High-fidelity transmission of auditory symbolic material is associated with reduced right–left neuroanatomical asymmetry between primary auditory regions

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The intergenerational stability of auditory symbolic systems, such as music, is thought to rely on brain processes that allow the faithful transmission of complex sounds. Little is known about the functional and structural aspects of the human brain which support this ability, with a few studies pointing to the bilateral organization of auditory networks as a putative neural substrate. Here, we further tested this hypothesis by examining the role of left–right neuroanatomical asymmetries between auditory cortices. We collected neuroanatomical images from a large sample of participants (nonmusicians) and analyzed them with Freesurfer's surface-based morphometry method. Weeks after scanning, the same individuals participated in a laboratory experiment that simulated music transmission: the signaling games. We found that high accuracy in the intergenerational transmission of an artificial tone system was associated with reduced rightward asymmetry of cortical thickness in Heschl's sulcus. Our study suggests that the high-fidelity copying of melodic material may rely on the extent to which computational neuronal resources are distributed across hemispheres. Our data further support the role of interhemispheric brain organization in the cultural transmission and evolution of auditory symbolic systems.

Key words: auditory asymmetries; cortical morphometrics; cultural transmission; neuroanatomy; transmission fidelity.

Introduction

An influential proposal in the field of human cultural evolution attributes stable cultural traditions and cumulative innovations to psychological processes capable of high-fidelity copying—i.e. the ability to faithfully learn and reproduce cultural information (Tomasello et al. 1993; Mesoudi 2011; Lewis and Laland 2012; Legare and Nielsen 2015). In cultural systems where oral transmission is still prominent, such as music (Le Bomin et al. 2016), processes such as social learning and transmission operate as a form of inheritance system (Tomasello et al. 1993; Tomasello 2009). When these processes are imprecise, they lead to erroneous reproductions ("innovations") and may promote the emergence of novel variants (Boyd and Richerson 1988; Caldwell et al. 2016). While social learning and transmission biases are often interpreted in cognitive terms (Sperber 1996, 2012; Chater and Vitányi 2003; Kirby et al. 2007; Ravignani et al. 2018), their neural underpinnings are still unclear (Lumaca, Haumann, et al. 2018). Understanding the organizational aspects of human brain networks that promote social learning and transmission, and assessing the origins of their variability across individuals, may ultimately be essential for understanding larger-scale cultural phenomena as different as music stability and diversification (Mesoudi 2011).

Experiments with signaling games suggest that the interhemispheric organization of temporal auditory networks may be a neural substrate for the faithful transmission of music (Lumaca et al. 2019, 2021). In a 2-session experiment, we collected neuroimaging and behavioral data from healthy participants (nonmusicians) (for more details, see "Study design"). The behavioral experiment consisted of a paradigm that mimics, under controlled laboratory settings, the intergenerational transmission of a melodic system: the signaling games (Moreno and Baggio 2015; Nowak and Baggio 2016; Lumaca and Baggio 2017, 2018). In signaling games, each participant plays first as a "receiver" (learner) of a melodic "code" (an artificial system of signals-states mappings). In a second game, the participant's role becomes that of "sender" (transmitter) and is asked to reproduce the original code by memory (Fig. 1). In our experiment, the signals were 5-tone melodic patterns, while the states were facial expressions representing music emotions (see Lumaca and Baggio 2017 for details on the stimuli). We assessed the participants' performance on 3 core cultural transmission behaviors: coordination (social learning), transmission (transmission fidelity), and innovation (reproduction errors). We found that the transmission fidelity could be predicted by the strength of homotopic functional connections between
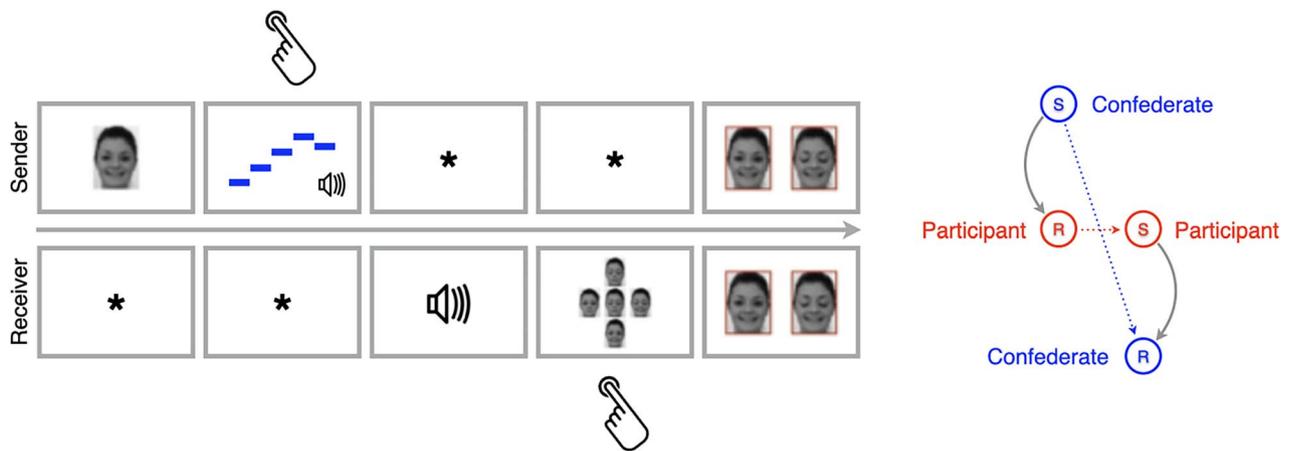
Fig. 1. Structure of a single trial in signaling games and experimental transmission design. On the left, an example of a single trial showing what the senders (top row) and receivers (bottom row) saw on the screen or listened to via headphones. At the start of each trial, the sender saw on the computer screen a facial expression (simple or compound emotions; "state") and was asked to compose an isochronous 5-tone sequence to be used as a "signal" to communicate the observed state to a receiver. The receiver listened to the signal via the headphones and responded by guessing which image the sender had seen. Feedback was presented simultaneously to both players, showing the state the receiver has seen (left) and the image the receiver has chosen (right), in a green frame (matching images; correct trial) or in a red frame (mismatching images; incorrect trial). The sender and the receiver converged over several trials on a shared mapping of signals (tone sequences) to states (emotions). Hand symbols indicate when the sender or the receiver had to produce a response. Time flows from left to right. On the right, the experimental transmission design in signaling games. The participant played as receiver (R) with a confederate of the experimenters playing as sender (S) in game 1. Roles switched in game 2.

bilateral auditory areas (Lumaca et al. 2019) and by the microstructural integrity of crosscallosal auditory fibers (Lumaca, Baggio, et al. 2021). Stronger functional connections, and larger fractional anisotropy in the callosal splenium crossed by interhemispheric auditory fibers, were associated with a more accurate transmission of the auditory symbolic material. These results support the hypothesis that neural characteristics enhancing interhemispheric cooperation and coordination can promote perceptuo-cognitive processes (Zaidel 1995; Banich 1998; Catani et al. 2007), including those behind the high-fidelity copying of tonal material. Little is known about how far this purported connection between interhemispheric organization and transmission biases may extend to auditory anatomy.

To examine this issue, we assessed another prominent aspect of the interhemispheric auditory organization: the anatomical asymmetry of auditory cortices. Asymmetry is a core organizational feature of human brain structure (Kertesz et al. 1986) whose degree is known to affect the hemispheric division of processing labor (Hugdahl 2011). In the auditory cortex, anatomical asymmetries have been reported at multiple spatial scales of brain architecture: from the microscopic organization of neuronal microcolumns (Buxhoeveden and Casanova 2000; Galuske et al. 2000) to the cortical morphology of entire auditory regions (e.g. Geschwind and Levitsky 1968; Jäncke and Steinmetz 1993; Penhune et al. 1996). Morphological asymmetries in the Heschl's gyrus have been reported for both adult musicians and nonmusicians, with and without tinnitus, in terms of volume, (Schneider et al. 2009) and for children, these have been reported in terms of cortical thickness (CT; Zoellner et al. 2019). Here, we assessed the left–right regional asymmetries using surface-based morphometry (SBM; Dale et al. 1999; Fischl, Sereno and Dale 1999). SBM is an automated quantitative tool for the fine-grained assessment of cortical morphometry in T1-weighted (T1w) anatomical images. It allows for the estimation of independent aspects of cortical morphology, such as surface area and CT, which are indicative of the cytoarchitectural organization of the cortical columns in the neocortex (Rakic 1988). Studies using SBM have reported general patterns of left–right asymmetries between auditory regions,

which are exhibited by the majority of individuals. Crucially, they found strong leftward asymmetries (left > right) in the volume and surface area of the planum temporale and Heschl's gyrus— the location of the primary auditory cortex in humans—and strong rightward asymmetries in the thickness of the transverse temporal sulcus (or Heschl's sulcus)—a small auditory region connecting the planum temporale and Heschl's gyrus (Koelkebeck et al. 2014; Meyer et al. 2014; Chiarello et al. 2016; Kong et al. 2018).

Auditory asymmetries are characterized by a large intersubject variability (Rademacher et al. 2001; Tzourio-Mazoyer et al. 2004; Desai et al. 2005; Mueller et al. 2013). In an attempt to understand the origins of this variability, Chiarello et al. (2016) related the strength of regional asymmetries to the degree of their variability across individuals. Their work demonstrates a larger between-subjects variability in the superior temporal plane for surface area, and in the planum temporale, Heschl's gyrus, and Heschl's sulcus, for CT. Critically, high-variability regions also exhibited a large degree of anatomical asymmetry. The author's suggestion is that biological constraints on the expression of brain asymmetries typically tend to limit the extent of their phenotypic variation. Regions with less strict biological constraints would instead be more sensitive to the influence of idiosyncratic factors, including experience-dependent plasticity. These regions would develop more independently across hemispheres, increasing the extent of asymmetry. If such phenotypic variation is meaningful and does not merely reflect noise (Kosslyn et al. 2002; Zilles and Amunts 2013), some degree of relationship is expected between asymmetry in highly lateralized superior temporal regions and performance in auditory behavior (Kanai and Rees 2011; Zatorre 2013; Marie and Golestani 2017).

This relationship has been mainly addressed for language acquisition (Golestani and Pallier 2007) and language lateralization (Jäncke and Steinmetz 1993; Heiervang et al. 2000; Josse et al. 2003; Dorsaint-Pierre et al. 2006; Chiarello et al. 2012; Greve et al. 2013). In music perception, the association with brain asymmetries has been only investigated in the context of music training and expertise (Schneider et al. 2005; Bermudez et al. 2009; Meyer et al. 2012; Ellis et al. 2013; Worschech et al. 2022).

However, we do not know whether auditory asymmetries in musically naive individuals—i.e. asymmetries that are not the outcome of training-induced plasticity—can promote the aspects of auditory function that support faithful encoding and transmission of musical sounds. This is especially relevant for the stability and diversification of folk music, given the key role of nonmusical experts in the vertical transmission of folk tunes and other popular songs (Fitch 2015; Le Bomin et al. 2016).

In this study, we aimed at addressing this hypothesis by examining whether the degree of anatomical asymmetries in auditory-related cortical areas of nonmusicians are associated with perceptual-cognitive biases in the acquisition and transmission of simple tone sequences (see "Study design" and "Study aims" for details). We predicted that some asymmetry phenotypes may confer some advantage (or predispositions) in the capacity for learning and imitating the tone material (Liem et al. 2014). If revealed true, we may infer that the distribution of auditory biases in human populations is partly shaped by small differences across individuals in the bilateral organization of the auditory cortex. Extended to cultural transmission and evolution, after several generations, these differences would partly drive large-scale cultural phenomena such as music stability and diversification (Dediu and Ladd 2007).

Materials and methods
Participants

A total of 52 participants (32 females, mean age = 24.5, range = 20–34) took part in this study. None of them reported a personal history of psychiatric or neurological disorders. One participant (female) decided to drop out of the second session. The participants were matched for age (males: mean = 25.15 ± 2.73; females: mean = 24.25 ± 2.90; *t*-test, *P* > 0.05) and handedness (right-handed). Fifty-one participants completed the experiment. None of the participants had received formal musical training (mean = 0.6 years ± 0.98) (Zhang et al. 2020). All participants gave their written consent and filled out an MRI safety form. This study is part of a larger project that aims to investigate the neural bases of cognitive biases in music transmission and regularization. This project involved the analysis of different neuroimaging modalities (fMRI, resting-state functional MRI [rs-fMRI], diffusion, anatomy) from the same group of participants in order to investigate the main hypothesis at multiple neural levels from auditory function to neuroanatomy (Supplementary Table S1) (Lumaca et al. 2019, 2021, 2022). The study was approved by the ethics committee of the Central Denmark Region (nr. 1083).

Study design

All participants underwent 2 separate sessions (∼20 days apart): an MRI session and a behavioral session. The MRI session (∼1 h) (see Session 1: MR session) consisted of 4 scans: for each participant, we collected rs-fMRI images, a high-resolution anatomical image (MP2RAGE), and functional MRI (T2∗-weighted) images acquired during an auditory oddball task and high-resolution diffusion MRI (dMRI) images. After the scans, the participants reported their musical skills and training using the Goldsmiths Musical Sophistication Index, Gold-MSI (Müllensiefen et al. 2014), and were then tested on their working memory and attention spans (backward and forward digit span) (Orsini et al. 1987).

During the behavioral session, the participants played 2 consecutive signaling games (see Session 2: signaling games). In the first game, each participant played as a receiver (learner) of an artificial melodic code that consisted of 5 5-tone auditory patterns. These patterns referred to distinct emotions (represented as a facial expression from an actor) (Supplementary Fig. S1). Participants were instructed to learn the original signaling code from a confederate of the experimenters. In the second game, the participant played as the sender (transmitter) and was asked to transmit a system that was as similar as possible to the original (Supplementary Fig. S2). The 2 games were always played by different confederates (*n* = 3). Here, we report the analysis of high-resolution anatomical images (MP2RAGE). The analysis of data in the other modalities (rs-fMRI, fMRI, and dMRI) is outside the scope of this study and is described in detail elsewhere (see Supplementary Table S1).

Study aims

The aim of this work is to test any relationship existing between the fidelity of music transmission and anatomical asymmetries in auditory-related cortical regions. We started by applying Freesurfer's SBM (Dale et al. 1999; Fischl et al. 1999) to the MP2RAGE anatomical images. Figure 2 shows the schematic flowchart of our data analysis. Using SBM, we estimated the 3 main indicators of cortical morphology (CT, cortical surface area [CSA], and cortical volume [CV]) (Liem et al. 2014; Meyer et al. 2014) for each anatomical region of Destrieux's brain atlas (*n* = 165) (Destrieux et al. 2010). An asymmetry coefficient (AC) was calculated for each brain region and morphological trait using the formula: ((right − left)/(right + left)/2; (Penhune et al. 1996; Golestani et al. 2011; see Schneider et al. 2005 for a similar formula). A positive value indicates rightward asymmetry, while a negative value indicates leftward asymmetry. Using coefficients of variation (Bedeian and Mossholder 2000), we first assessed whether the brain regions with higher between-subject variability of asymmetry are also the most asymmetrical (Chiarello et al. 2016). Then, we examined whether this variability is systematic, focusing on the superior temporal regions. Following Lumaca et al. (2019, 2021), we restricted our analysis to 3 auditory regions of interest (ROIs): transverse temporal regions (Heschl's gyrus and Heschl's sulcus) and planum temporale (Fig. 3). Using multiple regression analyses, we tested whether the anatomical asymmetry in the 3 auditory regions could predict the social learning, transmission, and innovation of auditory symbolic material in the signaling games.

Session 1: MR session
MRI data acquisition

Data were acquired at the Aarhus University Hospital on a 3T MRI scanner (Siemens Prisma). Participants laid supine position in the scanner, with cushions fit around their heads to reduce motion artifacts. An MP2RAGE sequence was used for the acquisition of a high-resolution T1w image (TR = 5,000 ms; TE = 2.87 ms; voxel size = 0.9 mm³; echo time = 2.87 ms; flip angle = 4°; number of sagittal slices = 192) (10 min). During the acquisition, the participants were instructed to remain still and to watch a subtitled silent movie.

Cortical morphometry

Cortical surface reconstruction and volumetric segmentation were performed using the Freesurfer image analysis software (FreeSurfer-Linux-centos6_x86_64-stable-pub-v5.3.0). SBM offers 3 main advantages over VBM. It allows to run separate analyses for multiple aspects of cortical structure and to map their measurements to the precise anatomical locations of brain atlases (Desikan et al. 2006; Destrieux et al. 2010). It achieves
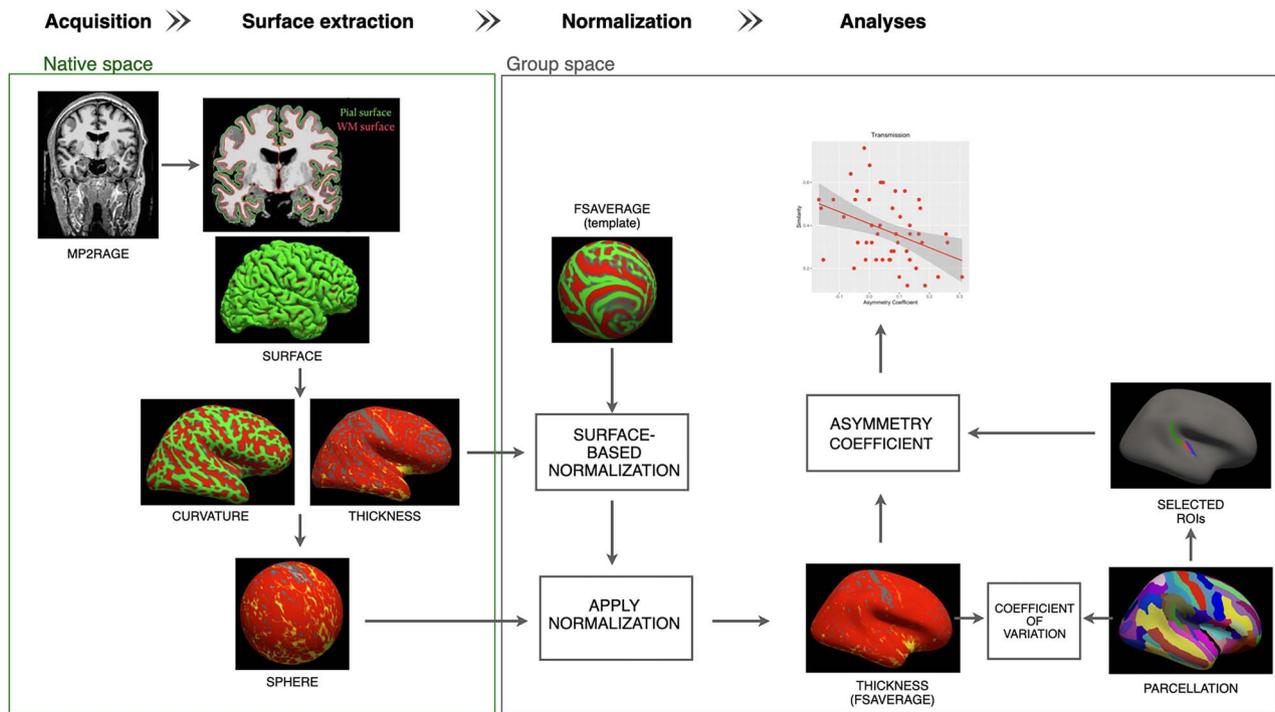
Fig. 2. Schematic flowchart of SBM analysis (see Zoellner et al. 2019 for a similar procedure). For each participant, we preprocessed high-resolution (MP2RAGE) anatomical images using the standard Freesurfer's preprocessing pipeline. Thickness (represented in the figure) and surface area were computed from the uniform grid (comprised of vertices) of the generated surface images. Cortical metrics were mapped to the inflate surface of each participant's reconstructed brain, which was inflated into a sphere. Subject-specific spheres were normalized to an average spherical surface (fsaverage) for the optimal alignment of sulcal and gyral features across participants. A coefficient of variation (SD/mean) was computed for each region of the Destrieux anatomical parcellation and cortical metrics, separately for each hemisphere ($n = 74$). The coefficient of variation estimates the extent of between-subject variability in thickness, area, or volume. Then, we selected 3 auditory-related cortical areas (Heschl's gyrus, Heschl's sulcus, and planum temporale). For each area, an AC of thickness, area, and volume was calculated. The AC estimates the degree to which a cortical metric is left- or right-lateralized. Multiple regression analyses were finally performed to test the relations between ACs of the auditory-related cortical regions and the signaling behaviors (coordination, transmission, and innovation).
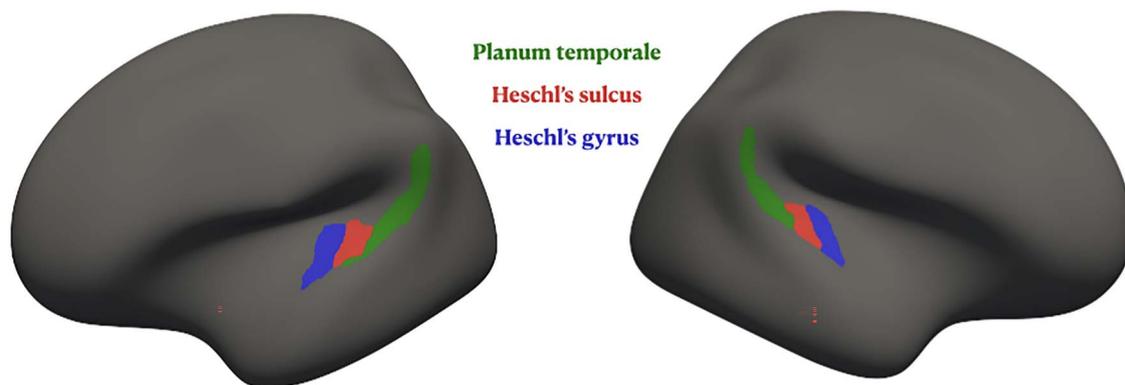

Fig. 3. The 3 selected auditory-related cortical regions are projected on the inflated left-hemisphere surface and the right-hemisphere surface of the Freesurfer's average (fsaverage) template.

finer spatial accuracy (subvoxel level). Finally, it avoids problems related to geometrical differences and interbrain (voxelwise) registration by using the cortical folding of the brain. The technical specifications of the preprocessing steps are described elsewhere (Dale and Sereno 1993; Sled et al. 1998; Dale et al. 1999; Fischl, Sereno and Dale 1999; Fischl et al. 1999; Ségonne et al. 2004). Briefly, we performed the standard recon-all pipeline using the -all flag, which performs all standard preprocessing steps, including motion correction, intensity normalization, and tesselation. Freesurfer reconstructs models of the participant's white-matter surface (the border between white matter and gray matter) and pial surface (the border between gray matter and

cerebrospinal fluid). For each participant, measures of CT and CSA were computed from the mesh grid of the surface images. CT reflects the number and the size of neurons within the columns and is calculated as the shortest distance between the white-matter surface and the pial surface. CSA may be related to the spatial distance between those columns and is calculated, for each vertex, as the mean area of the tessellation triangles that are part of that vertex. Finally, CV is calculated, which is the product between CT and CSA (Raznahan et al. 2011). CT, surface area, and volume were mapped to an inflated sphere of the participant's reconstructed brain and were registered to the Freesurfer common surface (FsAverage) where the gyri and the sulci of

all participants' images are optimally aligned (Fischl, Sereno, Tootell, et al. 1999). This procedure ensures that morphologically homologous cortical locations are accurately matched among participants. Thereafter, the cortex is automatically parcellated into units based on the gyral and sulcal features (Fischl et al. 2004; Desikan et al. 2006; Destrieux et al. 2010). In this study, the cortex was parcellated into 148 cortical regions (74 homologs) using Destrieux's atlas (aparc.a2009s annotation) (Destrieux et al. 2010). From these 148 anatomical structures, the following 3 ROIs were selected: Heschl's gyrus, Heschl's sulcus, and planum temporale.

Session 2: signaling games

Signaling games (Lewis 1969; Skyrms 2010) are popular models of coordination where 2 or more players exchange signals over repeated trials for sharing a common code: a scaled-down and artificial signaling system where "signals" refer to "states" of the world. In our study, we used signaling games with 2 players (1 sender and 1 receiver) exchanging 5-tone melodic patterns (signals), each referring to a distinct emotion (5 states). Emotions were represented as facial expressions from an actor. Moreno and Baggio (2015) showed that when the game is played with fixed roles, as opposed to switching roles, receivers tend to learn the code from senders, i.e. the net transmission of the code is from senders to receivers (role asymmetry). In this condition, signaling games turn from a game-theoretic model of coordination to a model of cultural transmission (see Lumaca and Baggio 2017 and Nowak and Baggio 2016 for more details). In the current study, we used the fixed-role variant of signaling games.

Stimuli

Signals are sequences of 5 pure tones drawn from the Bohlen-Pierce (BP) macrotonal scale (Mathews et al. 1988; Zarei et al. 2006). In this scale, a tritave scale (3:1 frequency ratio) is logarithmically divided into 13 equal steps, which are larger in size than the corresponding Western semitones (146 cents vs. 100 cents). The pitches in this scale are defined by the following equation: $F = k \times 3^{n/13}$, where k is the reference pitch frequency, and n is the number of steps on the scale (Loui et al. 2009). We set $k = 440$ Hz and $n = 0, 4, 6, 7, 10$. Signals were delivered through headphones at 70 dB. The unfamiliar BP scale prevents players from exploiting their schematic memory for mapping certain musical structures (e.g. the minor mode in the Western diatonic scale) with specific emotions (sadness). The states, denoted by the signals, were 5 emotions of different complexity: 3 simple (peace, joy, and sadness) and 2 compounds (peace × joy and peace × sadness), which were presented on the computer screen as facial expressions (Supplementary Fig. S2).

Trial structure

The game consisted of 70 trials. Each trial was organized as follows (Fig. 1). The sender observes privately a facial expression (state) on the computer screen (3-s duration) drawn from a set of 5 facial expressions and is asked to produce a 5-tone sequence (signal). To do so, the sender enters digits (1–5) via the computer keyboard, each mapped to a different BP tone. The sender may try different sequences at will and at their own pace before sending the favorite one to the receiver. Upon receiving the signal via headphones, the receiver selects 1 of the 5 facial expressions shown on the computer screen, the expression that is (thought to be) associated with the one presented to the sender (duration: self-paced). The selection occurs by using the number pad. Feedback (3 s) is then presented to both players, showing on their screens the expression the sender has seen (left-hand side) and the expression the

receiver has chosen (right-hand side). Players were sitting back to back in the same experimental room, with no possibility to look at each other screen or to communicate (verbally or otherwise). The experimenter used a video camera installed in the experimental room to monitor the players' behaviors.

Behavioral metrics

For each participant, we computed behavioral metrics for 3 core cultural behaviors (coordination, transmission, and innovation) using the normalized Hamming distance (HD) and similarity (1/HD) (Hamming 1986). The normalized HD is the number of pointwise substitutions (S), that are necessary to transform 1 signal (or string) into another of equal length (L), divided by the length of the signal (hence, HD = S/L). Two identical signals have HD = 0 and similarity = 1.

"Coordination" is a measure of learning and represents the similarity between the code produced by the sender (confederate) and the code learned by the receiver (participant) during game 1 (between-players and within-game measure). It is the mean similarity between the signal produced by the sender for a given state and the set of signals chosen by the receiver for the same state during the second half of game 1. A single score was calculated across all 5 code similarities, ranging from 0 (the participant did not learn the starting material) to 1 (accurate learning). "Transmission" represents how accurately the starting material was reproduced by the participant. It quantifies the similarity between the code produced by the sender of game 1 (confederate) and the sender of game 2 (participant) (between-players and between-game measure). The single score ranges from 0 (the code transmitted is entirely different from the one received) to 1 (faithful transmission). "Innovation" represents the extent to which the learned code was changed by the participant. It is the HD between the signal learned by the participant for a given state in game 1 and the signal produced by the same participant in game 2, averaged across all signals (within-player and between-games measure). It ranges from 0 (same codes learned and transmitted) to 1 (the code was entirely changed between games).

Statistical analyses

The coefficient of variation estimates the extent of between-subject variability in the thickness, volume, and area of a brain region. This coefficient was estimated for all brain regions of Destrieux's atlas using the formula: SD/mean (Bedeian and Mossholder 2000).

An AC was calculated from each homotopic region of the Destrieux's atlas using the formula: (right − left)/0.5∗(right + left) (Penhune et al. 1996; Golestani et al. 2011). Scores range from −1 (leftward lateralization) to 1 (rightward lateralization). Scores close to 0 denote symmetry in cortical metrics.

First, we used Pearson's correlations to relate the coefficients of variation and asymmetries coefficients (in absolute values) across brain regions. To do so, absolute values of ACs were averaged across participants within each parcellation and that value was paired with the (left or right) coefficient of variation of the same parcellation. The correlation was computed across the 74 regions separately for left and right hemispheres (Chiarello et al. 2016). Then, we focused on the auditory-related cortical ROIs (Heschl's Gyrus, Heschl's Sulcus, and planum temporale) assessing whether regional asymmetries were significantly different from 0 using 1-sample t-tests. Separately for each metric, we corrected the resulting P-values for multiple comparisons using Bonferroni's method ($P = 0.05/3 = 0.01$, where 3 is the number of independent

Table 1. Pearson correlations between the coefficient of variations and the ACs of brain parcellations for each cortical metric computed by hemisphere ($n = 74$).

	CT	CSA	CV
Left hemisphere	0.23[a]	0.31[b]	0.30[b]
Right hemisphere	0.23[a]	0.38[c]	0.30[b]

Abbreviations. AC = asymmetry coefficient; CT = cortical thickness; CSA = cortical surface area; CV = cortical volume. [a]$P < 0.05$. [b]$P < 0.01$. [c]$P < 0.001$.

tests involving each homotopic ROI (Meyer et al. 2014). Finally, multiple regression analyses were employed to test for a relationship between asymmetries in the cortical measures of the auditory ROIs and the 3 core cultural transmission behaviors modeled in signaling games: coordination, learning, and transmission. The GLMs were performed with AC as the explanatory variable and with signaling behavior as the response variable. We also included gender, Gold-MSI standardized score, and log-transformed intracranial volume (eICV) as nuisance regressors. Independently for each morphometrical character, we applied a false discovery rate (FDR) correction for multiple tests ($n = 9$; where 9 is the number of independent tests involving each behavioral variable and homotopic ROI). As a post hoc test, we assessed the relative contribution of the nuisance regressors in the fit of the regression model, that showed a significant relationship with signaling behaviors, after correction. We used the significant AC, gender, Gold-MSI, and eICV as the explanatory variables and signaling behavior (coordination, transmission, and innovation) as the response variable. At each step, the variables selected for the model were based on their *P*-values. The deviance of the model was used to determine the maximum number of variables to include in the final model. In a control analysis, we performed the same statistical regressions replacing ACs with the values of cortical metrics from single auditory regions. This analysis was performed to assess a putative relation of behavioral measures of learning and innovation with cortical properties of single auditory regions. The FDR correction was performed separately for each hemisphere and cortical morphometric in order to match the number of tests of the main analysis ($n = 9$; where 9 is the number of independent tests involving each behavioral variable and each auditory region of the same hemisphere).

Results
Between-subject variability and relationship to brain asymmetries

Table 1 displays the Pearson's correlations between the coefficients of variation (Supplementary Table S2) and the mean ACs expressed in absolute values (Supplementary Table S3) across all cortical parcellations ($n = 74$). In all measures of cortical structure, we found a positive correlation between the mean (absolute) ACs and coefficients of variation (see also Supplementary Fig. S3). Brain regions with the highest degree of variability across individuals were also the most asymmetrical.

Among the auditory ROIs, Heschl's sulcus was the region showing the largest values in the coefficient of variation regardless of the hemisphere and cortical metrics (Supplementary Table S2).

General patterns of auditory asymmetries

Figure 4 shows average regional asymmetries for CT, CSA, and CV (Table 2). Among the 3 ROIs, only Heschl's sulcus showed a significant asymmetry in CT (rightward). All the 3 ROIs showed strong leftward asymmetries in CSA and CV.

Auditory asymmetries and relationship to signaling behaviors

We assessed the relationship between anatomical asymmetries in the 3 auditory ROIs and measures of coordination, transmission, and innovation. Only 2 regression tests survived the FDR correction for multiple comparisons: those between CT asymmetry in Heschl's sulcus and intergenerational transmission behaviors (transmission and innovation) (Fig. 5). ACs for CT in this region showed significant positive correlations with innovation ($r = 0.39$; pFDR = 0.045) and negative correlations with transmission ($r = -0.38$; pFDR = 0.045) (Table 3). In other words, individuals who exhibited less rightward CT asymmetry in Heschl's sulcus displayed better transmission and less innovation.

Nuisance regressors (sex, Gold-MSI, and eICV) were only weakly associated to signaling behaviors (Supplementary Figs. S4 and S5). We further used stepwise linear regression to assess the contribution of these regressors in the fit of the model relative to CT asymmetry in Heschl's sulcus. For innovation and transmission, CT asymmetry in Heschl's sulcus was the only predictor included in the final model (mdl = y ~ 1 + AsymmetryCoeff_HS). No factors were included for coordination (mdl = y ~ 1). According to these findings, the CT asymmetry in Heschl's sulcus appears to be the main significant factor in the transmission of melodic material, while age, musical training, and intracranial volume do not have a determinant effect.

In a control analysis, we performed similar regressions replacing ACs with the values of cortical metrics from single regions. We analyzed each hemisphere separately in order to correct for the same number of tests. No result survived FDR correction for multiple comparisons (Supplementary Table S4).

Discussion

In this study, we found that left–right asymmetry of CT in an auditory area that is located in between Heschl's gyrus and planum temporale, Heschl's sulcus, predicted individual behavior in a laboratory experiment of music transmission. The fewer participants showing a reduced CT rightward asymmetry in Heschl's sulcus were better at transmitting the original melodic code (transmitters). The majority of participants with rightward CT asymmetries in Heschl's sulcus tended to introduce more changes in the melodic material (innovators). Transmission fidelity seems to be specifically related to the anatomical organization of bilateral auditory networks since we did not find any significant structural-behavioral correlation using morphological measurements from single auditory regions. This is the first time a neuroanatomical marker of interhemispheric brain organization has been associated with cultural transmission behaviors.

The asymmetry patterns found in our study replicate previous reports from Meyer et al. (2014) who also employed SBM with Destrieux's parcellation scheme (Destrieux et al. 2010) and focused their investigation on auditory-related cortical regions. Specifically, we replicated the strong leftward asymmetry for CSA and CV in all auditory ROIs (Heschl's gyrus, Heschl's sulcus, and planum temporale), and the rightward asymmetry for CT in Heschl's sulcus. Contrary to Meyer et al. (2014), we only found weak evidence of rightward asymmetries for thickness in Heschl's gyrus and planum temporale. This difference may be due to our smaller sample size ($n = 51$ vs. $n = 104$) and to other methodological differences between the studies. Chiarello et al. (2016)
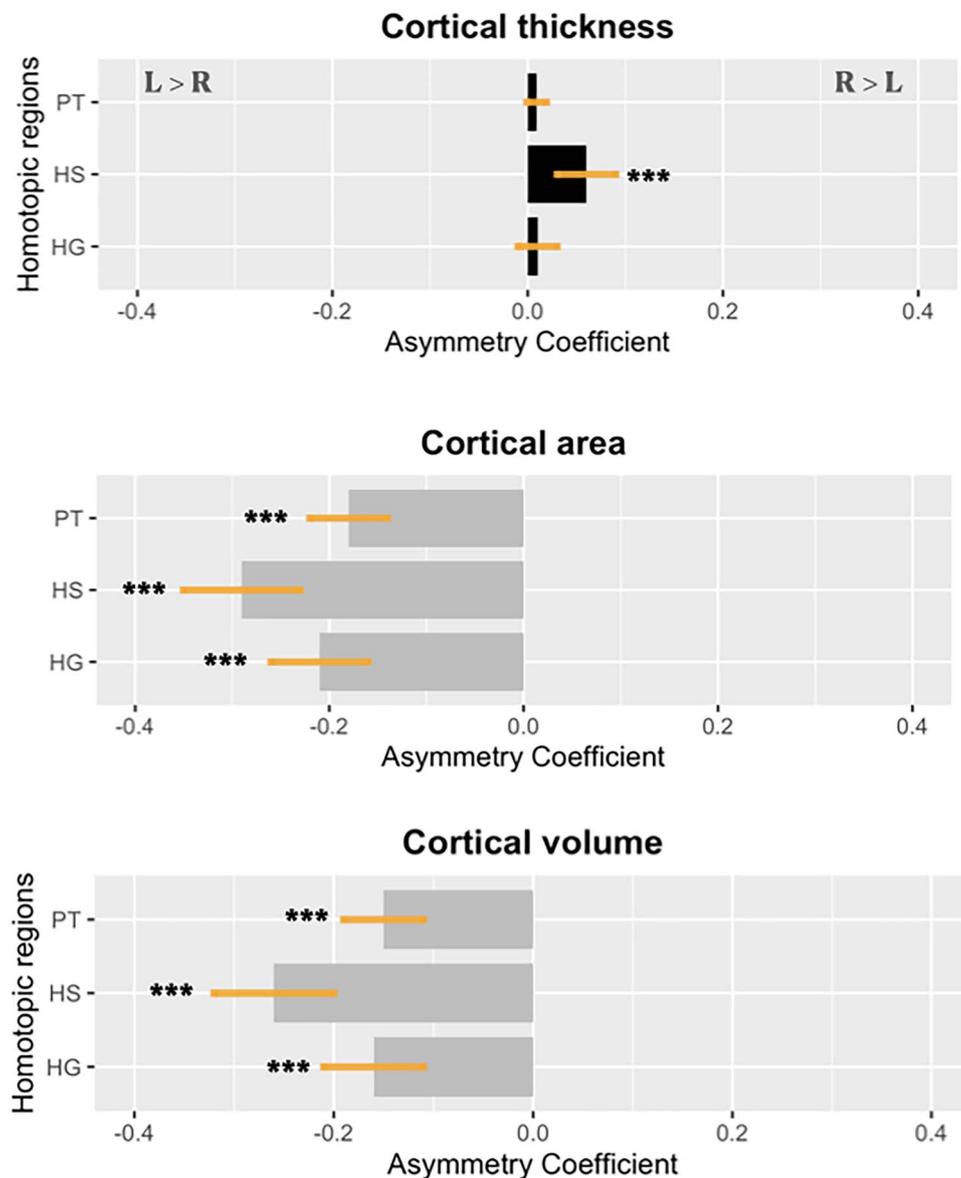
Fig. 4. Average regional asymmetries in CT, surface area, and volume across the 3 auditory-related cortical regions. ACs with positive values indicate rightward asymmetries (right > left; R > L), while coefficients with negative values indicate leftward asymmetries (left > right; L > R). Horizontal lines indicate the 95% confidence interval. Asterisks denote a significant asymmetry at $P < 0.001$ (see Table 2).

employed the same parcellation scheme and examined the anatomical asymmetries for the surface area and thickness at the whole-brain level. For surface area, they reported significant leftward asymmetries in the 3 auditory ROIs. For CT, they observed a rightward pattern of asymmetries, with the largest value in Heschl's sulcus. Similar asymmetry patterns were reported using a different parcellation scheme, the Desikan-Killiany atlas (Desikan et al. 2006). Koelkebeck et al. (2014) collected anatomical data from a large sample of healthy adults ($n = 101$). They showed pronounced asymmetries in a transverse temporal region, which included Heschl's gyrus and the anterior part of Heschl's sulcus. These asymmetries were left-lateralized for CSA and CV and were right-lateralized for CT. In the largest study to date ($n > 17,000$) on anatomical brain asymmetries in healthy adults, Kong et al. (2018) reported rightward asymmetries for CT and leftward asymmetries for CSA in the transverse temporal and the superior temporal parcellations. The consistency of our findings with those of studies using much larger samples, regardless of

the parcellation scheme in use, is indicative of the robustness of the method we employed. Our sample may well be representative of the distribution of auditory asymmetries in the healthy adult population of nonmusical experts. Beyond replicating previous findings, our study provides novel results on the relationship between individual deviations from the modal phenotype of brain asymmetries and auditory processing skills.

Our results suggest that departing from the general pattern of auditory asymmetries may confer an advantage in the neural processing of melodic material. The CT asymmetry in Heschl's sulcus was positively correlated with innovation and negatively correlated with transmission in the signaling games. Individuals whose CT asymmetries in Heschl's sulcus converged toward the general pattern (i.e. rightward) tended to introduce more changes in the artificial signaling system ("innovators"). Conversely, the fewer participants departing from this modal pattern tended to reproduce the original melodic code more accurately ("transmitters"). In a recent study, Liem et al. (2014) reported

Table 2. Mean values for cortical structures in the left and right auditory-related cortical regions. The AC is positive for rightward asymmetries (right > left) and negative for leftward asymmetries (left > right).

	Left hemisphere		Right hemisphere		AC (mean)
	Mean	SD	Mean	SD	
CT (mm)					
Planum temporale	2.55	0.13	2.58	0.16	0.009
Heschl's sulcus	2.42	0.19	2.57	0.23	0.06[a]
Heschl's gyrus	2.62	0.19	2.67	0.18	0.01
CSA (mm^2)					
Planum temporale	754.6	141	617.1	98.3	−0.18[a]
Heschl's sulcus	310.6	66	230.2	51.5	−0.29[a]
Heschl's gyrus	341.43	74.38	274.2	53.5	−0.21[a]
CV (mm^3)					
Planum temporale	2015	394	1784	278.3	−0.15[a]
Heschl's sulcus	636.1	136.9	485.9	112.4	−0.26[a]
Heschl's gyrus	1108	228.8	940	187.9	−0.16[a]

Abbreviation. AC = asymmetry coefficient. [a]Significant 1-sample *t*-tests (*P* < 0.001). Results are corrected for multiple comparisons using Bonferroni's method (*P* = 0.05/3 = 0.01).
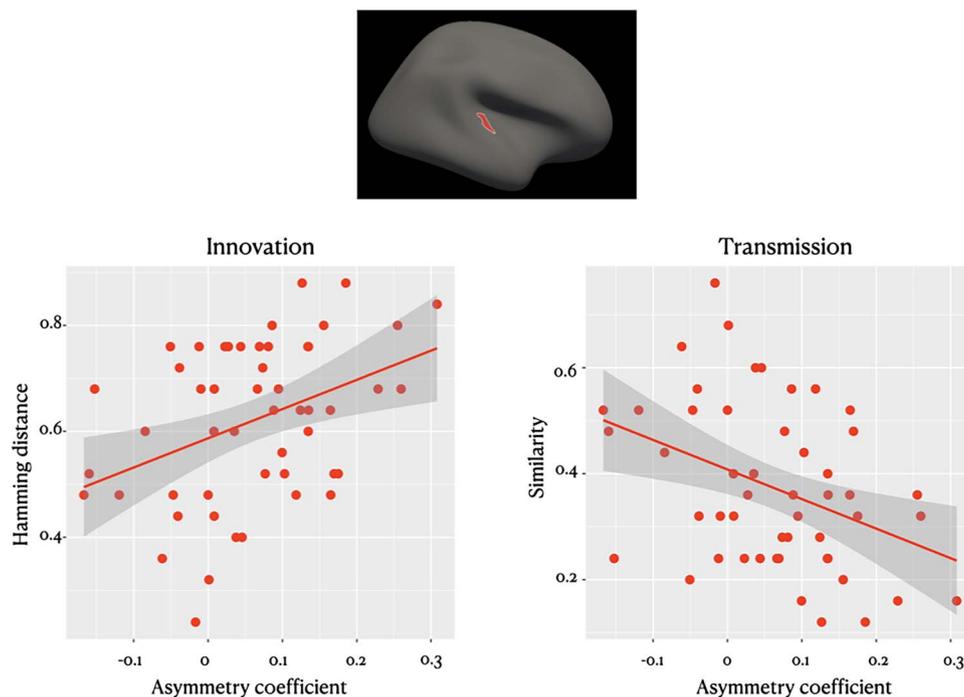

Fig. 5. Asymmetry of CT in Heschl's sulcus predicts intergenerational innovation and transmission. On the top, is Heschl's sulcus projected on the inflated fsaverage surface of the right hemisphere. On the bottom, are 2 scatterplots showing the significant relationship between CT ACs in Heschl's sulcus and measures of intergenerational innovation (*r* = 0.39) and transmission (*r* = −0.38) in signaling games. Each point in the scatterplot is one participant (*n* = 51).

similar results, relating left–right differences in the thickness of the planum temporale with performance in an auditory pattern-matching task (Saberi and Perrott 1999). In this task, a spoken sentence is followed by a probe stimulus with some local manipulations (temporal inversions) of various lengths. The participant was instructed to indicate whether the probe sentence was a sample from the original sentence. The difficulty in this task generally increases by increasing the length of the temporal manipulation. Using Freesurfer's SBM on anatomical images, the authors computed an AC for CT and CSA in 3 superior temporal regions (planum temporale, Heschl's gyrus, and the more posterior part of the superior temporal gyrus). In line with previous studies (Harasty et al. 2003; Koelkebeck et al. 2014; Meyer et al. 2014; Kong et al. 2018), they observed a general pattern of CT

asymmetry in the planum temporale that was right lateralized. Critically, they showed that the fewer participants with an opposite pattern of lateralization in the planum temporale (i.e. left > right) displayed better performance in the auditory task as compared to the larger right > left group. When local manipulations were longer, the left > right group outperformed the right > left group. The same analysis with CSA yielded no significant results. This finding supports the proposal that individual differences in the neuroanatomical asymmetry may be functionally relevant (Chiarello et al. 2016). In auditory-related cortical regions, individual deviations from the modal pattern of CT might confer an auditory processing advantage (see Catani et al. 2007 for a similar proposal with "white-matter" asymmetries in perisylvian regions).

Table 3. Pearson product–moment correlations (*r*) between the ACs of the selected homotopic auditory regions across morphological metrics, and behavioral measures related to social learning (coordination) and intergenerational transmission (transmission and innovation).

	Coordination	Transmission	Innovation
CT			
Heschl's gyrus	−0.17	−0.08	0.13
Planum temporale	−0.12	−0.12	0.26
Heschl's sulcus	−0.23	**−0.38**[a]	**0.39**[a]
CSA			
Heschl's gyrus	−0.05	0.17	−0.21
Planum temporale	0.02	−0.04	0.22
Heschl's sulcus	0.18	0.29	−0.17
CV			
Heschl's gyrus	−0.06	0.15	−0.15
Planum temporale	−0.001	−0.12	0.35
Heschl's sulcus	0.10	0.14	−0.03

Abbreviations. AC = asymmetry coefficient; CT = cortical thickness; CSA = cortical surface area; CV = cortical volume. [a]Correlation coefficients marked in bold and are significant in the multiple regression analysis with FDR correction (pFDR < 0.05). The correction was implemented separately for each morphological metric.

Why were structural-behavioral correlations only significant for CT asymmetries? And why was a decreased CT lateralization in this region associated with better transmission performance? These questions are difficult to address due to scarce research on the topic. Only a few studies have reported a significant association between music skills and measures of cortical structure from single auditory regions (Bermudez et al. 2009; Foster and Zatorre 2010; Worschech et al. 2022) or between auditory performance and anatomical asymmetries (Liem et al. 2014). It is not even clear whether a thinner cortex may confer some advantages in terms of processing speed and computational power as compared to a thicker cortex (Meyer et al. 2014). One hypothesis put forward by Liem et al. (2014) is that a thinner cortex in the right temporal regions, as observed by a decreased rightward lateralization of CT in the left > right group, would indicate the presence of a larger number of myelinated fibers in the same regions (Rakic 1988; Eickhoff et al. 2005). In turn, that would promote a faster analysis of suprasegmental cues, such as the longer segments in their probe stimuli, or pitch intervals and contour in our melodic stimuli (Poeppel 2003). Alternatively, a more equal distribution of neuronal material between bilateral auditory regions would promote an equal share of computational resources (see Chiarello et al. 2016 for a similar hypothesis). A more effective recruitment of bilateral auditory regions would promote the establishment of symmetrical auditory representations during the early stages of acoustic analyses (Hickok and Poeppel 2000; Poeppel 2001, 2003). Both scenarios are compatible with that of a less-asymmetric participant who would store a more accurate representation of the melodic material and transmit it without excessive information loss.

We did not observe any significant structural-behavioral correlation either using CSA or CV. CV is the product of 2 independent factors, CT and CSA (Raznahan et al. 2011). When CT and CSA develop in opposite directions, asymmetry measurements for CV are not easily interpretable (Panizzon et al. 2009; Meyer et al. 2014) and, we argue, could mask associations with auditory behaviors (see Song et al. 2022 for a similar account). A positive association has often been reported between the strength of CSA asymmetry and the degree of left-hemispheric language dominance (Vigneau et al. 2006) in perisylvian language-related regions such as PT (Foundas et al. 1994; Moffat et al. 1998) (but, see Dorsaint-Pierre et al. 2006; Bishop 2013; Greve et al. 2013 for studies where these correlations performed poorly). A larger surface area in the left

PT might be advantageous for the rapid acoustic analyses that take place in language perception: A larger distance between cortical microcolumns, concomitant with an increased amount of white matter volume, would promote a better differentiation and rapid processing of the auditory signal (Harasty et al. 2003; Meyer et al. 2014). Conversely, a thicker and less myelinated cortex would promote coarser-grained analyses in the temporal dimension (Harasty et al. 2003). Asymmetries in CT, rather than CSA, might thus be a better neuroanatomical marker of auditory processing at a suprasegmental level (150–300 ms), as also discussed by Liem et al. (2014). That might explain the significant correlations found in our study only between CT asymmetries and transmission performance.

Why were structural behavioral associations only found in Heschl's sulcus? Heschl's sulcus is a deep groove, in the superior temporal lobe, connecting Heschl's gyrus with the planum temporale. This region is thought to mark the caudal border of the primary auditory cortex (Rademacher et al. 1993) responsible for processing basic auditory information such as pitch, intensity, and location of sounds. The secondary auditory cortex, which is involved in perceiving complex sounds such as speech and music, may extend over Heschl's sulcus and onto Heschl's gyrus in some individuals. This suggests Heschl's sulcus can belong to either the primary or secondary auditory cortex depending on the specific individual and their brain anatomy (Morosan et al. 2001; Rademacher et al. 2001). Due to its position between the lower and higher auditory areas, Heschl's sulcus might play a critical role in the integration and segregation of the auditory input into 2 main auditory streams, the "what" ventro-lateral auditory pathway and the "where" dorso-posterior pathway (Romanski et al. 1999). Within the dorso-posterior pathway, Heschl's sulcus and other posterior regions (temporal and parietal) are involved in high-level abstract operations, including mental transformations of the auditory material (Foster and Zatorre 2010). However, for the current experimental task, this region may have a greater involvement in the functions of the ventro-lateral pathway that allows sound pattern identification, such as temporal integration. Temporal integration refers to the process of combining temporally separated auditory signals (tones) onto cohesive auditory pattern memory traces (Bregman and Ahad 1995). There is evidence supporting the role of Heschl's sulcus in melodic perception and production (Jäncke et al. 2001; Koelsch et al. 2002; Brown et al. 2006; Pando-Naude et al. 2021). One hypothesis is that the extent

of morphological asymmetry in this region may influence the efficiency of the hemispheric division of acoustic labor required to integrate auditory material (Clunies-Ross et al. 2015). In our study, Heschl's sulcus shows the strongest rightward CT asymmetry (see Chiarello et al. 2016 and Meyer et al. 2014 for a similar observation) associated with the largest between-subject variability when considering all 3 anatomical markers. Our positive findings limited to this region could be explained if that variability was systematic and not random. This conjecture is admittedly speculative and needs future experimental investigation. However, we do not claim that the cognitive processes relevant for the transmission task reside in Heschl's sulcus. Neurodevelopmental processes (e.g. pruning) and other factors that produce the large variability observed in this auditory region may also have affected regions outside the superior temporal gyrus. The collective outcome might finally produce the individual differences in learning and transmission behaviors as measured in our task.

One question in cultural evolution research concerns the existence of a causal relationship between the cultural and biological variabilities (Dediu and Ladd 2007; Dediu 2011; Pamjav et al. 2012; Brown et al. 2014), and more specifically, whether neurobiology can constrain culture. This question originates from the theory that symbolic systems, during their transmission, "evolve" by adapting to the (different) brains of their learners and users (Dehaene and Cohen 2007; Christiansen and Chater 2008; Christiansen and Müller 2015). This culture-biology relationship can be investigated with at least 2 complementary approaches. The idea that biological variability can constrain the cultural transmission of music can be tested using the quantitative (game-theoretical) models of population dynamics. Complementarily, we can zoom in into individual brains using tools from cognitive neuroscience (Lumaca et al. 2018). In previous work, we provided a first experimental support that the latter approach is viable using electrophysiology (Lumaca and Baggio 2016; Lumaca, Haumann, et al. 2018). We showed that differences across individuals in the timing of event-related auditory processes are linked to between-subject variability in auditory biases. Participants with faster auditory processes were faithful transmitters, while innovators exhibited slower auditory latencies. The ability to rapidly process auditory material across hierarchical stages of the auditory networks (Christiansen and Chater 2008) may be impaired in individuals with poorer auditory integration capabilities (Bishop 2007; Williamson and Stewart 2010), leading to weaker memory of auditory material during music transmission. Following this work, we used neuroimaging to identify the functional and neuroanatomical characteristics of the temporal auditory networks that may constrain the faithful transmission of music (Lumaca et al. 2019; Lumaca, Baggio, et al. 2021). In Lumaca et al. (2019), we targeted differences across individuals in resting-state auditory connectivity—variations in how strongly bilateral core auditory regions (Lumaca, Dietz, et al. 2021) are connected when measured at rest. We showed that tiny interindividual differences are linked to how participants learn and transmit musical sounds. A stronger connectivity between homotopic auditory areas was associated with a better capacity to retain and transmit melodic sounds. Interhemispheric oscillatory synchronization is thought to be a key mechanism for the temporal integration of acoustic features and serial material in language and music (Preisig and Sjerps 2019; Preisig et al. 2021). Higher synchronization might promote efficient communication between homotopic auditory areas (Varela et al. 2001; Fries 2005); it would induce more accurate formation of melodic representations (Andoh and Zatorre 2011; Elmer et al. 2016, 2017) and ultimately lead to the faithful transmission

of music material. In humans, crosshemispheric communication and integration relies on the structural connections linking the relevant homotopic sensory cortices in both hemispheres (Gazzaniga 2000). This led us to investigate the splenium—the posterior subdivision of the corpus callosum that is crossed by crosshemispheric auditory fibers—as a putative structural basis for auditory integration and communication. In Lumaca et al. (2021), we used diffusion-tensor imaging and showed that faithful transmitters, compared to innovators, displayed a cluster of significantly higher fractional anisotropy (i.e. higher integrity) on the midsagittal area of the splenium. Lower white-matter integrity in this region may constitute a neuroanatomical bottleneck in information transmission, in terms of speed and bandwidth, leading to lower integration (Westerhausen et al. 2006, 2009) and poorer transmission performance. Our proposal is that auditory symbolic systems, when culturally transmitted, might adapt to each individual's brain based on how efficiently and rapidly bilateral auditory networks share information processing labor. A less efficient hemispheric coordination could be a source of variability in the cultural system.

The present study extends this and probes how culture adapts to brain anatomy; it suggests that the differences in the left–right auditory asymmetries may determine the variability in the division of labor between the auditory areas of the 2 hemispheres (Banich 1998). One further hypothesis is that biological constraints in the expression of hemispheric asymmetries may ultimately affect the emergence and the distribution of cultural variants in a population. Chiarello et al. (2016) showed that brain regions with a larger variability across individuals in cortical measures are more likely to be asymmetrical at a population level. Our study supports this finding in our study by showing a significant correlation between the coefficients of variation and (absolute) values of ACs across all 3 measures of cortical structure. Chiarello et al. (2016) argued that variability in asymmetries could be the outcome of more relaxed biological constraints on hemispheric development: Some brain regions would be freer to develop independently from their homotopic areas, due to experiential or environmental factors, thereby increasing asymmetry. The Heschl's sulcus is affected by experiential factors, as shown by a bilateral CT increase after just 6 months of piano learning (Worschech et al. 2022). If regions like Heschl's sulcus are also involved in specific cognitive functions, less strict developmental constraints would ultimately manifest into interindividual differences in the relevant behaviors. We support this proposal. We suggest that more relaxed constraints on the ontogeny of bilateral auditory networks might ultimately express as (interindividual) phenotypic variation in the transmission and innovation of auditory symbolic material.

By definition, cultural evolution relies on transmission acts sampled from a continuum between faithful transmission and innovation according to bio-cognitive biases. Music, we argue, may follow this pattern too. Transmission acts may be heterogeneous at an "intraindividual" level, which in our case, would translate into single individuals alternating between transmitting and innovating (Heyes 2018; Tamariz 2019). Alternatively, heterogeneity may emerge at an "interindividual" level, resulting in a mixed population of transmitters and innovators (Mesoudi 2009; Charbonneau 2015). The latter explanation better fits our previous and present data, and it seems more parsimonious to assume that different brains, which embed largely stable neurocognitive architectures, each produce different phenotypes rather than mixes of phenotypes. From a broader evolutionary perspective, there may be a biological pressure on brain development to

exhibit different degrees of asymmetry so that the resulting group dynamics produce a more stable outcome (Grabisch and Li 2020).

A number of questions arise such as: Which genes control the developmental path of bilateral auditory networks? Which regulatory gene factors induce more relaxed constraints on brain asymmetries? How does that bridge to the evolution of large-scale cultural phenomena such as stability and diversification? We hope these questions will be tackled in future research on the biological roots of culture and music, in particular.

Limitations

We acknowledge 3 major limitations in the current study. The first relates to the correlational nature of our data analyses. In this study, we use the term "prediction" to indicate that a brain measure collected in a sample at an initial point in time correlates with a behavioral measure collected in that sample at some later point in time (in-sample correlation) (Gabrieli et al. 2015). Our findings cannot be generalized to out-of-sample individuals (true prediction). Crossvalidation techniques will be useful in the future to address this issue (Dubois and Adolphs 2016). Second, we are aware of the risks in interpreting correlational data. From our results, we cannot infer that interindividual variability in auditory asymmetries produces variation in transmission fidelity (though, that is 1 possibility). In this work, we make no claims about causality. We only demonstrate that a reliable neuroanatomical-behavioral association exists and that it partly supports our previous findings. In doing so, we provide further material for theory testing (Kosslyn et al. 2002).

A second limitation of this experiment is its ecological validity. First, we used an artificial tone system with acoustic properties that differ significantly from real musical systems (however, see Loui et al. 2009 for studies using the same artificial musical scale to study auditory pattern perception). Second, 1-generation transmission experiments allow drawing limited conclusions and are far from the timescale of cultural transmission and evolution. However, we argue, this reduced external validity is compensated by an increased internal validity, allowing for precise manipulation and control. In our study, the BP scale enabled us to control for music schemas that participants might use to compose stimuli. A 1-generation transmission experiment allowed us to isolate the individual learning biases and relate them to the individual's brain characteristics. Note that these experiments are not meant to replicate the historical evolution of musical systems but rather to isolate microevolutionary mechanisms in small-scale, short-term contexts and to generate data that align with actual historical patterns. Previous work, using the same material and paradigm, demonstrated that transmitted artificial systems ultimately contain the same core properties, such as proximity, continuity, and symmetry, of the actual cultural systems being modeled (Lumaca and Baggio 2017). These properties reflect the cumulative sum of small innovations similar to those observed in our experiment (Supplementary Fig. S6). These kinds of experiments have limited value in isolation, but they can be grounded in real-life cultural phenomena when informed by historical patterns, theoretical work, and empirical data (Scott-Phillips and Kirby 2010).

The third limitation is that we only present findings for asymmetries in the gray matter. Future work should investigate asymmetries of white-matter fiber tracts (Catani et al. 2010) in an attempt to obtain a more complete picture of how the bilateral organization of brain networks affects cultural behaviors. In a previous study, Catani et al. (2007) showed a strong left-lateralization of language pathways for the majority of participants (62%). However, they reported that the fewer individuals with more symmetrical pathways (17%) were better at remembering verbal material. Future experiments should test whether the individual divergence from the modal pattern of white-matter asymmetries in a population, in addition to gray-matter asymmetries, may enhance the learning and transmission of tonal material.

Conclusion

Our results show a relationship between the left–right asymmetry in the thickness of a core auditory region, Heschl's sulcus, and 2 core cultural transmission behaviors: transmission and innovation. Faithful transmitters could be distinguished from innovators by the extent to which their asymmetry patterns departed or converged, respectively, from the modal pattern that is observed at the population level. A less right-lateralized distribution of gray matter in Heschl's sulcus was associated with better transmission performance and lower innovation. Our data support previous findings from our lab, suggesting that biases in music learning and transmission might be partly rooted in the small individual differences in the organization of bilateral auditory networks and their efficiency to share information processing labor.

CRediT authors statement

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Supplementary material

Supplementary material is available at *Cerebral Cortex Journal* online.

Data availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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