Brain Research 1657 (2017) 62–73

Contents lists available at ScienceDirect

Brain Research

journal homepage: www.elsevier.com/locate/bres

Research report

# Dance and music share gray matter structural correlates

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## ARTICLE INFO

*Article history:*
Received 25 May 2016
Received in revised form 23 November 2016
Accepted 25 November 2016
Available online 5 December 2016

*Keywords:*
Dance
Music
Brain
Cortical thickness
Superior temporal gyrus

## ABSTRACT

Intensive practise of sensorimotor skills, such as music and dance, is associated with brain structural plasticity. While the neural correlates of music have been well-investigated, less is known about the neural correlates of dance. Additionally, the gray matter structural correlates of dance versus music training have not yet been directly compared. The objectives of the present study were to compare gray matter structure as measured by surface- and voxel-based morphometry between expert dancers, expert musicians and untrained controls, as well as to correlate gray matter structure with performance on dance- and music-related tasks. Dancers and musicians were found to have increased cortical thickness compared to controls in superior temporal regions. Gray matter structure in the superior temporal gyrus was also correlated with performance on dance imitation, rhythm synchronization and melody discrimination tasks. These results suggest that superior temporal regions are important in both dance- and music-related skills and may be affected similarly by both types of long-term intensive training. This work advances knowledge of the neural correlates of dance and music, as well as training-associated brain plasticity in general.

## 1. Introduction

Investigating the neural correlates of specialized training, such as dance and music, allows us to better understand human brain plasticity and the interaction between the brain and behaviour. Many studies have examined the neural correlates of music training (for a review, see Herholz and Zatorre, 2012 or Schlaug, 2015), and there is growing interest to study the neural correlates of dance (for a review, see Karpati et al., 2015). As in music training, dance training is structured and can be quantified. Although both music and dance share many skills, such as sensorimotor integration, the specific skills learned in each form of training differ considerably, which motivates the study of what brain mechanisms and behaviours might be shared or distinct between these skills. For example, dance generally has a stronger reliance on whole-body movements and following sound, while music typically relies on effector-specific movements and the production of sound. The comparison of the gray matter structural correlates of dance versus music training has not yet been examined, and can provide insight into brain characteristics that may be associated with auditory-motor artistic training in general (i.e., are similarly correlated with music and dance) or those that may be associated with learning specific skills (i.e., are differently associated with music and dance). To these aims, the present study investigated gray matter (GM) structural differences between expert dancers, expert musicians and untrained controls in correlation with performance on dance- and music-related tasks.

### 1.1. Brain structural differences between expert musicians/dancers and untrained controls

Several studies have found GM structural differences between expert musicians and non-musicians. Many of these studies have used voxel-based-morphometry (VBM) to reveal GM concentration differences between musicians and non-musicians in distributed cortical regions including primary motor (M1) and somatosensory areas (i.e., pre- and postcentral gyri), premotor cortex (PMC), superior (SPL) and inferior parietal lobules, inferior temporal gyrus, Heschl's gyrus, superior temporal gyrus (STG), orbitofrontal gyrus and inferior frontal gyrus (IFG)/Broca's area (Abdul-Kareem et al., 2011; Amunts et al., 1997; Fauvel et al., 2014; Gaser and Schlaug,

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http://dx.doi.org/10.1016/j.brainres.2016.11.029
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2003; Han et al., 2009; James et al., 2014; Schlaug, 2001; Schneider et al., 2002; Sluming et al., 2002). While VBM allows analysis of the cerebellum and subcortical structures, surface-based morphometry avoids confounds caused by the position and shape of the cortical mantle (Good et al., 2001) since the data are extracted directly from the GM surface (Kim et al., 2005; Lerch and Evans, 2005; MacDonald et al., 2000). Applying VBM in combination with surface-based morphometry provides more information on the underlying nature of GM differences (Hutton et al., 2009; Palaniyappan and Liddle, 2012). To this aim, Bermudez et al. (2009) used VBM and cortical thickness (CT) methods together to reveal thicker cortex in musicians versus non-musicians in superior and middle temporal regions, PMC, lingual gyrus and superior frontal gyrus as well as increased GM concentration in superior temporal regions.

Relative to studies on music, less is known about the GM structural correlates of dance training. Using VBM, Hänggi et al., 2010 found reduced GM volume in the PMC, supplementary motor area (SMA) and superior frontal gyrus in professional female ballet dancers compared to non-dancers, mainly in the left hemisphere. Also using VBM, Nigmatullina et al. (2015) found reduced GM in the posterior cerebellum in expert dancers compared to non-dancer rowers, and also found group differences in the correlations between structure in this region and performance on a vestibular task. However, these above studies have some important limitations. Neither study correlated GM structure with dance performance. Moreover, they included limited GM measures (only VBM) that provided little information about the underlying nature of GM differences. Finally, the results may not be generalizable to all dancers since they included very select groups of only female ballet dancers.

Taken together, this body of work suggests that both music and dance training are associated with GM structure in various sensorimotor brain areas. However, brain-behavioural studies in musicians and dancers are important to further understand the relationship between the brain and music/dance ability.

### 1.2. Brain-behaviour correlations in music and dance

Various studies have examined brain-behaviour correlations in music and dance each separately. In music-related contexts, studies examining the correlation between brain function and structure with performance on melody and rhythm tasks are especially relevant to the present work. Foster and Zatorre (2010a) found that performance on a melodic discrimination task showed increased activation compared to an auditory control in the precentral gyrus (PrG), pre-supplementary motor area (preSMA), and STG. Structurally, CT in the right auditory cortex, bilateral intraparietal sulcus and PrG was positively correlated with performance on this same melodic task (Foster and Zatorre, 2010b). In addition to melody, rhythm is an important aspect of music training. Chen et al. (2008) found that performance on a rhythm synchronization task was correlated with activity in the preSMA, SMA, PMC, dorsolateral prefrontal cortex and inferior parietal lobule. Bailey et al. (2014) found GM structure in the PMC to be correlated with performance on a similar rhythm task. Finding and tapping to a beat has been correlated with activation in the STG, PMC and prefrontal cortex (Kung et al., 2013). Taken together, these findings point to the importance of auditory and motor brain regions in music, and namely in melody- and rhythm-related skills.

Much of the work investigating the neural correlates of dance has focused on functional neuroimaging studies during dance observation, and has demonstrated the importance of the action observation and simulation systems (PMC, SMA, M1, superior temporal sulcus (STS) and parietal cortex) in dance (e.g., Cross et al., 2006; Jola et al., 2013; Pilgramm et al., 2010). A few studies have employed innovative techniques to study the neural correlates of actual dance performance. Brown et al. (2006) scanned the brains of amateur tango dancers using positron emission tomography (PET) imaging while they performed tango-related leg movements. They found that the STG, SPL, frontal operculum, cerebellum, putamen, thalamus and motor cortical regions including PMC and M1 were activated during this dance task. More recent studies by Tachibana et al. (2011) and Ono et al. (2014) applied functional near infrared spectroscopy (fNIRS) in a sample of non-dancers while they performed a dance video game involving stepping to match visual stimuli. They found that superior and middle temporal gyri, SPL and frontopolar cortex were active during this task. The above studies on dance point to the importance of auditory and motor brain regions, including frontal and superior temporal regions, in dance observation and performance.

Taken together, studies investigating brain-behaviour correlations in music- and dance-related contexts have demonstrated the importance of a variety of regions in these skills, particularly those implicated in auditory, motor or multimodal integration functions. There is some overlap in the regions associated with performance of music- and dance-related tasks, including the STG, but a direct comparison of the neural correlates of music- versus dance-related tasks has not yet been conducted.

### 1.3. The role of superior temporal cortex in music and dance

As described above, the STG has been shown to be active during performance of both music- and dance-related tasks, pointing to its role in artistic auditory-motor training. Superior temporal cortex is classically known as an auditory processing region including primary and secondary auditory cortex (Mendoza, 2011). This has been supported by studies using musical tasks, which observed that the STG and STS are active during melodic processing (Bengtsson and Ullen, 2006; Foster and Zatorre, 2010a; Klein and Zatorre, 2015; Lappe et al., 2013; Lee et al., 2011; Schlaug, 2015). Superior temporal regions also play a role in functions other than purely auditory processing. For example, the planum temporale area of the STG has been proposed to be a computational hub (Griffiths and Warren, 2002) which processes and sorts sounds and then sends those with a motor relevance to more anterior motor regions. This is consistent with the involvement of the STG in an auditory-motor integration network (Bangert et al., 2006; Hickok et al., 2003; Romanski, 2012; Zatorre et al., 2007) and the role of the STG in auditory (e.g., listening to musical stimuli), motor (e.g., pressing piano keys) (Bangert et al., 2006; Baumann et al., 2007; Hickok et al., 2003) and auditory-feedback tasks (Pfordresher et al., 2014). The auditory-motor integration network is especially relevant to dance and music training as they both involve auditory and motor processing, and rely extensively on their integration. Specifically, dancers often synchronize their movements with auditory stimuli and musicians execute movements in order to produce sound on their instrument.

Other functions relevant to both dance and music in which superior temporal regions have been associated include the temporal control of movements (Bengtsson et al., 2004), multisensory integration (Jola et al., 2013; Pantev et al., 2015; Tachibana et al., 2011) and action imitation (Iacoboni et al., 2001; Molenberghs et al., 2010). The STG has also been implicated in more dance-relevant functions, such as balance (Karim et al., 2014), posture prediction (Gardner et al., 2015), form and motion processing (Cross et al., 2010; Giese and Poggio, 2003) and biological motion observation (Gilaie-Dotan et al., 2013; Han et al., 2013; Peuskens et al., 2005). Overall, the work described here supports the involvement of superior temporal regions in a variety of music- and dance-relevant functions.

### *1.4. Objectives and hypotheses*

The first objective of the present study was to compare the GM structural correlates of dance versus music training. The second aim was to relate any training-associated brain modifications to specific measures of dance and music abilities. To these aims, expert dancers, expert musicians and untrained controls were tested on a battery of dance and music-related tasks including dance imitation, rhythm synchronization and melody discrimination tasks, and completed a structural MRI brain scan. A novel multi-metric GM analysis approach was used including the combination of gray matter concentration (GMC), CT, and cortical surface area (SA) to provide complementary and detailed analyses of GM structure in these groups.

Since both dance and music training involve auditory processing, motor planning and execution, as well as auditory-motor integration, common GM structural differences were expected in auditory and motor regions (i.e., superior temporal auditory areas, as well as frontal motor areas) in both dancers and musicians compared to controls. However, larger and more diffuse brain changes were expected in musicians in auditory regions due to the importance of detailed sound analysis required in music training, while in dancers larger changes in motor regions were expected due to dancers' intensive practise of whole-body movements. The brain-behaviour correlations were expected to support the findings of the group comparison, with regions showing differences in musicians being correlated with performance on music-related tasks and regions showing differences in dancers being correlated with dance-related tasks.

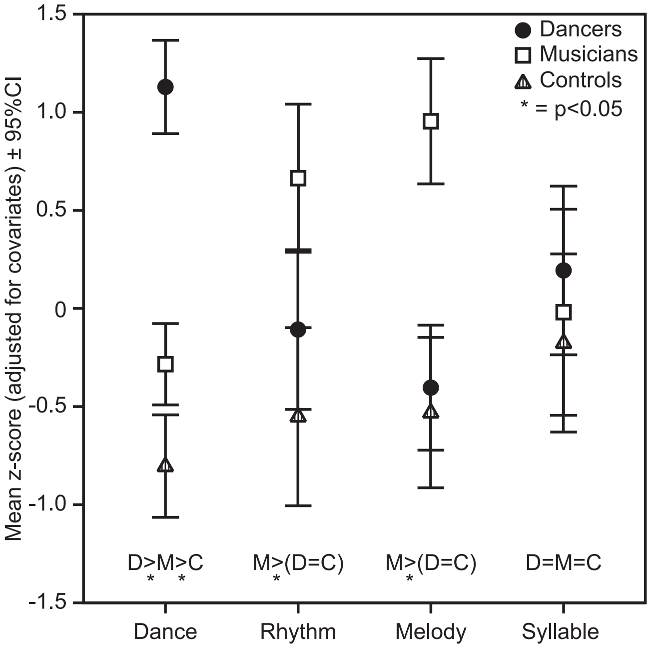

**Fig. 1.** Behavioural results. Performance across the three groups (dancers, musicians and controls) as measured by z-scores (standardized scores) adjusted for covariates are shown across tasks on a continuum from more dance-related (dance imitation), the rhythm synchronization, to more music-related (melody discrimination) as well as the syllable control task. As shown, dancers perform best on the dance task, and the musicians perform best on the melody and rhythm tasks. Adapted from Karpati et al. (2016).

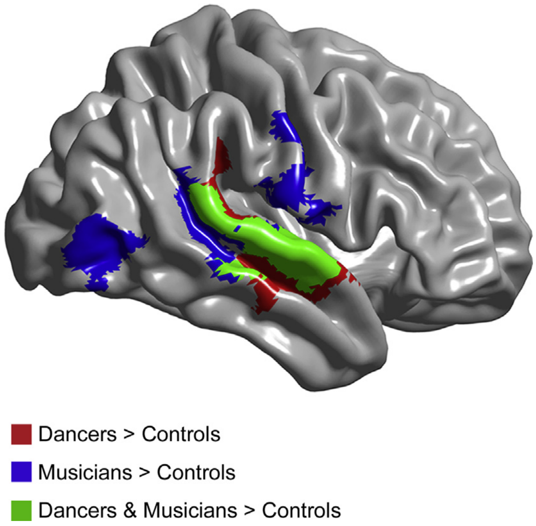

**Fig. 2.** Group differences in cortical thickness. Regions where dancers have greater cortical thickness (CT) than controls are shown in red, regions where musicians have greater CT than controls are shown in blue, and regions where both dancers and musicians have greater CT than controls are shown in green. Clusters shown are significant at $p \leqslant 0.05$ after correction for family-wise error using random field theory. See Table 1 for more detailed information on these results.

## 2. Results

### *2.1. Behavioural results (Fig. 1)*

On the dance imitation task, dancers outperformed both musicians and controls ($p < 0.001$), and musicians performed better than controls ($p = 0.003$). On both the rhythm synchronization and melody discrimination tasks, musicians outperformed both dancers and controls ($p \leqslant 0.007$) while dancers and controls performed similarly ($p \geqslant 0.19$). No significant group differences were found in the syllable sequence discrimination task ($p > 0.7$).

### *2.2. Group differences in GM structure (Fig. 2, Table 1)*

**CT**: F-tests conducted to determine the presence of group differences in CT revealed a significant cluster in the right superior temporal gyrus ($p = 0.02$). Post hoc pairwise comparisons showed greater CT in the dancers compared to controls in a cluster including the right STG, STS and middle temporal gyrus (MTG) ($p < 0.001$). Musicians showed greater CT than controls in a cluster including the right STG, STS and MTG, as well as two additional clusters in the right postcentral gyrus and right middle occipital gyrus ($p \leqslant 0.04$). No significant differences in CT were found between dancers and musicians.

**SA**: An F-test conducted on SA did not show any significant group differences.

**GMC**: An F-test conducted on GMC did not show any significant group differences.

### *2.3. GM structure correlations with behavioural tasks (Fig. 3)*

#### *2.3.1. Dance imitation (Table 2)*

**CT**: Across all participants, a trend towards a positive correlation between task performance and CT was observed in the left STG ($p = 0.08$). No correlations were found in the control group separately.

**SA**: No significant correlations were found between SA and dance task performance.

**GMC**: Across all participants, performance on the dance imitation task was positively correlated with GMC in bilateral clusters covering the STG and IFG and extending into more inferior temporal regions on the right ($p \leqslant 0.02$). In the control group separately,

**Table 1**
Group differences in cortical thickness.

| Comparison | Cluster | | Peak (MNI coordinates) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | P-value (2-tailed) | Extent | Brain region | Brodmann area | x | y | z | t-Value | Average group difference in CT (mm) |
| Dancers > Controls | <0.001 | 1438 vertices/3367 $mm^2$ | R STG | 22 | 58 | −7 | −6 | 4.07 | 0.20 |
| | | | R STG | 22 | 65 | −40 | 14 | 3.58 | 0.18 |
| | | | R pSTG/supramarginal gyrus | 22 | 56 | −35 | 25 | 3.47 | 0.15 |
| | | | R MTG | 21 | 60 | −25 | −6 | 3.34 | 0.18 |
| | | | R STG | 22/38 | 45 | 3 | −15 | 3.10 | 0.22 |
| | | | R MTG | 21 | 66 | −17 | −18 | 2.64 | 0.15 |
| | | | R Heschl's gyrus | 41 | 48 | −11 | 5 | 2.42 | 0.13 |
| Musicians > Controls | <0.001 | 1353 vertices/3097 $mm^2$ | R MTG | 21 | 63 | −30 | −5 | 3.73 | 0.23 |
| | | | R STG | 22 | 67 | −12 | 0 | 3.72 | 0.24 |
| | | | R STS | 22/39 | 55 | −43 | 17 | 3.45 | 0.19 |
| | | | R STG | 52 | 46 | −9 | −5 | 3.09 | 0.25 |
| | | | R Heschl's gyrus | 42 | 53 | −16 | 6 | 2.97 | 0.18 |
| | | | R STG | 22 | 67 | −37 | 10 | 2.94 | 0.18 |
| | | | R STG | 22/38 | 61 | 2 | −3 | 2.84 | 0.20 |
| | | | R MTG | 21 | 50 | −39 | 3 | 2.75 | 0.19 |
| | 0.003 | 401 vertices/1092 $mm^2$ | R PoG | 3 | 60 | −12 | 41 | 3.41 | 0.24 |
| | | | R CS | 3/4 | 57 | −7 | 25 | 3.27 | 0.16 |
| | | | R rolandic operculum | 43 | 55 | −5 | 10 | 2.78 | 0.16 |
| | 0.04 | 349 vertices/981 $mm^2$ | R MOG | 19 | 46 | −74 | 1 | 3.88 | 0.20 |

Clusters are significant at $p \leqslant 0.05$ after correction for family-wise error using random field theory.
CS = central sulcus; MTG = middle temporal gyrus; MOG = middle occipital gyrus; PoG = postcentral gyrus; STG = superior temporal gyrus; pSTG = posterior superior temporal gyrus; STS = superior temporal sulcus.

task performance was significantly positively correlated with GMC in clusters including the right IFG and left STG ($p \leqslant 0.03$), with a trend in the right STG ($p = 0.08$).

### 2.3.2. Rhythm synchronization (Table 3)

**CT**: Across all participants, performance on the rhythm task was positively correlated with CT in the right pre- and postcentral gyri and central sulcus ($p < 0.001$), and a trend was observed in the left STG extending into the supramarginal gyrus ($p = 0.07$). In the control group, CT in the right STG was positively correlated with rhythm task performance ($p < 0.01$).

**SA**: No significant correlations were found between SA and rhythm task performance.

**GMC**: Across all participants, GMC in the right postcentral gyrus was positively correlated with rhythm task scores ($p = 0.05$). In the control group, a trend was observed in a cluster including the left IFG and STG ($p = 0.07$).

### 2.3.3. Melody discrimination (Table 4)

**CT**: Across all participants, performance on the melody task was positively correlated with CT in a cluster centered on the left MTG and extending into the STG and ITG, two clusters covering the right STG, STS and MTG, and a fourth cluster containing the right ventral pre- and postcentral gyri and central sulcus ($p < 0.01$). No correlations were found in the control group separately.

**SA**: No significant correlations were found between SA and melody task performance.

**GMC**: No significant correlations were found between GMC and melody task performance.

## 3. Discussion

This is the first study to examine the GM structural correlates of dance training using multiple analysis techniques, as well as the first to compare the GM structural correlates of dance versus music training. Both dancers and musicians showed increased CT compared to controls in the STG, and increased GM in this region was correlated with better performance on dance imitation, rhythm synchronization and melody discrimination tasks. These findings suggest that the STG is involved in both music- and dance-related functions and may be affected similarly by both types of training. In addition, GMC in the IFG was correlated with performance on the dance task.

### 3.1. GM structure in superior temporal regions is associated with both music and dance

Both musicians and dancers had greater CT than controls in overlapping right temporal regions, including the STG, STS and MTG. These results are consistent with previous work that found GM structural differences between musicians and non-musicians in similar brain areas (Bermudez et al., 2009; Fauvel et al., 2014). Neither study that has previously investigated GM structure in dancers versus non-dancers (Hänggi et al., 2010; Nigmatullina et al., 2015) found group differences in temporal regions. This difference may be due to the fact that both previous studies included only female ballet dancers, while the present study included a more generalizable group of both male and female dancers with varied training backgrounds. Additional factors that may contribute to this difference include the small sample size of 10 participants per group in Hänggi et al. (2010)'s study, as well as the use of a specialized athlete control group in Nigmatullina et al. (2015)'s study. The non-specialized control group used in the present study is a better representation of non-dancers in general.

The involvement of the STG in both music and dance is further supported by the results of the brain-behaviour correlations. Across all groups, CT in the STG was positively correlated with all three music- and dance-related tasks. This correlation was also observed between GMC in the STG and performance on the dance imitation task. The correlations across groups are likely driven by differences in behavioural performance. Importantly, however, in the control group alone we found similar correlations between GMC in the STG and dance task performance, as well as between CT in the STG and rhythm task performance. These results suggest that the STG is implicated in individual differences in task performance in the absence of training.

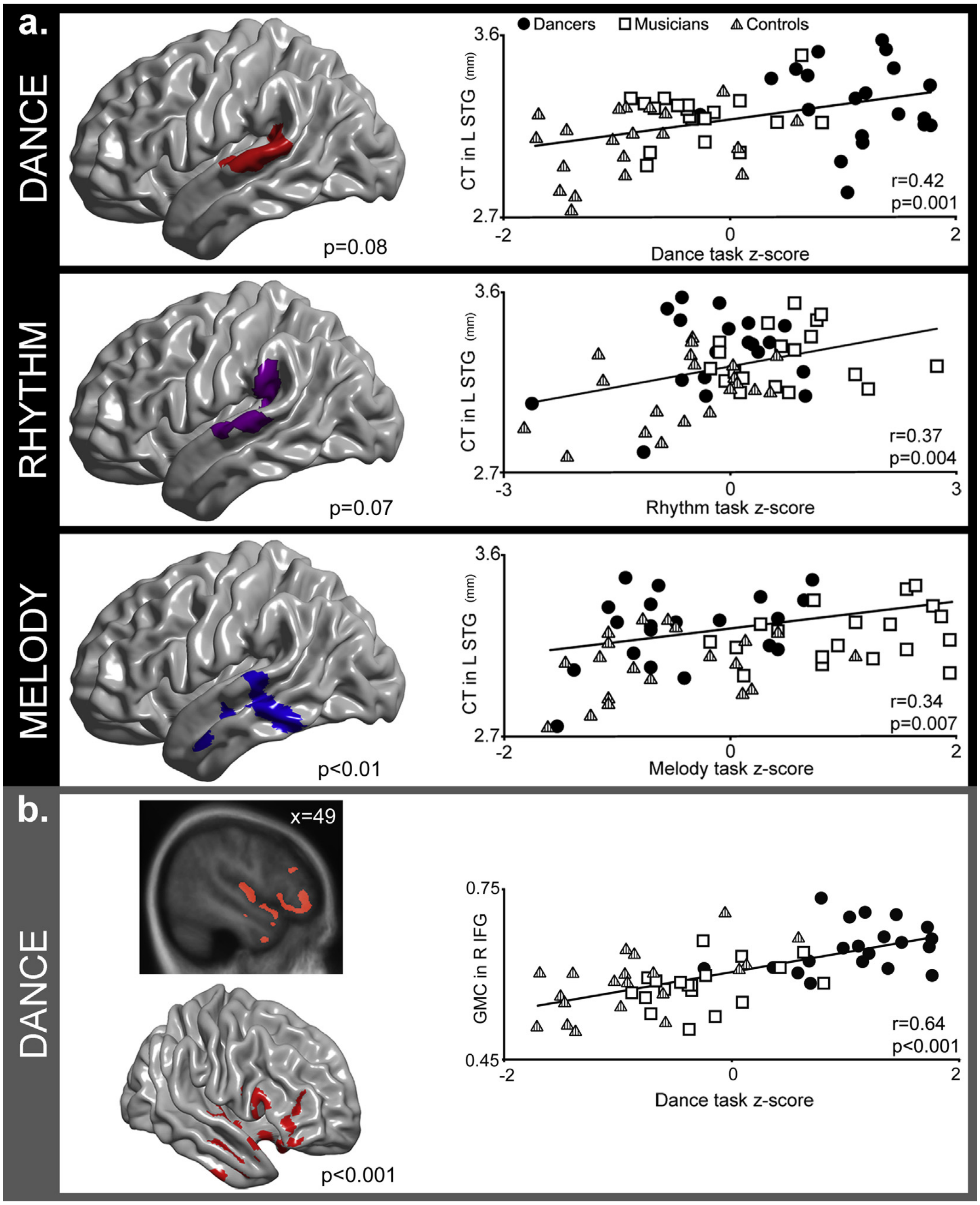

**Fig. 3.** Correlations between brain structure and task performance. Brain structure correlations with behavioural tasks across all groups are shown, including significant clusters at $p \leqslant 0.05$ and trending clusters at $p < 0.1$ after correction for family-wise error using random field theory. Regions of the left superior temporal gyrus (STG) where cortical thickness (CT) is correlated with dance (top-red), rhythm (middle-purple) and melody task performance (bottom-blue), as well as their corresponding scatterplots, are presented in panel (a). Panel (b) shows the correlation between gray matter concentration (GMC) in the right inferior frontal gyrus (IFG)/STG and dance task performance, as demonstrated by a saggital section, surface rendering showing the significant cluster and the corresponding scatterplot. See Tables 2–4 for more detailed information on these results.

The present findings of positive correlations between GM structure in the STG and performance on dance- and music-related tasks are consistent with previous functional and structural studies using similar tasks. For example, previous functional studies found STG activation during dance-related tasks, such as dance observation and simulation (Cross et al., 2006; Jola et al., 2013), performance of tango steps (Brown et al., 2006) and performance of a dance video game focusing on lower limb movement (Tachibana et al., 2011). Activation of the STG has also been observed during rhythm tasks, such as rhythm discrimination (Foster and Zatorre, 2010a), beat finding (Kung et al., 2013) and synchronizing taps to an auditory stimulus (Krause et al., 2010; Lewis et al., 2004). CT in the STG has also been positively correlated with rhythm discrimination (Foster and Zatorre, 2010b). Finally, the present correlation of CT in the STG with melodic discrimination is consistent with previous findings using this same melody task in musicians and non-musicians, which showed both a positive correlation between CT and melody task performance in the STG (Foster and Zatorre, 2010b), as well as melody task-related activation in the STG (Foster and Zatorre, 2010a).

Further support for the role of the STG in music and dance comes from studies on auditory-motor integration. The STG is an

**Table 2**
Brain structure correlations with the dance imitation task.

| Participants | Brain structural metric | Cluster | | Peak (MNI coordinates) | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | P-value (2-tailed) | Extent | Brain region | Brodmann area | x | y | z | t-value |
| All | *CT* | *0.08* | *649 vertices/1583 mm$^2$* | *L STG* | *22* | *-62* | *-35* | *7* | *3.62* |
| | | | | *L pSTG* | *41* | *-47* | *-39* | *20* | *2.97* |
| | | | | *L STG* | *42/22* | *-58* | *-20* | *8* | *2.77* |
| | GMC | <0.001 | 12046 voxels/mm$^3$ | R IFG | 44 | 56 | 13 | 19 | 5.48 |
| | | | | R IFG | 47 | 35 | 22 | -22 | 4.33 |
| | | | | R MFG | 46 | 43 | 44 | 10 | 3.87 |
| | | | | R insula | 13 | 42 | -5 | -10 | 3.85 |
| | | | | R rolandic operculum | 6 | 48 | -13 | 11 | 3.73 |
| | | | | R MTG | 21 | 56 | -3 | -18 | 3.72 |
| | | | | R IFG | 47 | 45 | 21 | -4 | 3.62 |
| | | | | R STG | 22 | 59 | -4 | 1 | 3.50 |
| | | | | R ITG | 21 | 52 | 4 | -36 | 3.42 |
| | | | | R MFG | 46 | 51 | 29 | 24 | 3.30 |
| | | | | R ITG | 20 | 64 | -16 | -25 | 3.19 |
| | | | | R subcallosal gyrus | 34 | 23 | 6 | -14 | 3.13 |
| | | | | R IFG | 47 | 47 | 42 | -12 | 3.10 |
| | | | | R IFG | 45 | 54 | 27 | 9 | 2.93 |
| | | | | R STG/temporal pole | 38 | 52 | 10 | -11 | 2.87 |
| | | 0.02 | 5392 voxels/mm$^3$ | L STG/temporal pole | 38 | -41 | 18 | -21 | 4.13 |
| | | | | L rolandic operculum | 6 | -49 | -5 | 5 | 4.08 |
| | | | | L insula | 13 | -46 | 13 | -7 | 3.60 |
| | | | | L IFG | 47 | -36 | 24 | -2 | 2.62 |
| Controls | GMC | 0.02 | 5598 voxels/mm$^3$ | R MFG | 9 | 46 | 20 | 43 | 6.27 |
| | | | | R IFG | 44 | 51 | 17 | 29 | 5.98 |
| | | | | R IFG | 45 | 46 | 34 | 1 | 5.86 |
| | | | | R IFG | 44/45 | 54 | 22 | 15 | 4.30 |
| | | | | R putamen | N/A | 23 | 15 | 4 | 2.99 |
| | | | | R IFG | 47 | 44 | 39 | -13 | 2.67 |
| | | 0.03 | 5215 voxels/mm$^3$ | L PoG | 43 | -68 | -14 | 28 | 6.44 |
| | | | | L supramarginal gyrus | 40 | -61 | -31 | 40 | 5.62 |
| | | | | L STG | 22 | -65 | -34 | 10 | 4.68 |
| | | | | L PrG | 6 | -63 | 4 | 27 | 4.54 |
| | | | | L STG | 22 | -69 | -17 | 0 | 4.42 |
| | | | | L STG | 41 | -44 | -37 | 11 | 3.75 |
| | | | | L PoG | 4 | -62 | -5 | 39 | 2.99 |
| | | *0.08* | *4728 voxels/mm$^3$* | *R supramarginal gyrus* | *22* | *68* | *-23* | *20* | *5.70* |
| | | | | *R MTG* | *21* | *67* | *-6* | *-11* | *5.01* |
| | | | | *R STS* | *22* | *68* | *-20* | *-1* | *4.78* |
| | | | | *R STG* | *22* | *53* | *-10* | *7* | *4.61* |
| | | | | *R supramarginal gyrus* | *40* | *67* | *-19* | *38* | *2.93* |

Results are listed for each brain structural metric (CT or GMC) across all participants and in the control group separately. Significant clusters at $p \leqslant 0.05$ and trending clusters at $p < 0.1$ after correction for family-wise error using random field theory are reported. Trending clusters are listed in italics.
CT = cortical thickness; GMC = gray matter concentration; IFG = inferior frontal gyrus; ITG = inferior temporal gyrus; MFG = middle frontal gyrus; MTG = middle temporal gyrus; PoG = postcentral gyrus; PrG = precentral gyrus; STG = superior temporal gyrus; pSTG = posterior superior temporal gyrus; STS = superior temporal sulcus.

**Table 3**
Brain structure correlations with the rhythm synchronization task.

| Participants | Brain structural metric | Cluster | | Peak (MNI coordinates) | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | P-value (2-tailed) | Extent | Brain region | Brodmann area | x | y | z | t-Value |
| All | CT | <0.001 | 548 vertices/1353 mm$^2$ | R CS | 3 | 44 | −14 | 35 | 4.04 |
| | | | | R CS/PrG | 3/4 | 43 | −10 | 50 | 3.19 |
| | | | | R CS | 4 | 61 | −1 | 19 | 3.10 |
| | | *0.07* | *616 vertices/1739 mm$^2$* | *L supramarginal gyrus* | *40* | *−47* | *−33* | *20* | *3.10* |
| | | | | *L STG* | *22* | *−62* | *−28* | *4* | *3.00* |
| | | | | *L supramarginal gyrus* | *40* | *−60* | *−36* | *32* | *2.85* |
| | | | | *L STG* | *22* | *−64* | *−9* | *1* | *2.77* |
| | GMC | 0.05 | 3018 voxels/mm$^3$ | R CS | 6 | 44 | −14 | 48 | 3.75 |
| | | | | R PoG | 4 | 40 | −26 | 58 | 3.73 |
| Controls | CT | <0.01 | 117 vertices/185 mm$^2$ | R STG | 22/42 | 45 | −5 | −10 | 5.23 |
| | | | | R STG | 22/42 | 43 | −18 | 0 | 2.75 |
| | *GMC* | *0.07* | *3166 voxels/mm$^3$* | *L insula* | *13* | *−39* | *18* | *−9* | 5.82 |
| | | | | *L STG* | *41* | *−43* | *1* | *−16* | 4.94 |
| | | | | *L IFG* | *47* | *−47* | *37* | *−15* | 4.54 |
| | | | | *L IFG* | *47* | *−50* | *26* | *−2* | 3.81 |

Results are listed for each brain structural metric (CT or GMC) across all participants and in the control group separately. Significant clusters at $p \leqslant 0.05$ and trending clusters at $p < 0.1$ after correction for family-wise error using random field theory are reported. Trending clusters are listed in italics.
CS = central sulcus; CT = cortical thickness; GMC = gray matter concentration; IFG = inferior frontal gyrus; PoG = postcentral gyrus; PrG = precentral gyrus; STG = superior temporal gyrus.

**Table 4**
Cortical thickness correlations with the melody discrimination task across all participants.

| Cluster | | Peak (MNI coordinates) | | | | | |
|---|---|---|---|---|---|---|---|
| P-value (2-tailed) | Extent | Brain region | Brodmann area | x | y | z | t-Value |
| <0.001 | 1065 vertices/2746 mm$^2$ | R ventral PoG | 43 | 65 | −14 | 20 | 4.06 |
| | | R rolandic operculum | 43 | 51 | −9 | 15 | 3.64 |
| | | R ventral PrG | 43 | 62 | 5 | 19 | 3.41 |
| | | R PoG | 4 | 57 | −15 | 48 | 3.21 |
| | | R CS/PoG | 4 | 55 | −8 | 30 | 3.09 |
| | | R IFG/precentral sulcus | 6 | 49 | 9 | 13 | 2.70 |
| | | R CS | 3/4 | 43 | −15 | 37 | 2.50 |
| <0.001 | 1159 vertices/2580 mm$^2$ | R MTG | 21 | 62 | −26 | −6 | 4.03 |
| | | R STG/STS | 22 | 52 | −45 | 22 | 4.01 |
| | | R STS | 21/22 | 49 | −38 | 9 | 3.71 |
| | | R STG | 22 | 63 | −13 | 6 | 3.01 |
| | | R STG | 22 | 67 | −36 | 9 | 2.76 |
| <0.01 | 197 vertices/314 mm$^2$ | R STG | 52 | 43 | −3 | −14 | 3.70 |
| | | R STG | 52 | 42 | −14 | −5 | 3.07 |
| <0.01 | 640 vertices/1925 mm$^2$ | L ITG | 37/20 | −59 | −44 | −16 | 3.68 |
| | | L MTG | 21 | −57 | −29 | −4 | 3.61 |
| | | L MTG | 21/38 | −59 | 1 | −24 | 2.92 |
| | | L MTG/STS | 21 | −55 | −12 | −13 | 2.88 |
| | | L STG | 22 | −62 | −20 | 9 | 2.66 |

Clusters are significant at $p \leqslant 0.05$ after correction for family-wise error using random field theory are reported. No significant clusters in GMC or in the control group separately were found.
CS = central sulcus; IFG = inferior frontal gyrus; ITG = inferior temporal gyrus; MTG = middle temporal gyrus; PoG = postcentral gyrus; PrG = precentral gyrus; STG = superior temporal gyrus; STS = superior temporal sulcus.

important component of the auditory-motor integration network (Bangert et al., 2006; Hickok et al., 2003; Zatorre et al., 2007) and has been implicated in processing sounds and sending those with a motor relevance to motor regions (Griffiths and Warren, 2002). Auditory-motor integration is crucial to both dance and music training, since dancers are trained to synchronize movements to auditory stimuli and musicians are trained to execute movements to produce sound. Functional brain plasticity associated with such training has been demonstrated by the finding of functional enhancements of this auditory-motor network in expert musicians compared to amateur musicians (Lotze et al., 2003) and non-musicians (Bangert et al., 2006; Chen et al., 2008). This has not yet been investigated in dancers compared to non-dancers, however the present results of structural enhancements in both dancers and musicians in the STG suggests that both dance and music training may have effects on this network. The STG has also been associated with temporal control of movements (Bengtsson et al., 2004), which is highly relevant to both dancers and musicians as both are trained to execute movement sequences in a precisely timed manner. Studies using both music- and dance-related tasks have implicated the STG in multisensory integration (Jola et al., 2013; Pantev et al., 2015; Tachibana et al., 2011), which is crucial to both dance and music training as they require the integration of auditory (e.g., music one is dancing to or producing), visual (e.g., observing a choreographer or a conductor), and somatosensory (e.g., contact between body and floor or a musical instrument) information. In addition, STG activation has been demonstrated during other dance-related tasks, such as balancing (Karim et al., 2014) and posture prediction (Gardner et al., 2015).

The present GM structural differences found in dancers and musicians were both unilateral and bilateral between groups and in the brain-behavioural correlations. For example, some correlations were left-lateralized (e.g., the dance-CT correlation across all participants), others were right-lateralized (e.g., the rhythm-CT correlation in controls) and others were bilateral (e.g., the dance-GMC correlations across all participants and in controls, as well as the melody-CT correlations across all participants). Moreover, both the group comparison and brain-behavioural analyses yielded GM differences located across a wide extent of the STG. For example, the CT-dance task correlation was in the middle-posterior area of the STG, however the GMC-dance task correlation included more anterior regions of the STG. Taken together, the above results are consistent with previous findings of widespread and bilateral structural brain differences in the STG in both music- and dance-related functions. For example, activation over much of the STG has been found during melodic processing (Bengtsson and Ullen, 2006), beat finding (Kung et al., 2013) and dance observation (Jola et al., 2013).

The group differences in CT observed in the present study also extended beyond the STG into the STS and MTG. The observed area of the STS has been associated with music- and dance-relevant functions such as melodic processing (Klein and Zatorre, 2015; Lee et al., 2011), audiovisual integration (Powers et al., 2012; van Atteveldt et al., 2004; Werner and Noppeney, 2010), movement-sound congruency (Schmitz et al., 2013), and human motion perception (Han et al., 2013; Puce and Perrett, 2003). Dance-related functions have been associated with the MTG as well. The MTG has been implicated in audiovisual integration and movement timing during the performance of a dance video game (Ono et al., 2014), and its plasticity in response to dance training has been suggested by its greater activation to observing trained than untrained dance movements (Calvo-Merino et al., 2005; Cross et al., 2009). In combination with the present findings, this work suggests that the STS and MTG, in addition to the STG, are involved in music and dance.

Overall, the present findings support previous work showing the importance of superior temporal regions in dance- and music-relevant functions separately, and expand on the literature by demonstrating that GM structure related to dance and music overlaps in superior temporal areas.

### *3.2. GM structure in the inferior frontal cortex is correlated with dance task performance*

In addition to the STG, GMC in the IFG was positively correlated with performance on the dance imitation task across all groups as well as in the control group separately. The correlation in the control group suggests that GMC in the IFG is positively correlated with dance imitation ability in the absence of dance (or music) training. These correlations were observed throughout the IFG, including the opercular, triangular and orbital areas (Brodmann areas 44, 45, and 47).

This finding extends previous work suggesting the involvement of the IFG in a variety of dance-relevant functions. It has been suggested that the IFG works with the STG in the above-described auditory-motor network (Bangert et al., 2006; Hickok et al., 2003; Romanski, 2012; Zatorre et al., 2007), which is furthered by findings of anatomical connections between these areas (for a review, see Romanski, 2012). Its role in this network may be associated with its involvement in action selection. It has been proposed that Brodmann area 44 (Broca's area and its right homolog) is the hub of a motor repertoire-dependent hearing-doing network (Lahav et al., 2007) and selects premotor representations based on context (Koechlin et al., 2003). This is supported by findings that the IFG is activated when listening to sounds with associated motor actions (Chen et al., 2009; Lahav et al., 2007). It has also been implicated in sequence prediction (Fiebach and Schubotz, 2006; Schubotz and von Cramon, 2003) as well as functions of the mirror neuron system (Molnar-Szakacs et al., 2005; Rizzolatti et al., 2001) including action observation and execution (Grezes and Decety, 2001). These functions are crucial to dance training, since it requires the observation, imitation and execution of movement sequences as well as the synchronization of movements to auditory stimuli.

The involvement of the IFG in dance contexts is supported by the finding of its greater activation to observing and simulating trained compared to untrained dance movements (Calvo-Merino et al., 2005; Cross et al., 2009; Gardner et al., 2015), suggesting its role in action embodiment, as well as its activation during performance of tango steps (Brown et al., 2006). Additional functional studies have demonstrated activity in the IFG during beat-finding (Kung et al., 2013), encoding a body's postural configuration (Cross et al., 2010) and balancing (Karim et al., 2014), all of which are highly relevant to dance performance.

More anterior regions of the IFG (Brodmann areas 45–47) have been associated with cognitive functions relevant to dance, including active memory retrieval (Cadoret et al., 2001) of spatial and nonspatial visual information (Kostopoulos and Petrides, 2003), monitoring information in working memory (Champod and Petrides, 2007; Petrides, 2000a,b) particularly during visuomotor integration; and processing the order of visual stimuli (Amiez and Petrides, 2007). These functions are relevant to dance's reliance on retrieval of previously learned ordered movements using auditory and visual cues. The present results expand on this functional literature by demonstrating that GM structure in the IFG is associated with dance imitation ability.

### 3.3. A multi-metric approach to study brain structural correlates of dance versus music

In the present study, three GM structural measures (i.e., GMC, CT and SA) were used to examine brain structural differences between dancers, musicians and controls. Using such a novel multi-metric GM approach provides complementary and more detailed analyses of GM structure in these groups. In the group comparison, significant differences between dancers, musicians and controls were found only in CT and not in GMC or SA. This is consistent with the study by Bermudez et al., 2009 who found less and smaller significant differences between musicians and nonmusicians using GMC compared to CT. Differences in findings between these measures may be related to differences in the aspects of GM structure that they measure. GMC provides a more global measure of gray matter structure and takes into account a variety of factors including CT, SA and gyrification (Palaniyappan and Liddle, 2012; Kong et al., 2015). Using surface-based measures in addition to GMC can help distinguish the nature of the GM differences by measuring such factors individually. Therefore, each measure may have different sensitivities depending on the nature of the GM structural differences in the examined sample. GMC would likely be more sensitive to general shape and position differences, while CT and SA would likely be more sensitive to differences in their respective measure. This is supported by the demonstration that this CT analysis can detect group differences of less than 1 mm (Lerch and Evans, 2005). The present findings of group differences in CT but not GMC or SA suggest that the brain plasticity associated with auditory-motor training may be related to the GM structure underlying CT (i.e., number of cells within a cortical column, cell size and packing density), rather than GM structure underlying other characteristics such as SA (i.e., number and spacing of cortical columns) (Gittins and Harrison, 2004; Rakic, 1988, 1995; Rakic et al., 2009).

The complementarity of these GM measures is furthered supported by the brain-behaviour correlations. Both GMC and CT in the left STG were found to be positively correlated with dance task performance, and the GMC results expanded on this with additional clusters in the right STG and bilateral IFG. Overlap between these measures was also found in correlations between GM structure in the right central sulcus and rhythm task performance, however some differences in correlations between this task and GM structure in superior temporal and inferior frontal regions were found between measures. Correlations with the melody task were only found in CT. Additional confidence in the results is provided when both methods converge, and differences in results may be attributed to the different sensitivities of each measure as described above. Overall, the present results support previous multi-method studies (e.g., Bermudez et al., 2009; Foster and Zatorre, 2010b; Hutton et al., 2009; Palaniyappan and Liddle, 2012) in demonstrating that these measures provide different but complementary information regarding GM structure.

Overall, our findings of differences in CT between musicians and controls in sensorimotor regions support the previous literature demonstrating brain structural effects of musical expertise. Various methodological differences across studies might account for why we did not find significant differences in GMC here between musicians and non-musicians. For example, the present study included musicians who played a variety of instruments, and we conducted a whole-brain analysis, and corrected our results for multiple comparisons. In contrast, some previous work that has reported GMC differences in musicians versus non-musicians has included only pianists/keyboard players in the musician group (Gaser and Schlaug, 2003; Han et al., 2009), only included region of interest analyses (Abdul-Kareem et al., 2011; Amunts et al., 1997; Schneider et al., 2002; Sluming et al., 2002), or not corrected results for multiple comparisons (Fauvel et al., 2014).

While the present study focused on detailed analyses of GM structure in dance versus music, previous work from our laboratory revealed additional findings of white matter (WM) differences in dance versus music using Diffusion Tensor Imaging in an overlapping sample of participants (Giacosa et al., 2016). More specifically, dancers had increased diffusivity and reduced coherence in sensorimotor pathways compared to musicians and these differences were related to performance on dance and music tasks. Whole-body dance training and effector-specific music training have opposite effects on sensorimotor pathways. Increased diffusivity in dancers may result from larger axonal diameter, increased fanning or enhanced crossing of fibres. Taken together, the findings from our GM and WM studies suggest that the characteristics that dance and music share (e.g., sensorimotor integration) may have a greater association with GM structure, while their differences (e.g., whole-body versus effector-specific movements) may have a greater association with WM.

## 4. Conclusions and future directions

This is the first study to compare the effects of long-term dance versus music training on GM structure in relation to behaviour. Specifically, GM structure was compared between expert dancers, expert musicians and untrained controls, and correlated with performance on dance- and music-related tasks. Both dancers and musicians showed increased GM relative to controls in superior temporal regions, and correlations between GM and performance on dance- and music-related tasks were found in these regions. Taken together, the results indicate that both dance and music training may shape GM structure in a similar way, particularly in the STG.

This work increases our understanding of brain plasticity associated with auditory-motor artistic training, and brain-behaviour correlations in the contexts of music and dance. Moreover, the present findings motivate several important areas of future study. For example, we are currently conducting structural covariance (He et al., 2007; Lerch et al., 2006) and functional resting state connectivity (Barkhof et al., 2014) analyses to investigate potential brain connectivity differences in dancers and musicians. Future longitudinal studies will be important to investigate the contribution of genetic versus environmental factors to dance and music training. Finally, this study may serve as a foundation for future clinical work to develop music- or dance-based therapies for special populations.

## 5. Experimental procedure

### 5.1. Participants

Three groups of participants (aged 18–40 years old) 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 5). 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 (Bailey and Penhune, 2010; Coffey et al., 2011). Dancers and musicians had on average approximately 15 years of experience in their respective disciplines, and controls had on average less than one year of experience in dance, music, figure skating and aerobics. All participants were physically active (e.g., biking, running, or other fitness activities). 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 5). Participants had no past or current learning or developmental disorder, neurological or psychiatric condition, or alcohol or substance abuse. This study was conducted in accordance with the Declaration of Helsinki and approved by the Research Ethics Board at the Montreal Neurological Institute and Hospital. Written informed consent was obtained from all participants.

### 5.2. Behavioural testing and analyses

The behavioural battery included three dance- and music-related tasks. The most dance-related task was a dance imitation task, in which 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. Participants imitated seven dance routines of varying difficulty selected from the video game Dance Central for Xbox Kinect version 1 (Harmonix, http://www.harmonixmusic.com). Movements were recorded by the Kinect sensor, which provided a measure of percent moves correct. This task assesses the ability to observe and imitate whole body dance movements in real time with music.

A rhythm synchronization task was chosen as a task related to both dance and music. Participants heard rhythmic stimuli twice, and were asked to listen to the first presentation and tap a finger on a computer mouse button in synchrony with the second. They completed 2 blocks of 36 trials each. The task was scored using the absolute value inter-tap interval (ITI) deviation, which is the ratio of the time between two of the participant's taps to the time between the two corresponding sounds in the stimulus. This task assesses auditory-motor integration and fine motor response, and has been previously applied in musician and non-musician samples (Bailey and Penhune, 2010; Bailey et al., 2014; Chen et al., 2008).

The most music-related task was a melody discrimination task (Foster and Zatorre, 2010a,b) in which participants were asked to determine if pairs of melodies were the same or different based on changes in pitch. Participants completed 4 blocks of 30 trials each. This task measures auditory processing and pitch discrimination and was scored using percent of trials correct. As a control for the melody task and a test of auditory working memory, participants were also tested on a syllable sequence discrimination task (Foster and Zatorre, 2010a,b), in which they heard two syllable

**Table 5**
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 (D) | 20 | 25.1 ± 3.9 | 14F, 6 M | 21.7 ± 2.2 | 15.3 ± 5.2 | 1.8 ± 1.9 | 2.35 ± 0.6 |
| Musicians (M) | 19 | 22.9 ± 3.4 | 12F, 7 M | 22.5 ± 3.2 | 1.0 ± 1.8 | 15.4 ± 3.4 | 2.32 ± 1.0 |
| Controls (C) | 20 | 25.4 ± 5.1 | 13F, 7 M | 21.8 ± 3.2 | 0.4 ± 0.8 | 0.5 ± 1.0 | 2.6 ± 1.1 |
| Comparison between groups | | D = M = C<br>F(2,56) = 2.1<br>p = 0.13 | | D = M = C<br>F(2,55) = 0.38<br>p = 0.68 | D > M (p < 0.0001)<br>D > C (p < 0.0001)<br>M = C (p = 1) | M > D (p < 0.0001)<br>M > C (p < 0.0001)<br>D = C (p = 0.27) | D = M = C<br>F(2,56) = 56<br>p = 0.57 |

F = females; M = males; SD = standard deviation.
Education levels for each participant were calculated on a scale of 1–5, where 1 is the lowest (completed high school) and 5 is the highest (completed doctorate degree).

sequences and were asked to determine if they were the same or different. Participants completed 2 blocks of the syllable task, each consisting of 30 trials, and this task was scored using percent of trials correct.

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. To allow for between-task comparisons, overall scores for the dance, rhythm and melody tasks were converted to z-scores (i.e., standardized scores) across all participants. 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. Group differences in the syllable sequence discrimination task were tested using a univariate ANCOVA. To control for effects of age and sex on task performance, these variables were included as covariates of no interest in all task analyses.

Additional details about these above tasks as well as behavioural analyses on this sample have been reported elsewhere (Karpati et al., 2016), and thus only brief descriptions of the behavioural measures and results are reported here.

### 5.3. MRI data acquisition and analyses

T1-weighted brain images were acquired for all participants at the Montreal Neurological Institute (MNI) on a 3T Siemens Trio MR scanner with a 32-channel head coil. MRI scanning parameters were as follows: echo time = 2.98 ms, repetition time = 2300 ms, voxel size 1 mm × 1 mm × 1 mm. Earplugs and headphones, as well as foam pads were used to reduce noise perception and head motion, respectively.

Images were processed using the CIVET pipeline (version 1.1.11, Ad-Dab'bagh et al., 2006; http://www.bic.mni.mcgill.ca/ServicesSoftware/CIVET1112). They were registered to the ICBM152 nonlinear model (Collins et al., 1994; Grabner et al., 2006) with 12 degrees of freedom for registration, and corrected for signal intensity nonuniformity (Sled et al., 1998). Images were segmented into gray and white matter, cerebrospinal fluid and background (Tohka et al., 2004; Zijdenbos et al., 1998).

Multiple GM measures (gray matter concentration [GMC], CT, and cortical surface area [SA]) were used together to compare GM structure between groups and correlate GM structure to task performance. CT and SA allow for the analysis of cortical structures without confounds of the shape and position of the cortical mantle (Good et al., 2001), while GMC allows for the investigation of the cerebellum and subcortical structures. Furthermore, each of these methods provides complementary information regarding GM structure. GMC provides a more global measure of GM structure which may be affected by several factors including CT, SA, and cortical folding (Hutton et al., 2009; Palaniyappan and Liddle, 2012). GMC alone cannot distinguish which of these factors may be associated with significant findings, however it allows for the sensitive detection of findings that may be associated with general shape or position differences or the combination of sub-threshold differences in multiple factors. CT and SA provide more specific measures of GM structure, with each measuring only one of these factors. Therefore, the biological interpretation of CT and SA findings are more concretely interpretable than GMC results. For example, CT may be related to the number of cells within a cortical column while SA may be related to the number and spacing of columns (Rakic, 1988, 1995; Rakic et al., 2009). It has also been suggested that CT is affected by cell size and packing density (Gittins and Harrison, 2004).

#### 5.3.1. Surface-based morphometry

For the surface-based analyses, deformable models were fitted to the images in order to extract the boundaries between GM and each of white matter and cerebrospinal fluid (Kim et al., 2005; MacDonald et al., 2000), resulting in two surfaces with 81920 polygons each. Following the surface extraction, participants' cortical mid-surfaces (calculated using the mid-points of the linked inner and outer surfaces) were nonlinearly aligned using the SURFTRACC algorithm and a depth-potential function to a hemisphere-unbiased iterative surface template in order to establish intersubject vertex correspondence (Boucher et al., 2009; Lyttelton et al., 2007; Robbins et al., 2004). Then, a CT map was calculated for each participant, where CT (the distance between the pia mater and gray/white matter boundary) was measured at each vertex (Ad-Dab'bagh et al., 2005; Lerch and Evans, 2005) and then blurred with a 20 mm surface-based blurring kernel (Chung and Taylor, 2004). Surface area (SA) of each vertex was calculated as one third of the area of all adjoining vertex triangles (Lyttelton et al., 2009) and blurred with a 40 mm surface-based blurring kernel.

#### 5.3.2. Voxel-based morphometry

For the voxel-based morphometry analyses, images containing voxels classified as GM for each participant were smoothed using a 3-dimensional Gaussian blurring kernel with an 8 mm full-width half-maximum. Lastly, a mask to include only GM in the analyses was created by including all voxels that were classified as GM in at least 25% of participants.

#### 5.3.3. Statistical analyses

General linear models were performed using SurfStat software (http://www.math.mcgill.ca/keith/surfstat/) across the whole brain to determine group differences in CT, SA, and GMC (Eq. (1)), as well as regions where each measure was correlated with performance on the dance, rhythm and melody tasks (Eq. (2)). These correlations were examined across all participants, as well as in the control group separately (to examine brain-behaviour correlations in the absence of training). Both F-tests and post hoc pairwise comparisons (where appropriate) were conducted in the group difference analysis. Age, sex and a proxy measure of brain volume (pBV; Karama et al., 2011) were included as covariates of no interest in all analyses. Clusters were defined using a forming threshold of $p < 0.01$, and correction for family-wise error using random field theory (Friston et al., 1994) was then applied at the cluster level.

$$\text{Tissue measure}^{*} = 1 + \text{Group} + \text{Age} + \text{Sex} + \text{pBV} \tag{1}$$

$$\text{Tissue measure}^{*} = 1 + \text{Task}^{**} + \text{Age} + \text{Sex} + \text{pBV} \tag{2}$$

$^{*}$CT, SA or GMC.

$^{**}$Dance imitation, rhythm synchronization or melody discrimination.

## Author contributions

All authors contributed to the conception and design of the study. F.K. and C.G. collected the data. F.K., C.G. and N.F. analyzed the data. All authors contributed to interpretation of the results. F.K. wrote the manuscript, and all authors reviewed and approved the manuscript.

## Acknowledgements

We would like to thank our participants for their time, as well as Alessia Di Cesare, Veronica Yuk, and Dana Boebinger for their assistance in the data collection process. This work was funded by a grant from the Natural Sciences and Engineering Council of Canada (NSERC) to Dr. Krista Hyde.

## References

Abdul-Kareem, I.A., Stancak, A., Parkes, L.M., Sluming, V., 2011. Increased gray matter volume of left pars opercularis in male orchestral musicians correlate positively with years of musical performance. J. Magn. Reson. Imaging 33, 24–32.

Ad-Dab'bagh, Y., Singh, V., Robbins, S., Lerch, J., Lyttelton, O., Fombonne, E., Evans, A. C., 2005. Native space cortical thickness measurement and the absence of correlation to cerebral volume. In: Zilles, K. (Ed.), Proceedings of the 11th Annual Meeting of the Organization for Human Brain Mapping, Toronto, Canada.

Ad-Dab'bagh, Y., Einarson, D., Lyttelton, O., Muehlboeck, J.S., Mok, K., Ivanov, O., Vincent, R.D., Lepage, C., Lerch, J., Fombonne, E., Evans, A.C., 2006. The CIVET image-processing environment: a fully automated comprehensive pipeline for anatomical neuroimaging research. In: Corbetta, M. (Ed.), Proceedings of the 12th Annual Meeting of the Organization for Human Brain Mapping, Florence, Italy.

Amiez, C., Petrides, M., 2007. Selective involvement of the mid-dorsolateral prefrontal cortex in the coding of the serial order of visual stimuli in working memory. Proc. Natl. Acad. Sci. U.S.A. 104, 13786–13791.

Amunts, K., Schlaug, G., Jancke, L., Steinmetz, H., Schleicher, A., Dabringhaus, A., Zilles, K., 1997. Motor cortex and hand motor skills: structural compliance in the human brain. Hum. Brain Mapp. 5, 206–215.

Bailey, J.A., Penhune, V.B., 2010. Rhythm synchronization performance and auditory working memory in early- and late-trained musicians. Exp. Brain Res. 204, 91–101.

Bailey, J.A., Zatorre, R.J., Penhune, V.B., 2014. Early musical training is linked to gray matter structure in the ventral premotor cortex and auditory–motor rhythm synchronization performance. J. Cogn. Neurosci. 26, 755–767.

Bangert, M., Peschel, T., Schlaug, G., Rotte, M., Drescher, D., Hinrichs, H., Heinze, H.J., Altenmuller, E., 2006. Shared networks for auditory and motor processing in professional pianists: evidence from fMRI conjunction. NeuroImage 30, 917–926.

Barkhof, F., Haller, S., Rombouts, S.A., 2014. Resting-state functional MR imaging: a new window to the brain. Radiology 272, 29–49.

Baumann, S., Koeneke, S., Schmidt, C.F., Meyer, M., Lutz, K., Jancke, L., 2007. A network for audio-motor coordination in skilled pianists and non-musicians. Brain Res. 1161, 65–78.

Bengtsson, S.L., Ehrsson, H.H., Forssberg, H., Ullen, F., 2004. Dissociating brain regions controlling the temporal and ordinal structure of learned movement sequences. Eur. J. Neurosci. 19, 2591–2602.

Bengtsson, S.L., Ullen, F., 2006. Dissociation between melodic and rhythmic processing during piano performance from musical scores. NeuroImage 30, 272–284.

Bermudez, P., Lerch, J.P., Evans, A.C., Zatorre, R.J., 2009. Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. Cereb. Cortex 19, 1583–1596.

Boucher, M., Whitesides, S., Evans, A., 2009. Depth potential function for folding pattern representation, registration and analysis. Med. Image Anal. 13, 203–214.

Brown, S., Martinez, M.J., Parsons, L.M., 2006. The neural basis of human dance. Cereb. Cortex 16, 1157–1167.

Cadoret, G., Pike, G.B., Petrides, M., 2001. Selective activation of the ventrolateral prefrontal cortex in the human brain during active retrieval processing. Eur. J. Neurosci. 14, 1164–1170.

Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., Haggard, P., 2005. Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb. Cortex 15, 1243–1249.

Champod, A.S., Petrides, M., 2007. Dissociable roles of the posterior parietal and the prefrontal cortex in manipulation and monitoring processes. Proc. Natl. Acad. Sci. U.S.A. 104, 14837–14842.

Chen, J.L., Penhune, V.B., Zatorre, R.J., 2008. Moving on time: brain network for auditory-motor synchronization is modulated by rhythm complexity and musical training. J. Cogn. Neurosci. 20, 226–239.

Chen, J.L., Penhune, V.B., Zatorre, R.J., 2009. The role of auditory and premotor cortex in sensorimotor transformations. Ann. N.Y. Acad. Sci. 1169, 15–34.

Chung, M.K., Taylor, J., 2004. Diffusion smoothing on brain surface via finite element method. In: Proceedings of the IEEE International Symposium on Biomedical Imaging: Nano to Macro, pp. 432–435.

Coffey, E.B.J., Herholz, S.C., Scala, S., Zatorre, R.J., 2011. Montreal Music History Questionnaire: a tool for the assessment of music-related experience in music cognition research. In: Proceedings of the Neurosciences and Music IV: Learning and Memory. Edinburgh, UK.

Collins, D.L., Neelin, P., Peters, T.M., Evans, A.C., 1994. Automatic 3D inter-subject registration of MR volumetric data in standardized talairach space. J. Comput. Assist. Tomogr. 18, 192–205.

Cross, E.S., Hamilton, A.F., Grafton, S.T., 2006. Building a motor simulation de novo: observation of dance by dancers. NeuroImage 31, 1257–1267.

Cross, E.S., Kraemer, D.J., Hamilton, A.F., Kelley, W.M., Grafton, S.T., 2009. Sensitivity of the action observation network to physical and observational learning. Cereb. Cortex 19, 315–326.

Cross, E.S., Mackie, E.C., Wolford, G., Hamilton, A.F., 2010. Contorted and ordinary body postures in the human brain. Exp. Brain Res. 204, 397–407.

Fauvel, B., Groussard, M., Chetelat, G., Fouquet, M., Landeau, B., Eustache, F., Desgranges, B., Platel, H., 2014. Morphological brain plasticity induced by musical expertise is accompanied by modulation of functional connectivity at rest. NeuroImage 90, 179–188.

Fiebach, C.J., Schubotz, R.I., 2006. Dynamic anticipatory processing of hierarchical sequential events: a common role for Broca's area and ventral premotor cortex across domains? Cortex 42, 499–502.

Foster, N.E., Zatorre, R.J., 2010a. A role for the intraparietal sulcus in transforming musical pitch information. Cereb. Cortex 20, 1350–1359.

Foster, N.E., Zatorre, R.J., 2010b. Cortical structure predicts success in performing musical transformation judgments. NeuroImage 53, 26–36.

Friston, K.J., Worsley, K.J., Frackowiak, R.S., Mazziotta, J.C., Evans, A.C., 1994. Assessing the significance of focal activations using their spatial extent. Hum. Brain Mapp. 1, 210–220.

Gardner, T., Goulden, N., Cross, E.S., 2015. Dynamic modulation of the action observation network by movement familiarity. J. Neurosci. 35, 1561–1572.

Gaser, C., Schlaug, G., 2003. Brain structures differ between musicians and non-musicians. J. Neurosci. 23, 9240–9245.

Giacosa, C., Karpati, F.J., Foster, N.E.V., Penhune, V.B., Hyde, K.L., 2016. Dance and music training have different effects on white matter diffusivity in sensorimotor pathways. NeuroImage 135, 273–286.

Giese, M.A., Poggio, T., 2003. Neural mechanisms for the recognition of biological movements. Nat. Rev. Neurosci. 4, 179–192.

Gilaie-Dotan, S., Kanai, R., Bahrami, B., Rees, G., Saygin, A.P., 2013. Neuroanatomical correlates of biological motion detection. Neuropsychologia 51, 457–463.

Gittins, R., Harrison, P.J., 2004. A quantitative morphometric study of the human anterior cingulate cortex. Brain Res. 1013, 212–222.

Good, C.D., Johnsrude, I., Ashburner, J., Henson, R.N., Friston, K.J., Frackowiak, R.S., 2001. Cerebral asymmetry and the effects of sex and handedness on brain structure: a voxel-based morphometric analysis of 465 normal adult human brains. NeuroImage 14, 685–700.

Grabner, G., Janke, A.L., Budge, M.M., Smith, D., Pruessner, J., Collins, D.L., 2006. Symmetric atlasing and model based segmentation: an application to the hippocampus in older adults. In: Larsen, R., Nielsen, M., Sporring, J. (Eds.), Medical Image Computing and Computer-Assisted Intervention – MICCAI, pp. 58–66.

Grezes, J., Decety, J., 2001. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum. Brain Mapp. 12, 1–19.

Griffiths, T.D., Warren, J.D., 2002. The planum temporale as a computational hub. Trends Neurosci. 25, 348–353.

Han, Y., Yang, H., Lv, Y.T., Zhu, C.Z., He, Y., Tang, H.H., Gong, Q.Y., Luo, Y.J., Zang, Y.F., Dong, Q., 2009. Gray matter density and white matter integrity in pianists' brain: a combined structural and diffusion tensor MRI study. Neurosci. Lett. 459, 3–6.

Han, Z., Bi, Y., Chen, J., Chen, Q., He, Y., Caramazza, A., 2013. Distinct regions of right temporal cortex are associated with biological and human-agent motion: functional magnetic resonance imaging and neuropsychological evidence. J. Neurosci. 33, 15442–15453.

Hänggi, J., Koeneke, S., Bezzola, L., Jancke, L., 2010. Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. Hum. Brain Mapp. 31, 1196–1206.

He, Y., Chen, Z.J., Evans, A.C., 2007. Small-world anatomical networks in the human brain revealed by cortical thickness from MRI. Cereb. Cortex 17, 2407–2419.

Herholz, S.C., Zatorre, R.J., 2012. Musical training as a framework for brain plasticity: behavior, function, and structure. Neuron 76, 486–502.

Hickok, G., Buchsbaum, B., Humphries, C., Muftuler, T., 2003. Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt. J. Cogn. Neurosci. 15, 673–682.

Hutton, C., Draganski, B., Ashburner, J., Weiskopf, N., 2009. A comparison between voxel-based cortical thickness and voxel-based morphometry in normal aging. NeuroImage 48, 371–380.

Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Rizzolatti, G., 2001. Reafferent copies of imitated actions in the right superior temporal cortex. Proc. Natl. Acad. Sci. U.S.A. 98, 13995–13999.

James, C.E., Oechslin, M.S., Van De Ville, D., Hauert, C.A., Descloux, C., Lazeyras, F., 2014. Musical training intensity yields opposite effects on grey matter density in cognitive versus sensorimotor networks. Brain Struct. Funct. 219, 353–366.

Jola, C., McAleer, P., Grosbras, M.H., Love, S.A., Morison, G., Pollick, F.E., 2013. Uni- and multisensory brain areas are synchronised across spectators when watching unedited dance recordings. i-Perception 4, 265–284.

Karama, S., Colom, R., Johnson, W., Deary, I.J., Haier, R., Waber, D.P., Lepage, C., Ganjavi, H., Jung, R., Evans, A.C.Brain Development Cooperative G, 2011. Cortical thickness correlates of specific cognitive performance accounted for by the general factor of intelligence in healthy children aged 6 to 18. NeuroImage 55, 1443–1453.

Karim, H.T., Sparto, P.J., Aizenstein, H.J., Furman, J.M., Huppert, T.J., Erickson, K.I., Loughlin, P.J., 2014. Functional MR imaging of a simulated balance task. Brain Res. 1555, 20–27.

Karpati, F.J., Giacosa, C., Foster, N.E., Penhune, V.B., Hyde, K.L., 2015. Dance and the brain: a review. Ann. N.Y. Acad. Sci. 1337, 140–146.

Karpati, F.J., Giacosa, C., Foster, N.E., Penhune, V.B., Hyde, K.L., 2016. Sensorimotor integration is enhanced in dancers and musicians. Exp. Brain Res. 234, 893–903.

Kim, J.S., Singh, V., Lee, J.K., Lerch, J., Ad-Dab'bagh, Y., MacDonald, D., Lee, J.M., Kim, S.I., Evans, A.C., 2005. Automated 3-D extraction and evaluation of the inner and outer cortical surfaces using a Laplacian map and partial volume effect classification. NeuroImage 27, 210–221.

Klein, M.E., Zatorre, R.J., 2015. Representations of invariant musical categories are decodable by pattern analysis of locally distributed BOLD responses in superior temporal and intraparietal sulci. Cereb. Cortex 25, 1947–1957.

Koechlin, E., Ody, C., Kouneiher, F., 2003. The architecture of cognitive control in the human prefrontal cortex. Science 302, 1181–1185.

Kong, L., Herold, C.J., Zöllner, F., Salat, D.H., Lässer, M.M., Schmid, L.A., Fellhauer, I., Thomann, P.A., Essig, M., Schad, L.R., Erickson, K.I., Schröder, J., 2015. Comparison of grey matter volume and thickness for analysing cortical changes in chronic schizophrenia: a matter of surface area, grey/white matter intensity contrast, and curvature. Psychiatry Res. 231, 76–83.

Kostopoulos, P., Petrides, M., 2003. The mid-ventrolateral prefrontal cortex: insights into its role in memory retrieval. Eur. J. Neurosci. 17, 1489–1497.

Krause, V., Schnitzler, A., Pollok, B., 2010. Functional network interactions during sensorimotor synchronization in musicians and non-musicians. NeuroImage 52, 245–251.

Kung, S.J., Chen, J.L., Zatorre, R.J., Penhune, V.B., 2013. Interacting cortical and basal ganglia networks underlying finding and tapping to the musical beat. J. Cogn. Neurosci. 25, 401–420.

Lahav, A., Saltzman, E., Schlaug, G., 2007. Action representation of sound: audiomotor recognition network while listening to newly acquired actions. J. Neurosci. 27, 308–314.

Lappe, C., Steinstrater, O., Pantev, C., 2013. Rhythmic and melodic deviations in musical sequences recruit different cortical areas for mismatch detection. Front. Hum. Neurosci. 7, 260.

Lee, Y.S., Janata, P., Frost, C., Hanke, M., Granger, R., 2011. Investigation of melodic contour processing in the brain using multivariate pattern-based fMRI. NeuroImage 57, 293–300.

Lerch, J.P., Evans, A.C., 2005. Cortical thickness analysis examined through power analysis and a population simulation. NeuroImage 24, 163–173.

Lerch, J.P., Worsley, K., Shaw, W.P., Greenstein, D.K., Lenroot, R.K., Giedd, J., Evans, A.C., 2006. Mapping anatomical correlations across cerebral cortex (MACACC) using cortical thickness from MRI. NeuroImage 31, 993–1003.

Lewis, P.A., Wing, A.M., Pope, P.A., Praamstra, P., Miall, R.C., 2004. Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. Neuropsychologia 42, 1301–1312.

Lotze, M., Scheler, G., Tan, H.R., Braun, C., Birbaumer, N., 2003. The musician's brain: functional imaging of amateurs and professionals during performance and imagery. NeuroImage 20, 1817–1829.

Lyttelton, O., Boucher, M., Robbins, S., Evans, A., 2007. An unbiased iterative group registration template for cortical surface analysis. NeuroImage 34, 1535–1544.

Lyttelton, O.C., Karama, S., Ad-Dab'bagh, Y., Zatorre, R.J., Carbonell, F., Worsley, K., Evans, A.C., 2009. Positional and surface area asymmetry of the human cerebral cortex. NeuroImage 46, 895–903.

MacDonald, D., Kabani, N., Avis, D., Evans, A.C., 2000. Automated 3-D extraction of inner and outer surfaces of cerebral cortex from MRI. NeuroImage 12, 340–356.

Mendoza, J.E., 2011. Auditory cortex. In: Kreutzer, J., DeLuca, J., Caplan, B. (Eds.), Encyclopedia of Clinical Neuropsychology. Springer-Verlag, New York, p. 301.

Molenberghs, P., Brander, C., Mattingley, J.B., Cunnington, R., 2010. The role of the superior temporal sulcus and the mirror neuron system in imitation. Hum. Brain Mapp. 31, 1316–1326.

Molnar-Szakacs, I., Iacoboni, M., Koski, L., Mazziotta, J.C., 2005. Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. Cereb. Cortex 15, 986–994.

Nigmatullina, Y., Hellyer, P.J., Nachev, P., Sharp, D.J., Seemungal, B.M., 2015. The neuroanatomical correlates of training-related perceptuo-reflex uncoupling in dancers. Cereb. Cortex 25, 554–562.

Ono, Y., Nomoto, Y., Tanaka, S., Sato, K., Shimada, S., Tachibana, A., Bronner, S., Noah, J.A., 2014. Frontotemporal oxyhemoglobin dynamics predict performance accuracy of dance simulation gameplay: temporal characteristics of top-down and bottom-up cortical activities. NeuroImage 85, 461–470.

Palaniyappan, L., Liddle, P.F., 2012. Differential effects of surface area, gyrification and cortical thickness on voxel based morphometric deficits in schizophrenia. NeuroImage 60, 693–699.

Pantev, C., Paraskevopoulos, E., Kuchenbuch, A., Lu, Y., Herholz, S.C., 2015. Musical expertise is related to neuroplastic changes of multisensory nature within the auditory cortex. Eur. J. Neurosci. 41, 709–717.

Petrides, M., 2000a. The role of the mid-dorsolateral prefrontal cortex in working memory. Exp. Brain Res. 133, 44–54.

Petrides, M., 2000b. Dissociable roles of mid-dorsolateral prefrontal and anterior inferotemporal cortex in visual working memory. J. Neurosci. 20, 7496–7503.

Peuskens, H., Vanrie, J., Verfaillie, K., Orban, G.A., 2005. Specificity of regions processing biological motion. Eur. J. Neurosci. 21, 2864–2875.

Pfordresher, P.Q., Mantell, J.T., Brown, S., Zivadinov, R., Cox, J.L., 2014. Brain responses to altered auditory feedback during musical keyboard production: an fMRI study. Brain Res. 1556, 28–37.

Pilgramm, S., Lorey, B., Stark, R., Munzert, J., Vaitl, D., Zentgraf, K., 2010. Differential activation of the lateral premotor cortex during action observation. BMC Neurosci. 11, 89.

Powers 3rd, A.R., Hevey, M.A., Wallace, M.T., 2012. Neural correlates of multisensory perceptual learning. J. Neurosci. 32, 6263–6274.

Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358, 435–445.

Rakic, P., Ayoub, A.E., Breunig, J.J., Dominguez, M.H., 2009. Decision by division: making cortical maps. Trends Neurosci. 32, 291–301.

Rakic, P., 1995. A small step for the cell, a giant leap for mankind: a hypothesis of neocortical expansion during evolution. Trends Neurosci. 18, 383–388.

Rakic, P., 1988. Specification of cerebral cortical areas. Science 241, 170–176.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661–670.

Robbins, S., Evans, A., Collins, D., Whitesides, S., 2004. Tuning and comparing spatial normalization methods. Med. Image Anal. 8, 311–323.

Romanski, L.M., 2012. Convergence of auditory, visual, and somatosensory information in ventral prefrontal cortex. In: Murray, M.M., Wallace, M.T. (Eds.), The Neural Bases of Multisensory Processes. CRC Press/Taylor and Francis, Boca Raton, pp. 667–678.

Schlaug, G., 2001. The brain of musicians. a model for functional and structural adaptation. Ann. N.Y. Acad. Sci. 930, 281–299.

Schlaug, G., 2015. Musicians and music making as a model for the study of brain plasticity. Prog. Brain Res. 217, 37–55.

Schmitz, G., Mohammadi, B., Hammer, A., Heldmann, M., Samii, A., Münte, T.F., Effenberg, A.O., 2013. Observation of sonified movements engages a basal ganglia frontocortical network. BMC Neurosci. 14, 32.

Schneider, P., Scherg, M., Dosch, H.G., Specht, H.J., Gutschalk, A., Rupp, A., 2002. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. Nat. Neurosci. 5, 688–694.

Schubotz, R.I., von Cramon, D.Y., 2003. Functional-anatomical concepts of human premotor cortex: evidence from fMRI and PET studies. NeuroImage 20 (Suppl. 1), S120–S131.

Sled, J.G., Zijdenbos, A.P., Evans, A.C., 1998. A non-parametric method for automatic correction of intensity non-uniformity in MRI data. IEEE T Med. Imaging 17, 87–97.

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

Tachibana, A., Noah, J.A., Bronner, S., Ono, Y., Onozuka, M., 2011. Parietal and temporal activity during a multimodal dance video game: an fNIRS study. Neurosci. Lett. 503, 125–130.

Tohka, J., Zijdenbos, A., Evans, A., 2004. Fast and robust parameter estimation for statistical partial volume models in brain MRI. NeuroImage 23, 84–97.

van Atteveldt, N., Formisano, E., Goebel, R., Blomert, L., 2004. Integration of letters and speech sounds in the human brain. Neuron 43, 271–282.

Werner, S., Noppeney, U., 2010. Distinct functional contributions of primary sensory and association areas to audiovisual integration in object categorization. J. Neurosci. 30, 2662–2675.

Zatorre, R.J., Chen, J.L., Penhune, V.B., 2007. When the brain plays music: auditory-motor interactions in music perception and production. Nat. Rev. Neurosci. 8, 547–558.

Zijdenbos, A., Forghani, R., Evans, A., 1998. Automatic quantification of MS lesions in 3D MRI brain data sets: validation of INSECT. In: Wells, W.M., Colchester, A., Delp, S. (Eds.), Medical Image Computing and Computer-Assisted Intervention (MICCAI98). Springer-Verlag, Cambridge, pp. 439–448.