Brain Structure and Function (2019) 224:1711–1722
https://doi.org/10.1007/s00429-019-01868-y

ORIGINAL ARTICLE

Wired for musical rhythm? A diffusion MRI-based study of individual differences in music perception

Archith Rajan[1] · Jeffrey M. Valla[1] · Jacob Antony Alappatt[1] · Megha Sharda[2] · Apurva Shah[3] · Madhura Ingalhalikar[3,4] · Nandini C. Singh[1]

Received: 15 July 2018 / Accepted: 25 March 2019 / Published online: 4 April 2019

Abstract

Music perceptual abilities are subjective and exhibit high inter-individual variability. Twenty-nine participants with varying degrees of musical training were tested for musical perception ability with the Profile of Music Perception Skills (PROMS) and brain structural measures obtained via diffusion tensor imaging. Controlling for the period of training, TBSS results showed that individuals with better musical perception abilities showed increased deviations from linear anisotropy in the corpus callosum. Specifically, mode of anisotropy in the genu and body of the corpus callosum was negatively correlated with music perception score suggesting the presence of crossing fibers. A multi-compartment model of crossing fibers revealed a significant positive relation for partial volumes of secondary fiber populations with timing aspects of music perception. Our results suggest that inter-hemispheric connectivity differences in the anterior parts of the corpus callosum may reflect innate differences in the processing of the rhythmic aspects of music.

Keywords Music perception · Diffusion-weighted imaging · Corpus callosum · Rhythm · Tempo · TBSS · PROMS-S

Introduction

The origin of musical expertise has long been a fascination for lay and academic audiences alike. While one view suggests that experts are "born", in that innate ability is the determining factor in performance achievement (i.e., "Nature") the opposing view is that experts are "made" and training overshadows any effects of innate ability to determine the ultimate level of performance (Macnamara et al. 2014) (i.e., "Nurture"). While the latter view, also referred to as the 'deliberate practice theory' (Ericsson et al. 1993) has gathered much support and attraction (Charness and Ericsson 1994; Ericsson et al. 2007a, b) it has also been sharply criticized (Gardner 1995; Sternberg 1996) because of its inability to explain results from behavioral genetics (Galton 1869) that have demonstrated that excellence in music, as well as science, art, sports, and other domains, is both inherited and innate (Macnamara et al. 2014). Furthermore, the degree and likelihood of deliberate practice itself may be under genetic control (Galton 1869). Genetic and environmental factors can modulate intelligence, personality and creative achievement in arts and science domains differently. A recent study using monozygotic and dizygotic twins has shown that genetic factors associated with intelligence had a greater role in scientific creative achievement than artistic creative achievement. Artistic achievement was related more to openness and divergent thinking abilities than intelligence (de Manzano and Ullén 2018). Another study (Hambrick and Tucker-Drob 2015) on 800 pairs of twins demonstrated evidence for moderate-to-strong genetic influences on skilled music performance. However, this study also showed that the genetic effect only partially explained (25%) music accomplishment and suggested that factors other than practice also contribute to individual differences in music accomplishment (Hambrick and Tucker-Drob 2015). An important but

✉ Nandini C. Singh
nandini@nbrc.ac.in

1 Language Literacy and Music Laboratory, National Brain Research Centre, Manesar 122051, India

2 International Laboratory for Brain, Music and Sound (BRAMS), University of Montreal, Montreal, QC H2V 2J2, Canada

3 Symbiosis Center for Medical Image Analysis, Symbiosis International (Deemed University), Pune 412115, India

4 Department of Electronics and Tele Communication, Symbiosis Institute of Technology, Symbiosis International (Deemed University), Pune 412115, India

relatively poorly investigated notion in all such research has been the definition of 'musical ability'. There has been little consensus on how musical ability may be objectively assessed. The concept of musical ability embraces a variety of definitions that range from exceptional ability as a consequence of both extended deliberate practice (Ericsson et al. 1993) and expertise that results from innate giftedness (Mosing et al. 2014). The notion that musical ability is a combination of both nature and nurture was also demonstrated by a recent study using monozygotic and dizygotic twin pairs by Seesjärvi et al. (2016). Their results showed predominantly additive genetic effects in the pitch discrimination task, shared environmental effects in the Out-of-key task and non-shared environmental effects in the rhythm (Offbeat) task and thus demonstrated that while both genetic and environmental factors play a role in our ability to perceive music, there is variability in the extent of influence on different aspects of music cognition.

Past studies investigating differences in musical perception abilities have rested heavily on the binary classification of participants into musician and non-musician groups, and the implicit assumption that musical ability differs as a result of musical training—i.e., that samples selectively recruited from musical academic and professional circles have better musical perception skills than controls. However, given the variation in musical perception abilities some non-musicians may possess musical abilities that have remained untapped and underestimated and provide an opportunity to investigate individual differences in musical ability. Predisposition to musical abilities could enhance the learning rates of such individuals if they were to receive musical training later on in life (Zatorre 2013).

Past studies exploring neural correlates of music perception have suggested that when it comes to musical ability, Nature works in tandem with Nurture. These studies have primarily demonstrated structural neural plasticity in a number of cortical areas of the brain, which include the auditory, parietal and premotor cortices, inferior frontal areas (Halwani et al. 2011) and their right hemispheric homologues (Cheung et al. 2018) between musically trained and untrained individuals. For instance, keyboard players exhibit greater grey matter volumes in the motor, auditory and visual regions in both hemispheres, compared to non-musicians (Gaser and Schlaug 2003). Grey matter volume in the Heschl's gyrus, a major component of the primary auditory cortex has shown correlated increases with musicianship status (Schneider et al. 2005), and with self-reported hours of practice (Foster and Zatorre 2010). Similarly, cortical thickness differences between musicians and non-musicians have also been observed in the planum temporale, an area which has been attributed to absolute pitch in people (Elmer et al. 2016; Limb 2006). Regions associated with processing temporal aspects of music, such as the supplementary motor area and the premotor cortex similarly have greater grey matter volume in musicians versus non-musicians (Bermudez et al. 2008). Most of these studies have used methods like voxel-based morphometry and surface-based cortical thickness metrics to inform studies of training-related changes in grey matter.

With advances in magnetic resonance imaging technology, recent studies have focused on examining the role of white matter (WM) tracts (regions in the nervous systems that are composed of myelinated axons) to skill training and coordinating communication between different brain regions. Consequently, white matter architecture has provided explanations for dance and music training (Giacosa et al. 2016; Karpati et al. 2015; Moore et al. 2014). The most commonly used diffusion-weighted imaging measures are scalar-invariant indices like fractional anisotropy (FA) and mean diffusivity (MD), which roughly measure the coherence of white matter organization and the overall spread of white matter tracts, respectively. Specifically, FA is the normalized difference measure of the three eigenvalues corresponding to diffusion along parallel (principal eigen vector) and perpendicular directions within a fiber, which measures the degree of diffusion anisotropy within a voxel (Mori and Zhang 2006) while MD is the average of the three eigen-values and provides a measure of the overall diffusion within an imaging voxel (Giacosa et al. 2016). Motor tracts like corticospinal tract (CST), association tracts like the superior longitudinal fasciculus (SLF), the inferior longitudinal fasciculus (ILF) and the uncinate fasciculus (UF), and commissural tracts like the CC have shown group differences primarily in FA and MD of which the latter CC has exhibited the most consistent musician versus non-musician differences (for a detailed review, see Moore et al. 2014). More recently, the arcuate fasciculus (AF) has also been shown to play an important role in music. Studies have shown that the microstructure of the arcuate, which is a crucial auditory-motor pathway, to be different in musicians when compared to non-musicians. In fact, singers and instrumentalists were both found to have a larger tract volume and higher FA in the arcuate bilaterally (Halwani et al. 2011). Specifically, the AF has been shown to have a role in predicting learning. For example, Engel et al. 2014 found that FA values in the anterior segment of the right AF could predict the learning rate and speed of learning in non-musicians, who learned to perform short melodies on a keyboard in a pure audio-motor training condition. Another study (Vaquero et al. 2018) showed that FA values and tract volumes in the right anterior and long segments of the AF could predict performance in rhythm and melody tasks, respectively, in non-musicians. These results have hinted towards the fact that WM micro-architecture (or neuroanatomical structure) might also play a role in predicting musical abilities.

Here, we undertake a study of music perception abilities along with neuroanatomical structure and connectivity in a group of individuals with varying levels of musical training, in an attempt to understand how micro-architecture might predict music perception. We hypothesize that pre-existing neural architecture may be a factor in explaining individual differences in musical abilities, specifically those in music perception. In this case, musical ability differences are gauged via standardized assessment, rather than binary vocational classification. We propose that some non-musicians, even without musical training, could possess a neural architecture that is primed with unrealized musical potential, and musicians with years of musical training may not have aptitudes commensurate with their self-reported "professional" status. Thus, even with years of musical training and degrees, a musician may not be as proficient as assumed ("Sleeping Musicians"), whereas even without any musical training, a non-musician could show superior musical proficiency ("Musical Sleepers") since an absence of musical training does not essentially mean an absence of musical ability (Law and Zentner 2012). We tested for individual differences in music perception skills and their relation to brain architecture in an adult population with heterogeneous musical backgrounds. The PROMS-S (Profile of Music Perception Skills-Short version)—a test battery specially designed to quantify individual differences in music perception—was used to assess different aspects of music perception in a normative population with varying degrees of musical training (Zentner and Strauss 2017). The PROMS was used since it is a test constructed to assess the processing of elementary patterns of rhythm and pitch—acoustic features that are common across most musical systems and traditions (Savage et al. 2015). Diffusion-weighted imaging (DWI), an in vivo technique that uses the properties of diffusion of water molecules was used to infer underlying variations in white matter microarchitecture in the whole brain.

We hypothesized that diffusion tensor metrics quantifying diffusivity and geometry (tensor shape) would be related to music perception abilities, especially in regions like the corpus callosum and auditory-motor pathways. Specifically, we postulated that microstructural differences in cross-hemispheric tracts like the CC may be correlated with enhanced music perception ability as measured by PROMS-S scores since it is a test constructed to assess the processing of elementary patterns of temporal, tonal and qualitative domains of music (Law and Zentner 2012). The rationale was that although a number of factors could account for individual differences in music perception skills, controlling for years of training would allow us to carefully dissociate the effects of musical training from these differences. The use of a heterogeneous group with varied amounts of music training would allow us to identify fine gradations in music perception skills amongst them. Due to the potential confound of binary classification in previous studies, we made no prior assumptions regarding the direction of changes in these regions.

Materials and methods

Participants

Thirty-three healthy, right-handed adult participants were recruited for this study. A heterogeneous group with varying degrees of self-reported musical expertise was selected. The study was approved by the Institutional Ethics Committee of the National Brain Research Centre, Manesar. All participants provided written and informed consent. All participants were graduates and had undergone at least 15 years of formal instruction. Four subjects were removed from the analysis either due to image artifacts or missing behavioral data resulting in $n=29$ participants (16 males, age 24.7 ± 3.66 years; see Table 1 for full demographics). There were 17 participants who had reported any form of previous musical training. The kind of training varied from vocal, keyboard, string instruments (guitar, ukulele, and violin), flute and percussion instruments (tabla, drums) and the duration of training ranged from 1 to 18 years. Based on self-report, the participants described themselves as non-musicians (no training in music and minimal listening to music, $n=4$), music loving non-musicians (no training in music but avid listening to music, $n=8$), amateur musicians (have had a little exposure to musical training and occasionally play musical instruments as a part of a hobby; $n=5$), semi-professional musicians (at least 5–7 years or more of musical training and occasionally performs professionally although music not being the mainstream profession; $n=7$), and professional musicians (trained mainstream professional musicians; $n=5$).

Participants without normal hearing or those under medication for depression or other neuro-psychiatric and neurological conditions or with a history of any of these conditions were not included.

Table 1 Demographics table showing the self-reported musical ability of the participants ($N=29$)

Age (mean ± SD)	Sex (M/F)	Years of training (mean ± SD)
24.7 years ± 3.66	16/13	7.09 ± 5.07
Range: 19–32 years		Range: 0–18

Evaluation of music perception abilities

To observe behavioral differences in terms of musical perception, we employed the Profile of Music Perception Skills-Short (PROMS-S). This standardized test gauges skill level in temporal and tonal domains of music using eight subtests: Standard Rhythm, Embedded Rhythm, Accent, Tempo, Melody, Pitch, Timbre, and Tuning (Zentner and Strauss 2017). It takes approximately 30 min to administer and was conducted in a soundproof room. All stimuli were delivered at a constant volume using the same set of headphones for all the participants. The test involved auditory tasks in a series of blocks, drawn from the aforementioned subtests, each of which focuses on a different aspect of music. The system of stimuli presentation was identical in all sequences. Participants were exposed to two presentations of the same musical piece. The third presentation was the target sequence, and participants were required to rate the musical piece as 'Same' or 'Different' compared to the earlier tone, on a five-point Likert Scale ('Definitely Same', 'Maybe Same', 'Don't Know', 'Maybe Different', 'Definitely Different'). The level of chance performance was calculated and the raw scores converted to the d's (d-prime) using the standard d′ model (Micheyl et al. 2008). Hits were defined as correctly identified same-stimuli and weighted 1 or 0.5 points based on certainty ratings. False alarms were defined as same-stimuli that were incorrectly classified as different-stimuli. The difference between z-scores of hits and false alarms constituted the d′ scores. These scores (Table 2) were used to examine all the brain–behavior relations.

Imaging

All imaging was performed at a single site, using the Philips Achieva 3T scanner with 8 channel head coil. All participants underwent 37-min MRI scans that included a T1 acquisition and a diffusion MRI acquisition. T1-weighted MPRAGE structural images were acquired using TR/TE = 7.1/3.2 ms with a voxel size $1 \times 1 \times 1$ mm^3. The diffusion MRI sequence was acquired using the following parameters: TR/TE = 8000/75 ms, slice thickness = 2 mm, 64 diffusion directions with $b = 2000$ s/mm^2 and a single $b = 0$ (b_0) image. Sixty-four 2 mm contiguous axial slices of 128×128 matrix yielded $2 \times 2 \times 2$ mm^3 data.

Table 2 Mean ± SD of d′ sub-scores

PROMS-S score	Mean ± SD
Melody	0.51 ± 0.17
Tuning	0.76 ± 0.32
Tempo	0.97 ± 0.18
Accent	0.62 ± 0.2
Pitch	0.42 ± 0.24
Rhythm	0.70 ± 0.19
Timbre	0.76 ± 0.14
Embedded Rhythm	0.72 ± 0.29
Total	0.52 ± 0.058

Diffusion images were preprocessed using standard FSL tools (version 5.0.9) and included brain extraction and eddy current correction by registering the gradient images to the baseline b_0 volume and rotating back the gradients according to the rotation parameter. For the preliminary analysis, we fitted the diffusion tensor model (Basser et al. 1994) followed by TBSS (Tract Based Spatial Statistics) analyses (Smith et al. 2006) on all the diffusion metrics (FA, MD, AD, RD, and MO). The FMRIB58_FA template was used as the reference template in MNI space for all the analyses. Based on our hypothesis of microstructural differences in fiber architecture, we computed the mode of anisotropy (MO) that encapsulates the distinction between linear and planar anisotropy and thus delineates fiber architecture. MO is a measure that is often related to the presence of crossing fibers within an imaging voxel (Ennis and Kindlmann 2006; Douaud et al. 2011; Yoncheva et al. 2016) and it varies from − 1 (planar anisotropic-two large eigen-values, disk-shaped) through 0 (orthotropic-all eigen-values of similar magnitude, spherical) to 1 (linear anisotropic-one large eigen-value, pencil-shaped).

To attain deeper insights into the white matter integrity in the important regions derived from the MO analysis; our subsequent analysis involved fitting a higher order ball-and-stick model (Behrens et al. 2007; Jbabdi et al. 2010). A three-fiber model was chosen to test for the presence of more than one secondary fiber population. This ball-and-stick model takes into account the presence of multiple fiber populations within a voxel-each with its own distinct orientation. The amounts of space occupied by each of these populations are given by the partial volume fraction estimates (3 in our case: F1, F2, and F3) for each voxel. These directional measures provide more insights and interpretability than the regular diffusion tensor-based metrics like FA, especially in regions suggesting a crossing fiber population such as the CC.

Voxel-wise statistical analysis that employed a general linear model (GLM) with contrasts to test for positive or negative linear associations of the d′ total scores was carried out on the MO images using the TBSS framework with non-parametric permutation testing (5000 permutations) for multiple comparisons correction and a threshold-free cluster enhancement (TFCE). Mean centered age, years of training and gender were added as nuisance covariates. (Resulting GLM: $\text{MO} = 1 + \beta_{1\times} d'$ total score $+ \beta_{2\times}$ age $+ \beta_{3\times}$ gender $+ \beta_{4\times}$ years of training.) Results were considered significant at $p < 0.05$, TFCE-corrected for multiple comparisons. The significant clusters from this analysis were marked and used as a mask for further analyses. The voxels limited to this mask were employed in a subsequent GLM-based regression analysis that was performed using a 3-compartment fiber crossing model (Behrens et al. 2007) with the PROMS-S total d′ scores, as well as with the *d*′s of the PROMS-S sub-scores. F1, F2 and F3 partial volumes were correlated with the musical scores using a similar general linear model. Since the preliminary analysis with MO showed little effects of gender, it was avoided from any further analysis. Multiple comparisons correction was performed using 5000 permutations and TFCE and significance was considered at $p < 0.05$.

As a secondary analysis, the effects of self-reported years of training were also analyzed by correlating the PROMS-S scores with years of training. The self-reported years of training was correlated with all the PROMS-S scores. TBSS was also run on all the subjects with GLMs consisting of years of training and the sub-scores in the model.

Results

The PROMS-S scores showed inter-individual gradations in different music perception skills. The sub-scores of measures like tuning, pitch, and embedded rhythms, in particular, captured fine variations and showed high variability. The participants generally performed well for the tempo discrimination tasks and most poorly for pitch discrimination tasks (Fig. 1 and Table 2). The main analyses aimed at examining inter-individual differences in overall music perception skills (as measured by the total *d*′ scores) unexplained by musical training, and reflected in white matter architecture. The TBSS analysis of all the diffusion measures using a DTI model (FA, MD, AD, RD, MO) against PROMS-S scores and a subsequent follow up TBSS analysis using partial volume measures from a ball-and-stick model are presented. To specifically assess for inter-individual differences in music perception not explained by musical training, all analyses were controlled for the years of training.

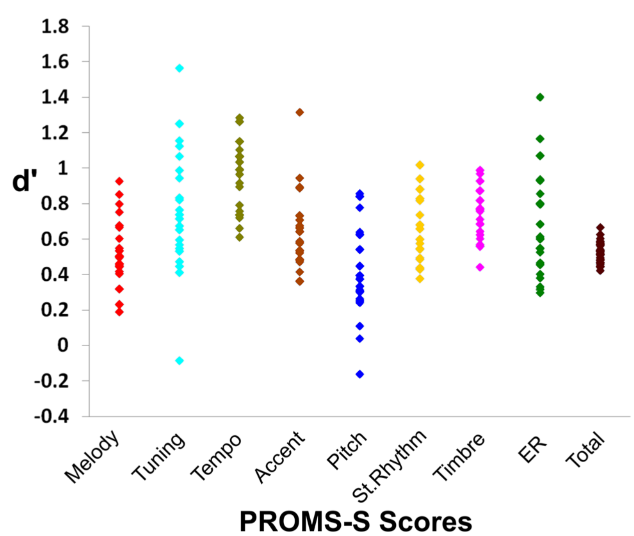

Fig. 1 Range of d′ measures for each PROMS-S sub-score: *St. Rhythm* Standard Rhythm, *ER* Embedded Rhythm

Since different diffusion measures give complementary and often orthogonal information about white matter microstructure (Ennis and Kindlmann. 2006), multiple comparisons across measures and across sub-scores were not carried out. However, each individual analysis was corrected for multiple comparisons using Threshold Free Cluster Enhancement (TFCE).

Fractional anisotropy and diffusivity indices

There was no relation between fractional anisotropy (FA), mean, radial or axial diffusivity (MD, AD, and RD) and music perception ability as measured by the PROMS-S scores.

Mode of anisotropy

The mode of anisotropy (MO) revealed a significant negative association with PROMS-S total *d*′ scores, in the genu, the body of the CC, and the superior and anterior parts of the corona radiata as displayed in Fig. 2a and Table 3 ($p < 0.05$, TFCE-corrected). These indicated a departure from linear anisotropy in CC in individuals with better music perception skills, strongly indicating the possibility of more than one dominant fiber population. This provided the motivation for a secondary analysis fitting a multi-compartment model to unravel and capture subtle differences in these areas of interest.

The multi-compartment model (Jbabdi et al. 2010) models the isotropic (free-moving) compartment within a voxel with a ball and anisotropic (restricted) compartments with sticks, with each of the sticks corresponding to the partial volume of a fiber within the voxel. The multi-compartment model accounts for the presence of distinct fiber bundle populations, each with a different orientation within a single voxel. Analyzing each of these distinct fiber bundles facilitates better interpretations especially in the voxels with crossing fibers.

Partial volumes of crossing fibers

Since the direction of association suggested the presence of crossing fibers, further analyses were performed that were restricted to the significant clusters obtained from earlier analysis, where MO showed a negative linear association with the total d′ scores. A multi-compartment model with a single isotropic component and three anisotropic

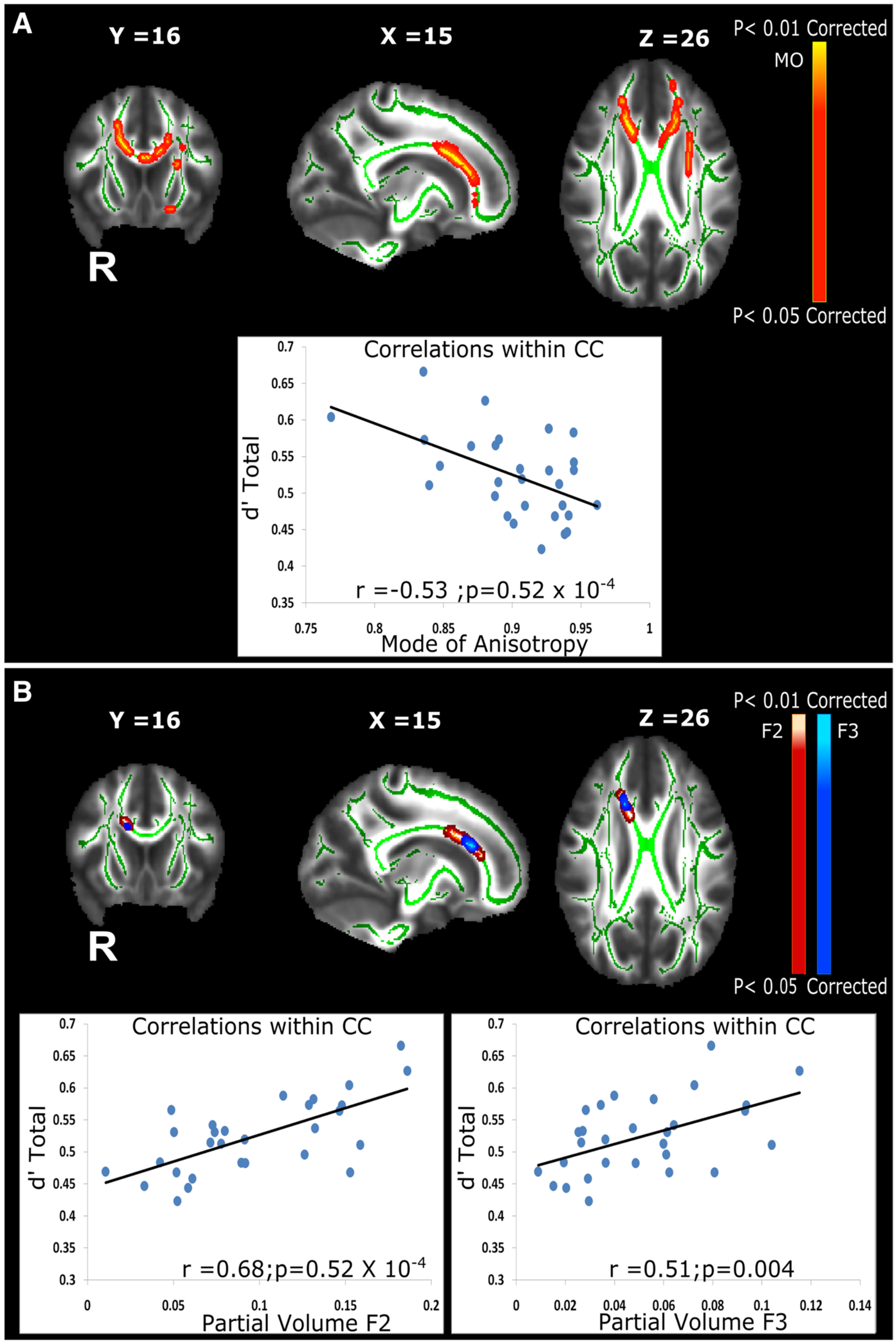

Fig. 2 **a** TBSS results showing a negative linear association of mode of anisotropy with the total d′ score in the corpus callosum (genu and body) and parts of anterior corona radiata ($p < 0.05$, TFCE corrected). The significant clusters (orange) were highlighted using the *tbss_fill* command in FSL and overlaid on the mean FA image. The correlation plot depicts the negative relationship between d′ total PROMS-S scores and the mean mode of anisotropy within the three significant callosal clusters ($r = -0.53$, $p = 0.003$). **b** TBSS results showing clusters with a positive linear association between the total PROMS-S scores and the partial volumes of secondary fiber populations F2 and F3. The analyses were restricted to voxels with a significant correlation between MO and d′ total. The significant clusters (green—F2, red—F3) were highlighted using the *tbss_fill* command in FSL and overlaid on the mean FA image. The correlations between these measures in the regions of the CC, from the average values within the mask obtained from **a** also showed a similar trend and are shown below (F2: $r = 0.68$, $p = 0.52 \times 10^{-4}$, F3: $r = 0.51$, $p = 0.004$). *R* right. Mean FA skeleton is also overlaid on the mean FA image in green. MNI coordinates (mm) are also reported

components corresponding to partial volumes of three crossing fibers (F1, F2, and F3) within each voxel was fitted to the diffusion-weighted images (Behrens et al. 2007). This voxel-wise regression analysis revealed a significant positive relation for partial volumes only of the secondary fiber populations (after TFCE correction for multiple comparisons) with the PROMS-S total d′ scores, suggesting an increase in crossing fiber population with increase in music perception skills (F2: $r = 0.68$, $p = 0.52 \times 10^{-4}$, F3: $r = 0.51$, $p = 0.004$). The results are displayed in Fig. 2b.

To further investigate which aspect of music perception skills best correlated with white matter of the CC, the d′ scores of each of the PROMS-S subtests were correlated individually with partial volume estimates of F1, F2, and F3 for all significant areas of interest. Results revealed that the secondary fiber populations extracted from F2 and F3 were significantly associated with temporal PROMS-S subtests like Accent (F2: $r = 0.48$, $p = 0.008$), Embedded Rhythm (F2: $r = 0.52$, $p = 0.004$, F3: $p = 0.01$), and Tempo (F2: $r = 0.50$, $p = 0.006$. F3: $r = 0.45$, $p = 0.043$). The F3–Accent

Table 3 Local maxima (MO) of white matter pathways that significantly correlated with the PROMS-S total scores

Cluster	# of voxels	Max (*x*, *y*, z; mm)	Structures (based on JHU ICBM-DTI-81 White-Matter Labels)
1	476	−11, 31, 12	Genu of corpus callosum Body of corpus callosum
2	317	13, 20, 23	Genu of corpus callosum Body of corpus callosum
3	55	−12, 32, −3	Genu of corpus callosum
4	11	−24, 34, −3	Anterior corona radiata left

correlation was marginally non-significant, but trended similarly (F3: $r = 0.31$, $p = 0.096$). PROMS-S subscales concerning tonal and qualitative aspects of music perception (Melody, Pitch, Timbre, Tuning), however, were unrelated to F2 and F3 volumes (Fig. 3).

Training-related effects

To dissociate music perception skills from musical training-related skills, self- reported years of training were correlated with all the PROMS-S scores, and an additional TBSS analysis was also performed with musical training included in the GLM model. The total scores were correlated with the years of training (Spearman's $\rho = 0.60$, $p = 0.005$, FDR corrected across scores). Out of the sub-scores, all except one of the scores that correlated were non-temporal, with the Tuning sub-score showing the highest correlations ($\rho = 0.57$, $p = 0.005$, FDR corrected across scores). Other sub-scores that significantly correlated with self-reported years of training were Embedded Rhythms ($\rho = 0.46$, $p = 0.03$, FDR corrected across scores), Timbre ($\rho = 0.45$, $p = 0.03$, FDR corrected across scores) and Melody ($\rho = 0.43$, $p = 0.03$), FDR corrected across scores). However, there were no significant effects for any diffusion metrics related to the years of training.

In order to obtain some information about which grey matter regions, the genu, and body of the CC might connect to, probabilistic tractography was performed on a single subject who was musically trained and scored highest in the PROMS-S. The significant clusters for F2 and F3 from the three sub-scores indicated in Fig. 3 were averaged to form two seed masks for F2 and F3. A three-fiber model was fitted on the preprocessed diffusion-weighted images as mentioned in the "Materials and methods" section. Probabilistic tractography was performed with each seed as a single mask to generate individual connectivity distribution maps for each mask, which were thresholded at their respective mean values and binarized (Fig. 4). The connectivity distribution extended mostly to bilateral frontal and subcortical regions, with some parietal and insular cortices also showing connectivity. The cortical regions included superior and middle frontal, inferior frontal, insula, cingulate, precuneus, lingual, and parahippocampal cortices. Several subcortical regions like the hippocampus, caudate, putamen and thalamus were also shown to be connected.

Discussion

This study examined, for the first time, the association between music perception abilities and white matter microstructure in a diverse population of individuals with varying musical ability. The specific objective was to identify individual differences in music listening abilities that were not a result of musical training alone. A cohort of 29 individuals with varying degrees of musical training was tested for music perception skills in temporal (Rhythm, Embedded Rhythm, Accent, Tempo), tonal (Melody, Pitch) and qualitative (Tuning, Timbre) domains. The PROMS-S scores showed inter-individual differences in different music perception skills. The overall performance was better in temporal discrimination tasks like tempo, but poor for pitch discrimination tasks (Table 2). After controlling for effects of years of training, white matter microstructure analyses with the total d′ PROMS score, using TBSS (Fig. 2a) revealed several interesting features. Firstly, we found a departure from linear anisotropy in anterior parts of the corpus callosum (CC) specifically in the genu and body related to music perception abilities, regardless of musical training. This deviation in anisotropy was captured by the mode of anisotropy (MO) in individuals with better music perception skills. As discussed earlier, the MO gives complementary information to FA and changes from −1 to 1 as the nature of anisotropy changes from planar (for example, in cases where more than one prominent white matter fiber orientation is present, leading to a "pancake"-shaped diffusion profile) to linear (for example, in cases where there is only a single white matter fiber orientation present, leading to a "cigar" shaped diffusion profile) and thereby provided the possibility of more than one dominant fiber population. In order to test the role of secondary fiber populations, subsequent analysis was carried out which involved fitting a multi-compartment model to three distinct anisotropic compartments with distinct orientations for each fiber component. The results of this model confirmed an increase in partial volumes of secondary fiber (F2 and F3) populations in individuals with increased musical perception ability (Figs. 2b, 3) suggesting thereby that a certain type of neural architecture, in this case, the presence of crossing fibers in the CC might provide an advantage for the perception of musical features. Of special mention here, is the absence of correlations of any of the behavioral scores with F1 fibers, thereby indicating no differences in primary fiber structure. On the other

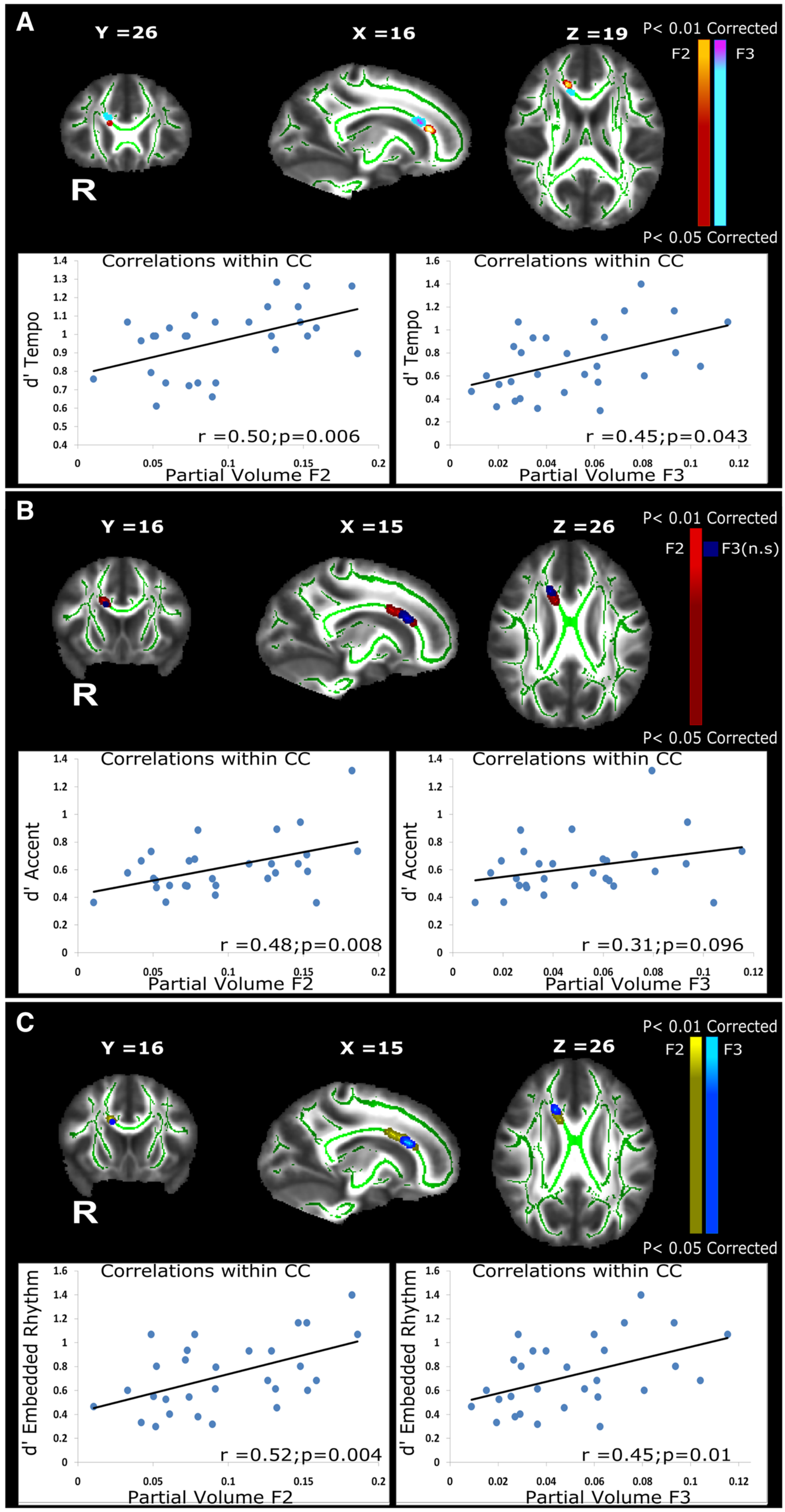

Fig. 3 **a** TBSS results showing sub-clusters with a positive linear association between the PROMS-S Tempo sub-score and the partial volumes of secondary fiber populations F1 and F2 (red–yellow—F2, light blue–pink—F3). The analyses were restricted to voxels with a significant correlation between MO and d′ total. Similar trends were also observed in the correlations between the measures in the regions of the CC, from the average values within the mask obtained from significant CC clusters in Fig. 2a (F2: $r=0.50$, $p=0.006$, corrected, F3: $r=0.45$, $p=0.043$). R = right. Mean FA skeleton is also overlaid on the mean FA image in green. MNI coordinates (mm) are also reported. Similar results from TBSS and correlation analyses for **b**. Accent sub-scores (F2: $r=0.48$, $p=0.008$, F3: $r=0.31$, $p=0.096$, n.s. = not significant) and **c**. Embedded Rhythm sub-scores (F2: $r=0.52$, $p=0.004$, F3: $r=0.45$, $p=0.01$)

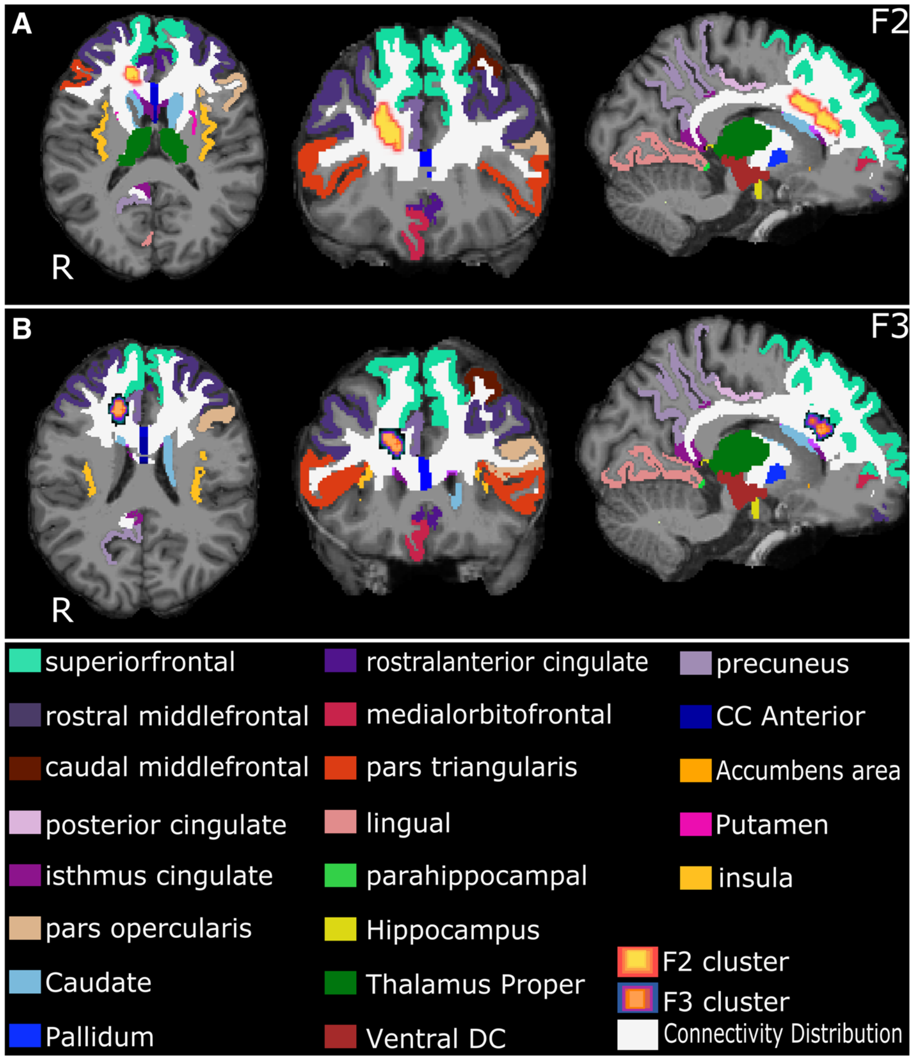

Fig. 4 Probabilistic tractography from significant clusters in F2 (**a**) and F3 (**b**) along with their connectivity distribution maps for a single subject. The clusters in MNI space corresponding to all the sub-scores from Fig. 3 were averaged for each partial volume measure. These were non-linearly registered to FA map of the individual using ANTs' SyN registration (Avants et al. 2008). Probabilistic tractography was performed in the subject space using FSL's probtrackx. The probabilistic connectivity distribution images were thresholded at their respective mean values and binarized. The cortical regions from a FreeSurfer (Fischl 2012) based parcellation using the Desikan Killiany atlas (Desikan et al. 2006) which were connected to the thresholded connectivity distribution maps are shown, with their FreeSurfer labels indicated below

hand, significant correlations were found between F2 and F3 fibers with musical sub-scores specifically with temporal sub-scores (Tempo, Accent, and Embedded rhythm). These findings indicate that differences in secondary fiber structure might be responsible for differences in music perception scores in the temporal domain. We, therefore, suggest that the complexity of white matter architecture in the form of crossing fiber tracts is directly related to temporal music perception abilities (Fig. 3). In the sections below we discuss the implications of these results for individual differences in music perception abilities.

The corpus callosum has been reported as an important tract involved in music processing. It is the largest inter-hemispheric commissural tract, divided into different regions based on connectivity profiles. The genu is the majority of the anterior third (rostrum, genu, body, isthmus splenium and tapetum) of the human CC, containing fibers interconnecting frontal association areas. As the primary white matter tract connecting regions of the hemispheres, the CC is thought to be involved in aspects like bimanual coordination (Johansen-Berg et al. 2007). Comparison of professional keyboard and string musicians to non-musician controls found larger anterior CC regions in the former group (Schlaug et al. 1995). A longitudinal training study which involved children in an instrumental training experimental group also reported increased CC size after 29 months of training (Schlaug et al. 2009). Similarly, fiber integrity (FA) in the CC was also found to be positively correlated with the number of hours of instrumental practice from childhood to early adulthood in professional musicians (Bengtsson et al. 2005). More recent studies have reported more specific regions of the CC with musicianship. For instance, early-trained musicians show greater FA in the mid-genu, body, and isthmus of the CC, suggesting a critical developmental period of neuroplasticity during which musical training can maximize structural influence (Steele et al. 2013). Similar evidence in the CC was recently reported in a longitudinal study that followed school going children who had taken up after school musical training for 2 years. The children were compared with two groups of matched controls—one group that had taken up sports training and the other which was not involved in any systematic after school training (Habibi et al. 2017). Changes in microstructural connectivity were found in pathways connecting superior frontal, sensory, and motor segments of the CC, which were attributed to musical training.

The CC has thus been well established to play a role in music perception and production due to its involvement in a variety of tasks that require inter-hemispheric transfer and are also crucial for musical skills—like bimanual coordination and inter-hemispheric transfer of visual information (Patston et al. 2007) for example. Our results not only corroborate earlier findings, in that individual differences in the microstructure of the CC could explain differences in music perception abilities, they also provide novel insights into how differences in specific acoustic features of music perception may be reflected in white matter architecture. The use of an objective music perception scale (in this case the PROMS-S) revealed that overall musical perception ability as quantified by the PROMS-S score showed associations with anterior regions of the CC that have connections with frontal and motor areas (Aboitiz et al. 1992). Our results thus confirm that music perception abilities as measured by a global music perception aptitude score might be reflected in white matter architecture seen in the CC (after controlling for years of training). This could probably be an indication of an efficient microstructural organization which is more dispersed (more crossings or fanning out, for example) especially in the inter-hemispheric regions connecting the frontal and motor areas that are also necessary for music perception (Chen et al. 2008). It is noteworthy that the sub-scores of temporal measures like Tempo, Accent and Embedded Rhythm positively correlated with the partial volumes of secondary fibers in these regions (Fig. 3), while no such correlations were found for tonal (e.g., Melody, Tuning, Pitch) and textural (e.g., Timbre) subtests. This is in line with a recent cross-cultural study which showed that the temporal properties of music like rhythm are much more deeply embedded and basic to human cognition (Ravignani et al. 2017). In this study, musically untrained individuals performed an imitation task of randomly generated drumming sequences, whose imitation attempts served as training basis for the successive participants. By perceiving and imitating from each other, these initially random sequences were converted into more structured and distinctive rhythms upon a series of such repeated imitations. In line with our results and emerging research, we speculate that the cortical architecture reported in our study might minimize callosal constraints (Aboitiz et al. 2003) of inter-hemispheric information flow, which would, in turn, enhance the frontal–motor interactions necessary for enhanced temporal-related music perception. It is also interesting to note that these results with the partial volumes were right lateralized, which is in line with what most music perception literature had shown.

These findings suggest a small but definite role for cortical connectivity in music perception. Since the (CC) is a structure that has over the years shown consistent and convergent evidence in the white matter literature for musicians (Moore et al. 2014), future studies could further investigate the microstructural properties of this very structure in musicians using more advanced measures than regular DTI metrics. Better microstructural compartment modeling of the CC (Thapaliya et al. 2017) could be made and measures like axon diameter (Assaf et al. 2008), g-ratio (Stikov et al. 2011) or apparent fiber density (Raffelt et al. 2012) could be analyzed using high-resolution diffusion imaging techniques to characterize better how musical abilities are related to the white matter microstructure.

Taken together, our results reveal a fundamental relation of the crossing fiber architecture with music perception. Subjects, irrespective of musical training, with higher musical perception are structured to facilitate interhemispheric information flow and frontal–motor area integration. We demonstrated that musical perception is highly related to secondary fiber populations in the genu of CC and motor regions conferring an efficient system for processing musical information. Interestingly, studies investigating the functional anatomy of music perception have primarily used spectral measures like perfect pitch (Ohnishi et al. 2001) or have used reported years of formal training (Schmithorst 2005) to establish musical proficiency. Despite the fact that rhythm and melody are two of the most important universal features of music, their individual roles on overall musical aptitude remain unclear. Our results indicate that the origins of both timing- and melody-based measures may be different and that temporal measures like rhythm may be linked to the presence of such secondary fiber structures in the corpus callosum. Our study thus presents unique insights into the neural substrates of rhythm perception.

While a detailed connectivity analysis to ascertain the specific cortical regions that these callosal fibers connect to, is beyond the scope of this study, a preliminary tractography analysis was attempted on a single subject. The connectivity profile revealed that the fibers connected to several frontal and subcortical regions bilaterally (Fig. 4). While this only provides a preliminary qualitative picture about the nature of connections and the regions that are connected, and conclusive evidence is still lacking, further detailed functional and structural connectivity based studies exploring the role of the corpus callosum and the grey matter regions it connects could reveal detailed insights.

Although the current study used a cross-sectional approach and coarse self-reported measures like years of training which could have only partially controlled for music practice, it does provide a starting point for future longitudinal studies that might focus on the development of CC and its interaction with musical skills in the temporal domain and training in a larger population. A limitation of this study was the inability to replicate earlier results on music practice and FA which we attribute to the use of a coarse measure like self-reported years of training and a large variation in the extent of music training. However, our approach provided a dissociation of music perception skills that might have minimal contributions from musical training in a heterogeneous group of individuals with different levels of training in a possibly unconfounded manner. Similarly, future studies could also look at the behavioral scores in each task collectively as to how well they align along temporal and tonal domains in such a heterogeneous population using dimensionality reduction approaches. This could better interpret the roots of modularity in music perception skills.

Our findings also provide an interesting twist to the Nature/Nurture question posed by the title of this study. If the neuroarchitecture underlying high rhythmic aptitude is independent of musical training, then Nature may outweigh Nurture where temporal aspects of musical aptitude are concerned. Thus, we might ask: are we wired for rhythm? We hope further studies which include genetics with larger populations in larger cohorts might shed light on the effects of musical aptitude (Turker et al. 2017) and musical training.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional research committee of the National Brain Research Centre, Manesar, and were in compliance with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Written and informed consent was obtained from all individual participants included in the study.

References

Aboitiz F, Scheibel AB, Fisher RS, Zaidel E (1992) Fiber composition of the human corpus callosum. Brain Res 598:143–153

Aboitiz F, López J, Montiel J (2003) Long distance communication in the human brain: timing constraints for inter-hemispheric synchrony and the origin of brain lateralization. Biol Res 36:89–99

Assaf Y, Blumenfeld-Katzir T, Yovel Y, Basser PJ (2008) AxCaliber: a method for measuring axon diameter distribution from diffusion MRI. Magn Reson Med 59:1347–1354

Avants BB, Epstein CL, Grossman M, Gee JC (2008) Symmetric diffeomorphic image registration with cross-correlation: evaluating automated labeling of elderly and neurodegenerative brain. Med Image Anal 12:26–41

Basser PJ, Mattiello J, LeBihan D (1994) Estimation of the effective self-diffusion tensor from the NMR spin echo. J Magn Reson 103:247–254

Behrens TE, Berg HJ, Jbabdi S, Rushworth MFS, Woolrich MW (2007) Probabilistic diffusion tractography with multiple fiber orientations: what can we gain ? Neuroimage. 34:144–155

Bengtsson SL, Nagy Z, Skare S, Forsman L, Forssberg H, Ullén F (2005) Extensive piano practicing has regionally specific effects on white matter development. Nat Neurosci 8:1148

Bermudez P, Lerch JP, Evans AC, Zatorre RJ (2008) Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. Cereb Cortex 19:1583–1596

Charness N, Ericsson KA (1994) Expert performance: its structure and acquisition. American Psychology. 49:725–747

Chen JL, Penhune VB, Zatorre RJ (2008) Listening to musical rhythms recruits motor regions of the brain. Cereb Cortex 18:2844–2854

Cheung VK, Meyer L, Friederici AD, Koelsch S (2018) The right inferior frontal gyrus processes nested non-local dependencies in music. Sci Rep 8:3822

de Manzano Ö, Ullén F (2018) Genetic and environmental influences on the phenotypic associations between intelligence, personality, and creative achievement in the arts and sciences. Intelligence 69:123–133

Desikan RS, Ségonne F, Fischl B, Quinn BT, Dickerson BC, Blacker D, Albert MS (2006) An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. Neuroimage 31:968–980

Douaud G, Jbabdi S, Behrens TE, Menke RA, Gass A, Monsch AU, Rao A, Whitcher B, Kindlmann G, Matthews PM, Smith S (2011) DTI measures in crossing-fiber areas: increased diffusion anisotropy reveals early white matter alteration in MCI and mild Alzheimer's disease. Neuroimage 55:880–890

Elmer S, Hänggi J, Jäncke L (2016) Interhemispheric transcallosal connectivity between the left and right planum temporale predicts musicianship, performance in temporal speech processing, and functional specialization. Brain Struct Funct 221:331–344

Engel A, Hijmans BS, Cerliani L, Bangert M, Nanetti L, Keller PE, Keysers C (2014) Inter-individual differences in audio-motor learning of piano melodies and white matter fiber tract architecture. Hum Brain Mapp 35:2483–2497

Ennis DB, Kindlmann G (2006) Orthogonal tensor invariants and the analysis of diffusion tensor magnetic resonance images. Magn Reson Med 146:136–146

Ericsson KA (2007) Deliberate practice and the modifiability of body and mind: toward a science of the structure and acquisition of expert and elite performance. Int J Sport Psychol 38:4

Ericsson KA, Krampe RT, Romer CT (1993) The role of deliberate practice in the acquisition of expert performance. Psychol Rev 100:363–406

Ericsson KA, Roring RW, Nandagopal K (2007) Giftedness and evidence for reproducibly superior performance: an account based on the expert performance framework. High Ability Stud 18:3–56

Fischl B (2012) FreeSurfer. Neuroimage 62:774–781

Foster NEV, Zatorre RJ (2010) Cortical structure predicts success in performing musical transformation judgments. Neuroimage 53:26–36

Galton F (1869) Hereditary genius: an inquiry into its laws and consequences. 27: (Macmillan, 1869)

Gardner H (1995) "Multiple Intelligences" as a Catalyst. Engl J 84:16–18

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

Giacosa C, Karpati FJ, Foster NE, Penhune VB, Hyde KL (2016) Dance and music training have different effects on white matter diffusivity in sensorimotor pathways. Neuroimage 135:273–286

Habibi A, Damasio A, Ilari B, Veiga R, Joshi AA, Leahy RM, Haldar JP, Varadarajan D, Bhushan C, Damasio H (2017) Childhood music training induces change in micro and macroscopic brain structure: results from a longitudinal study. Cereb Cortex 28:4336–4347

Halwani GF, Loui P, Rueber T, Schlaug G (2011) Effects of practice and experience on the arcuate fasciculus: comparing singers, instrumentalists, and non-musicians. Front Psychol 2:156

Hambrick DZ, Tucker-Drob EM (2015) The genetics of music accomplishment: evidence for gene–environment correlation and interaction. Psychon Bull Rev 22:112–120

Jbabdi S, Behrens TE, Smith SM (2010) Crossing fibers in tract-based spatial statistics. Neuroimage 49:249–256

Johansen-Berg H, Della-Maggiore V, Behrens TE, Smith SM, Paus T (2007) Integrity of white matter in the corpus callosum correlates with bimanual co-ordination skills. Neuroimage 36:16–21

Karpati FJ, Giacosa C, Foster NE, Penhune VB, Hyde KL (2015) Dance and the brain: a review. Ann N Y Acad Sci 1337:140–146

Law LN, Zentner M (2012) Assessing musical abilities objectively: construction and validation of the profile of music perception skills. PLoS One 7:e52508

Limb CJ (2006) Structural and functional neural correlates of music perception. Anat Record 288:435–446

Macnamara BN, Hambrick DZ, Oswald FL (2014) Deliberate practice and performance in music, games, sports, education, and professions: a meta-analysis. Psychol Sci 25:1608–1618

Micheyl C, Kaernbach C, Demany L (2008) An evaluation of psychophysical models of auditory change perception. Psychol Rev 115:1069

Moore E, Schaefer RS, Bastin ME, Roberts N, Overy K (2014) Can musical training influence brain connectivity? Evidence from diffusion tensor MRI. Brain Sci 4:405–427

Mori S, Zhang J (2006) Principles of diffusion tensor imaging and its applications to basic neuroscience research. Neuron 51:527–539

Mosing MA, Madison G, Pedersen NL, Kuja-Halkola R, Ullén F (2014) Practice does not make perfect: no causal effect of music practice on music ability. Psychol Sci 25:1795–1803

Ohnishi T, Matsuda H, Asada T, Aruga M, Hirakata M, Nishikawa M, Katoh A, Imabayashi E (2001) Functional anatomy of musical perception in musicians. Cereb Cortex 11:754–760

Patston LL, Kirk IJ, Rolfe MHS, Corballis MC, Tippett LJ (2007) The unusual symmetry of musicians: Musicians have equilateral interhemispheric transfer for visual information. Neuropsychologia 45:2059–2065

Raffelt D, Tournier JD, Rose S, Ridgway GR, Henderson R, Crozier S, Salvado O, Connelly A (2012) Apparent fiber density: a novel measure for the analysis of diffusion-weighted magnetic resonance images. Neuroimage 59:3976–3994

Ravignani A, Delgado T, Kirby S (2017) Musical evolution in the lab exhibits rhythmic universals. Nat Hum Behav 1:0007

Savage PE, Brown S, Sakai E, Currie TE (2015) Statistical universals reveal the structures and functions of human music. Proc Natl Acad Sci 112:8987–8992

Schlaug G, Jancke L, Huang Y, Staiger JF, Steinmetz H (1995) Increased corpus callosum size in musicians. Neuropsychologia 33:1047–1055

Schlaug G, Forgeard M, Zhu L, Norton A, Norton A, Winner E (2009) Training-induced neuroplasticity in young children. Ann N Y Acad Sci 1169:205–208

Schmithorst VJ (2005) Separate cortical networks involved in music perception: preliminary functional MRI evidence for modularity of music processing. Neuroimage. 25:444–451

Schneider P, Sluming V, Roberts N, Bleeck S, Rupp A (2005) Structural, functional, and perceptual differences in Heschl's gyrus and musical instrument preference. Ann N Y Acad Sci 1060:387–394

Seesjärvi E, Särkämö T, Vuoksimaa E, Tervaniemi M, Peretz I, Kaprio J (2016) The nature and nurture of melody: a twin study of musical pitch and rhythm perception. Behav Genet 46:506–515

Smith SM, Jenkinson M, Johansen-Berg H, Rueckert D, Nichols TE, Mackay CE, Watkins KE, Ciccarelli O, Cader MZ, Matthews PM, Behrens TE (2006) Tract-based spatial statistics: voxelwise analysis of multi-subject diffusion data. Neuroimage 31:1487–1505

Steele CJ, Bailey JA, Zatorre RJ, Penhune VB (2013) Early musical training and white-matter plasticity in the corpus callosum: evidence for a sensitive period. J Neurosci 33:1282–1290

Sternberg RJ (1996) Costs of expertise. In: Ericsson KA (ed) The road to excellence: the acquisition of expert performance in the arts and sciences, sports, and games. Lawrence Erlbaum, Mahwah, pp 347–354

Stikov N, Perry LM, Mezer A, Pauly JM, Wandell BA, Dougherty RF (2011) Modeling and measuring the myelin g-ratio. Proc Intl Soc Magn Reson Med 19:225

Thapaliya K, Vegh V, Bollmann S, Barth M (2017) Assessment of microstructural signal compartments across the corpus callosum using multi-echo gradient recalled echo at 7 T. Neuroimage 182:407–416

Turker S, Reiterer SM, Seither-preisler A, Schneider P (2017) 'When music speaks': auditory cortex morphology as a neuroanatomical marker of language aptitude and musicality. Front Psychol 8:1–17

Vaquero L, Ramos-Escobar N, François C, Penhune V, Rodríguez-Fornells A (2018) White-matter structural connectivity predicts short-term melody and rhythm learning in non-musicians. NeuroImage 181:252–262

Yoncheva YN, Somandepalli K, Reiss PT, Kelly C, Di Martino A, Lazar M, Zhou J, Milham MP, Castellanos FX (2016) Mode of anisotropy reveals global diffusion alterations in attention-deficit/hyperactivity disorder. J Am Acad Child Adolesc Psychiatry 55:137–145

Zatorre RJ (2013) Predispositions and plasticity in music and speech learning: neural correlates and implications. Science 342:585–589

Zentner M, Strauss H (2017) Assessing musical ability quickly and objectively: development and validation of the Short-PROMS and the Mini-PROMS. Ann N Y Acad Sci 1400:33–45