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Auditory cortex anatomy reflects multilingual phonological experience

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This report details **convincing** evidence that experience with multilingualism in general, and with larger phonological inventories specifically, is related to differences in the structure of the transverse temporal gyri. The project is notable for using a relatively large sample, and confirming the primary finding in a second sample. The **important** findings strongly point to experience-dependent plasticity related to language experience as a driver of neuroanatomy of the auditory cortex.

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Abstract

This study explores the relationship between the anatomy of the auditory cortex and multilingual experience, shedding light on the complex mechanisms of auditory processing in humans. Integrating previous research on auditory information processing and the impact of bi- and multilingualism on brain structure, we investigate how the morphology of auditory brain regions reflects individuals' language experience and, more specifically, their phonological repertoire. Leveraging two distinct samples comprising over 200 participants, each exposed to between 1 and 7 languages encompassing 36 different languages, we explore whether the morphological variability of auditory brain regions reflects individual language experience, specifically focusing on the phonological repertoire. Additionally, we examine the potential influence of typological distances between languages spoken by multilingual individuals on the neural signatures of multilingualism within the auditory cortex. Our findings revealed a relationship between the average thickness of the left and right second transverse temporal gyrus (TTG) and participants' language experience. Model comparisons demonstrated that the inclusion of phoneme-level information in the language experience index accounted for the greatest variance in average TTG thickness (bilaterally). The direction of this effect was negative, indicating that a more extensive and more phonologically diverse language experience was associated with thinner cortices in the

second TTG. Across two independent datasets, we provide robust evidence linking the degree of language experience and typological distance between languages to cortical thickness in early auditory brain regions. We propose that this phenomenon may reflect experience-driven pruning and neural efficiency, warranting further investigation through longitudinal studies of language acquisition. Moreover, our findings support the notion that experiences with typologically similar languages differ from those with typologically distant languages, offering valuable insights into the intricate relationship between language diversity and brain structure. Our findings also indicate that early auditory regions seem to represent phoneme-level cross-linguistic information, contrary to the most established models of language processing in the brain, which suggest that phonological processing happens in more lateral posterior STG and STS.

1 Introduction

Processing of complex auditory stimuli is fundamental to vocal communication. In humans with typical development, auditory processing has been shown to depend on multiple regions within the temporal cortex spreading across the superior and lateral aspects of the superior temporal gyrus (STG). The superior aspect of the STG hosts tonotopically organized primary auditory regions, which have been shown to be located in regions including the first transverse temporal gyrus (TTG), i.e., Heschl's gyrus (HG) (Dick et al., 2012; Moerel et al., 2014). The planum polare (PP) is immediately anterior to HG, while the planum temporale (PT) borders it posteriorly. Of note, TTG shows high variability in shape and size, some individuals having one single gyrus, others presenting duplications (with a common stem or fully separated) or multiplication of TTG (Geschwind and Levitsky, 1968; Marie et al., 2015). The superior temporal sulcus (STS) lies directly below the STG and separates it from the middle temporal gyrus. Understanding functional contributions of these different brain areas to processing of sound and vocal stimuli has been advanced by lesion studies (Hillis et al., 2017), ablation, and resection case studies (Hamilton et al., 2021; Hullett et al., 2022), functional magnetic resonance imaging (Booth et al., 2002; da Costa et al., 2011; Humphries et al., 2014), and intracranial recordings (Hamilton et al., 2021; Mesgarani et al., 2014). To date, however, no single functional parcellation of the human auditory cortical areas is generally agreed upon (Hamilton et al., 2021; Moerel et al., 2014). For example, in contrast to hierarchical models of auditory processing (e.g., Binder et al., 2000; Humphries et al., 2014; Scott and Johnsrude, 2003; Wessinger et al., 2000), recent proposals of sound processing postulate that processing of speech is distributed, and happens in parallel in different regions of the auditory cortex (Hamilton et al., 2021). According to parallel processing models, the posterior STG has been shown to be a crucial and essential locus for language and phonological processing (Bhaya-Grossman and Chang, 2022; Hillis et al., 2017), and to encode acoustic-articulatory features of speech sounds (Lakertz et al., 2021; Mesgarani et al., 2014). The primary auditory regions, including Heschl's gyrus, have been argued not to be necessary for speech perception (Hamilton et al., 2021; Hullett et al., 2022).

Structural brain imaging provides another route for gaining insight into the functional roles of cortical subregions, albeit at a different timescale. Quantifying individual differences in behavioral skill and/or language experience and relating them to cortical morphology can inform us about the relative influences of experience-dependent plasticity and of potential predisposition, in different domains. Of note, distinct influences (environmental *versus* genetic) tend to be reflected by different underlying anatomical characteristics of the brain. Indeed, a recent large-scale genome-wide association meta-analysis suggests that cortical surface area is relatively more influenced by genetics and that cortical thickness tends to reflect environmentally-driven neuroplasticity (Grasby et al., 2020). Such environmental effect on cortical thickness might in turn be tied to microstructural changes to the underlying brain tissue, such as modifications in dendritic length and branching, synaptogenesis or synaptic pruning, growth of capillaries and glia, all previously tied to some kind of environmental enrichment and/or skill learning (see Lövdén et al., 2013; Zatorre et al., 2012 for overviews). Increased cortical thickness may reflect synaptogenesis and dendritic growth, while cortical thinning observed with MRI may be a result of increased myelination (Natu et al., 2019) or synaptic pruning.

In the context of multilingualism, structural brain imaging can offer insights into whether and how the brain accommodates experience with different languages, and into what type of linguistic information is encoded, stored, and processed by particular brain structures. Previous findings point to an influence of experience-dependent plasticity on thickness of regions associated with speech processing, including the left posterior STG and left PT (Hervais-Adelman et al., 2017), as well as the STG (Mårtensson et al., 2012). Moreover, Ressel and colleagues (2012) associated lifelong bilingualism with increased volume of the Heschl's gyrus, a finding interpreted as reflecting experiencerelated plasticity related to the acquisition of novel phonology.

Languages differ from each other in many ways and to different degrees: language similarities vary per linguistic domain, with distinct typological distances that can be computed between the languages' phonological, lexical, and syntactic systems. The present study investigates whether there are brain structural signatures of multilingualism in the auditory cortex, and whether typological distances between spoken languages further modulate those signatures. Given our focus on auditory brain regions, we quantified how the languages spoken by the participants differed from each other in terms of their phonological systems. Specifically, we investigated whether the neuroanatomical indices describing the auditory cortex regions were related to cross-linguistic phonological information at different levels: acoustic and articulatory feature-level, phoneme-level, or (more abstract) counts of phonological classes.

To investigate the relationship between the individual variability in the morphology of the auditory cortex and variability in language experience, we analyzed the anatomical brain scans of 204 healthy, right-handed participants from the PLORAS database (Seghier et al., 2016). The sample was split into two groups according to the date of data acquisition. The main sample included 136 participants speaking between 1 to 7 languages (2.65 languages on average), and representing a relatively wide range of linguistic diversity (34 different languages in total), see **Figure 1** for a visual representation of the sample's language experience. The replication sample included 68 participants speaking to up to 5 languages, 2.44 languages on average. All MRI anatomical images were processed with FreeSurfer's brain structural pipeline (Fischl et al., 2004). Multilingualism was operationalized in a continuous way, without artificially dichotomizing the sample into multi-, bi-, and monolinguals (cf. DeLuca et al., 2019; Luk and Bialystok, 2013). Given the focus on auditory brain regions and on potential associations with language distance at the phonological level, and the fact that phonological perceptual space is known to be shaped relatively early in life (e.g., Werker and Hensch, 2015), we used information regarding the age of onset(s) of acquisition (AoA) of the different languages spoken by participants, and weighed each language by its AoA. For this, we operationalized the language experience in a continuous and quantitative measure for each participant, using Shannon's (1948) entropy equation (see Materials and Methods, Section 2.2), with high entropy values indicating more diverse language experience. In addition to the language experience index not accounting for typological features ('Language experience - no typology'), three measures combining language experience with typological distances at different levels were constructed: (1) 'Language experience – features', (2) 'Language experience – phonemes', and (3) 'Language experience – phonological classes'.

Our analyses aimed at a fine localization of the structural effects of multilingualism. We predicted (see Bhaya-Grossman and Chang, 2022; Hamilton et al., 2021; Lakertz et al., 2021; Mesgarani et al., 2014) that the cortical thickness of posterior STG would be related to the composite measures of language experience in our multilingual participants, and to the differences between their languages at the acoustic and articulatory feature level. In terms of the predicted direction of these effects, according to most current views, multilingualism is hypothesized to be a dynamic

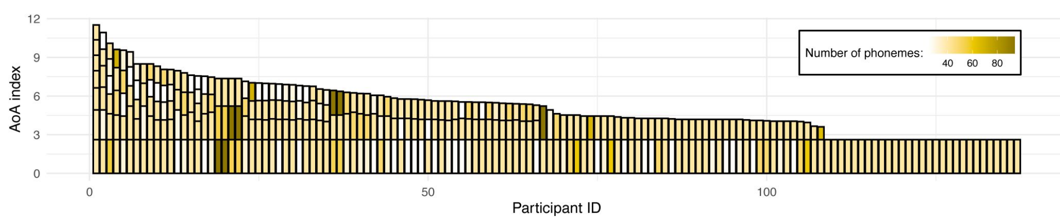


Figure 1.

Illustration of the sample's language experience.

Each bar represents a single participant's overall language experience; the height of the stacked bars within each bar represents the AoA index for individual languages (the taller the bar, the earlier in life a given language was acquired). The color of each stacked bar refers to the number of phonemes in each language's phonological inventory. For reference, English phonological inventory has 40 phonemes (Stanford Phonology Archive, 2019a). Prior to plotting, data was sorted by the overall language experience based on a sum of AoA index for participants' individual languages; consequently, data of participants with most diverse language experience can be found on the left-hand side of the figure, and the right-hand side includes data from monolinguals (i.e., exposed only to one language).

process reshaping brain structure and inducing both increases (in initial stages) and decreases (in peak efficiency) in brain morphological indices as a function of quantity of the multilingual experience (Pliatsikas, 2020). Furthermore, acquisition of multiple languages is thought to have additive effects on brain structure, and to induce cortical and subcortical adaptations in order to accommodate the additional languages (see e.g., Hervais-Adelman et al., 2018). The exact nature of such adaptations for multiple languages of phonologically diverse repertories on auditory brain regions is to date unknown. A positive relationship between the thickness of auditory regions and the degree of multilingualism (weighted by greater phonological distance) would indicate that the auditory regions need to expand in order to accommodate the variability of phonological input in the environment; a negative one would suggest a specialization of the auditory system in relation to such variability (Pliatsikas, 2020).

2 Materials and Methods

2.1 Participants

Main sample. The full sample consisted of N = 146 participants (M_{age} = 35.79, SD = 15.77; 85 females; 31 monolinguals) exposed to up to 7 languages (2.65 languages on average), with n = 136 complete cases. **Replication sample.** The replication sample consisted of N = 69 participants (M_{age} = 32.04, SD = 11.68; 38 females; 29 monolinguals) exposed to up to 5 languages (2.44 languages on average), with n = 68 complete cases. **Table 1** breaks down the samples according to how many languages were spoken by which number of participants; further information on participants' language background (languages spoken by each participant) is included in **Table S1**.

main sample							
number of languages	1	2	3	4	5	6	7
number of participants	29	40	36	18	10	2	1
replication sample							
number of languages	1	2	3	4	5	6	7
number of participants	30	4	16	14	5	0	0

Table 1.

Breakdown of participants by number of languages they spoke.

2.2 Language experience

To describe the diverse language background of our participants, we expressed age of onset(s) of acquisition (AoA) of different languages in a continuous quantitative measure. First, AoA of individual languages was log-transformed to minimize differences between values for languages learned later in life, and the values were inverted to express early AoAs as the highest values; a constant value of 1 was added to the index before log-transformation and after inverting the values, each time to avoid values equal to zero. Next, the AoAs of participants' different languages were combined into one "language experience" index per participant. It was computed using Shannon's entropy equation (Shannon, 1948):

$$H = -\sum_{i=0}^{n} p_i \, log_2 \, p_i$$

where, n stands for the total number of languages a participant has been exposed to and p_i is the AoA index calculated as above. High entropy values indicated more diverse language experience.

2.3 Typological distance measures

Across the two samples, the participants spoke a total of N = 36 different languages (n = 34 in the main sample, and n = 20 in the replication sample): Arabic, Bengali, Cantonese, Creole (Antiguan), Czech, Danish, Dutch, English, Farsi, Finnish, French, German, Greek, Gujarati, Hakka, Hebrew, Hindi, Hokkien, Hungarian, Irish, Italian, Japanese, Korean, Luxembourgish, Malay, Mandarin, Portuguese, Punjabi, Russian, Sindhi, Spanish, Swahili, Swedish, Swiss German, Urdu and Vietnamese. The PHOIBLE database (Moran et al., 2019) and open-source software (Dediu and Moisik, 2016) were used to construct three measures of typological distance between the languages: distances between the distinctive phonological features describing the phonemes of each phonological inventory, distances between the sets of phonemes of the phonological inventories, and similarity in counts of phonological classes that share certain features, as detailed below. **Figure S 2** provides a visual representation of the three distance matrices between all the languages. The three distance measures were all related to each other, as evidenced by low to moderate positive correlations between them, see **Table 2**. **Figure S3** shows the distribution of values for each of the distance measures.

	Features distances	Phoneme distances	Phonological classes distances
Features distances	1		
Phoneme distances	.42	1	
Phonological classes distances	.24	.51	1

Table 2.

Pearson correlations between the three phonological distance measures.

2.3.1 Acoustic and articulatory features

For each documented phonological inventory, PHOIBLE includes their phonemes (see **Section 2.3.2** below) and the lower-level distinctive acoustic and articulatory features describing the phonemes. These features offer a qualitative description of differences between discrete sound categories, and are based on articulatory phonology (Hayes, 2011). Every phoneme in every language is described by the following 37 binary features: tone, stress, syllabic, short, long, consonantal, sonorant, continuant, delayed release, approximant, tap, trill, nasal, lateral, labial, round, labiodental, coronal, anterior, distributed, strident, dorsal, high, low, front, back, tense, retracted tongue root, advanced tongue root, periodic glottal source, epilaryngeal source, spread glottis, constricted glottis, fortis, raised larynx ejective, lowered larynx implosive, click. Individual languages were described in terms of presence or absence of these features across all phonemes belonging to the given phonological inventory, and represented as vectors. For a given pair of language feature vectors, a pairwise distance was computed as cosine distance using the scipy.spatial.distance function in Python.

2.3.2 Phonemes

Phonemes are individual speech sounds such as vowels and consonants, representing the smallest units of sound that can change the meaning of a word when substituted. Lists of phonemes belonging to each of the languages represented in the data-base were exported from PHOIBLE

(Moran et al., 2019) and represented as strings. For a given pair of languages A and B, a pairwise string distance between phonemes of both languages was computed with the Jaccard distance method:

$$1 - J(A, B) = \frac{|A \cap B|}{|A \cup B|}$$

representing the inverse of the ratio between the size of the intersection and the size of the union of the two sets of phonemes, and varying between 0 (both languages having exactly the same phonemes) and 1 (no phonemes in common).

In addition, using the language-specific phoneme-level information, we constructed a cross-linguistic description of individual languages and used it to compute a measure of cumulative phoneme inventory for each participant. We counted how many unique phonemes each participant was exposed to across all their languages (i.e., phonemes that overlapped between languages were counted only once). For example, the cumulative phoneme inventory of a participant who was exposed only to English was equal to 40, while an English-French bilingual's cumulative phoneme inventory would be equal to 64 (both English and French have 40 unique phonemes (Stanford Phonology Archive, 2019b, 2019a), with 16 phonemes overlapping across the two inventories).

2.3.3 Counts of phonological classes

Both the lists of phonemes and phonological features describing them can be used to derive a more abstract, higher-level description of individual languages in terms of which and how many *phonological classes* their phonological inventories contain. Using the PHOIBLE inventories and feature system, Dediu and Moisik (2016) proposed a comprehensive list of 167 phonological classes, along with a method for selecting a language's phonemes belonging to given classes and computing their counts. The system describes how many "segments", "consonants", "vowels", "diphthongs" etc. a given language has, and counts segments belonging to classes that share certain features (e.g., "bilabial consonants", "front vowels", "clicks", see Supplementary Information, Section 7.8 for the full list). Per language, we created a vector representing the counts of all 167 phonological classes, and computed pairwise distances between the languages spoken by the participants in our database with cosine distance (as above).

2.4 Combining typology and language experience (indexed by AoA)

Quantifying diverse language experience with Shannon's entropy equation does not account for similarities and differences between the languages. Therefore, using Rao's quadratic entropy equation (*QE*) (De Bello et al., 2007; Pavoine and Bonsall, 2011; Rao, 1982), the language experience index was combined with each of the above typological distance measures, separately, to generate weighted measures accounting for the three different types of cross-linguistic phonological distances. The summed phonological distances (feature-level, phoneme-level or based on counts of phonological classes) between all language pairs were weighted by the log-transformed and inverted AoA index for each language, as follows:

If the AoA index for *i*-th language in a participant's repertoire of a total of S languages is p_i and the dissimilarity between language i and j is d_{ij}, then language experience index accounting for typological information has the form:

$$QE = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} \, p_i \, p_j$$

where d_{ij} varies from 0 (i.e., where the two languages have exactly the same phonological systems) to 1 (i.e., the two languages have completely different phonological systems). The SYNCSA R package (Debastiani and Pillar, 2012) (*https://rdrr.io/cran/SYNCSA/*) was used to perform calculations.

For a similar methodology, but applied to lexical distance measures, see Kepinska et al. (2023). In sum, apart from the language experience index not accounting for typological features ('Language experience - no typology'), three measures combining typology and language experience were constructed: (1) 'Language experience – features', (2) 'Language experience – phonemes', and (3) 'Language experience – phonological classes'

2.5 Neuroimaging data acquisition and processing

For all participants, structural MRIs with 176 sagittal slices were acquired using a T1-weighted three-dimensional (3D) Modified Driven Equilibrium Fourier Transform (MDEFT) sequence. The resulting images had a matrix size of 256 × 224, yielding a final resolution (voxel size) of 1 × 1 × 1 mm. Repetition time (TR)/echo time (TE)/inversion time (TI) was: [12.24/3.56/530 ms] for the main sample (from a 1.5T Siemens Sonata scanner), and 7.92/ 2.48/910 ms for the replication sample (from a 3T Siemens Trio scanner). The T1 images were denoised using the spatially adaptive non-local means filter (SANLM; Manjón et al., 2010) in MATLAB within the CAT12 toolbox. The images were then processed with FreeSurfer's (version 7.2) brain structural pipeline (Fischl et al., 2004), which consists of motion correction, intensity normalization, skull stripping, and reconstruction of the volume's voxels into white and pial surfaces.

2.6 Parcellation of the auditory regions

The reconstructed surfaces were parcellated into regions using an atlas-based procedure (Destrieux et al., 2010). The auditory regions were delineated using the following labels from the Destrieux atlas: planum polare of the superior temporal gyrus (G_temp_sup-Plan_polar; PP), anterior transverse temporal gyrus (of Heschl) (G_temp_sup-G_T_transv; referring to HG, or to the anterior-most TTG), transverse temporal sulcus (S_temporal_transverse; HS), planum temporale, or temporal plane of the superior temporal gyrus (G_temp_sup-Plan_tempo; PT), superior temporal sulcus (parallel sulcus) (S_temporal_sup; STS), and lateral aspect of the superior temporal gyrus (G_temp_sup-Lateral; STG). The STG and the STS labels were further divided into smaller regions using Free-Surfer's freeview software and FreeSurfer command line tools. For this, on the inflated surface of the fsaverage template, we first drew additional ROIs, dividing the STG into anterior and posterior parts, with the transverse temporal sulcus as the dividing landmark (Hamilton et al., 2021). We further divided the STS into anterior, middle and posterior parts. The anterior versus mid-STS were divided by again aligning the boundary with the posterior border of the anterior TTG, and the midversus posterior STS were divided by aligning the boundary with the posterior border of STG. **Figure S 4** shows an example of the parcellation in the native space of one of the participants. Next, we transformed the new ROIs into the participants native space (using mri_surf2surf), and intersected them with individual subjects' unaltered STG and STS labels. Cortical volume, surface area and average thickness were computed and extracted from the final labels (with mris_anatomical_stats), and were used in the linear mixed models reported in **Section 3.1**.

For analysis on the TTG along the superior temporal plane (i.e., on the superior aspect of the STG) (see Results, **Section 3.2**), we used an automated toolbox (TASH; Dalboni da Rocha et al., 2020). TASH runs on the output of the FreeSurfer Destrieux atlas structural segmentation, and provides a finer segmentation not only of HG – whether a single gyrus or a common stem duplication (default version of TASH) – but also of additional TTGs when present (extended version of TASH, called 'TASH_complete'; (Dalboni da Rocha et al., 2023). Volume, surface area and average thickness of the resulting labels were extracted. To explore the significant interaction between average thickness of PT and language experience in the exploratory analysis on all auditory regions (Section 3.1), we used 'TASH_complete'; this allowed us to explore possible relationships with additional TTGs, when present. We performed a visual selection of the gyri segmented by TASH_complete, excluding from the analysis gyri that lay along the portion of the superior temporal plane that curved vertically (i.e., within the parietal extension, Honeycutt et al., 2000), when present. The volume, surface area and average thickness of the resulting labels were extracted, and used as dependent variables in the statistical analysis (see Results, see Section 3.2).

3 Results

Table 3 provides an overview of the performed analyses and of results.

3.1 Auditory cortex and language experience

In a first, exploratory analysis, we investigated relationships between the composite language experience measure ('Language experience - no typology') and the volume, surface area, and average thickness of the following auditory subregions: STG, STS, HG, HS, PT and PP, as parcellated by FreeSurfer (Destrieux et al., 2010). Given the large size of STG and STS, we refined their segmentations by dividing the STG into anterior and posterior part, and the STS into anterior, middle, and posterior parts (see Materials and Methods, Section 2.6 for details). Using the lme4 R package (Bates et al., 2015), we fit three linear mixed models to the extracted anatomical measures (volume, surface area, average thickness), with participants modeled as random effects, language experience, region of interest (ROI), and hemisphere as fixed effects, controlling for the covariates of age, sex and whole-brain volume, area, or mean thickness. Interaction terms for language experience, ROI, and hemisphere were included in the models to determine whether language experience would differentially affect any of the segmented regions. Significance was calculated using the lmerTest package (Kuznetsova et al., 2017), which applies Satterthwaite's method to estimate degrees of freedom and generate p-values for mixed models. Out of all investigated cortical measures, only average thickness of the PT, bilaterally, was related to participants' language experience at $p = .01$, see **Table S 2**. Specifically, participants with more extensive and diverse language experience had a significantly thinner PT.

3.2 Superior temporal plane and language experience

Given that full TTG duplications, triplications etc. by definition belong to the PT, and that previous work has shown relationships between TTG duplications patterns and language aptitude (Turker et al., 2017), we wanted to better pinpoint the location of the above effects within PT subregions. To this end, and to gain more detailed insight into the localization of the relationship between the thickness of the PT and participants' language experience, we ran three follow-up analyses, an ROI-based one, a vertex-wise based one, as well as an analysis investigating the effect of language proficiency.

First, we used an automatic toolbox (TASH; Dalboni da Rocha et al., 2020) to segment gyri along the superior temporal plane (HG, or 1st TTG, and additional TTG(s), when present), and to extract their cortical thickness, surface area and volume. Note that FreeSurfer does not segment additional TTGs specifically, but provides measures for the PT as a whole. We included HG in these follow-up analyses (i.e., even though we had included the Freesurfer HG ROI in the above, broader analyses), given that the default FreeSurfer pipeline is not fine-tuned for the segmentation of this small and variable region, and is thus error-prone for this ROI (Dalboni da Rocha et al., 2020). As expected from previous work, the TTG showed large individual variability in overall duplication patterns in the sample. Segmentations revealed different numbers of gyri across hemispheres and participants, ranging from a single gyrus to four identified TTGs, see **Table 4**. On average, participants had 2.375 gyri in the left hemisphere (SD = 0.63), and 1.84 in the right (SD = 0.64). The

	ANALYSIS	REGION(S)	MEASURE(S)	MOTIVATION	RESULTS
1.	Language experience and auditory regions (Section 3.1)	Auditory regions segmented by FreeSurfer (anterior STG, posterior STG, anterior STS, posterior STS, HG, HS, PT and PP)	cortical volume, surface area and thickness	Exploratory first step	Relationship between the average thickness of the PT (bilaterally) and language experience (p = .01)
2.	Language experience and TTG (Section 3.2)	Transverse temporal gyri segmented by TASH	cortical volume, surface area and thickness and number of gyri	To elucidate above exploratory results	Relationship between the average thickness of the 2^{nd} TTG (bilaterally) and language experience (p = .01)
3.	Vertex-wise analysis (Section 3.2)	Whole-brain	cortical thickness	To confirm above exploratory results	Cluster of vertices negatively related to participants' language experience at $p < .0001$ (uncorrected), located in the superior aspect of the left STG, corresponding to the location of the second TTG
4.	Effects of language proficiency (Section 3.2)	2^{nd} TTG	cortical thickness	To confirm the results obtained from AoA-based language experience index	Relationship between the average thickness of the 2^{nd} TTG (bilaterally) is confirmed using a different metric to calculate language experience (p = .018 for left, and p = .065 for right hemisphere)
5.	Language typology and 2^{nd} TTG (Section 3.3)	2^{nd} TTG	cortical thickness	To assess the effect of language typology within the identified region	Quantifying the distance between languages based on phoneme-level information explains the most variance in the average thickness of the bilateral second TTG
6.	Language experience expressed as 'cumulative phoneme inventory' (Section 3.3)	2^{nd} TTG	cortical thickness	To account for language experience in participants with different L1s	Relationship between the thickness of the left 2^{nd} TTG and the specific characteristics of languages at the phoneme-level of their phonological inventories (p = .004)
7.	Language experience in participants with a single TTG (Section 3.4)	Right HG (1^{st} TTG) and right PT	cortical thickness	To assess the effect of language experience in participants without multiple TTGs	Positive relationship between the thickness of right HG and language experience (p = .007); no relationship between the thickness of right PT and language experience (p = .81)
8.	Replication analysis (Section 3.5)	2^{nd} TTG	cortical thickness	To replicate the main result (analysis #2 and #5) in an independent sample	Relationship between the average thickness of the 2^{nd} TTG and language experience partially replicated (for left hemisphere, p = .047)

Table 3.

Overview of the performed analyses.

number of gyri was not related to participants' language experience, either in the left (β = 0.10, t = 0.97, p = .335), or in the right hemisphere (β = −0.01, t = −0.13, p = .90), according to a linear model with number of gyri as dependent and language experience as independent variables (controlling for participants' age and sex).

To localize the effect of language experience on the cortical thickness of the segmented gyri, we fit another linear mixed model with participants modeled as random effects, language experience ('Language experience - no typology'), gyrus (first, second, third), and hemisphere as fixed effects, controlling for the covariates of age, sex, and mean thickness (including interaction terms for language experience, gyrus, and hemisphere). We also ran two additional models on the volume and surface area values of the segmented regions, to confirm that the results were specific to the average thickness values, as in the model above (including all auditory regions, see **Section 3.1**). Out of all investigated cortical measures, only average thickness of the second TTG (bilaterally) was related to participants' language experience at p < .01, see **Table S 3**.

Second, to confirm the above result, we also ran a whole-brain vertex-wise analysis in FreeSurfer. We fit a general linear model to the cortical thickness surface maps of all subjects (smoothed with a 5-mm kernel), testing for a significant effect of the language experience index ('Language experience - no typology') across the whole brain. We found one cluster of vertices negatively related to participants' language experience at p < .0001 (uncorrected), located in the superior aspect of the left STG, corresponding to the location of the second TTG, see **Figure S 5**. At the same threshold, no vertices were found in the right hemisphere, possibly due to greater, known anatomical variability in right compared to left auditory regions (cf. Dalboni da Rocha et al., 2020).

We also explored whether the proficiency attained in the spoken languages was related to the thickness of the 2^{nd} TTG. Analyses calculating cumulative language experience based on the participants' proficiency instead of AoA yielded similar results as above, with a significant negative relationship between the proficiency-based cumulative language experience index and the thickness of the left 2^{nd} TTG, and a trend towards significance for the right 2^{nd} TTG (see Section 7.6 for details).

3.3 Second transverse temporal gyrus and effects of language typology

Building on the above result, we investigated whether the thickness of participants' 2^{nd} TTG was related to cross-linguistic phonological information describing the languages they spoke, *above and beyond* being related to mere experience of speaking several languages. The analysis below was therefore performed on a sub-sample of participants who had multiple TTGs (n = 130 in the left and n = 96 in the right hemisphere). We constructed Click or tap here to enter text.three indices of language experience accounting for different typological relations between languages (see Kepinska et al., 2023 for a similar approach applied to lexical distances): (1) 'Language experience – features', (2) 'Language experience – phonemes', and (3) 'Language experience – phonological classes'. We used these indices as dependent variables in a set of multiple regression analyses fit to the average thickness values of the left and right second TTG, and performed a model comparison procedure to gauge which of the typological measure was most related to the thickness of the second TTG. Model comparison was performed by computing differences in explained variance (*ΔR^2 Adjusted*) compared to the baseline model (i.e., with language experience without typological information), and using the Bayesian information criterion (BIC) (Schwarz, 1978), where the difference between two BICs was converted into a Bayes factor using the below equation, following Wagenmakers (2007):

$$BF_{10} = \exp \frac{\Delta BIC_{01}}{2}$$

	left				right				whole sample:
total number of gyri:	1	2	3	4	1	2	3	4	
N	6	78	47	5	40	78	18	0	**136**
Male/Female	0/6	28/50	23/24	3/2	10/30	33/45	11/7	-	**54/82**
proportion Male/proportion Female	0/0.07	0.61/0.51	0.29/0.42	0.05/0.02	0.18/0.37	0.61/0.55	0.20/0.09	-	
Age (mean)	42.95	35.95	36.29	28.48	35.12	36.49	36.63	-	**36.11**
Language experience - no typology (mean)	0.69	0.79	0.83	0.93	0.85	0.80	0.76	-	**0.807**
Language experience - no typology (min)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	**0.000**
Language experience - no typology (max)	1.09	1.89	1.76	1.56	1.76	1.89	1.34	-	**1.893**

Table 4.

Number of participants, their demographic and language experience characteristics displaying different overall shapes of the TTG (i.e., total number of identified gyri in the left and right hemisphere).

Last column lists whole sample's descriptive statistics.

The model without typological information ('Language experience - no typology') served as baseline for the comparisons. The analyses showed that out of the three language experience indices - (1) 'Language experience – features', (2) 'Language experience – phonemes', and (3) 'Language experience – phonological classes' - the model containing **phoneme** level information explained the most variance in the average thickness of the bilateral second TTG. It also outperformed the model containing the language experience index not accounting for any typological information ('Language experience - no typology'), see **Table 5**. None of the other phonological distance measures combined with language experience performed better than language experience alone. The direction of the relationship between language experience weighted by typological distance was negative, and had a small effect size ($\beta = -0.35$, $t = -2.96$, $p = .004$, $f^2 = 0.07$ and $\beta = -0.26$, $t = -1.98$, $p = .05$, $f^2 = 0.04$ for left and right hemisphere, respectively), showing that the more extensive one's language experience, and the more varied at the phoneme level one's languages are, the thinner the second TTG cortex (see **Figure 2**). The statistics for the overall regression models are presented in the Supplementary Materials, **Section 7.4**.

To further establish that our results reflected the relationship between TTG structure and **phonological** diversity specifically (as opposed to language diversity in a more general sense), we derived an additional measure of language experience, where the AoA index of different languages was weighted by lexical distances between the languages. Here, we followed the methodology described in Kepinska, Caballero, et al. (2023): We used Levenshtein Distance Normalized Divided (LDND) (Wichmann et al., 2010) which was computed using the ASJP.R program by Wichmann (*https://github.com/Sokiwi/InteractiveASJP01*). Information on lexical distances was combined with language experience information per participant using Rao's quadratic entropy equation in the same way as for the phonological measures. We then entered this language experience measure accounting for lexical distances between the languages into linear models predicting the thickness of the second left and right TTG (controlling for participants' age, sex and mean hemispheric thickness) and observed that the index of multilingual language experience accounting for lexical distances between languages explained less variance than the index incorporating phoneme-level distances between languages, both in the left and the right hemisphere ($R^2 = 0.164$ and $R^2 = 0.116$ for left and right respectively). This further strengthens our conclusion that our results reflected the relationship between TTG structure and **phonological** diversity specifically, as opposed to language diversity in a more general sense.

To further probe how cross-linguistic sound inventories may modulate the effect of language experience on the brain, and to account for language experience in participants with different mother tongues (L1s), we constructed a crosslinguistic description of individual languages (see Methods, *Section 2.3.2*) and used it to calculate a measure of cumulative phoneme inventory for each participant. Here, we counted how many unique phonemes each participant was exposed to across all their languages (i.e., phonemes that overlapped between languages were counted only once), irrespective of when these languages were acquired. We used this measure as an independent variable in another linear model fit to the average thickness values of the second TTG (controlling for age, sex, hemispheric thickness, and accounting for language experience irrespective of language typology) (see *Section 2.3.2*, Supplementary Materials, *Section 7.4.1* and **Table S 4**). In the left hemisphere, this measure explained variance in the thickness of the second TTG *above and beyond* language experience ($\beta = -0.004$, $t = -2.910$, $p = .004$), with a small effect size ($f^2 = 0.06$). In the right hemisphere, the thickness of the second TTG was not significantly related to the 'cumulative phoneme inventory' measure ($p = .76$), when also accounting for overall language experience irrespective of typology. This result shows that the thickness of the left second TTG in these participants was related to the specific characteristics of languages at the phoneme-level of their phonological inventories, irrespective of when these languages were acquired, while the thickness of the right second TTG was relatively more related to when and

Figure 2.

Multilingual language experience and thickness of the second TTG.

Average thickness of the second TTG in the left and right hemisphere were negatively related to the multilingual language experience index weighted by their phoneme-level phonological distances. Plots show residuals, controlling for age, sex and mean hemispheric thickness.

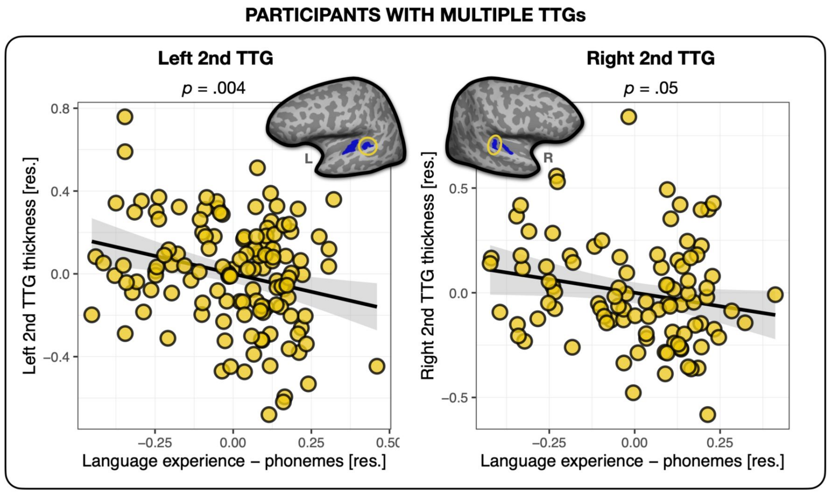


Table 5.

Left and right second transverse temporal gyri and language experience.

Multiple regression model parameters (parameter estimates and standard errors, in brackets; *p*-values are listed according to the coding presented underneath the table) for the average cortical thickness values of the second TTG, as predicted by the four language experience indices: (1) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (2) acoustic/articulatory features, (3) phonemes, and (4) counts of phonological classes. Last two rows present model comparison results (additional variance explained and BF_{10} values). *NB*. all models including typological information were compared against the 'No typology' model.

		left				*right*			
Language experience models:		No typology	Features	Phonemes	Phonological classes	No typology	Features	Phonemes	Phonological classes
(Intercept)	β	0.00	-0.01	0.00	-0.01	0.01	0.01	0.01	0.01
	SE	(0.03)	(0.03)	(0.03)	(0.03)	(0.03)	(0.04)	(0.03)	(0.03)
Language Experience	β	-0.12**	-0.33	-0.35**	-0.60*	-0.10+	-0.25	-0.26+	-0.44
	SE	(0.05)	(0.23)	(0.12)	(0.29)	(0.05)	(0.27)	(0.13)	(0.33)
Age	β	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SE	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Mean thickness (left/right)	β	1.40***	1.41***	1.37***	1.41***	0.94*	0.99*	0.92*	0.99**
	SE	(0.30)	(0.31)	(0.30)	(0.30)	(0.37)	(0.38)	(0.37)	(0.37)
Sex	β	0.00	0.01	0.00	0.01	-0.01	-0.01	-0.01	0.00
	SE	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)
Num.Obs.		*130*	*130*	*130*	*130*	*96*	*96*	*96*	*96*
R^2		*0.20*	*0.17*	*0.21*	*0.18*	*0.16*	*0.13*	*0.16*	*0.14*
R^2 *Adj.*		*0.17*	*0.14*	*0.18*	*0.16*	*0.12*	*0.09*	*0.12*	*0.10*
AIC		*18.5*	*23.5*	*16.9*	*21.2*	*11.9*	*14.9*	*11.8*	*14.0*
BIC		*35.7*	*40.7*	*34.1*	*38.4*	*27.3*	*30.3*	*27.2*	*29.4*
Log.Lik.		*-3.23*	*-5.75*	*-2.43*	*-4.62*	*0.04*	*-1.47*	*0.10*	*-0.99*
F		*7.80*	*6.32*	*8.29*	*6.98*	*4.30*	*3.46*	*4.33*	*3.72*
RMSE		*0.25*	*0.25*	*0.25*	*0.25*	*0.24*	*0.25*	*0.24*	*0.24*
ΔR^2 *Adjusted*		-	*-0.03*	*0.01*	*-0.02*	-	*-0.03*	*0.00*	*-0.02*
BF_{10}		-	*0.08*	*2.23*	*0.25*	-	*0.22*	*1.08*	*0.36*

. $p < 0.1$, + $p = 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

how many languages were learned (even though the typological distance information did improve the model fit, see **Table 5**), see **Figure S 6** and **Table S 4**, and Supplementary Materials, **Section 7.4**.

3.4 Language experience in participants with a single TTG

So far, we revealed associations between phonological language experience and the cortical thickness of the 2nd TTG bilaterally in multilinguals. Yet, 40 participants out of 136 (29.4%) had a single TTG (Heschl's gyrus) in the right hemisphere (*versus* only 6 participants, i.e., 4.4% in the left; see **Table 4**). We therefore repeated the above analysis in the 40 participants with a single TTG in the right hemisphere in order to investigate the relationship between TTG anatomy and language experience in this sample. The analysis revealed that in participants without posterior TTGs in the right hemisphere, the thickness of the first TTG was indeed related to their language experience. The nature of this relation proved however to be different than that for multilingual participants with multiple TTGs. First, the language experience index accounting for most variance in the thickness of the first TTG was the index not accounting for typological relations between multilinguals' languages ('Language experience - no typology'), see **Table S 5**. Second, the direction of this effect was inverse to that found for participants with multiple TTGs: the more extensive one's language experience, the thicker the HG (β = 0.15, t = 2.89, p = .007; medium effect size: f^2 = 0.237), see **Figure 3**. Of note, we did not find any significant relationship between the thickness of the PT and language experience in this sub-group of participants (β = 0.02, t = 2.43, p = .81). In addition, for PT thickness, compared to a model including only covariates of no-interest, the model including the language experience index offered moderate evidence against it (BF_{10} = 0.16), suggesting that the observed effects between cortical thickness and language experience in the superior temporal plane are specific to gyri only, see **Table S 5**, and Supplementary Materials, **Section 7.5**.

3.5 Replication analysis

In an effort to strengthen the inferences that can be made from the above results, we tested whether the relationship between multilingual language experience and thickness of the second TTG could be replicated in an independent sample of 68 participants. Note that too few participants presented single gyri in the left (n = 7) and the right hemisphere (n = 14), therefore the replication analysis focused on the second TTG results only. Using linear regression, we fit models to the average thickness values of participants' left and right second TTG. As in the analyses on the original sample, we first fit a model using the language experience index irrespective of typology ('Language experience - no typology'), and then we fit models that additionally accounted for the three types of typological relations between languages (features, phonemes, and counts of phonological classes), controlling for covariates of age, sex, scanner model, and mean hemispheric thickness. We again observed that language experience ('Language experience - no typology') did significantly predict the average thickness of the second TTG, but only in the right hemisphere (β = −0.13, t = −2.05, p = .046; small effect size: f^2 = 0.087), see **Table 6**. Furthermore, similarly to the analysis on the main sample (see **Section 3.3**), the language experience index weighted by phonological information at the phoneme level ('Language experience – phonemes'), showed a better fit than the model without typological information, explaining 3% of additional variance in the average thickness of the right second TTG. In contrast to the results of the main sample, however, this time the model including phonological feature-level information ('Language experience – features') had a better fit to the thickness data and explained an additional 14% of the variance (11% more variance than the model with language experience weighted by phoneme-level distances), see **Table 6** and **Figure 4C**. No language experience indices were significantly related to the average thickness values of second TTG in the left hemisphere (β = −0.03, t = −0.53, p = .60, and β = −0.09, t = −0.58, p = .57, for language experience index without and with typological phoneme-level information, respectively), see **Figure 4** and **Table 6**.

Figure 3.

Thickness of the right first TTG and PT in participants with a single TTG in the right hemisphere.

Average thickness of HG in the right hemisphere was positively related to the amount of multilingual experience, irrespective of typological relations between languages (left panel). The average thickness of the right PT was not related to language experience (right panel). Plots show residuals, controlling for age, sex, and mean hemispheric thickness.

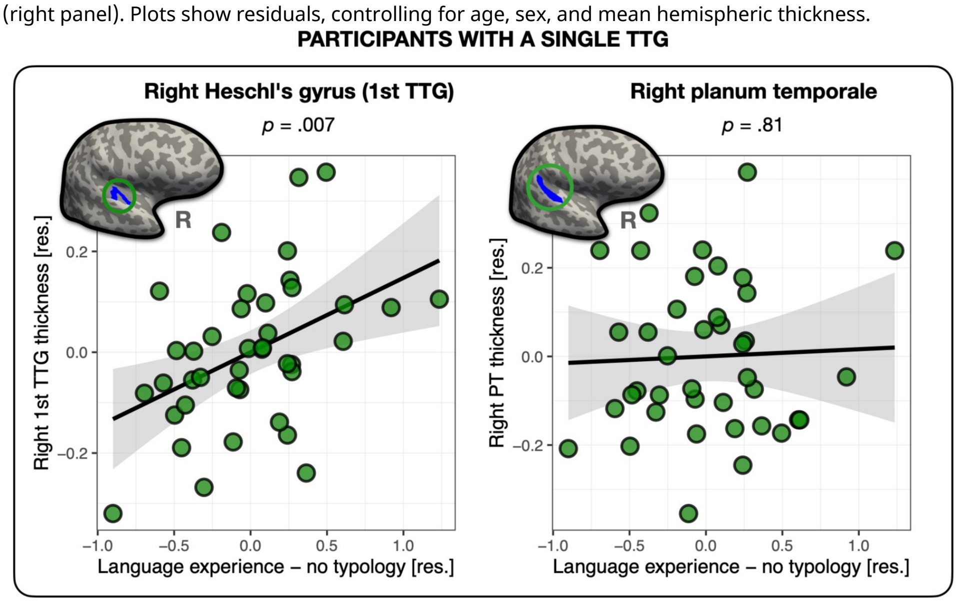
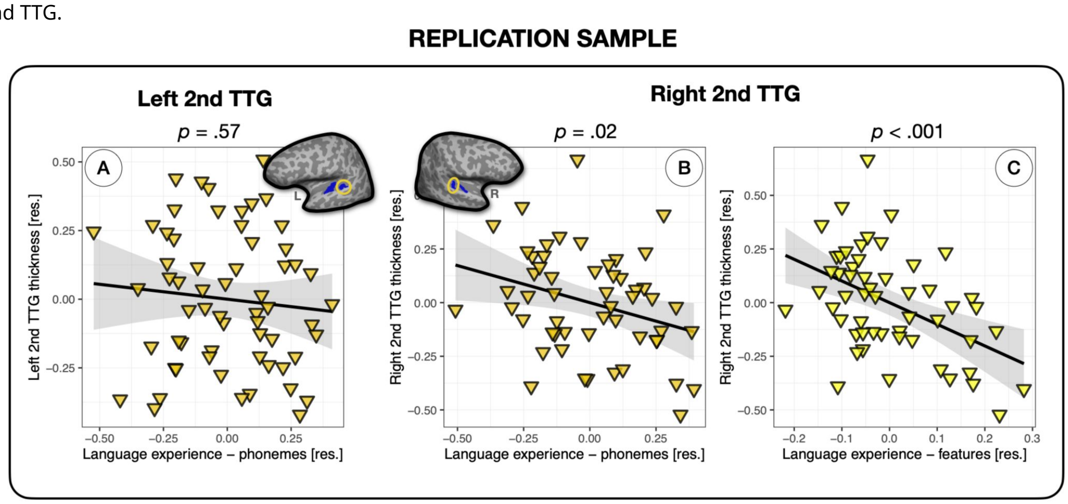


Figure 4.

Multilingual language experience and thickness of the second TTG in an independent sample of participants.

(A) Average thickness of the left second TTG was not significantly related to the language experience index; average thickness of the right second TTG was significantly related to the language experience indices accounting for phoneme-level phonological overlaps between multilinguals' languages (B) and feature level information (C). The model including phonological feature level information presented in panel (C) had the best fit to the average thickness data of the right second TTG.



		left				*right*			
Language experience models:		No typology	Features	Phonemes	Phonological classes	No typology	Features	Phonemes	Phonological classes
(Intercept)	β	1.00	1.12	0.99	1.24	-1.85	-2.20.	-2.09	-1.21
	SE	(1.14)	(1.10)	(1.13)	(1.09)	(1.34)	(1.21)	(1.33)	(1.30)
Language Experience	β	-0.03	-0.09	-0.09	0.32	-0.13*	-1.02***	-0.38*	-0.75
	SE	(0.06)	(0.28)	(0.15)	(0.49)	(0.06)	(0.27)	(0.15)	(0.49)
Scanner	β	-0.08	-0.09	-0.08	-0.09	0.10	0.09	0.11	0.09
	SE	(0.07)	(0.07)	(0.07)	(0.07)	(0.08)	(0.07)	(0.08)	(0.08)
Age	β	0.00	0.01	0.00	0.01	0.01*	0.01**	0.01*	0.01*
	SE	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Sex	β	0.09	0.09	0.09	0.07	0.00	0.03	0.01	-0.02
	SE	(0.07)	(0.07)	(0.07)	(0.07)	(0.07)	(0.06)	(0.07)	(0.07)
Mean thickness (left/right)	β	0.57	0.52	0.58	0.42	1.72**	1.86***	1.81***	1.52**
	SE	(0.44)	(0.42)	(0.44)	(0.42)	(0.52)	(0.46)	(0.51)	(0.50)
Num.Obs.		*61*	*61*	*61*	*61*	*54*	*54*	*54*	*54*
R2		*0.092*	*0.089*	*0.092*	*0.094*	*0.225*	*0.350*	*0.253*	*0.196*
R2 Adj.		*0.009*	*0.006*	*0.010*	*0.012*	*0.144*	*0.282*	*0.175*	*0.112*
AIC		*13.9*	*14.1*	*13.8*	*13.7*	*7.6*	*-1.9*	*5.6*	*9.5*
BIC		*28.7*	*28.9*	*28.6*	*28.5*	*21.5*	*12.0*	*19.5*	*23.5*
Log.Lik.		*0.047*	*-0.046*	*0.077*	*0.130*	*3.205*	*7.947*	*4.196*	*2.229*
F		*1.109*	*1.072*	*1.120*	*1.142*	*2.781*	*5.158*	*3.244*	*2.342*
RMSE		*0.24*	*0.24*	*0.24*	*0.24*	*0.23*	*0.21*	*0.22*	*0.23*
ΔR^2 Adjusted		-	*> -0.01*	*< 0.01*	*< 0.01*	-	*0.14*	*0.03*	*-0.03*
BF_{10}		-	*0.91*	*1.03*	*1.09*	-	*114.68*	*2.70*	*0.38*

. $p < 0.1$, + $p = 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 6.

Thickness of left and right second TTGs and language experience in an independent sample of participants.

Multiple regression model parameters (parameter estimates and standard errors, in brackets; *p*-values are listed according to the coding presented underneath the table) for the average cortical thickness of the second TTG, as predicted by the four language experience indices: (1) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (2) features, (3) phonemes, and (4) counts of phonological classes. The last two rows present model comparison results (additional variance explained and BF_{10} values). NB. all models including typological information were compared against the ‘No typology’ model.

4 Discussion

Multilingual language experience, quantified in a continuous manner, is related to the structure of the auditory cortex. Using two independent samples of participants, we find replicable effects showing that multilingual language experience, weighed by the age of acquisition of the respective languages, is specifically related to the thickness of gyri (TTGs) of the superior temporal plane. Moreover, we show that the typological distances between multilinguals' languages, in particular typological distance measures based on phonemes of the different languages (and to some degree on their acoustic and articulatory features), explains variation in TTG thickness *above and beyond* the effect of AoA alone.

The effects we find are specific to the second transverse temporal gyrus in people having at least one full posterior duplication, and to the first TTG in people having only one gyrus. The anterior-most TTG, i.e. HG, is the first cortical relay station for auditory input. HG and the TTG as a whole exhibit large individual variation in shape and size: some individuals have a single TTG, but duplications (complete or partial) and multiplications of the gyrus are also common, and have been observed both *ex-vivo* (Geschwind and Levitsky, 1968) and *in-vivo* (Marie et al., 2015). The TTG are known to be formed before birth, *in utero* (Chi et al., 1977). Further, genes known to be involved in speech processing, in the development of the nervous system, and in X-linked deafness, have been related to the surface area and thickness of the left and right HG (Cai et al., 2014). A body of work has shown relationships between both HG volume and TTG shape (i.e., duplication patterns) and auditory and language abilities that are thought to be relatively stable and thus possibly arising from predisposition, such as speech sound processing and learning abilities (Golestani et al., 2011, 2007), linguistic tone learning (Wong et al., 2008), and general language aptitude (Turker et al., 2017). Studies have also shown larger HG and more TTG duplications in professional musicians (Schneider et al., 2005), and longitudinal work in children undergoing musical training shows that the grey matter volume of this region is relatively stable over the course of a year (Seither-Preisler et al., 2014). To date, however, little evidence has been shown supporting experience-dependent plasticity of TTG. Ressel et al. (2012) showed that lifelong, non-elective bilingual language experience with Spanish and Catalan was associated with a larger bilateral HG volume in comparison to monolingual experience. Importantly, the bilinguals in their study were not self-selected, so unlikely to have learned a second language because of a special talent for languages. The findings of the Ressel et al. study thus suggested that the HG volume differences arose from experience with a different phonological system, since Spanish and Catalan are quite similar at the lexical level but have different phonologies. This finding was partially replicated in our study, in a sub-sample of participants with a single gyrus in the right hemisphere. More generally, our results show that experience with multiple languages is associated with differences in the thickness of the TTG, and that increasing degrees of multilingualism are linearly related to the structure of the transverse temporal gyrus. Establishing that non-pathological environmental experiences are related to the morphology of TTG offers important insights into the adaptability of this early sensory region, and has important implications for our understanding of the neural underpinnings of auditory processing in general, which we outline below.

We find an effect of multilingualism on the cortical thickness of the second TTG in individuals with a second such gyrus, but on the thickness of the first gyrus in individuals without a full TTG duplication. The result aligns with recent findings of cortical surface area being relatively more associated with genetic factors and of cortical thickness being relatively more associated with environmental factors (e.g., Eyler et al., 2012; Grasby et al., 2020). Individual differences in the shape (i.e., duplication patterns) of the TTG seem to, however, be related to *how* multilingualism will be accommodated by the thickness of the auditory brain regions: increasing thickness of the first gyrus when no duplications are present, and decreasing thickness of the second gyrus for participants with more than one TTG.

The fact that the most multilingual participants in the current sample had thinner cortex in their second TTG might not automatically point to the conclusion that multilingual language *experience* is associated with this specific neural marker. In fact, polyglotism and multilingualism could partly result from innate predispositions (i.e., language aptitude), which in turn have been associated with brain structural markers within the TTG (Turker et al., 2021, 2017). However, we observed that accounting for typology (i.e., including information regarding how languages spoken by the participants differed from each other in terms of their phonological systems) explained more variance in the cortical thickness data of the 2nd TTG than an index of language experience accounting for the age of exposure to different languages alone. The contribution of typological distance to our results is important, since it strengthens our interpretation that the observed results are more likely to be due to experience-induced plasticity and not to predispositions: it is far less likely that specific brain anatomical features would induce individuals to learn specific language combinations. It also has to be noted, however, that research has established relationships between population-level genetic factors (distribution of DCDC2 READ1 regulatory element) and characteristics of phoneme inventory of language(s) predominant in that population (DeMille et al., 2018; Tang et al., 2020), and that genetic influences on auditory cortex anatomy have previously been observed (Cai et al., 2014; Guadalupe et al., 2014), making it possible that our results may in some part also be related to genetic rather than purely environmental factors.

Our data show that, within the auditory cortex, language experience is particularly related to gyri in the superior temporal plane, and not to the rest of the planum temporale (as shown in the analysis investigating the sub-sample of participants with a single gyrus in the right hemisphere), nor to other auditory regions such as posterior STG, as shown in the first, exploratory analysis across broader auditory cortex sub-regions. The posterior STG, has been previously shown to be an essential site for language and phonological processing (Bhaya-Grossman and Chang, 2022; Hamilton et al., 2021; Hillis et al., 2017), and for representing acoustic-phonetic features of speech sounds (Lakertz et al., 2021; Mesgarani et al., 2014). We had predicted that we would find effects of differences between our multilingual participants' languages at the acoustic and articulatory feature level within posterior STG, however indices related to the degree of multilingualism in our sample were not related to its structure. Tuning to the different acoustic-phonetic features might be an experience-independent feature of the posterior STG (i.e., it might be sensitive to features both present and absent from the languages a person knows), and therefore multilingualism might not induce any neuroplastic changes to this region. Alternatively, our findings may suggest that current language models might underestimate the role of early auditory regions (i.e., of HG and 2nd TTG, when present) in phonological processing, and support their role beyond an initial spectro-temporal analysis of speech sounds. Future research, using both structural and functional mapping, is needed to clarify the respective roles of TTG(s) and STG in phonological processing.

With regards to the specific typological features that did best explain our results, we found that accounting for overlaps between languages in terms of their phoneme-level sound structure (i.e., discrete sound categories present in the individual languages' phonological inventories) was the best predictor of the thickness of the second TTG, and that a measure of how many unique phonemes each participant was exposed to across all their languages explained variance in the thickness of the left second TTG *above and beyond* language experience (in the larger main sample). Functional neuroimaging work by Fisher and colleagues (2018) has shown that speech sounds, and specifically vowel formants, are encoded in tonotopic auditory regions including HG and the STG, suggesting that even early auditory regions such as HG and second TTG (when present) are involved in speech sound processing. Similarly, Bonte et al. (2017) found that vowels can be decoded from fMRI signal of (among others) the temporal plane, Heschl's gyrus and sulcus (see also Jäncke et al., 2002; Obleser and Eisner, 2009; van Atteveldt et al., 2004) for findings of processing of isolated phonemes in the HG and PT regions), and Rutten et al. (2019) showed that attending to speech sounds (stop consonants) in pseudowords results in an increase in the neural processing of higher temporal modulations in regions as early as HG and also in the PT. It is therefore plausible that our finding of an association between greater multilingual language experience and decreased thickness of the second TTG arises from increased processing demands (and associated cortical pruning, see below) inherent to the acquisition and mastery of many non-overlapping phonological inventories. Moreover, to the best of our knowledge, previous studies did not account for fine variation in the exact individual anatomy of the TTG (i.e., single *versus* multiplicated gyri). Our results may thus call for a re-evaluation of the specific anatomical site within the superior temporal plane in which phonemes are preferentially processed: based on our results, the second TTG (when present) could be a possible candidate.

Apart from the phoneme-based typological distance measure explaining more variance in cortical thickness of the 2nd TTG in the main sample, the data from the replication sample showed that phonological feature-level language distance measure explained additional variance (to the composite language experience measure) in the thickness values. We believe that this inconsistency across samples might be related to the smaller sample size in the replication analysis (and therefore lower power to detect the effect) and the particular phonological characteristics of participants' languages. Specifically, the replication sample included 31 individuals (i.e., 46% of participants) who spoke German and English, a language combination that has a phonological feature distance of zero. In contrast, the main sample included a more heterogenous mix of 34 different languages. Notably, however, in the replication sample, the phonemes-based typological distance measure numerically explained more variance in the thickness of the 2nd TTG than a composite language experience measure based on AoA of different languages, as observed in the main sample.

The decreased thickness of the second TTG in relation to greater multilingualism may arise from different, non-exclusive microstructural and physiological mechanisms, including functional remapping, experience-driven pruning and neural efficiency, or learning-related increased myelination. Primary auditory cortex is known to lie within the anterior-medial part of HG (i.e., the first TTG; Rademacher et al., 1993), although there is no exact correspondence between cytoarchitectural and macrostructural boundaries (Rademacher et al., 2001). *In-vivo* markers for human primary auditory cortex have been identified, including tonotopy, increased myelination (Dick et al., 2017), and decreased cortical thickness (Zoellner et al., 2019). Also, there is evidence that in professional musicians, functional activation extends to posterior TTGs during listening to musical sounds, while activation is confined to HG in non-musicians (Schneider et al., unpublished findings). Our findings of thinning in relation to extensive multilingual language experience with a wider diversity of speech sounds could be speculatively interpreted as arising from spatial expansion of primary-like functionality to the second TTG, when present. This spreading of primary-like processing may subsequently induce specialization and pruning of the more posterior gyrus. Alternatively, it could be that the secondary auditory regions beyond HG may be specialised for the processing of (cross-linguistic) phonological information, and this might result in experience-driven pruning. Experience-induced pruning is essential for maintaining an efficient and adaptive neural network. It reinforces relevant neural circuits for faster more efficient information processing, while diminishing those that are less active, or less beneficial. The cortical specialization may need to arise because phonologically more diverse language experience requires that the mapping of acoustic signal to sound categories is denser, more detailed and more intricate. As a result, the brain may need to engage in more intensive processing to discriminate between and accurately perceive the sound categories of each language. This increased cognitive demand may, in turn, require the auditory and language processing regions of the brain to adapt and become more efficient. Over time, this heightened effort for successful speech perception and sound discrimination may lead to neural plasticity, resulting in cortical specialization. This means that cortical areas become more finely tuned and specialized for processing the unique phonological features of language(s) spoken by individuals. Why this occurs in the second TTG and not in non-gyral portions of the superior temporal plane (i.e., in the PT more generally) remains to be explored in future work, but one possibility is that gyri are more likely to host such a specialised function due to their greater neuronal density or to specific micro-anatomical features and connectivity properties (i.e., greater proximity and thus more direct, local functional and structural connectivity of neurons within the gyrus, as opposed to with neurons within the sulcal parts). Either way, the neural efficiency account would be in line with the Dynamic Restructuring Model of bilingualism (Pliatsikas, 2020), according to which the "peak efficiency" stage of multilingual functioning comes hand in hand with reductions in local volume. Of note, our supplementary analysis (see Section 7.6) investigating second TTG thickness in relation to proficient *versus* non-proficient languages points to the tentative conclusion that the observed reduced thickness results might be driven by experience with proficiently spoken languages (more so than with non-proficiently spoken ones), aligning with the predictions of the Dynamic Restructuring Model. Another potential microstructural mechanism underlying the thinner cortex result could be increased myelination of 2^{nd} TTG; this would again be in line with the idea that multilingual language experience leads to modifications such that the of 2^{nd} TTG becomes more 'primary-like', since HG is characterized by higher myelination. It has been suggested that the apparent thinning of the ventral temporal cortex during childhood (as argued by e.g., Sowell et al., 2004) is actually driven by increased myelination, since increased myelination in deep cortical layers can shift the apparent gray–white boundary in MR images (Natu et al., 2019); see also Mediavilla et al. (2022) for evidence on learning-related contraction of gray matter being associated with adaptive myelination in rodents. Given the cross-sectional design of the current study, the above explanations remain hypotheses to be tested in further longitudinal studies of language acquisition, preferably ones using myelin mapping (Lutti et al., 2014; Marques et al., 2010) to explore the underlying physiological mechanisms in more details.

Future research should also further increase the degree of detail in describing the multilingual language experience, as both AoA and proficiency (used here) are not sensitive to other aspects of multilingualism, such as intensity of the exposure to the different languages, or quantity and quality of language input. Since these aspects have been convincingly shown to be associated with neural changes (e.g., Romeo, 2019), incorporating further, more detailed measures describing individuals' language experience could further enhance our understanding of cortical plasticity in general, and how the brain accommodates variable language experience in particular.

Interestingly, in individuals who have only one TTG (i.e., no duplications), we find that multilingualism is related to thickness but in the opposite direction (note that we did not perform a replication analysis of the positive correlation between HG (1^{st} TTG) thickness and language experience in the replication sample due to the limited number of individuals presenting with only one gyrus.) We speculate that there might be different mechanisms underlying plasticity in regions more likely to contain primary *versus* secondary auditory cortex. In other words, it may be more likely that experience-induced pruning occurs in secondary compared to primary regions, and that in primary regions, greater efficiency comes at the cost of a neuronal 'bulking'. Alternately but non-exclusively, it could be that in people who do not have a second TTG, HG needs to accommodate both lower-level auditory processing and also the processing of more complex speech sounds. Further research, especially with larger samples of participants with a single TTG, is needed to elucidate the opposite direction of the relationship between multilingualism and cortical thickness in HG *versus* the second TTG in our results.

Different methodological tools are available for capturing the variability of TTG. Most previous studies used either manual labelling, whole-brain approaches involving normalizing structural images to a common template space in order to assess regional variation in grey or white matter probability, or automated pipelines serving to segment and label different regions of interest (e.g.

VBM or FreeSurfer). Both approaches have important advantages, the former allowing for high precision in capturing details of individual variation, the latter two being far less time-consuming and labor-intensive, and therefore more applicable to large datasets. In the current study, we capitalized on recent developments in cortical segmentation efforts and used an automatic toolbox (TASH; Dalboni da Rocha et al., 2020) specifically designed for fine delineation of auditory cortex gyri, and extraction of measures describing their anatomy. Coupled with visual inspection of the data, TASH provides a “best-of-both-worlds” approach, by being anatomically precise while involving little manual involvement with the data (which also tends to be error-prone). The measures we obtained align with the high degree of variability reported in previous literature, but they also seem to be more sensitive, since we identify more multiplications of the TTG than previously reported. For example, in Marie et al. (2015), out of 232 subjects, 204 (88%) had one gyrus (including partially duplicated) in the left hemisphere, 28 (12%) had a complete posterior duplication; the prevalence of further multiplications was not assessed in that study. In our data, a minority of participants (4%) presented only one gyrus in the left hemisphere, and most of them had either two (57%) or three (35%) separate gyri. TASH identifies gyri based on anatomical landmarks and curvature values, and unlike previous descriptive work is surface-based rather than volume-based. It therefore might be more sensitive to shallow cortical folds that might otherwise not be discernable in volume-based manual labelling. The precise functional relevance of these multiplications remains to be uncovered in future research, and more work is needed to further ascertain anatomical accuracy of the segmentation of posterior gyri in the superior temporal plane.

Notably, such variability in shape of the auditory regions is absent from other, evolutionarily older, species: macaques’ auditory cortex is flat, and some chimpanzees have only a single gyrus (Hackett et al., 2001). By showing that a human-specific experience, i.e., speaking multiple languages, is reflected in the anatomy of cortical regions that seem to be evolutionarily particular to humans, we contribute to informing both models of neuroplasticity and of language evolution.

A large body of work has provided insights into both how the brain processes auditory information and speech signals (see Bhaya-Grossman and Chang, 2022; Moerel et al., 2014 for overviews), and into how bi- and multilingualism are related to the structure of the brain (see García-Pentón et al., 2016; Li et al., 2014; Pliatsikas, 2020 for overviews). In the current study, we brought together both strands of research in an effort to investigate how the auditory cortex accommodates multilingual experience, thereby providing insights into the intricate functioning of auditory processing in humans. Apart from showing that individual anatomy appears to constrain the architecture of phonological representations, our findings also support the idea that experience with typologically similar languages might be different from experience with typologically distant languages (Antoniou, 2018; Berthele, 2020; Li et al., 2014). Indeed, across two independent datasets, we show, for the first time, that cortical thickness of early auditory brain regions is related to the degree of one’s language experience coupled with typological distance between the languages one knows. These findings indicate that early auditory regions seem to represent (or be shaped by) phoneme-level cross-linguistic information, contrary to the most established models of language processing in the brain, which suggest that phonological processing happens in more lateral posterior STG and STS.

7 Supplementary Information

main sample								
	L1	L2	L3	L4	L5	L6	L7	Number of languages
1	Czech	Russian	German	Korean	Vietnamese	French	English	7
2	Swiss_German	German	French	Greek	Italian	English		6
3	German	Italian	English	French	Portuguese	Spanish		6
4	English	French	German	Spanish	Mandarin			5
5	German	English	French	Dutch	Italian			5
6	English	French	German	Italian	Spanish			5
7	German	English	French	Spanish	Russian			5
8	English	German	Luxembourgish	French	Danish			5
9	English	German	French	Spanish	Italian			5
10	English	Italian	French	German	Spanish			5
11	Portuguese	English	Spanish	French	Italian			5
12	Hakka	Mandarin	Malay	English	Cantonese			5
13	English	French	Italian	Spanish	Mandarin			5
14	German	English	French	Japanese				4
15	English	French	German	Danish				4
16	German	English	French	Spanish				4
17	German	English	French	Italian				4
18	German	English	Italian	French				4
19	English	French	German	Italian				4
20	German	English	Greek	French				4
21	French	German	English	Spanish				4
22	Spanish	Hebrew	English	French				4
23	English	German	Spanish	French				4
24	German	English	French	Italian				4
25	Portuguese	English	French	Italian				4
26	Greek	English	French	Spanish				4
27	Greek	English	French	Spanish				4
28	Greek	English	Italian	Spanish				4
29	Hakka	English	Mandarin	German				4
30	Cantonese	English	Mandarin	Italian				4
31	Cantonese	English	Mandarin	French				4
32	German	English	Dutch					3
33	English	Spanish	Portuguese					3
34	English	French	Swedish					3
35	English	Hindi	Portuguese					3
36	German	English	French					3

Table S1.

Languages spoken by each participant in the main and replication samples.

37	German	English	Dutch	3
38	German	English	French	3
39	German	English	Spanish	3
40	Greek	English	French	3
41	Greek	English	Spanish	3
42	Greek	English	German	3
43	Greek	English	German	3
44	Greek	English	French	3
45	Greek	English	French	3
46	Greek	English	French	3
47	Greek	English	French	3
48	Greek	English	Italian	3
49	Mandarin	Cantonese	English	3
50	Cantonese	English	Mandarin	3
51	Cantonese	Mandarin	English	3
52	Cantonese	Mandarin	English	3
53	English	French	Mandarin	3
54	Cantonese	English	Mandarin	3
55	English	Mandarin	German	3
56	Cantonese	English	Mandarin	3
57	English	French	Mandarin	3
58	English	French	Mandarin	3
59	English	German	Mandarin	3
60	Bengali	Hindi	English	3
61	Bengali	Hindi	English	3
62	Hindi	English	Urdu	3
63	Hindi	English	Urdu	3
64	Bengali	English	Hindi	3
65	Bengali	English	Hindi	3
66	English	Spanish	French	3
67	Farsi	English	Arabic	3
68	English	German		2
69	English	French		2
70	Dutch	English		2
71	English	Creole		2
72	English	Irish		2
73	German	English		2
74	German	English		2
75	German	English		2
76	German	English		2
77	English	German		2

Table S1. (continued)

78	German	English	2
79	Italian	English	2
80	Hebrew	English	2
81	English	Hebrew	2
82	Spanish	English	2
83	German	English	2
84	German	English	2
85	Greek	English	2
86	Greek	English	2
87	Greek	English	2
88	Greek	English	2
89	Greek	English	2
90	Greek	English	2
91	Greek	English	2
92	Greek	English	2
93	Mandarin	English	2
94	Cantonese	English	2
95	Cantonese	English	2
96	English	Mandarin	2
97	Mandarin	English	2
98	Cantonese	English	2
99	Mandarin	English	2
100	Mandarin	English	2
101	Mandarin	English	2
102	Gujarati	English	2
103	Gujarati	English	2
104	Gujarati	English	2
105	English	Hungarian	2
106	English	French	2
107	English	French	2
108	English		1
109	English		1
110	English		1
111	English		1
112	English		1
113	English		1
114	English		1
115	English		1
116	English		1
117	English		1
118	English		1

Table S1. (continued)

	L1	L2	L3	L4	L5	L6	L7	Number of languages
119	English							1
120	English							1
121	English							1
122	English							1
123	English							1
124	English							1
125	English							1
126	English							1
127	English							1
128	English							1
129	English							1
130	English							1
131	English							1
132	English							1
133	English							1
134	English							1
135	English							1
136	English							1
replication sample								
	L1	L2	L3	L4	L5	L6	L7	Number of languages
1	German	English	French	Spanish	Italian			5
2	German	English	Italian	French	Arabic			5
3	Sindhi	English	Hindi	French	Russian			5
4	English	Irish	French	German	Italian			5
5	German	English	French	Italian	Spanish			5
6	English	French	German	Russian				4
7	German	English	Italian	French				4
8	German	English	French	Italian				4
9	English	French	German	Spanish				4
10	English	French	Spanish	German				4
11	Swiss_German	German	English	French				4
12	German	English	French	Spanish				4
13	German	English	French	Swahili				4
14	German	English	French	Swedish				4
15	German	English	French	Spanish				4
16	German	Portuguese	English	French				4
17	German	Dutch	English	French				4
18	Swiss_German	German	French	English				4
19	German	English	French	Spanish				4

Table S1. (continued)

Table S1. (continued)

20	Hungarian	English	French	3
21	German	English	French	3
22	English	German	Spanish	3
23	Punjabi	English	French	3
24	English	French	German	3
25	English	French	German	3
26	English	French	Italian	3
27	English	French	Mandarin	3
28	German	Italian	English	3
29	German	English	Finnish	3
30	German	English	French	3
31	German	English	Spanish	3
32	German	English	Dutch	3
33	German	English	Dutch	3
34	German	English	Spanish	3
35	German	Russian	English	3
36	Swahili	English		2
37	English	Czech		2
38	German	English		2
39	English	Spanish		2
40	English			1
41	English			1
42	English			1
43	English			1
44	English			1
45	English			1
46	English			1
47	English			1
48	English			1
49	English			1
50	English			1
51	English			1
52	English			1
53	English			1
54	English			1
55	English			1
56	English			1
57	English			1
58	English			1
59	English			1
60	English			1
61	English			1
62	English			1
63	English			1
64	English			1
65	English			1
66	English			1
67	English			1
68	English			1
69	English			1

Figure S 1.

Illustration of the replication sample's language experience.

As in **Figure 1**, each bar here represents a single participant's overall language experience; the height of the stacked bars within each bar represents the AoA index for individual languages (the taller the bar, the earlier in life a given language was acquired). The color of each stacked bar refers to the number of phonemes in each language's phonological inventory.

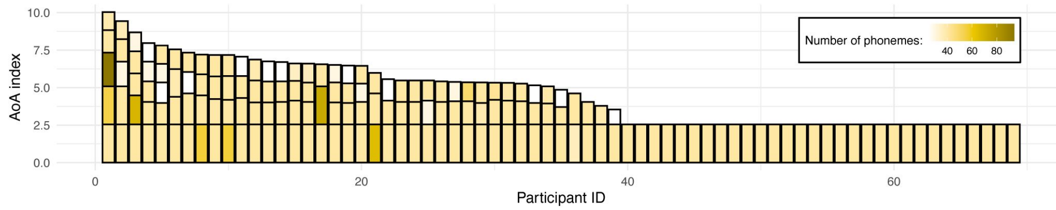


Figure S 2.

Similarity matrices of typological distances between all languages represented in the study (*N* = 36) based on: (1) distances in distinctive acoustic and articulatory features describing the phonemes of each language (e.g., "short", "long"); (2) distances in sets of phonemes belonging to each language; and (3) distances based on counts of phonological classes that share certain features (e.g., "consonants", "front rounded vowels", "clicks"). Data for individual languages were collected from the PHOIBLE database (Moran et al., 2019) and open-source software (Dediu & Moisik, 2016). The figure was generated in R, with the package pheatmap (Kolde, 2019), version 1.0.12.

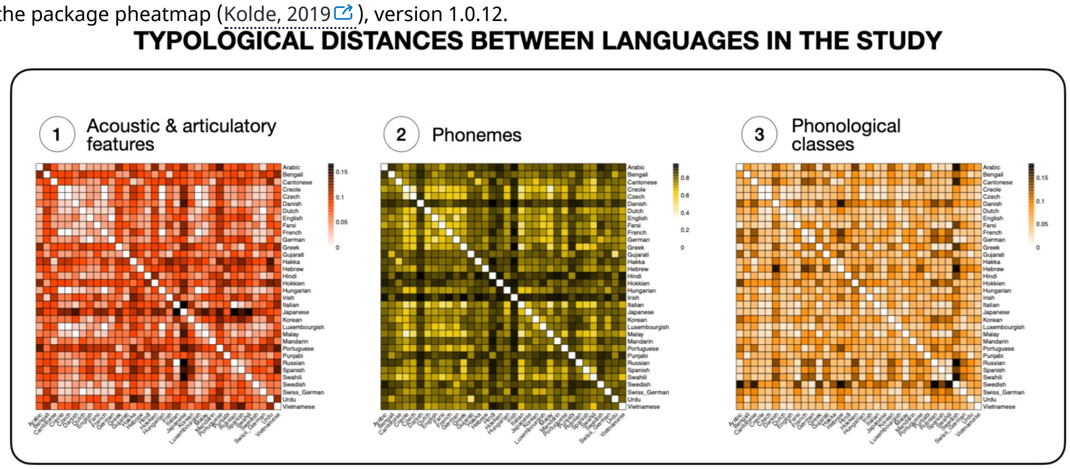


Figure S 3.

Distributions of the three distance measures used in the study based on: (1) distances in distinctive acoustic and articulatory features describing the phonemes of each language (in red); (2) distances in sets of phonemes belonging to each language (in yellow); and (3) distances based on counts of phonological classes (in orange).

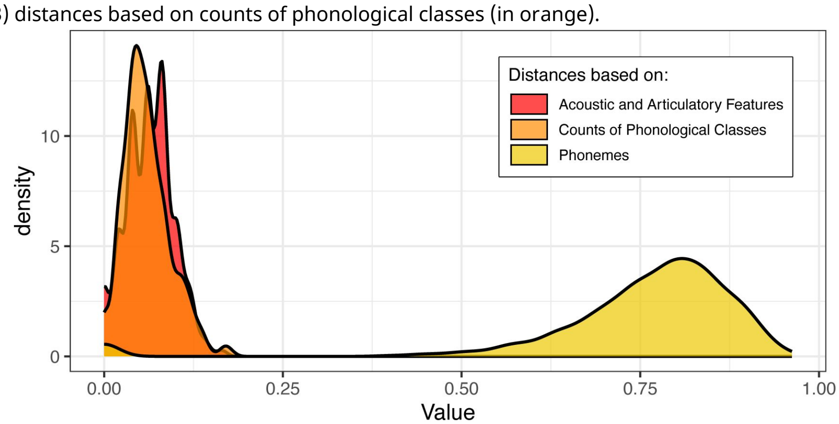
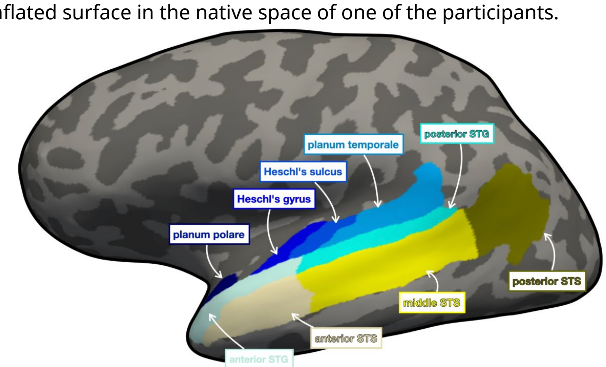


Figure S 4.

Auditory ROIs used in the analysis.

The ROIs are overlaid on an inflated surface in the native space of one of the participants.



7.1 Auditory cortex regions and language experience

		VOLUME	AREA	THICKNESS
(Intercept)	β	1711.89***	58.10***	0.58***
	SE	(35.28)	(11.85)	(0.02)
Age	β	1.01	0.07	0.00
	SE	(0.88)	(0.24)	(0.00)
Sex	β	0.63	-7.41	0.02
	SE	(26.07)	(8.07)	(0.01)
Whole-brain: Volume / Area / Thickness	β	0.00***	0.01***	0.77***
	SE	(0.00)	(0.00)	(0.09)
Language experience	β	41.50	7.45	0.03
	SE	(66.09)	(22.33)	(0.03)

Posterior STG	β	-1548.51***	-257.01***	-0.34***
	SE	(46.38)	(15.85)	(0.02)
Anterior STS	β	-2465.10***	-190.57***	-0.77***
	SE	(46.38)	(15.85)	(0.02)
Middle STS	β	-688.17***	646.88***	-1.01***
	SE	(46.38)	(15.85)	(0.02)
Posterior STS	β	-185.92***	861.89***	-1.01***
	SE	(46.38)	(15.85)	(0.02)
PT	β	-2064.07***	-163.35***	-0.80***
	SE	(46.38)	(15.85)	(0.02)
HG	β	-2886.10***	-482.40***	-0.78***
	SE	(46.38)	(15.85)	(0.02)
HS	β	-3416.84***	-552.82***	-0.97***
	SE	(46.38)	(15.85)	(0.02)
PP	β	-1870.15***	-316.73***	0.19***
	SE	(46.38)	(15.85)	(0.02)
Hemisphere	β	-478.00***	-103.17***	0.02
	SE	(46.38)	(15.85)	(0.02)
Language experience x Posterior STG	β	-54.04	-20.53	-0.02
	SE	(90.37)	(30.88)	(0.05)
Language experience x Anterior STS	β	-104.26	-28.61	-0.01
	SE	(90.37)	(30.88)	(0.05)
Language experience x Middle STS	β	23.56	28.91	-0.02
	SE	(90.37)	(30.88)	(0.05)
Language experience x Posterior STS	β	40.34	38.03	-0.05
	SE	(90.37)	(30.88)	(0.05)
Language experience x PT	β	-172.20.	-35.12	-0.12*
	SE	(90.37)	(30.88)	(0.05)
Language experience x HG	β	-39.06	-4.31	-0.02
	SE	(90.37)	(30.88)	(0.05)
Language experience x HS	β	-82.13	-25.18	-0.01
	SE	(90.37)	(30.88)	(0.05)
Language experience x PP	β	-91.67	-9.65	-0.07
	SE	(90.37)	(30.88)	(0.05)
Language experience x Hemisphere	β	41.88	-17.55	0.02
	SE	(90.37)	(30.88)	(0.05)
Posterior STG x Hemisphere	β	407.62***	99.63***	0.02
	SE	(65.60)	(22.42)	(0.03)
Anterior STS x Hemisphere	β	371.93***	67.74**	-0.05
	SE	(65.60)	(22.42)	(0.03)
Middle STS x Hemisphere	β	440.40***	43.39.	0.11**
	SE	(65.60)	(22.42)	(0.03)
Posterior STS x Hemisphere	β	1186.10***	435.79***	0.01
	SE	(65.60)	(22.42)	(0.03)
PT x Hemisphere	β	222.12***	7.78	0.04
	SE	(65.60)	(22.42)	(0.03)
HG x Hemisphere	β	255.17***	19.78	0.09**
	SE	(65.60)	(22.42)	(0.03)
HS x Hemisphere	β	363.43***	23.36	0.16***
	SE	(65.60)	(22.42)	(0.03)
PP x Hemisphere	β	486.42***	146.40***	-0.15***
	SE	(65.60)	(22.42)	(0.03)
Language experience x Posterior STG x Hemisphere	β	-36.81	32.36	-0.02
	SE	(127.81)	(43.68)	(0.07)
Language experience x Anterior STS x Hemisphere	β	75.05	52.32	0.01
	SE	(127.81)	(43.68)	(0.07)
Language experience x Middle STS x Hemisphere	β	15.40	16.32	0.01
	SE	(127.81)	(43.68)	(0.07)
Language experience x Posterior STS x Hemisphere	β	50.84	52.48	-0.03
	SE	(127.81)	(43.68)	(0.07)
Language experience x PT x Hemisphere	β	31.46	33.64	0.03
	SE	(127.81)	(43.68)	(0.07)
Language experience x HG x Hemisphere	β	-71.22	8.23	0.00
	SE	(127.81)	(43.68)	(0.07)
Language experience x HS x Hemisphere	β	-13.56	24.11	0.02
	SE	(127.81)	(43.68)	(0.07)
Language experience x PP x Hemisphere	β	-37.13	13.98	0.02
	SE	(127.81)	(43.68)	(0.07)
SD (Intercept id)		*91.84*	*24.92*	*0.06*

SD (Observations)	*382.49*	*130.71*	*0.20*
Num.Obs.	*2448*	*2448*	*2448*
R2 Marg.	*0.904*	*0.937*	*0.793*
R2 Cond.	*0.910*	*0.939*	*0.812*
AIC	*35864.3*	*30661.7*	*-580.1*
BIC	*36102.2*	*30899.7*	*-342.2*
ICC	*0.1*	*0.0*	*0.1*
RMSE	*374.14*	*128.27*	*0.19*

STG: superior temporal gyrus, STS: superior temporal sulcus, PT: planum temporale, HG: Heschl's gyrus, HS: Heschl's sulcus, PP: planum polare

. $p < 0.1$, + $p = 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table S2.

Results of linear mixed models (parameter estimates and standard errors, in brackets; *p*-values are listed according to the coding presented underneath the table) testing the effect of language experience on the structure (volume, area, and average thickness) of the auditory regions: planum polare, Heschl's gyrus, Heschl's sulcus, planum temporale, anterior and posterior superior temporal gyrus, and anterior, middle, and posterior superior temporal sulcus. Anterior STG was used as the reference level.

7.2 Superior temporal region and language experience

		VOLUME	AREA	THICKNESS
(Intercept)	β	-86.44***	-31.09***	0.05**
	SE	(14.45)	(4.14)	(0.01)
Language experience	β	-4.83	0.92	-0.06*
	SE	(32.25)	(9.24)	(0.03)
Age	β	-1.33	-0.30	0.00
	SE	(0.86)	(0.22)	(0.00)
Sex	β	14.78	2.72	0.01
	SE	(12.69)	(3.66)	(0.01)
Whole-brain: volume / area / thickness	β	0.00***	0.00***	0.98***
	SE	(0.00)	(0.00)	(0.16)
2nd gyrus	β	351.19***	119.93***	-0.13***
	SE	(17.05)	(4.89)	(0.01)
3rd gyrus	β	-169.80***	-50.83***	0.01
	SE	(17.55)	(5.03)	(0.02)
Hemisphere	β	51.04***	19.58***	-0.04**
	SE	(14.42)	(4.13)	(0.01)
Language experience x 2nd gyrus	β	-30.18	-14.89	0.09**
	SE	(36.03)	(10.33)	(0.03)
Language experience x 3rd gyrus	β	-5.66	3.50	-0.05
	SE	(36.88)	(10.57)	(0.03)
Language experience x hemisphere	β	-27.16	-7.25	0.00
	SE	(31.46)	(9.02)	(0.03)
2nd Gyrus x hemisphere	β	8.34	8.32.	-0.02
	SE	(17.01)	(4.88)	(0.01)
3rd Gyrus x hemisphere	β	-18.79	-6.34	-0.01
	SE	(17.55)	(5.03)	(0.02)
Language experience x 2nd gyrus x hemisphere	β	-11.32	-2.86	-0.02
	SE	(36.04)	(10.34)	(0.03)
Language experience x 3rd gyrus x hemisphere	β	30.25	11.01	-0.03
	SE	(36.88)	(10.57)	(0.03)
SD (Intercept id)		*0.01*	*0.00*	*0.07*
SD (Observations)		*257.90*	*73.94*	*0.22*
Num.Obs.		*567*	*567*	*567*
R2 Marg.		*0.521*	*0.596*	*0.254*
R2 Cond.		*0.521*		*0.324*
AIC		*7836.9*	*6455.5*	*66.9*
BIC		*7910.7*	*6529.3*	*140.7*
ICC		*0.0*		*0.1*
RMSE		*254.47*	*72.95*	*0.21*

. $p < 0.1$, + $p = 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table S3.

Results of the linear mixed models testing the effect of Language Experience on the structure (volume, area and average thickness) of the gyri in the superior temporal region: first, second and third TTG. Anterior TTG was used as the reference level.

7.3 Vertex-wise analysis

Figure S 5.

Results of a whole-brain vertex-wise analysis, aimed at establishing relations between the language experience index and whole-brain cortical thickness.

Overlaid on the inflated surface of the fsaverage template brain is the thresholded at $p < .0001$ (uncorrected) significance map from the conducted *F*-test showing a negative relationship between cortical thickness in the highlighted region and the degree of multilingual language experience.

7.4 Second transverse temporal gyrus and effects of language typology

Kolmogorov-Smirnov normality tests were run on all models' residuals, revealing that parametric linear models were appropriate for the present data (all *ps* > .4). According to a frequentist analysis of the data, all eight overall regression models were statistically significant: (1) Left hemisphere: $F(4,125) = 7.802$, $p < .001$, $F(4,125) = 6.32$, $p < 0.001$, $F(4,125) = 8.287$, $p < 0.001$, $F(4,125) = 6.98$, $p < 0.001$, respectively for the models with the four language experience indices: (a) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (b) acoustic/articulatory features, (c) phonemes, and (d) counts of phonological classes; and (2) Right hemisphere: $F(4,91) = 4.295$, $p = 0.003$, $F(4,91) = 3.461$, $p = 0.01$, $F(4,91) = 4.331$, $p = 0.002$, $F(4,91) = 3.722$, $p = 0.007$, respectively for the models with the four language experience indices: (a) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (b) acoustic/articulatory features, (c) phonemes, and (d) counts of phonological classes.

7.4.1 Cumulative phoneme inventory and the second TTG

The two models including the 'cumulative phoneme inventory' measure were statistically significant: (1) Left hemisphere: $F(5,124) = 8.308$, $p < .001$, and (2) Right hemisphere: $F(5,90) = 3.42$, $p = 0.007$, see further **Table S 4**. **Figure S 6** presents the relationship between the thickness of the second TTG (left and right) and the cumulative phoneme inventory.

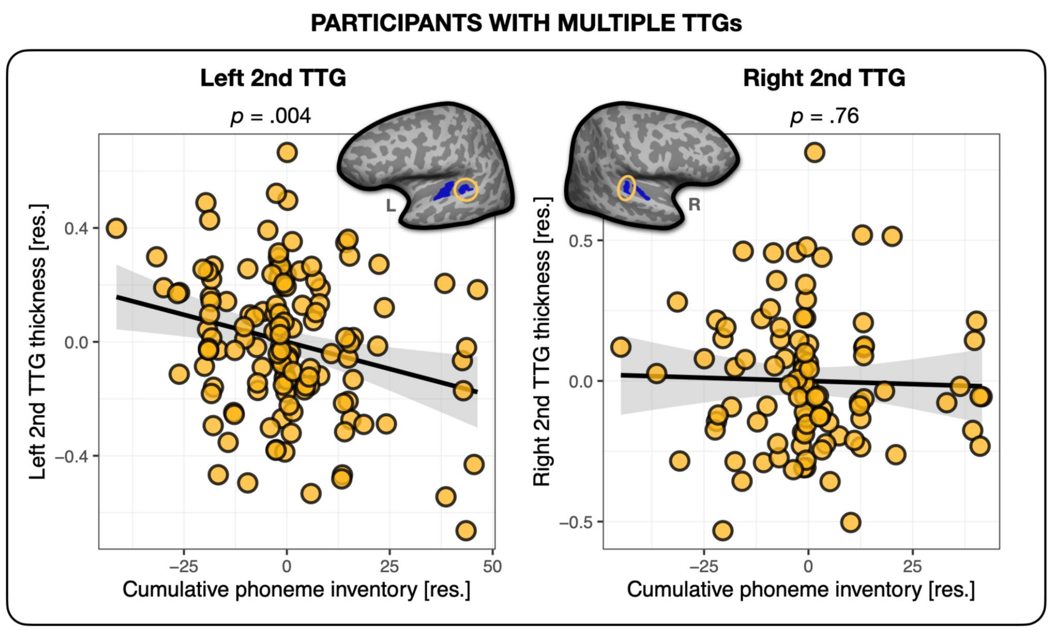


Figure S 6.

Cumulative phoneme inventory and thickness of the second TTG.

Average thickness of the second TTG in the left and right hemisphere in relation to the number of unique phonemes each participant was exposed to across all their languages (the plotted values are residuals controlled for age, sex, mean hemispheric thickness and the language experience index irrespective of typology).

Language experience Models:		left			right		
		Cumulative Phoneme inventory	Language experience	Language experience (Phonemes)	Cumulative phoneme inventory	Language experience	Language experience (Phonemes)
(Intercept)	β	0.00	0.00	0.00	0.00	0.00	0.00
	SE	(0.02)	(0.02)	(0.02)	(0.03)	(0.03)	(0.03)
Language experience	β	0.05	-0.12**	-	-0.08	-0.10+	-
	SE	(0.07)	(0.05)	-	(0.09)	(0.05)	-
Phonemes	β	0.00**	-	-	0.00	-	-
	SE	(0.00)	-	-	(0.00)	-	-
Language experience (Phonemes)	β	-	-	-0.35**	-	-	-0.26+
	SE	-	-	(0.12)	-	-	(0.13)
Age	β	0.00.	0.00	0.00	0.00	0.00	0.00
	SE	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Mean thickness (left/right)	β	1.43***	1.40***	1.37***	0.95*	0.94*	0.92*
	SE	(0.29)	(0.30)	(0.30)	(0.37)	(0.37)	(0.37)
Sex	β	0.00	0.00	0.00	0.01	0.00	0.01
	SE	(0.02)	(0.02)	(0.02)	(0.03)	(0.03)	(0.03)
Num.Obs.		*130*	*130*	*130*	*96*	*96*	*96*
R2		*0.251*	*0.200*	*0.210*	*0.160*	*0.159*	*0.160*
R2 Adj.		*0.221*	*0.174*	*0.184*	*0.113*	*0.122*	*0.123*
AIC		*11.9*	*18.5*	*16.9*	*13.8*	*11.9*	*11.8*
BIC		*31.9*	*35.7*	*34.1*	*31.8*	*27.3*	*27.2*
Log.Lik.		*1.062*	*-3.232*	*-2.430*	*0.085*	*0.036*	*0.101*
F		*8.308*	*7.802*	*8.287*	*3.420*	*4.295*	*4.331*
RMSE		*0.24*	*0.25*	*0.25*	*0.24*	*0.24*	*0.24*
ΔR2 Adjusted		-	*-0.04*	*-0.03*	-	*0.01*	*0.01*
BF_{10}		-	*0.15*	*0.34*	-	*9.33*	*9.96*
BF_{01}		-	*6.43*	*2.88*	-	*0.11*	*0.10*

. $p < 0.1$, + $p = 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table S4.

left and right second transverse temporal gyri and cumulative phoneme inventory. Multiple regression model parameters (parameter estimates and standard errors, in brackets; *p*-values are listed according to the coding presented underneath the table) for the average cortical thickness of the second TTG (left and right), as predicted by the "cumulative phoneme inventory" index. For comparison, models with the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of phonemes are also reported. Last two rows present model comparison results (additional variance explained and BF_{10} and BF_{01} values are also reported).

7.5 Language experience in participants with a single TTG

Kolmogorov-Smirnov normality tests were run on all models' residuals, revealing that parametric linear models were appropriate for the present data (all *p*s > .29). According to a frequentist analysis of the data, all eight overall regression models were statistically significant: (1) Right Heschl's gyrus: $F(4,35) = 6.365$, $p < .001$, $F(4,35) = 4.851$, $p = 0.003$, $F(4,35) = 5.403$, $p = 0.002$, $F(4,35) = 5.72$, $p = 0.001$, respectively for models with the four language experience indices: (a) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (b) acoustic/articulatory features, (c) phonemes, and (d) counts of phonological classes; and (2) Right planum temporale: $F(4,35) = 2.655$, $p = 0.049$, $F(4,35) = 2.639$, $p = 0.050$, $F(4,35) = 2.66$, $p = 0.048$, $F(4,35) = 2.685$, $p = 0.049$, respectively for models with the four language experience indices: (a) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (b) acoustic/articulatory features, (c) phonemes, and (d) counts of phonological classes.

		Right Heschl's gyrus				*Right planum temporale*			
		No typology	Features	Phonemes	Phonological classes	No typology	Features	Phonemes	Phonological classes
(Intercept)	β	-0.01	-0.01	-0.01	-0.13*	2.52***	2.52***	2.52***	2.50***
	SE	(0.03)	(0.03)	(0.03)	(0.06)	(0.03)	(0.03)	(0.03)	(0.07)
Language experience indices	β	0.15**	0.48+	0.35*	0.82*	0.02	0.03	0.06	0.11
	SE	(0.05)	(0.24)	(0.15)	(0.32)	(0.07)	(0.30)	(0.19)	(0.41)
Age	β	0.00	0.00	0.00	0.00	-0.00	-0.00	-0.00	-0.00
	SE	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Sex	β	0.05	0.03	0.05	0.04	0.06	0.05	0.06	0.06
	SE	(0.05)	(0.06)	(0.06)	(0.05)	(0.07)	(0.07)	(0.07)	(0.07)
Mean Thickness (right)	β	0.93**	0.99**	0.96**	0.93**	0.90*	0.90*	0.91*	0.90*
	SE	(0.30)	(0.31)	(0.30)	(0.30)	(0.38)	(0.39)	(0.38)	(0.38)
Num.Obs.		40	40	40	40	40	40	40	40
R2		*0.42*	*0.36*	*0.38*	*0.40*	*0.23*	*0.23*	*0.23*	*0.23*
R2 Adj.		*0.36*	*0.28*	*0.31*	*0.33*	*0.15*	*0.14*	*0.15*	*0.15*
AIC		*-36.6*	*-32.4*	*-34.0*	*-34.9*	*-15.6*	*-15.5*	*-15.6*	*-15.6*
BIC		*-26.5*	*-22.3*	*-23.8*	*-24.7*	*-5.4*	*-5.4*	*-5.5*	*-5.4*
Log.Lik.		*24.30*	*22.19*	*22.99*	*23.43*	*13.79*	*13.76*	*13.81*	*13.79*
RMSE		*0.13*	*0.14*	*0.14*	*0.13*	*0.17*	*0.17*	*0.17*	*0.17*
ΔR2 Adjusted		-	*-0.07*	*-0.04*	*-0.03*	-	*> -0.01*	*< 0.01*	*< 0.01*
BF_{10}		-	*0.12*	*0.27*	*0.42*	-	*0.97*	*1.02*	*1.01*

. $p < 0.1$, + $p = 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table S5.

Right superior temporal plane (Heschl's gyrus and planum temporale) and language experience in participants with one TTG.

Multiple regression model parameters (parameter estimates and standard errors, in brackets; *p*-values are listed according to the coding presented underneath the table) for the average cortical thickness of the right Heschl's gyrus, and the right planum temporale, as predicted by the four language experience indices: (1) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (2) phonemes, (3) acoustic/articulatory features and (4) counts of phonological classes. Last two rows present model comparison results (additional variance explained and BF_{10} values); NB. all models including typological information were compared against the 'No typology' model.

7.6 Effects of language proficiency

The findings of thinner cortex in the second TTG (when present) were further followed up by an analysis investigating the effect of proficiency attained by the participants in their individual languages. Here, we again constructed cumulative language experience measures per participant using the Shannon's entropy equation (Shannon, 1948), but this time from the self-reported proficiency ratings (on a scale from 0 to 10) of each of participants' languages. First, we computed a general proficiency score and used it in two linear models to establish whether the AoA-derived cumulative language experience measure could be replicated by the proficiency-derived measure, since AoA and proficiency are known to be highly correlated. This analysis therefore served as a 'sanity check' for the results obtained from the analyses reported in Section 3.2. Indeed, we observed that the thickness of the second TTG (when present) was negatively related to the cumulative language experience measure derived from proficiency ratings. This effect was significant for the left hemisphere 2nd TTG thickness, and showed a trend towards significance for the right ($\beta = -0.11$, $t = -2.41$, $p = .018$, small effect size: $f^2 = 0.05$; and $\beta = -0.10$, $t = -1.87$, $p = .065$, small effect size: $f^2 = 0.05$, for left and right 2nd TTG respectively).

Given the hypothesis that multilingualism is a dynamic process reshaping brain structure and inducing both increases (in initial stages) and decreases (in peak efficiency) in brain morphological indices (Pliatsikas, 2020), we further explored the effect of proficiency of different languages by investigating the role of languages spoken proficiently and non-proficiently on the structure of the 2nd TTG. Here, we computed two further different indices per participant: (1) derived only from languages spoken proficiently (rated at 7 and higher out of 10 on a self-reported proficiency scale), and (2) derived from languages spoken at a low level of proficiency (rated lower than 7 out of 10). We subsequently used these indices in two further analyses to test the hypothesis that decreases in brain morphological indices (here in cortical thickness) are driven by peak efficiency of language functioning (operationalized here as high proficiency in many languages). We did observe that the thickness of the 2nd TTG was related to the measure of language experience derived from languages spoken proficiently, however this effect was only significant in the right hemisphere ($\beta = -0.18$, $t = -2.89$, $p = .005$, small effect size: $f^2 = 0.11$; and $\beta = -0.02$, $t = -0.44$, $p = .66$, for right and left 2nd TTG respectively). 2nd TTG's thickness was not related to the language experience measure derived from languages spoken at low level of proficiency ($\beta = -0.01$, $t = -0.11$, $p = .91$; and $\beta = -0.12$, $t = -1.69$, $p = .097$ for right and left 2nd TTG respectively), see **Figure S 7**.

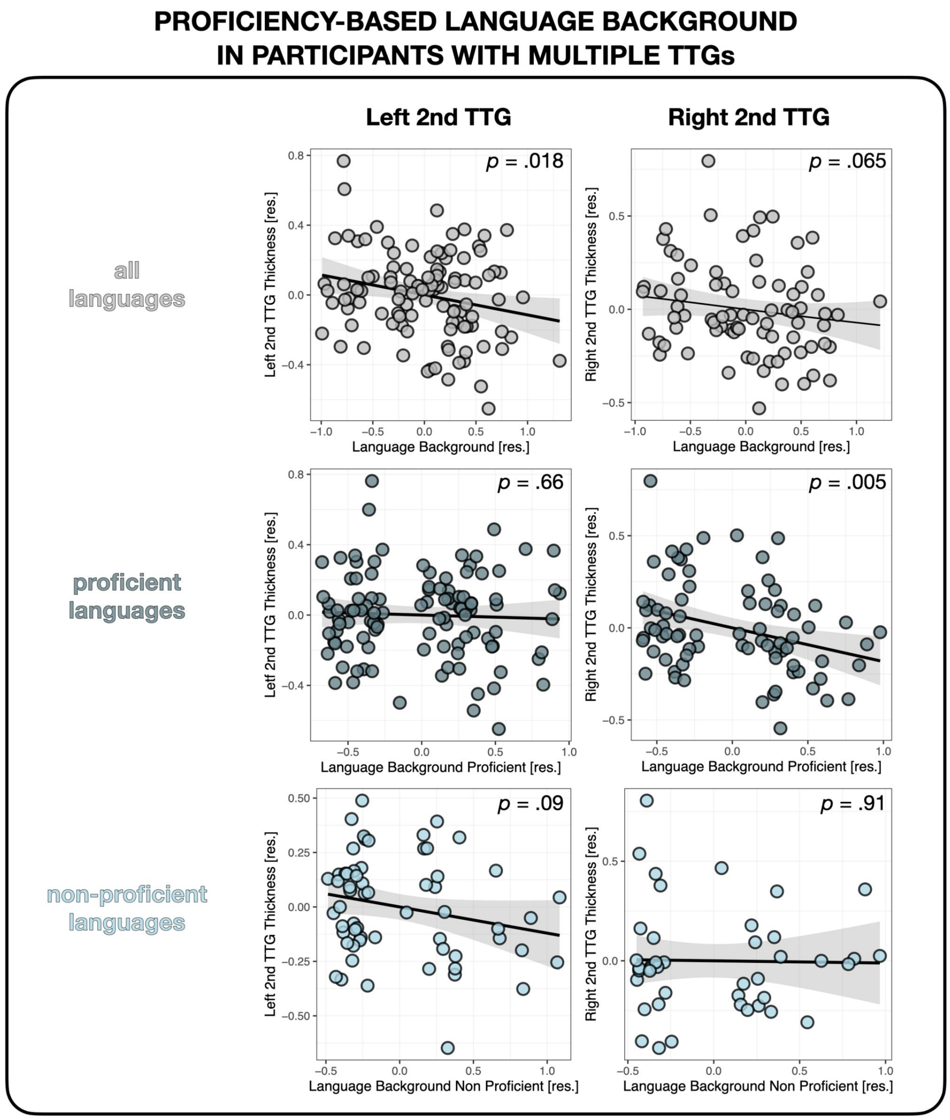


Figure S 7.

Multilingual proficiency and thickness of the second TTG.

Average thickness of the second TTG in the left and right hemisphere as a function of language proficiency in all languages of each participant (top panel), only their proficient languages (middle panel) and only their non-proficient languages (bottom panel). Plots show residuals, controlling for age, sex and mean hemispheric thickness.

7.7 Replication analysis

Kolmogorov-Smirnov normality tests were run on all models' residuals, revealing that parametric linear models were appropriate for the present data (all *p*s > .5). According to a frequentist analysis of the data, all four overall regression models for left hemisphere data were statistically not significant: $F(5,55) = 1.109$, $p < .001$, $F(5,55) = 1.12$, $p = .36$, $F(5,55) = 8.287$, $p = .37$, $F(5,55) = 1.072$, $p = .38$, respectively for models with the four language experience indices: (a) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (b) acoustic/articulatory features, (c) phonemes, and (d) counts of phonological classes. Models for the right hemisphere data were all statistically significant, apart from the counts of phonological classes model: $F(5,48) = 2.781$, $p = 0.03$, $F(5,48) = 5.158$, $p < 0.001$, $F(5,48) = 3.244$, $p = 0.013$, $F(5,48) = 2.342$, $p = 0.06$, respectively for models with the four language experience indices: (a) the cumulative language experience measure not accounting for typology, and cumulative language experience weighted by overlaps between languages at the level of (b) acoustic/articulatory features, (c) phonemes, and (d) counts of phonological classes.

7.8 Phonological classes as defined by Dediu and Moisik (2016)

(v = vowels, c = consonants) segments, vowels, monophtongs, diphtongs, triphtongs, heights.v, lengths.v, long.v, nasal.v, round.v, high.v, mid.v, low.v, front.v, back.v, tense.v, lax.v, atr.v, rtr.v, raised.v, retracted.v, fronted.v, glottalized.v, unique.v, unique.nasal.v, heights_mono.v, heights_di.v, heights_tri.v, lengths_mono.v, lengths_di.v, lengths_tri.v, long_mono.v, long_di.v, long_tri.v, nasal_mono.v, nasal_di.v, nasal_tri.v, round_mono.v, round_di.v, round_tri.v, high_mono.v, high_di.v, high_tri.v, mid_mono.v, mid_di.v, mid_tri.v, low_mono.v, low_di.v, low_tri.v, front_mono.v, front_di.v, front_tri.v, back_mono.v, back_di.v, back_tri.v, tense_mono.v, tense_di.v, tense_tri.v, lax_mono.v, lax_di.v, lax_tri.v, atr_mono.v, atr_di.v, atr_tri.v, rtr_mono.v, rtr_di.v, rtr_tri.v, raised_mono.v, raised_di.v, raised_tri.v, retracted_mono.v, retracted_di.v, retracted_tri.v, fronted_mono.v, fronted_di.v, fronted_tri.v, glottalized_mono.v, glottalized_di.v, glottalized_tri.v, unique_mono.v, unique_di.v, unique_tri.v, unique.nasal_mono.v, unique.nasal_di.v, unique.nasal_tri.v, consonants, places.c, bilabial.c, labiodental.c, dental.c, alveolar.c, dental_alveolar.c, palatoalveolar.c, alveolopalatal.c, postalveolar.c, true_retroflex.c, palatal.c, velar.c, uvular.c, pharyngeal_epiglottal.c, glottal.c, labial.c, coronal.c, dorsal.c, guttural.c, manners.c, obstruent.c, voiced_obstruent.c, voiceless_obstruent.c, aspirated_obstruent.c, glottalized_obstruent.c, stop.c, voiced_stop.c, voiceless_stop.c, aspirated_stop.c, glottalized_stop.c, fricative.c, voiced_fricative.c, voiceless_fricative.c, affricate.c, sonorant.c, voiced_sonorant.c, voiceless_sonorant.c, glottalized_resonant.c, nasal.c, approximant.c, tapflap.c, trill.c, trill_tap.c, coronal_trill_tap.c, glottalized.c, uvt.c, uvt.stops.c, uvt.fricatives.c, uvt.affricates.c, uvt.nasals.c, uvt.approximants.c, lvt.c, lvt.stops.c, lvt.fricatives.c, lvt.affricates.c, lvt.nasals.c, lvt.approximants.c, ratio.voiced.voiceless.obstruents, ratio.voiced.voice-less.stops, ratio.obstruents.sonorants, egressive, implosive, ejective, click, voiceless, voiced, breathy, creaky, tones, bilabial.fricatives, labiodental.fricatives, alveolar.fricatives, nonsibilant.dental.fricatives, sibilant.dental.fricatives, bilabi-allabiodental.affricates, bilabial.affricates, retroflex.stops, retroflex.fricatives, retroflex.affricates, retroflex.nasals, retroflex.approximants

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Reviewer #1 (Public review):

Summary:

The goal of this project is to test the hypothesis that individual differences in experience with multiple languages relate to differences in brain structure, specifically in the transverse temporal gyrus. The approach used here is to focus specifically on the phonological inventories of these languages, looking at the overall size of the phonological inventory as well as the acoustic and articulatory diversity of the cumulative phonological inventory in people who speak one or more languages. The authors find that the thickness of the transverse temporal gyrus (either the primary TTG, in those with one TTG, or in the second TTG, in people with multiple gyri) was related to language experience, and that accounting for the phonological diversity of those languages improved the model fit. Taken together, the evidence suggests that learning more phonemes (which is more likely if one speaks more than one language) leads to experience-related plasticity brain regions implicated in early auditory processing.

Strengths:

This project is rigorous in its approach--not only using a large sample but replicating the primary finding in a smaller, independent sample. Language diversity is difficult to quantify, and likely to be qualitatively and quantitatively distinct across different populations, and the authors use a custom measure of multilingualism (accounting for both number of languages as well as age of acquisition) and three measures of phonological diversity. The team has been careful in discussion of these findings, and while it is possible that pre-existing differences in brain structure could lead to an aptitude difference which could drive one to learn more than one language, the fine-grained relationships with phonological diversity seem less likely to emerge from aptitude rather than experience.

The authors have satisfied my curiosity regarding other potential confounds in the data, including measurements of lexical distance as well as phonological typology.

https://doi.org/10.7554/eLife.90269.2.sa3

Reviewer #2 (Public review):

This work investigates the possible association between language experience and morphology of the superior temporal cortex, a part of the brain responsible for the processing of auditory stimuli. Previous studies have found associations between language and music proficiency as well as language learning aptitude and cortical morphometric measures in regions in the primary and associated auditory cortex. These studies have most often, however, focused on finding neuroanatomical effects of difference between features in a few (often two) languages or from learning single phonetic/phonological features and have often been limited in terms of N. On this background, the authors use more sophisticated measures of language experience that take into account the age of onset and the differences in phonology between languages the subjects have been exposed as well as a larger number of subjects (N = 146 + 69) to relate language experience to the shape and structure of the superior temporal cortex, measured from T1-weighted MRI data. It shows solid evidence for there being a negative relationship between language experience and the right 2nd transverse temporal gyrus as well as some evidence for the relationship representing phoneme-level cross-linguistic information.

Strengths

The use of entropy measures to quantify language experience and include typological distance measures allows for a more general interpretation of the results and is an important step toward respecting and making use of linguistic diversity in neurolinguistic experiments.

A relatively large group of subjects with a range of linguistic backgrounds.

The full analysis of the structure of the superior temporal cortex including cortical volume, area, as well as the shape of the transverse gyrus/gyri. There is a growing literature on the meaning of the shape and number of the transverse gyri in relation to language proficiency and the authors explore all measures given the available data.

The authors chose to use a replication data set to verify their data, which is applaudable. However, see the relevant point under "Weaknesses".

Weaknesses

Even if the language experience and typological distance measures are a step in the right direction for correctly associating language exposure with cortical plasticity, it still is a measure that is insensitive to the intensity of the exposure.

Only the result from the multiple transverse temporal gyri (2nd TTG) is analyzed in the replicated dataset. Only the association in the right hemisphere 2nd TTG is replicated but this is not reflected in the discussion or the conclusions. The positive correlation in the right TTG is thus not attempted to be replicated.

The replication dataset differed in more ways than the more frequent combination of English and German experience, as mentioned in the discussion. Specifically, the fraction of monolinguals was higher in the replication dataset and the samples came from different scanners. It would be better if the primary and replication datasets were more equally matched.

https://doi.org/10.7554/eLife.90269.2.sa2

Reviewer #3 (Public review):

Summary:

The study uses structural MRI to identify how the number, degree of experience, and phonemic diversity of language(s) that a speaker knows can influence the thickness of different sub-segments of auditory cortex. In both a primary and replication sample of adult speakers, the authors find key differences in cortical thickness within specific subregions of cortex due to either the age at which languages are acquired (degree of experience) or the diversity of the phoneme inventories carried by that/those language(s) (breadth of experience).

Strengths:

The results are first and foremost quite fascinating and I do think they make a compelling case for the different ways in which linguistic experience shapes auditory cortex.

The study uses a number of different measures to quantify linguistic experience, related to how many languages a person knows (taking into account the age at which each was learned) as well as the diversity of the phoneme inventories contained within those languages. The primary sample is moderately large for a study that focuses on brain-behaviour relationships; a somewhat smaller replication sample is also deployed in order to test the generality of the effects.

Analytic approaches benefit from the careful use of brain segmentation techniques that nicely capture key landmarks and account for vagaries in the structure of STG that can vary across individuals (e.g., the number of transverse temporal gyri varies from 1-4 across individuals).

Weaknesses:

The specificity of these effects is interesting; some effects really do appear to be localized to left hemisphere and specific subregions of auditory cortex e.g., TTG. There is an ancillary analysis that examines regions outside auditory cortex to examine whether these are the only brain regions for which such effects occur. Expanding the search space to a whole-brain analysis, and a more lenient statistical threshold, does reveal only small patches of the brain outside auditory cortex show similar effects. Notably, these could be due to inflated type-1 error, but overall we would need a much larger sample to be certain.

Discussion of potential genetic differences underlying the findings is interesting. It does represent one alternative account that does not have to do with plasticity/experience, as the authors acknowledge.

The replication sample is useful and a great idea. It does however feature roughly half the number of participants. As the authors are careful to point out, that statistical power is weaker and given small effects in some cases we should not be surprised that the results only partially replicated in that sample.

https://doi.org/10.7554/eLife.90269.2.sa1

Author response:

The following is the authors' response to the original reviews.

> ***Reviewer #1 (Public Review):***
>
> *Summary:*
>
> *The goal of this project is to test the hypothesis that individual differences in experience with multiple languages relate to differences in brain structure, specifically in the transverse temporal gyrus. The approach used here is to focus specifically on the phonological inventories of these languages, looking at the overall size of the phonological inventory as well as the acoustic and articulatory diversity of the cumulative phonological inventory in people who speak one or more languages. The authors find that the thickness of the transverse temporal gyrus (either the primary TTG, in those with one TTG, or in the second TTG, in people with multiple gyri) was related to language experience, and that accounting for the phonological diversity of those languages improved the model fit. Taken together, the evidence suggests that learning more*

> *phonemes (which is more likely if one speaks more than one language) leads to experience-related plasticity in brain regions implicated in early auditory processing.*
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> *Strengths:*
>
> *This project is rigorous in its approach--not only using a large sample, but replicating the primary finding in a smaller, independent sample. Language diversity is difficult to quantify, and likely to be qualitatively and quantitatively distinct across different populations, and the authors use a custom measure of multilingualism (accounting for both number of languages as well as age of acquisition) and three measures of phonological diversity. The team has been careful in discussion of these findings, and while it is possible that pre-existing differences in brain structure could lead to an aptitude difference which could drive one to learn more than one language, the fine-grained relationships with phonological diversity seem less likely to emerge from aptitude rather than experience.*
>
> *Weaknesses:*
>
> *It is a bit unclear how the measures of phonological diversity relate to one another--they are partially separable, but rest on the same underlying data (the phonemes in each language). It would be helpful for the reader to understand how these measures are distributed (perhaps in a new figure), and the degree to which they are correlated with one another.*

Thank you for the comment. Indeed our description missed this important detail that we now included in the manuscript. Unsurprisingly, the distances all correlated with one another, which we present in Table 2 in Section 2.3 of the revised manuscript. We have also added a figure with distributions of the three distance measures (see Figure S3).

> *Further, as the authors acknowledge, it is always possible that an unseen factor instead drives these findings--if typological lexical distance measures are available, it would be helpful to enter these into the model to confirm that phonological factors are the specific driver of TTG differences and not language diversity in a more general sense. That said, the relationship between phonological diversity and TTG structure is intuitive.*

Thank you for the suggestion. To further establish that our results reflected the relationship between TTG structure and phonological diversity specifically (as opposed to language diversity in a more general sense), we derived a fourth measure of language experience, where the AoA index of different languages was weighted by lexical distances between the languages. Here, we followed the methodology described in Kepinska, Caballero, et al. (2023): We used Levenshtein Distance Normalized Divided (LDND) (Wichmann et al., 2010) which was computed using the ASJP.R program by Wichmann (https://github.com/Sokiwi/InteractiveASJP01). Information on lexical distances was combined with language experience information per participant using Rao's quadratic entropy equation in the same way as for the phonological measures.

We then entered this language experience measure accounting for lexical distances between the languages into linear models predicting the thickness of the second left and right TTG (controlling for participants' age, sex and mean hemispheric thickness) in the main sample, and compared these models with the corresponding models including the original three phonological distance measures (models 24 in Author response table 1), and the measure with no typological information (1).

Below, we list adjusted R2 values of all models, from which it is clear that the index of multilingual language experience accounting for lexical distances between languages (5) explained less variance than the index incorporating phoneme-level distances between languages (2), both in the left and the right hemisphere. This further strengthens our conclusion that our results reflected the relationship between TTG structure and phonological diversity specifically, as opposed to language diversity in a more general sense.

Author response table 1.

	Model	Adjusted R^2
left 2nd TTG	(1) No typology	0.174
	(2) Phonemes	0.184
	(3) Features	0.142
	(4) Phonological classes	0.156
	(5) Lexical	0.164
right 2nd TTG	(1) No typology	0.122
	(2) Phonemes	0.123
	(3) Features	0.094
	(4) Phonological classes	0.103
	(5) Lexical	0.116

We have added a description of this analysis to the manuscript, Section 3.3, lines 357-370.

> *One curious aspect of this paper relates to the much higher prevalence of split or duplicate TTG in the sample. The authors do a good job speculating on how features of the TASH package might lead to this, but it is unclear where the ground truth lies--some discussion of validation of TASH against a gold standard would be useful.*

The validation of the TASH toolbox in comparison to gold standard manual measurement involved assessing how well the measurements of left and right Heschl's gyrus (HG) volumes obtained using the TASH method correlated with those obtained through manual labeling (see Dalboni da Rocha et al., 2020 for details). This validation process was conducted across three independent datasets. Additionally, for comparison, the manually labeled HG volumes were also compared with those obtained using FreeSurfer's Destrieux parcellation of the transverse temporal gyrus in the same datasets. The validation process, therefore, involved rigorous comparisons of HG volumes obtained through manual labeling, FreeSurfer, and TASH across different datasets, along with an assessment of inter-rater reliability for the manual labeling procedure. This comprehensive approach ensures that the results are robust and reliable. TASH_complete, the version used in the present work, is an extension of the extensively validated TASH, which apart from the first gyrus, also identifies additional transverse temporal gyri (i.e. Heschl’s gyrus duplications and multiplications) situated in the PT, when present. Since work on the correspondence between manually identified TTG multiplications is still ongoing, as outlined in the Methods section, we complemented the automatic segmentation by extensive visual assessment of the identified posterior gyri. This process involved removing from the analysis those gyri that lay along the portion of the superior temporal plane that curved vertically (i.e., within the parietal extension, Honeycutt et al., 2000), when present. Given that TASH_complete and TASH operate on the same principles and are both based on FreeSurfer’s surface reconstruction and cortical parcellation (which have been extensively validated against manual tracing and other imaging modalities, showing good accuracy), and since we have visually inspected all segmentations, we are confident as to the accuracy of the reported TTG variability. It has to be further noted that the prevalence of TTG multiplications beyond 2nd full posterior duplications was not systematically assessed in previous descriptive reports (Marie, 2015). However, we acknowledge that more work is needed to further ascertain anatomical accuracy of the segmentations, and we elaborate on this point in the Discussion of the revised manuscript (lines 621-623).

> ***Reviewer #2 (Public Review):***
>
> *This work investigates the possible association between language experience and morphology of the superior temporal cortex, a part of the brain responsible for the*

> *processing of auditory stimuli. Previous studies have found associations between language and music proficiency as well as language learning aptitude and cortical morphometric measures in regions in the primary and associated auditory cortex. These studies have most often, however, focused on finding neuroanatomical effects of difference between features in a few (often two) languages or from learning single phonetic/phonological features and have often been limited in terms of N. On this background, the authors use more sophisticated measures of language experience that take into account the age of onset and the differences in phonology between languages the subjects have been exposed to as well as a larger number of subjects (N = 146 + 69) to relate language experience to the shape and structure of the superior temporal cortex, measured from T1weighted MRI data. It shows solid evidence for there being a negative relationship between language experience and the right 2nd transverse temporal gyrus as well as some evidence for the relationship representing phoneme-level cross-linguistic information.*
>
> *Strengths*
>
> *The use of entropy measures to quantify language experience and include typological distance measures allows for a more general interpretation of the results and is an important step toward respecting and making use of linguistic diversity in neurolinguistic experiments.*
>
> *A relatively large group of subjects with a range of linguistic backgrounds.*
>
> *The full analysis of the structure of the superior temporal cortex including cortical volume, area, as well as the shape of the transverse gyrus/gyri. There is a growing literature on the meaning of the shape and number of the transverse gyri in relation to language proficiency and the authors explore all measures given the available data.*
>
> *The authors chose to use a replication data set to verify their data, which is applaudable. However, see the relevant point under "Weaknesses".*
>
> *Weaknesses*
>
> *The authors fail to explain how a thinner cortex could reflect the specialization of the auditory cortex in the processing of diverse speech input. The Dynamic Restructuring Model (Pliatsikas, 2020) which is referred to does not offer clear guidance to interpretation. A more detailed discussion of how a phonologically diverse environment could lead to a thinner cortex would be very helpful.*

Thank you for bringing our attention to this point. We have now extended the explanation we had previously included in the Discussion by including the following passage on p. 20 (lines 557-566) of the revised manuscript:

“Experience-induced pruning is essential for maintaining an efficient and adaptive neural network. It reinforces relevant neural circuits for faster more efficient information processing, while diminishing those that are less active, or less beneficial. The cortical specialization may need to arise because phonologically more diverse language experience requires that the mapping of acoustic signal to sound categories is denser, more detailed and more intricate. As a result, the brain may need to engage in more intensive processing to discriminate between and accurately perceive the sound categories of each language. This increased cognitive demand may, in turn, require the auditory and language processing regions of the brain to adapt and become more efficient. Over time, this heightened effort for successful speech perception and sound discrimination may lead to neural plasticity, resulting in cortical specialization. This means that cortical areas become more finely tuned and specialized for processing the unique phonological features of language(s) spoken by individuals.”

We have also added a passage to the Introduction regarding the possible microscopic or physiological underpinnings of the brain structural differences that we observe macroscopically using structural MRI (lines 68-73):

"Such environmental effect on cortical thickness might in turn be tied to microstructural changes to the underlying brain tissue, such as modifications in dendritic length and branching, synaptogenesis or synaptic pruning, growth of capillaries and glia, all previously tied to some kind of environmental enrichment and/or skill learning (see Lövdén et al., 2013; Zatorre et al., 2012 for overviews). Increased cortical thickness may reflect synaptogenesis and dendritic growth, while cortical thinning observed with MRI may be a result of increased myelination (Natu et al., 2019) or synaptic pruning."

> *It is difficult to understand what measure of language experience is used when. Clearer and more explicit nomenclature would assist in the interpretation of the results.*

We have added more explicit list of indices used in the Introduction (lines 104-107 of the revised manuscript) and in Section 2.4 and used them consistently throughout the text:

(1) language experience index not accounting for typological features: 'Language experience - no typology'

(2) measures combining language experience with typological distances at different levels:

a. 'Language experience – features',

b. 'Language experience – phonemes',

c. 'Language experience – phonological classes'.

> *There is a lack of description of the language backgrounds of the included subjects. How many came from each of the possible linguistic backgrounds? How did they differ in language exposure? This would be informative to evaluate the generalizability of the conclusions.*

Thank you for raising this point. Given the complexity of participants' language experience, ranging between monolingual to speaking 7 different languages, we opted for a fully parametric approach in quantifying it. We used the Shannon's entropy and Rao's quadratic entropy equations to create continuous measures of language experience, without the constraints of a minimum sample size per language and the need to exclude participants with underrepresented languages. To add further details in our description of the language background, we summarize the language background of both samples in the newly added Table 1 presenting a breakdown of participants by number of languages they spoke, and Supplementary Table S1 listing all languages spoken by each participant.

> *Only the result from the multiple transverse temporal gyri (2nd TTG) is analyzed in the replicated dataset. Only the association in the right hemisphere 2nd TTG is replicated but this is not reflected in the discussion or the conclusions. The positive correlation in the right TTG is thus not attempted to be replicated.*

Thank you for bringing this point to our attention. Since only few participants presented single gyri in the left (n = 7) and the right hemisphere (n = 14), the replication analysis focused on the second TTG results only. We have now commented on this fact in Section 3.5 (lines 413-415), as well as in the Discussion (lines 594-596).

> *The replication dataset differed in more ways than the more frequent combination of English and German experience, as mentioned in the discussion. Specifically, the fraction of monolinguals was higher in the replication dataset and the samples came from different scanners. It would be better if the primary and replication datasets were more equally matched.*

Indeed, the replication sample did not fully mimic the characteristics of the main sample and a better match between the two samples would have been preferable. As elaborated in the Introduction, however, the data was split into two groups according to the date of data acquisition, which also coincided with the field strength of the scanners used for data acquisition: the first, main sample's data were acquired on a 1.5T, the replication sample's on 3T. We opted for keeping this split and not introducing additional noise in the analysis by using data from different field strengths at the cost of not fully matching the two datasets. Observing the established effects (even partially) in this somewhat different replication sample, however, seems in our view to further strengthen our results.

> *Even if the language experience and typological distance measures are a step in the right direction for correctly associating language exposure with cortical plasticity, it still is a measure that is insensitive to the intensity of the exposure. The consequences of this are not discussed.*

Indeed, we agree with the reviewer that there is still a lot of grounds to cover to fully understand the relationship between language experience and cortical plasticity. We have added a paragraph to the Discussion (lines 587-592 of the revised manuscript) to bring attention to this issue:

"Future research should also further increase the degree of detail in describing the multilingual language experience, as both AoA and proficiency (used here) are not sensitive to other aspects of multilingualism, such as intensity of the exposure to the different languages, or quantity and quality of language input. Since these aspects have been convincingly shown to be associated with neural changes (e.g., Romeo, 2019), incorporating further, more detailed measures describing individuals' language experience could further enhance our understanding of cortical plasticity in general, and how the brain accommodates variable language experience in particular."

> ***Reviewer #3 (Public Review):***
>
> *Summary:*
>
> *The study uses structural MRI to identify how the number, degree of experience, and phonemic diversity of language(s) that a speaker knows can influence the thickness of different sub-segments of the auditory cortex. In both a primary and replication sample of adult speakers, the authors find key differences in cortical thickness within specific subregions of the cortex due to either the age at which languages are acquired (degree of experience), or the diversity of the phoneme inventories carried by that/those language(s) (breadth of experience).*
>
> *Strengths:*
>
> *The results are first and foremost quite fascinating and I do think they make a compelling case for the different ways in which linguistic experience shapes the auditory cortex.*
>
> *The study uses a number of different measures to quantify linguistic experience, related to how many languages a person knows (taking into account the age at which each was*

learned) as well as the diversity of the phoneme inventories contained within those languages. The primary sample is moderately large for a study that focuses on brainbehaviour relationships; a somewhat smaller replication sample is also deployed in order to test the generality of the effects.

Analytic approaches benefit from the careful use of brain segmentation techniques that nicely capture key landmarks and account for vagaries in the structure of STG that can vary across individuals (e.g., the number of transverse temporal gyri varies from 1-4 across individuals).

Weaknesses:

The specificity of these effects is interesting; some effects really do appear to be localized to the left hemisphere and specific subregions of the auditory cortex e.g., TTG. However because analyses only focus on auditory regions along the STG and MTG, one could be led to the conclusion that these are the only brain regions for which such effects will occur. The hypothesis is that these are specifically auditory effects, but that does make a clear prediction that nonauditory regions should not show the same sort of variability. I recognize that expanding the search space will inflate type-1 errors to a point where maybe it's impossible to know what effects are genuine. And the fine-grained nature of the effects suggests a coarse analysis of other cortical regions is likely to fail. So I don't know the right answer here. Only that I tend to wonder if some control region(s) might have been useful for understanding whether such effects truly are limited to the auditory cortex. Otherwise one might argue these are epiphenomenal or some hidden factor unrelated to auditory experience predicting that we'd also see them in the non-auditory cortex as well, either within or outside the brain's speech network(s).

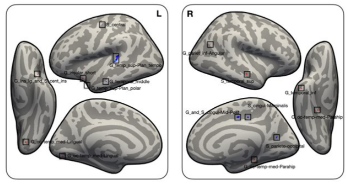
Thank you for raising this important issue. Our primary analyses indeed focused on the auditory regions, given their involvement in speech and language processing at different levels of processing hierarchy (from low – HG, to high – STG and STS). Here, we included a fairly broad range of ROIs (8 per hemisphere, 16 in total) and it has to be noted that it was only the bilateral planum temporale which showed an association with multilingualism. In the original submission we had indeed attempted at confirming the specificity of this result by performing a whole-brain vertex-wise analysis in freesurfer (see Table 3, Section 3.2, Figure S5), which again showed that the only cluster of vertices related to participants' language experience at $p < .0001$ (uncorrected) was located in the superior aspect of the left STG, corresponding to the location of planum temporale and the second TTG. Lowering the threshold of statistical significance to $p < .001$ (uncorrected) results in further clusters of vertices whose thickness was positively associated with the degree of multilingual language experience localized in:

• Left hemisphere: central sulcus (S_cenral), long insular gyrus and central sulcus of the insula (G_Ins_lg_and_S_cent_ins), lingual gyrus (G_oc-temp_med-Lingual), planum temporale of the superior temporal gyrus (G_temp_sup-Plan_tempo), short insular gyri (G_insular_short), middle temporal gyrus (G_temporal_middle), and planum polare of the superior temporal gyrus (G_temp_sup-Plan_polar)

• Right hemisphere: angular gyrus (G_pariet_inf-Angular), superior temporal sulcus (S_temporal_sup), middle-posterior part of the cingulate gyrus and sulcus (G_and_S_cingul-Mid-Post), marginal branch of the cingulate sulcus (S_cingul-Marginalis), parieto-occipital sulcus (S_parieto_occipital), parahippocampal gyrus (G_oc-temp_med-Parahip), Inferior temporal gyrus (G_temporal_inf)

We present the result of this analysis in Author response image 1, where clusters are labelled according to the Destrieux anatomical atlas implemented in FreeSurfer:

Author response image 1.



As the reviewer points out, establishing relationships between our dependent and independent variables at a lower threshold of statistical significance might not reflect a true effect, and it is statistically more probable that multilingualism-related cortical thickness effects seem to be specific to the auditory regions. We do not exclude that an analysis of other pre-defined ROIs, performed at a similar level of detail as our present investigation, would uncover further significant associations between multilingual language experience and brain anatomy, but such an investigation is beyond the scope of the present work.

> *The reason(s) why we might find a link between cortical thickness and experience is not fully discussed. The introduction doesn't really mention why we'd expect cortical thickness to be correlated (positively or negatively) with speech experience. There is some discussion of it in the Discussion section as it relates to the Pliatsikas' Dynamic Restructuring Model, though I think that model only directly predicts thinning as a function of experience (here, negative correlations). It might have less to say about observed positive correlations e.g., HG in the right hemisphere. In any case, I do think that it's interesting to find some relationship between brain morphology and experience but clearer explanations for why these occur could help, and especially some mention of it in the intro so readers are clearer on why cortical thickness is a useful measure.*

We have expanded the section of the Introduction introducing cortical thickness pointing to different microstructural changes previously associated with environmental enrichment and skill learning (lines 68-73), and hope the link between cortical thickness and multilingual language experience is clearer now:

“Such environmental effect on cortical thickness might in turn be tied to microstructural changes to the underlying brain tissue, such as modifications in dendritic length and branching, synaptogenesis or synaptic pruning, growth of capillaries and glia, all previously tied to some kind of environmental enrichment and/or skill learning (see Lövdén et al., 2013; Zatorre et al., 2012 for overviews). Increased cortical thickness may reflect synaptogenesis and dendritic growth, while cortical thinning observed with MRI may be a result of increased myelination (Natu et al., 2019) or synaptic pruning.”

In addition, we have also expanded the Discussion section providing more reasoning for the links between cortical thickness and multilingual language experience (lines 557-566):

“Experience-induced pruning is essential for maintaining an efficient and adaptive neural network. It reinforces relevant neural circuits for faster more efficient information processing, while diminishing those that are less active, or less beneficial. The cortical specialization may need to arise because phonologically more diverse language experience requires that the mapping of acoustic signal to sound categories is denser, more detailed and more intricate. As a result, the brain may need to engage in more intensive processing to discriminate between and accurately perceive the sound categories of each language. This increased cognitive demand may, in turn, require the auditory and language processing regions of the brain to adapt and become more efficient. Over time, this heightened effort for successful speech perception and sound discrimination may lead to neural plasticity, resulting in cortical specialization. This means that cortical areas become more finely tuned and specialized for processing the unique phonological features of language(s) spoken by individuals."

> *One pitfall of quantifying phoneme overlap across languages is that what we might call a single 'phoneme', shared across languages, will, in reality, be realized differently across them. For instance, English and French may be argued to both use the vowel /u/ although it's realized differently in English vs. French (it's often fronted and diphthongized in many English speaker groups). Maybe the phonetic dictionaries used in this study capture this using a close phonetic transcription, but it's hard to tell; I suspect they don't, and in that case, the diversity measures would be an underestimate of the actual number of unique phonemes that a listener needs to maintain.*

The PHOIBLE database uses transcription that reflects phonological descriptive data as closely as possible, according to the available descriptive sources. Different realizations of sounds are (as much as possible) marked in the database. For example, the open front unrounded vowel /a/ is listed as e.g., [a] or [a̟], with the "+" sign denoting a fronted realization. This is done in PHOIBLE by the use of diacritics (see https://phoible.org/conventions) which further specify variations on the language-specific realizations of the phonemes listed in the database. Further details are available in Moran (2012) (https://digital.lib.washington.edu/researchworks/items/0d26e54d-950a-4d0b-b72c-3afb4b1aa9eb). In our calculation of phoneme-based distances a sign with and without a diacritic were treated as different phonemes, and therefore the different realizations were accounted for.

That said, we fully agree with the reviewer that in fact any diversity measure will be an underestimation of the actual variation, as between-speaker micro-variation can never be fully reflected in largescale typological databases as the one used in the present study. To the best of our knowledge, however, PHOIBLE offers the most comprehensive way of allowing for quantifying cross-linguistic variation to date, and we are looking forward for the field to offer further tools capturing the linguistic variability at an ever-finer level of detail.

> *Discussion of potential genetic differences underlying the findings is interesting. One additional data point here is a study finding a relationship between the number of repeats of the READ1 (a factor of the DCDC2 gene) in populations of speakers, and the phoneme inventory of language(s) predominant in that population (DeMille, M. M., Tang, K., Mehta, C. M., Geissler, C., Malins, J. G., Powers, N. R., ... & Gruen, J. R. (2018). Worldwide distribution of the DCDC2 READ1 regulatory element and its relationship with phoneme variation across languages. Proceedings of the National Academy of Sciences, 115(19), 4951-4956.) Admittedly, that paper makes no claim about the cortical expression of that regulatory factor under study, and so more work needs to be done on whether this has any bearing at all on the auditory cortex. But it does represent one alternative account that does not have to do with plasticity/experience.*

We thank the reviewer for bringing this important line of research to our attention, which we now included in the Discussion (lines 494-498 of the revised manuscript).

> *The replication sample is useful and a great idea. It does however feature roughly half the number of participants meaning statistical power is weaker. Using information from the first sample, the authors might wish to do a post-hoc power analysis that shows the minimum sample size needed to replicate their effect; given small effects in some cases, we might not be surprised that the replication was only partial. I don't think this is a deal breaker as much as it's a way to better understand whether the failure to replicate is an issue of power versus fragile effects.*

Thank you for the suggestion. Indeed, the effect sizes established in the analyses using the main sample were small (e.g., f2 = 0.07). According to a power analysis performed with G*Power 3.1 (Faul et al., 2009), detecting an effect of this magnitude of the predictor of interest at alpha = .05 (two-tailed), in a linear multiple regression model with 4 predictors (i.e., 3 covariates of no-interest: sex, age, hemispheric thickness, and 1 predictor of interest), a sample of N = 114 is required to achieve 80% of power. Our partial lack of replicating the effect might therefore indeed be related to a lower power of the replication sample, rather than the effect itself being fragile.

> ***Recommendations for the authors:***
>
> ***Reviewer #1 (Recommendations for the Authors):***
>
> *A few remaining details that I think you can handle:*
>
> *(1) Was there any correction for multiple comparisons, especially when multiple anatomical measures were investigated in separate models? (e.g. ln 130).*

Since three different anatomical measures were investigated in Analysis 1 and Analysis 2 (see Table 1), the alpha level of the two linear mixed models was lowered to α = .0166. Note that the p-values of the predictors of interest were p = .012 (mixed model with all auditory regions) and p = .005 (mixed model with all identified TTGs).

> *(2) In Table 2, since your sample skews heavily female, it would be more useful to present the counts of Male/Female totals for 1, 2, 3, 4, etc TTGs as proportions of the total for that sex rather than counts, so that the distribution across sex is more obvious.*

Thank you for bringing this issue to our attention. We have now included an additional row in Table 4, with proportions of males and females presenting different total number of identified gyri in the left and the right hemisphere.

> *(3) (ln 161) It wasn't clear to me how you dealt statistically with the fact that some participants had only one TTG - did you simply enter "0" as a value for cortical thickness for 2, 3, etc. for those participants? If so, it's possible that this result could reflect the number of split/duplicated gyri rather than the thickness of those gyri.*

Indeed, if non-existing gyri were coded with a value of “0” (it being the lowest possible thickness value), the results would reflect the configuration of TTGs (single vs multiple gyri) rather than a relationship between thickness and language experience.

The model was, however, fit to all available thickness values, and the gyri labels (1st, 2nd, 3rd) were modeled as a fixed factor with 3 levels. This procedure allowed us to localize the effect of language experience to a specific gyrus. The following formula was used with the lmer package in R:

thickness ~ age + sex + whole_brain_thickness + language_experience* gyrus*hemisphere + (1 | participant_id)

We observed a significant interaction between language experience and the 2nd gyrus (NB. no significant 3-way interaction between language experience, the 2nd gyrus and hemisphere pointed to the effect being bilateral). This result was then followed up with two linear models: one for the thickness values of the 2nd left and one for the 2nd right gyrus, each fit to the available data only (n = 130 for the left hemisphere; n = 96 for the right), see Table 5. This procedure ensured that only the available cortical thickness data were considered when establishing their relationship with our independent variable (language experience).

> *(4) I think more could be done in the results section to distinguish your three phonological measures--these details are evident in the Methods section, but if readers consume this paper front to back they may find it difficult to figure out what each measure really means.*

Thank you. We have added more explicit list of indices used in the Introduction (lines 104-107) and in Section 2.4. As per Reviewer #2 comments, the Methods section was also moved before the Results section, hopefully further enhancing the readability of the paper.

> *Typos:*
>
> *ln 270: "weighed"--could you have meant "weighted"?*

Corrected, thank you!

> *ln 377: "Apart from phoneme-based typological distance measure explaining" --> "Apart from *the* phonemebased..."*

Corrected, thank you!

> ***Reviewer #2 (Recommendations for the Authors):***
>
> *The interpretation of the results would be much helped by the methods section being moved to precede it. Now, much of the results section is methods summaries that would not have been needed if the reader had been presented with the methods beforehand. This is especially true for the measures of language experience and typological distances used.*

Thank you. We have moved the Materials and Methods section before the Results section.

> *The equation in section "4.2 Language experience" should be H = - sum(p_i log2 (p_i)) and not H = - sum(p_i log2(i)).*

Corrected, thank you!

> *It is unclear what "S" represents in the equation in the section "4.4 Combining typology and language experience (indexed by AoA)".*

The explanation has been added, thank you!

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