



Auditory and frontal anatomic correlates of pitch discrimination in musicians, non-musicians, and children without musical training

María-Ángeles Palomar-García¹ · Mireia Hernández² · Gustau Olcina³ · Jesús Adrián-Ventura¹ · Víctor Costumero⁴ · Anna Miró-Padilla¹ · Esteban Villar-Rodríguez¹ · César Ávila¹

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Introduction

Pitch is a primary perceptual dimension of sounds, and it plays an important role in music and speech perception (Oxenham 2012). Pitch discrimination reflects the ability to encode regularities in music and detect tonal mismatching information. This capacity is developed at a very early age, as revealed by a processing bias toward unequal-step scales found in 9-month-old infants (Trehub et al. 1999; Benasich and Tallal 2002) and by studies showing that musical training at 9 months of age may improve the ability to detect tonal mismatching information (Zhao and Kuhl 2016). The fact that this precocious ability arises long before the individual engages in any musical training suggests that different cognitive processes (e.g., speech processing or working memory) exert an influence on its development. In fact, Benasich and Tallal (2002) found that auditory processing abilities at the age of 9 months were the best predictor of language outcomes at 2 years of age. The development of pitch discrimination continues until approximately the age of seven years,

which is when children are able to discriminate complex, brief tones—a capacity that is still lacking in 4–5 year-old children (Thompson et al. 1999). Furthermore, Schneider et al. (2005) emphasize that relative pitch of harmonic complex sounds, such as instrumental sounds, depends on spectral envelope and fundamental frequency information with different weighting, and it cannot be explained by a simple one-to-one relationship between perceived pitch and fundamental frequency. Specifically, they propose that greater GM volume and enhanced functional MEG activity in the left lateral Heschl's gyrus may predispose one to hear the fundamental frequency in an ambiguous tone, whereas in the right lateral Heschl's gyrus may lead to a dominant perception of spectral pitch or single harmonics.

The pitch discrimination ability, however, is not equally developed in all individuals. For instance, different studies with neurologically intact individuals show that a small proportion of the population has congenital amusia, commonly known as tone deafness (Ayotte et al. 2002; Peretz et al. 2002). Individuals with tone deafness show severe difficulties in detecting pitch changes and producing music that are believed to be independent of hearing loss, musical training, and intelligence. There is compelling evidence that different temporal and frontal brain areas and their connectivity are compromised in this condition. For instance, morphometric studies found anatomic differences in the gray and white matter volume of the left and right auditory cortex (AC) and the right inferior frontal gyrus (IFG) (Hyde et al. 2006, 2007; Mandell et al. 2007; Albouy et al. 2013). In addition, diffusion tensor imaging (DTI) studies have shown a reduced volume of the right arcuate fasciculus (AF) (Loui et al. 2009), which structurally connects temporal and frontal regions. In a similar vein, functional studies have reported a decrease in the connectivity between the right IFG and the right AC (Hyde et al. 2011; Albouy et al. 2013,

✉ María-Ángeles Palomar-García
mpalomar@uji.es

¹ Neuropsychology and Functional Neuroimaging Group, Department of Basic Psychology, Clinical Psychology and Psychobiology, Universitat Jaume I, Avda. Sos Baynat, s/n., 12071 Castellón de la Plana, Spain

² Cognition and Brain Plasticity Group, Department of Cognition, Development and Educational Psychology, Institut de Neurociències, University of Barcelona, Barcelona, Spain

³ Neuropsychology and Functional Neuroimaging Group, Department of Education, University Jaume I, 12071 Castellón, Spain

⁴ Center for Brain and Cognition, University Pompeu Fabra, Barcelona, Spain

2015; Leveque et al. 2016), as well as enhanced connectivity between the right and left auditory cortices (Hyde et al. 2011; Albouy et al. 2015). Consistent with these results for congenital amusia, the results of other studies suggest that damage to temporal, frontal, parietal, and subcortical areas of the right hemisphere and degeneration in different critical fronto-temporal, frontal, and inter-hemispheric pathways are associated with acquired amusia (Sihvonen et al. 2016, 2017). Overall, the studies on amusia—whether congenital or acquired—suggest that pitch discrimination deficits are associated with structural and functional anomalies in the right fronto-temporal network and in the connectivity between the left and right auditory cortices.

At the opposite pole, musicians have shown enhanced pitch discrimination compared to non-musicians (Bianchi et al. 2016, 2017). Different studies seem to indicate that acquiring musical performance skills is related to structural and functional variations in the brain. For example, morphometric studies have revealed differences between musicians and non-musicians in gray matter (GM) volume, surface area, and cortical thickness in different parts of the auditory cortices (Heschl's gyrus and planum temporale; Schneider et al. 2002, 2005; Gaser and Schlaug 2003; Bermudez et al. 2009; Elmer et al. 2013; Palomar-García et al. 2017) and in several motor and premotor areas that had been previously implicated in musical training (Sluming et al. 2002; Gaser and Schlaug 2003; Bermudez et al. 2009). Furthermore, Seither-Preisler et al. (2014) found a larger right Heschl's gyrus in children with musical training, compared to children without musical training. Other sources of evidence come from structural and functional connectivity studies. For instance, DTI studies have found that musicians have a larger right AF volume than non-musicians (Halwani et al. 2011), and also the surface area of the anterior corpus callosum (CC) is greater (Schlaug et al. 1995a). Similarly, resting-state studies have shown increased connectivity between the left AC and the right sensorimotor cortex and between the left and right AC (Klein et al. 2016) in musicians compared to non-musicians. Resting-state studies have also shown enhanced connectivity between the right AC and the right ventral premotor cortex in musicians (Palomar-García et al. 2017). Taken together, the results of these studies suggest that, compared to non-musicians, musicians present anatomical and functional differences in the AC and right IFG. Furthermore, previous studies have found that some people are able to classify pitches into tone categories without the use of a reference tone (Bachem 1937), and this ability is called absolute pitch (AP). Previous neuroimaging studies have reported a left-sided planum temporale anatomical asymmetry in AP musicians (Schlaug et al. 1995b; Luders et al. 2004), whereas other studies have found that gray matter volume in the right HG (Wengenroth et al. 2014)

and bilateral volume in the HG were highly correlated with AP proficiency (McKetton et al. 2019). In addition, DTI studies have found increased fractional anisotropy (FA) values in the left-sided white matter underlying the planum temporale and increased connectivity in the left superior longitudinal fasciculus in AP possessors (Oechslin et al. 2010; Burkhard et al. 2020). Furthermore, an AP-specific functional network has been reported, characterized by increased connectivity in the area of the AC (Jäncke et al. 2012), but also by increased connectivity within the parietal and frontal regions (Brauchli et al. 2019).

However, the presence of experience-dependent effects in the above-mentioned studies means that it is not possible to determine whether the individual differences in the auditory cortex and right frontal regions reflect an innate predisposition to musical skills or the effects of training. In this regard, the results of different studies seem congruent with the idea that innate, predisposing factors do exist. For example, Foster and Zatorre (2010) examined the anatomical correlates of the right AC and intraparietal sulcus of musical performance on different tasks in a group of participants with different amounts of musical training. Consistent with the results cited above, participants' performance on pitch discrimination, melody discrimination, and rhythm processing correlated with the GM volume of the right AC. Importantly, the correlation with pitch discrimination remained significant after partialling out the effect of hours of musical training. Likewise, Zatorre et al. (2012) found that participants who quickly learned how to perform a micromelody task had steeper fMRI responses to pitch changes in their bilateral AC, even before they were trained on the task. Consistent with the studies by Zatorre and collaborators, further evidence is provided by a few recent investigations carried out with non-musicians with the aim of ruling out the training component. These studies sought baseline brain measures that could predict learning. The results showed that enhanced BOLD-activity in the right AC during a pre-training period spent listening to familiar melodies was predictive of the learning rate (Herholz et al. 2016). In addition, the macro- and microstructural organizations of the AF (i.e., fractional anisotropy and volume) were found to predict the learning rate and speed of learning on rhythm and melody tasks (Engel et al. 2014; Vaquero et al. 2018). Furthermore, inter-hemispheric connectivity differences in the anterior parts of the corpus callosum could reflect innate differences in the processing of the rhythmic aspects of music (Rajan et al. 2019). It is of note, however, that the presumably predisposing effects found in the previously mentioned studies seem to be restricted to the auditory cortex, but they do not include the right IFG. This raises the question of whether individual differences in the auditory cortex reflect predisposing factors to pitch discrimination, whereas individual differences involving the right IFG are the consequence of

higher-level musical training. The sample types used in previous studies do not allow this question to be answered.

In the present study, we aim to disentangle predisposing and training-related individual differences associated with pitch discrimination. To do so, we investigate the anatomic correlates of pitch discrimination in three different types of samples: adult musicians, adult non-musicians, and children without musical instruction. In line with prior studies, we expect that greater GM volume in the auditory and frontal regions will be associated with better performance on the pitch discrimination task. Critically, however, we establish two hypotheses in this regard. First, the greater GM volume in auditory regions is a predisposing factor to enhanced pitch discrimination. Hence, greater GM volume in the Heschl's gyrus is particularly expected in individuals who, despite not having musical training (non-musicians and children), are good at pitch discrimination. Specifically, based on previous studies (Schneider et al. 2005), we expected to find bilateral differences in the gray matter volume in Heschl's gyrus depending on how they processed the pitch discrimination, that is: (i) more gray matter in the left HG associated with better perception of fundamental pitch; and (ii) more gray matter in the right HG associated with the ability to perceive spectral pitch. Second, greater GM volume in the right IFG is associated with musical training, and hence, it is only expected in musicians. Furthermore, we wanted to investigate whether there were differences in the GM volume depending on handedness. For this reason, we selected adult musicians and non-musicians who were left-handed and right-handed.

Methods

Participants

Adult sample

A total of 60 voluntary subjects participated in the study, 32 musicians [11 women; mean age = 20.09 years, standard deviation (SD) ± 2.01 ; range 18–26 years] and 28 non-musicians (12 women; mean age = 20.68 ± 2.21 years; range 18–27 years). Musicians had completed formal music studies (conservatory, private schools), and they were active musicians (age of commencement of training = 7.61 ± 1.5 years, range 6–9; all with a minimum of 9 years of formal training). Non-musicians had never played a musical instrument, and they had received no musical training beyond obligatory musical instruction at school. The two groups did not differ in age or gender distribution. In the musician group, 18 participants were left-handed, and 14 participants were right-handed; in the control group, 16 participants were left-handed, and 12 participants were right-handed, according to

the Edinburgh Handedness Inventory (Oldfield 1971). None of them had suffered from any neurological or psychiatric disorders, and they had no history of head injury with loss of consciousness. Written informed consent was obtained from all participants, following a protocol approved by the Universitat Jaume I, and they received monetary compensation.

Children sample

A total of 32 school-aged children participated in the study (17 girls; mean age = 8.5 ± 1.54 years; range 6–12 years). They had no previous formal musical instruction. 28 children were right-handed, and 4 children were left-handed according to the Edinburgh Handedness Inventory (Oldfield 1971). All of them had normal neuropsychological and psychiatric conditions and abilities. All parents gave written consent for their children to participate in this study, following a protocol approved by the Universitat Jaume I, and they received economic compensation for their participation.

Materials

Jake Mandell tone deaf test (JMT)

With the aim of measuring individual differences in pitch discrimination, we used the Jake Mandell Test (JMT), developed by Jake Mandell and previously used to assess individual differences in pitch discrimination (Hernández et al. 2019). This computerized test consists of 36 trials based on complex musical phrases that use different sonorities, such as organ, piano, percussion, or string instruments. These phrases are also heterogeneous in different features, such as duration, number of tones, number of short and long sounds, intensity changes, and the use of synthesized or natural sounds. The trials comprised paired brief musical phrases (i.e., melodies) performed in a variety of timbres and musical styles. In half of the pairs (18/36), the two melodies differ in the pitch of a single note, with 9/18 of the different notes falling outside the scale of the melody and 9/18 confined to the scale. The pitch difference of the single modified note from the initial and repeated phrase may vary by up to 11 semitones in pitch; variations greater than one octave are not used. In the other half of the pairs, the two melodies share the same melodic contour, rhythm, and timbre.

On each trial, the subject hears two short successive melodies and indicates whether they are equal (green button “same”) or different (red button “different”); pairs of melodies can be the same or have differences in one or more pitches. After receiving the instructions, the subject is given the opportunity to adjust the volume to a comfortable level, and four practice trials are presented. Then, 36 paired trials are presented to all subjects in the same order, without

arranging the items in the order of increasing difficulty. This test is available at <https://jakemandell.com/tonedeaf/>.

The test was designed to be challenging even for people with musical training, thus preventing clustering of scores by trained individuals. According to the author, the JMT is useful for measuring the average capacity for pitch perception, and it has been verified with a statistical analysis of 61,036 subjects. We used the subject's percentage of total correct answers as a score for pitch perception capacity.

Image acquisition

Adult sample

Images were acquired on a 3-T Philips Achieva. A 3D structural MRI was acquired for each subject using a T_1 -weighted magnetization-prepared rapid gradient-echo sequence (time repetition/time echo (TR/TE) = 8.4/3.8 ms, matrix = 224×269 , voxel size = $0.90 \times 0.89 \times 0.80$ mm).

Children sample

Images were acquired on a 1.5-T Siemens Avanto (Erlangen, Germany). A 3D structural MRI was acquired for each subject using a T_1 -weighted magnetization-prepared rapid gradient-echo sequence (time repetition/time echo (TR/TE) = 2200/3.8 ms, matrix = $256 \times 256 \times 160$, voxel size = $1 \times 1 \times 1$ mm).

Voxel-based morphometry analyses

Image preprocessing

Adult sample

Voxel-based morphometry (VBM) was performed with the Computational Anatomy Toolbox (CAT12; <https://www.neuro.uni-jena.de/cat/>) for the Statistical Parametric Mapping, SPM12 package (Wellcome Trust Centre for Neuroimaging, London, UK; <https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). The preprocessing steps were conducted following the standard default procedure suggested in the manual. This procedure includes the following steps: (1) segmentation of the images into GM, white matter (WM), and cerebrospinal fluid (CSF); (2) registration to a standard template provided by the International Consortium of Brain Mapping (ICBM); (3) DARTEL normalization of the GM segments to the Montreal Neurological Institute (MNI) template; (4) modulation of the normalization data; (5) data quality check (in which no outliers or incorrectly aligned cases were detected), and for each subject, the total intracranial volume (TIV) was estimated. Finally, images were

smoothed with an 8-mm Gaussian Kernel. Note that this procedure does not include any correction for global head size [e.g., intracranial volume correction (TIV)].

Children sample

First, a customized tissue probability map (TPM) template was created based on the pediatric sample of the Template-O-Matic (TOM8) toolbox (<https://irc.cchmc.org/software/tom.php>). Age and gender were also entered to obtain a more accurate template (based on our sample). After that, VBM was performed with the CAT12 (<https://www.neuro.uni-jena.de/cat/>) for the SPM12 package (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). Images were segmented into GM, WM, and CSF, and they were registered through affine regularization to the TPM. Further spatial registration was achieved with high-dimensional DARTEL normalization to MNI. Voxel values were modulated. Then, we performed a data quality check (in which no outliers or incorrectly aligned cases were detected), and for each children, the TIV was estimated. Finally, images were smoothed with an 8 mm Gaussian Kernel.

Statistical analysis

We applied a region of interest (ROI) analysis to investigate focal voxel-based morphometry differences in a priori regions of interest (ROIs). We took two critical regions for pitch discrimination as ROIs: the left and right Heschl's gyri (including H1 and H2) and the right IFG. These ROIs were defined using the probabilistic Harvard–Oxford cortical structural atlas, set at a probability of 50%. The modulated GM volumes were obtained for each structure via MATLAB script (https://www0.cs.ucl.ac.uk/staff/g.ridgway/vbm/get_totals.m). After that, partial correlations were performed using SPSS 20 (IBM, Chicago, IL, USA), including GM volumes and pitch discrimination scores as variables. In the adult sample, we controlled for the effects of TIV and handedness, whereas in the children's sample, we controlled for TIV, age, and gender. Results were considered at an alpha of 0.017 (based on Bonferroni correction for multiple comparisons), considering that there were three ROIs to be correlated with the JMT score ($p < 0.05/3$).

Results

Table 1 summarizes the performance on the JMT and the raw volume data for each group of participants (musicians, non-musicians, and children). Table 2 summarizes the partial correlations between JMT scores and volumetric measures in each group.

Table 1 Mean correct responses on the JMT, and volumetric brain measures in the musician, the non-musician, and children groups

	Musicians (<i>n</i> =32)	Non-musicians (<i>n</i> =28)	Children (<i>n</i> =32)
Jake Mandell test score	77.68 (8.24)	67.85 (10.43)	62.36 (8.43)
Left Heschl's gyrus (ml) ^a	1.36 (0.22)	1.30 (0.23)	1.37 (0.23)
Right Heschl's gyrus (ml) ^a	1.27 (0.19)	1.22 (0.21)	1.29 (0.17)
Right inferior frontal gyrus (ml) ^a	1.21 (0.12)	1.19 (0.13)	1.17 (0.14)

^aBrain measures are uncorrected raw volumes. We controlled for total intracranial volume when analyzing this variable. Values in parentheses are standard deviations

Table 2 Partial correlations between GM volume of a priori ROIs and scores obtained on the JMT

JMT scores	Right Heschl	Left Heschl	Right IFG
Musicians (<i>n</i> =32)	0.16	0.20	0.47*
Non-musicians (<i>n</i> =28)	0.28	0.41*	0.10
Musicians and non-musicians	0.26	0.33*	0.27
Children (<i>n</i> =32)	0.41*	0.14	0.26

One-tailed *t*-tests; **P*<0.05 FWE corrected

Behavioral results: JMT

We performed a one-way ANOVA with the JMT score as the dependent variable and group as a between-subject factor. The main effect of group was significant [$F(2, 89) = 23.65$, $p < 0.001$]. Post hoc analyses using Bonferroni revealed significant differences between musicians and non-musicians $t(89) = 4.21$, $p < 0.001$ and between musicians and children $t(89) = 6.79$, $p < 0.001$. The difference between non-musicians and children was not significant ($p = 0.07$).

ROI analyses

The multivariate ANOVA we ran to investigate possible differences as a function of group or handedness did not yield

any significant effects. Thus, ROIs did not differ in the overall sample or in any group ($p > 0.10$).

The results showed that JMT scores correlated positively with the GM volume of the right IFG ($r = 0.47$; $p < 0.017$) in the musician group (Table 2, Fig. 1a). In the case of non-musicians, JMT scores correlated positively with the GM volume of the left Heschl's gyrus ($r = 0.41$; $p < 0.017$; Table 2, Fig. 1b). This correlation approached significance in non-musicians' right Heschl's gyrus ($r = 0.28$; $p = 0.07$). In the group of children, JMT scores correlated positively with the GM volume of the right Heschl's gyrus ($r = 0.41$; $p < 0.017$; Table 2, Fig. 1c). Finally, it is worth noting that the volumes of the musicians' ROIs were not correlated with the age at which they started their musical training or with the hours of training.

Discussion

Using voxel-based morphometry, the present study examined the individual differences in the GM volume of the Heschl's gyrus and IFG regions related to pitch discrimination in three different groups: adult musicians and non-musicians, and children without musical training. The ROIs were selected due to their involvement in the pitch perception ability required to recognize modifications in noise based on differences in frequency. Our results showed that

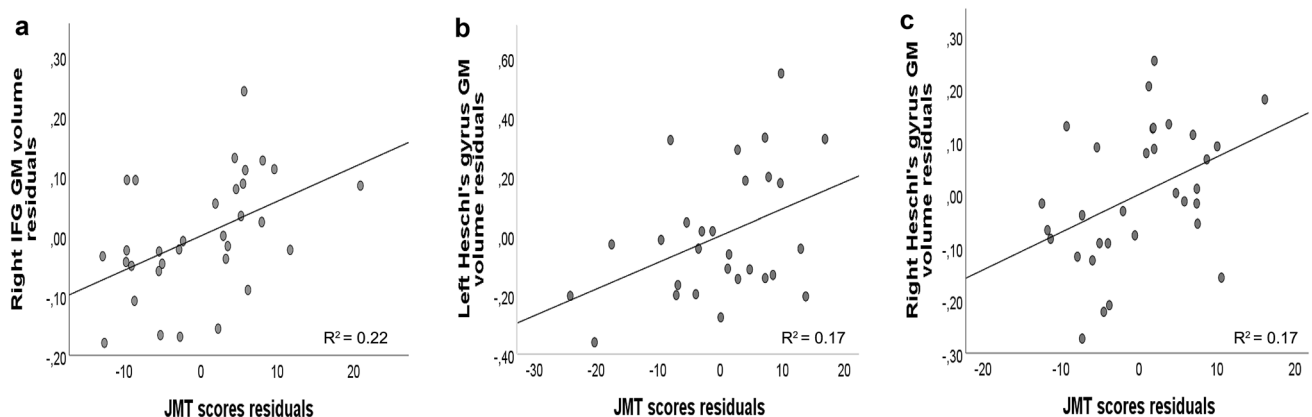


Fig. 1 Scatterplots of residuals illustrating the relationship between JMT scores with: **a** the right IFG GM volume in musicians; **b** the left Heschl's gyrus GM volume in non-musicians; and **c** the right Heschl's gyrus GM volume in children

musicians who performed the pitch discrimination task better had a greater volume in the right IFG, whereas the adults and children without musical training with better pitch discrimination had greater volume in auditory regions.

Regarding the behavioral data, the results showed that adult musicians performed the JMT better than non-musicians and children. Specifically, when comparing adult musicians and non-musicians, the scores were almost 10% higher for musicians than for non-musicians—importantly, however, musicians did not perform at ceiling. The present result is in line with different studies showing that, compared to non-musicians, musicians show higher sensitivity to certain acoustic features that are critical in music processing (Micheyl et al. 2006; Anderson and Kraus 2011; Bianchi et al. 2016). In addition, different contributions of expertise in music processing and performance have been associated with higher scores on the JMT (Hernández et al. 2019). The results also showed no differences between non-musicians and children in their pitch discrimination capacity. This is consistent with previous studies suggesting that the development of pitch discrimination is already established at the age of 6–7 years and hardly improves in the period from childhood to adulthood without specific training (Thompson et al. 1999; Ireland et al. 2019).

Regarding the VBM analysis, we did not find significant differences in any brain measures between adult musicians, non-musicians, and children. Specifically, our results differ from previous studies that found increases in GM volume in the Heschl's gyrus in musicians compared to non-musicians (Schneider et al. 2002, 2005; Gaser and Schlaug 2003; Bermudez et al. 2009; Palomar-García et al. 2017). However, other studies did not report differences in the Heschl's gyrus specifically (Vaquero et al. 2016; McKetton et al. 2019). One possible explanation for these discrepancies could be that the volume of Heschl's gyrus not only depends on musical training, but also on a predisposing ability to detect better pitch discrimination, as Drayna et al. (2001) and Mosing et al. (2014) proposed. Therefore, if the non-musicians have an innate pitch discrimination ability and, therefore, greater volume in Heschl's gyrus, as we have seen in our study, significant differences would not be found between musicians and non-musicians. In addition, we did not find significant differences in adult samples depending on handedness.

On the other hand, the correlation analyses between the GM volume and pitch discrimination scores revealed a differential pattern of results depending on the group. Specifically, in the non-musician adult group, we observed that those participants with more GM volume in the left Heschl's gyrus had better performance on the JMT. With a more liberal threshold, we found the same correlation in the right Heschl's gyrus. These regions have previously been associated with the type of pitch processing, irrespective of musical aptitude (Schneider et al. 2005). Specifically, they

have been related to a right-hemispheric specialization for spectral pitch perception and a left hemispheric specialization for fundamental pitch perception, in accordance with a functional imaging study contrasting the neural processing of rapid temporal and spectral variation (Zatorre and Belin 2001). As far as we know, this is the first study to report this relationship in a sample of adults without any musical training (i.e. beyond the obligatory training at school) or pitch discrimination problems. As expected, this result is consistent with previous studies that proposed the existence of two pitch centers that facilitate the extraction of fundamental and spectral pitch (Schneider et al. 2005), with studies comparing participants with congenital amusia and controls (Mandell et al. 2007), and with studies with AP possessors showing a greater gray matter volume of the right HG (Wengenroth et al. 2014) and the bilateral HG (McKetton et al. 2019), and higher fractional anisotropy values in the left-sided white matter underlying the planum temporale (Burkhard et al. 2020). Along the same lines, our results were also consistent with previous studies with non-musicians showing that the AC volume predicts the learning rate and speed of learning on rhythm and melody tasks (Engel et al. 2014; Herholz et al. 2016; Vaquero et al. 2018).

Perhaps the best way to separate the effects of predisposing factors from those of musical training would be a longitudinal study of children before the onset of their music training and continuing on into adulthood. To date, we are aware of few longitudinal studies in this area. The main finding of these studies is that music training produces structural brain and behavioral changes in children (Hyde et al. 2009; Habibi et al. 2014, 2018a, b). However, these changes observed after training were not predicted by pre-existing biological traits, including the AC volume. Furthermore, previous studies with children have found that short periods of musical training during childhood can improve children's discrimination of simple tones and melodies (Hyde et al. 2009; Habibi et al. 2016) and neural processing of musical sounds and pitches (Shahin et al. 2004; Schlaug et al. 2005; Fujioka et al. 2006; Besson et al. 2007; Putkinen et al. 2014). However, to our knowledge, the present study is the first to investigate, in children, the relationship between GM volume and pitch discrimination ability before musical training begins, that is, the predisposing morphometric characteristics of good pitch discrimination. Our results in this regard demonstrate that the children who had a greater right Heschl's gyrus volume performed better on the pitch discrimination task. This finding is congruent with what we observed in the adult sample: the volume in auditory regions in people without musical training helps them to perform an auditory pitch discrimination task. Specifically, based on the study by Schneider et al. (2005), the greater volume on the right may lead to a dominant perception of spectral pitch or single harmonics.

In addition, the present results with non-musicians and children without musical training are in line with previous studies showing that individual differences in musical abilities could be explained by the presence of pre-existing structural differences in the brain (Foster and Zatorre 2010; Seither-Preisler et al. 2014; Vaquero et al. 2018).

In light of the prior evidence mentioned above, our Heschl's gyrus findings probably indicate that differences in auditory regions are more related to musical aptitude, that is, to morphometric predisposing factors. In this regard, it is worth noting that the volume of the AC has been attributed a predisposing role in speech perception as well. For instance, different studies have shown that variability in the left auditory cortical structure and in related white-matter regions and functional networks predicts the ability to learn to discriminate speech sounds (Golestani et al. 2002, 2007; Ventura-Campos et al. 2013; Ressel et al. 2012). This speech-related evidence represents cumulative evidence in favor of the predisposing role of the AC in pitch sound-related abilities.

In the case of the musician group, we found a significant correlation between the pitch discrimination task and the right IFG, musicians who have more GM in the IFG performed the pitch discrimination test better. This finding is in line with an fMRI study in which pitch discrimination learning in the context of melodic patterns was associated with decreases in the neural activity of auditory regions and global increases in the neural activity of some right frontal regions (Zatorre et al. 2012). The IFG has been implicated in musical pitch encoding, melodic pitch memory, and non-local dependencies on musical tasks based on internal knowledge of the grammatical rules of musical syntax (Hyde et al. 2006, 2011; Cheung et al. 2018). In addition, in an fMRI study, Bianchi et al. (2017) found stronger cortical responses to pitch in a right fronto-temporal network in musicians compared to non-musicians. They found an increased neural signal in the IFG of musicians that was related to an extended neural network for pitch processing in these individuals (Bianchi et al. 2016). This observation is likely to reflect an involvement of auditory working memory in the processing and maintenance of pitch information (Maess et al. 2001; Koelsch et al. 2005; Zatorre et al. 2012; Bianchi et al. 2017; Leopold et al. 2019). Moreover, previous studies have reported that long-term consequences of musical training induce increases in the structural connectivity between the right frontal and auditory regions (Halwani et al. 2011), as well as an increase in their functional connectivity at rest (Palomar-García et al. 2017). Furthermore, several studies have revealed the importance of this fronto-temporal network in music processing and, specifically, in auditory discrimination (Chen et al. 2009; Herholz et al. 2016; Sihvonen et al. 2017). All these results seem to indicate that the right

fronto-temporal network becomes strengthened as a consequence of musical training. Therefore, we interpret that the correlation between the JMT scores and the right IFG volume that we found in musicians reflects the strengthening of the right fronto-temporal network in musicians with higher pitch discrimination capacity.

In conclusion, the current study shows that individual differences in the GM volume of different regions of the fronto-temporal network associated with the pitch discrimination capacity are due to both predisposing and training-related factors. Evidence from adult non-musicians and children without musical training indicates that the volume of the Heschl's gyrus is a predisposing factor for developing a good pitch discrimination capacity. Evidence from musicians suggests that the constant audio-motor interaction that comes with musical training enhances the volume of the right IFG.

Limitations

The present research may have some limitations. Specifically, different methods were used to define the boundaries and extent of the auditory regions. As previous studies have proposed (Zoellner et al. 2019), it might be a good idea to individually delineate the auditory regions in each participant. However, it is important to highlight that Desikan et al. (2006) found that the automated system for subdividing the cortex into regions of interest is valid when compared to manual procedures, and it has a very high degree of reliability. Future studies might be interested in exploring the reported results, individually delineating these regions (see Zoellner et al. 2019).

Author contributions M-ÁP-G, MH, and CÁ developed the study concept; M-ÁP-G, MH, GO, AM-P performed data collection; M-ÁP-G, JA-V, VC, and EV-R performed the data analysis; M-ÁP-G, MH, and CÁ wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final version of the manuscript for submission.

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Compliance with ethical standards

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

Ethics approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional Review Board of the Universitat Jaume I and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. This article does not contain any studies with animals performed by any of the authors.

Informed consent Informed consent was obtained from all adult participants included in the study. Furthermore, written informed consent was obtained from the parents for their children.

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