.1.1. 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 mentioned 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 $1 \times 1 \times 1$ 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.

2.3.3.1.2. 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).

2.3.3.1.3. 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.

2.3.3.2. 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.

2.3.4. 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.

2.3.4.1. 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.

2.3.4.2. Correlations of the subjectwise averaged extracted values with behavioural performance. Each of the non-directional and directional diffusivity measures was 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.

3. Results

3.1. Behavioural results

3.1.1. 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 1; Age: $F(2,53) = 2.12$, $p = 0.13$; BMI: $F(2,53) = 0.4$, $p = 0.67$). One-way ANOVAs

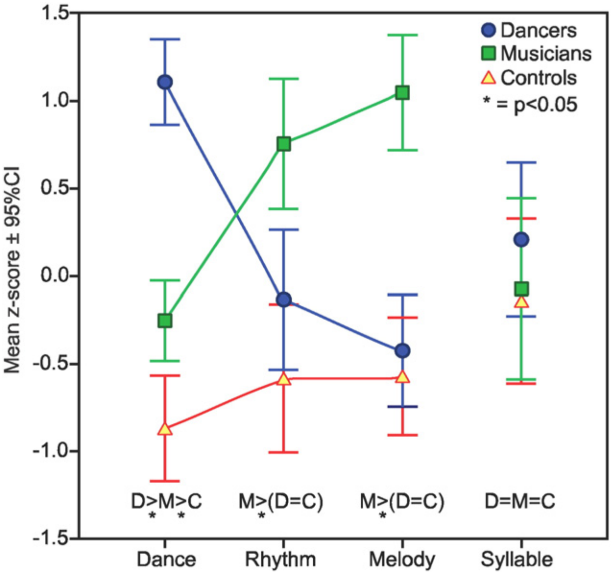

Fig. 1. Behavioural results. Performance on the behavioural tasks (z-scores) across the three groups.

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 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: $F(2,51) > 235$, $p < 0.0001$).

3.1.2. Dance and music tasks

Behavioural results for the full sample were reported previously (Karpati et al., 2015b). As described above, three participants (one from each group) were excluded due to unreliable MRI data. For the current sample we followed similar procedures and obtained consistent results with Karpati et al. (2015b). 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) 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 ($F(4,53) = 26.4$, $p < 0.0001$). In addition, 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.

3.1.3. 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). 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.

3.2. Diffusion tensor imaging results

3.2.1. 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 3 for specific peak p-values and localisation and Supplementary Table 1 for a summary).

Table 2
Cognitive results.

		Cognitive tasks			
Group		Letter number sequence	Matrix reasoning	Digit span	Syllable sequence discrimination
Dancers	Mean ± SD	10.05 ± 2.01	13.37 ± 1.3	9.05 ± 2.12	69.65 ± 7.42
	(range)	(8–15)	(11–16)	(7–13)	(53.33–86.67)
Musicians	Mean ± SD	12.50 ± 2.47	13.39 ± 2.03	10.11 ± 2.56	67.96 ± 9.24
	(Range)	(7–17)	(10–16)	(5–14)	(43.33–81.67)
Controls	Mean ± SD	10.00 ± 3.2	11.58 ± 2.91	9.89 ± 3.36	67.60 ± 8.57
	(range)	(5–18)	(2–15)	(5–18)	(51.67–83.33)
Total	Mean ± SD	10.82 ± 2.82	12.77 ± 2.31	9.68 ± 2.72	68.41 ± 8.32
	(range)	(5–18)	(2–16)	(5–18)	(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*

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.

Table 3
Localisation of TBSS results and statistical values.

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
			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
		AD	R body CC/*ATR*	37	0.049	3.45	−6	−26	24
			R SCR/–	18,495	0.004	6.43	21	−12	35
		MD	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
			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
		MO	L ILF-IFOF/=	38	0.049	2.46	42	−32	−12
			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
		F1	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
		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
	DvsM ROIs		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

WM = white matter; R = right; and L = left.
Regions are labelled according to the JHU ICBM-DTI-81 White-Matter Labels/JHU White-Matter Tractography Atlas.
– = 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; and UF = uncinate fasciculus.

3.2.1.1. 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. 2A). 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

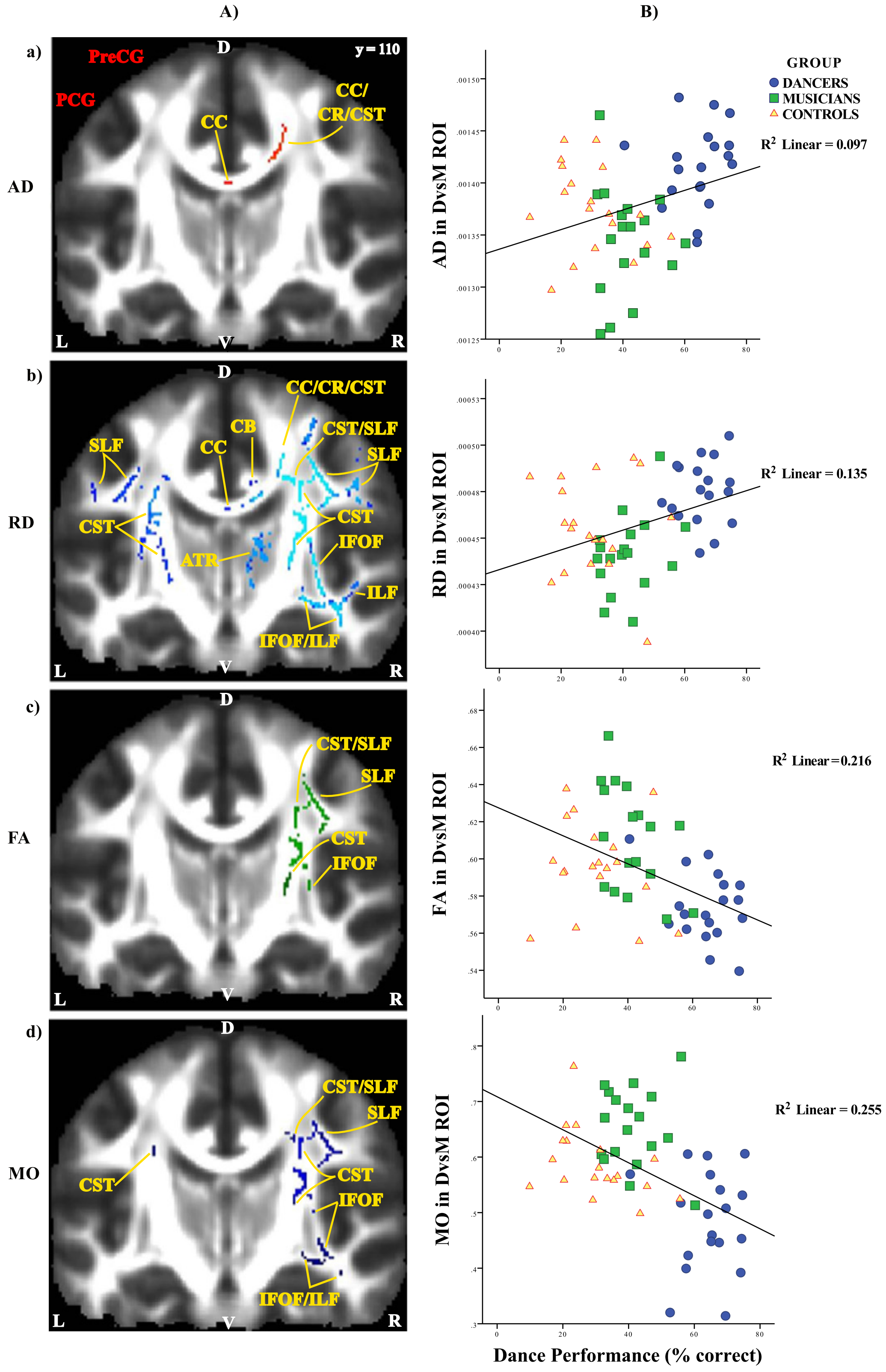

Fig. 2. Dancers versus musicians group comparisons and brain–behaviour correlations. The left column (A) illustrates the regions of significant difference between dancers and musicians for axial (AD), radial diffusivities (RD), fractional anisotropy (FA) and mode of anisotropy (MO). The right column (B) illustrates the correlations between diffusivity measures and dance performance. (A) In comparison to musicians, dancers had 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, specifically 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). (B) The extracted values of AD and RD, averaged over the 'Dancers versus Musicians' ROIs were positively correlated with dance performance (rows 1 and 2); those of FA and MO were 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.

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.

3.2.1.2. 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 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 2 for a summary).

3.2.1.3. 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) fibres, 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. 3A 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. 3C. No significant differences were found in F1 or F2 when comparing dancers to controls.

3.2.2. 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.

3.2.2.1. 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. 2B). 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.

3.2.2.2. 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, AD and MD, 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.

3.2.2.3. 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.

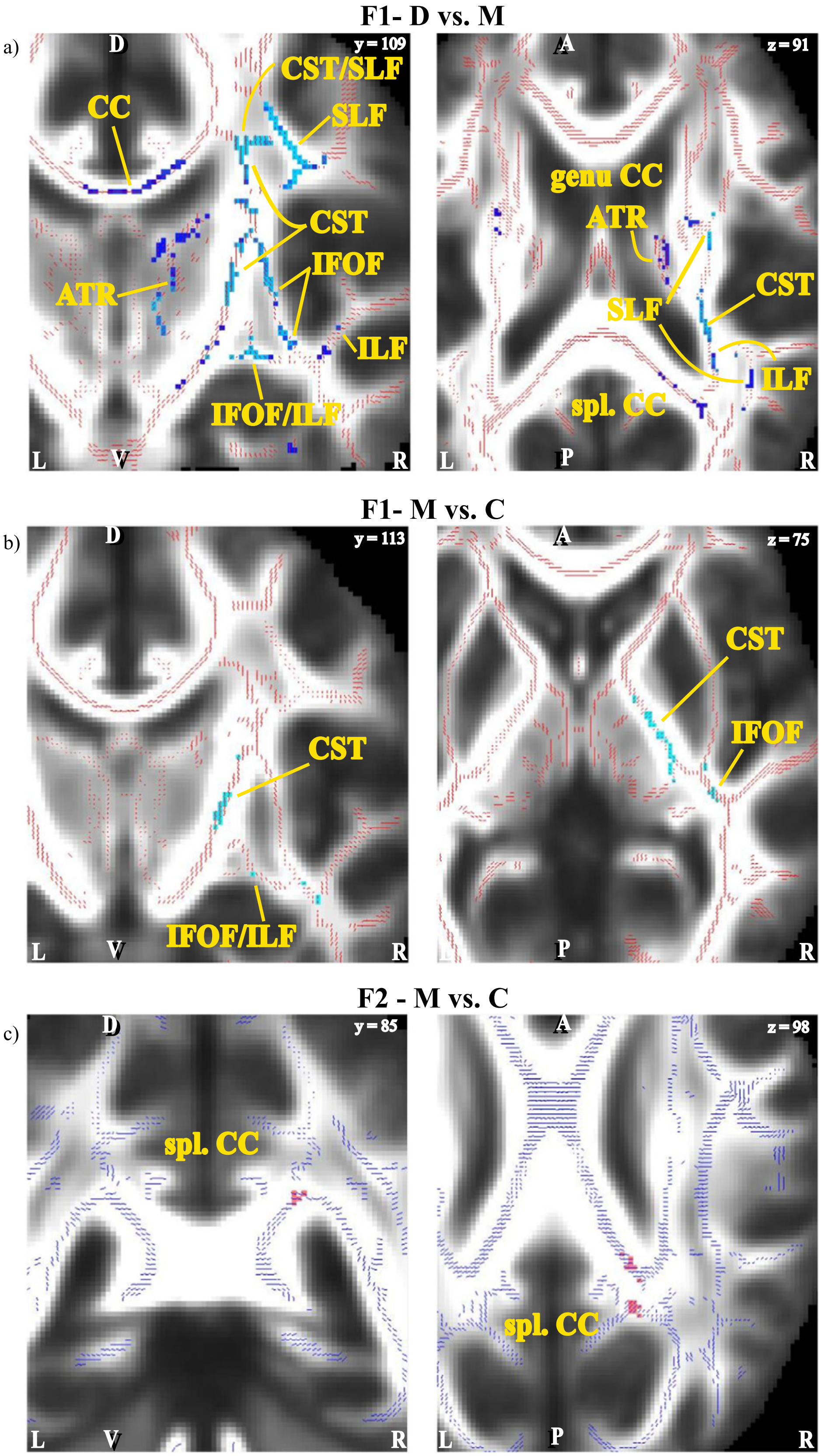

Fig. 3. Group comparisons of directional measures. The left panels illustrate the coronal view; the right panels show the axial view. Coordinates on the figures are in MNI space. 3a — Top row. Dancers versus Musicians, F1 (red lines). Musicians had higher F1: significant voxels range from dark blue ($p < 0.05$) 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 had 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 had 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; and spl. = splenium.

4. Discussion

4.1. 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 hypothesise that increased diffusivity in dancers may be either related to greater heterogeneity of fibre orientation within the above-mentioned 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.

4.2. 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; Douaud et al., 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 that connect 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 a 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 the 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. 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.

4.3. Region specific findings

4.3.1. 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., 2013; 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 plane formed by the CST and 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. 2B); melody performance was negatively associated with diffusivity and positively with anisotropy.

4.3.2. 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; Chechlacz et al., 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 visuomotor 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., 2013; Kamali et al., 2014), which is part of the AON. 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 hypothesised 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; Hufner 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.

4.3.3. 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 of the 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.

4.4. 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).

5. 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 brain structure (Takeuchi et al., 2011; Baer et al., 2015).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.04.048.

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