

Brain Structure Predicts the Learning of Foreign Speech Sounds

Narly Golestani^{1,2}, Nicolas Molko¹, Stanislas Dehaene¹, Denis LeBihan¹ and Christophe Pallier¹

¹Unité INSERM 562, Service Hospitalier Frédéric Joliot, CEA/DRM/DSV 4 Place du general Leclerc, 91401 Orsay cedex, France and ²Institute of Cognitive Neuroscience, University College London, London WC1N 3AR, UK

Previous work has shown a relationship between parietal lobe anatomy and nonnative speech sound learning. We scanned a new group of phonetic learners using structural magnetic resonance imaging and diffusion tensor imaging. Voxel-based morphometry indicated higher white matter (WM) density in left Heschl's gyrus (HG) in faster compared with slower learners, and manual segmentation of this structure confirmed that the WM volume of left HG is larger in the former compared with the latter group. This finding was replicated in a reanalysis of the original groups tested in Golestani and others (2002, Anatomical correlates of learning novel speech sounds. *Neuron* 35:997-1010). We also found that faster learners have a greater asymmetry (left > right) in parietal lobe volumes than slower learners and that the right insula and HG are more superiorly located in slower compared with faster learners. These results suggest that left auditory cortex WM anatomy, which likely reflects auditory processing efficiency, partly predicts individual differences in an aspect of language learning that relies on rapid temporal processing. It also appears that a global displacement of components of a right hemispheric language network, possibly reflecting individual differences in the functional anatomy and lateralization of language processing, is predictive of speech sound learning.

Keywords: brain anatomy, Heschl's gyrus, individual differences, phonetic perception, voxel-based morphometry, white matter

Introduction

There are marked individual differences in how quickly adults can learn to hear foreign speech sounds, in particular sounds that differ in terms of place of articulation, such as the *r/l* contrast for native Japanese listeners and such as the Hindi dental-retroflex for native English speakers (Pruitt and others 1990; Polka 1991; Bradlow and others 1997; Golestani and Zatorre 2004). The acoustic parameters that critically distinguish these phonemes are in the first 30-50 ms of the sounds, and thus, the ability to distinguish them relies on perceptual and neural systems designed to process very rapidly changing information. In previous work, we showed that nonnative listeners who are faster at learning to hear the dental-retroflex Hindi contrast have greater asymmetry (left > right) in the amount of white matter (WM) in the parietal lobes (Golestani and others 2002). Larger WM volumes in parietal regions can be due to myelination differences and/or differences in the number of WM fibers connecting intra- and interhemispheric language regions, resulting in more efficient neural processing. Thus, it is possible that individual differences in anatomical connectivity between anterior and posterior language regions in the left hemisphere, or between the auditory cortex and the

above regions, might in part predict individual differences in speech sound learning.

Previous studies have compared aspects of functional and structural anatomy as a function of proficiency in a second language. Using voxel-based morphometry (VBM), it has been shown that bilingual individuals have a higher gray matter (GM) "density" in the left parietal lobe compared with monolingual individuals. Further, it was shown that the degree of structural difference in this region is modulated by the proficiency attained and the age at acquisition in bilinguals, suggesting that there may be experience-dependent anatomical change in this region (Mechelli and others 2004). Chee and others (2004) examined the functional anatomy underlying phonological working memory (PWM) in bilinguals who were equally proficient in both languages ("equal bilinguals") and in bilinguals who were more proficient in one language than in the other ("unequal bilinguals"). They found greater left insula activation during a PWM task in the former compared with the latter group and suggested that more optimal engagement of regions involved in PWM in the former group may be related to greater proficiency in a second language in bilinguals (Chee and others 2004). Evidence for structural brain differences between people with different learning/experience histories has also been shown in domains other than language (Maguire and others 2000; Draganski and others 2004) including music (Schneider and others 2002; Gaser and Schlaug 2003). The above studies have all compared healthy individuals having attained a different "final state" due to learning and experience in a particular domain. Finally, studies have examined brain morphology in individuals diagnosed with dyslexia, a disorder that often involves speech sound processing difficulties. These studies have shown abnormal morphology of left angular, parietooccipital, and temporal regions in dyslexia (Rumsey and others 1986; Hynd and others 1990; Larsen and others 1990; Duara and others 1991; Kushch and others 1993) and in children with language disorders (Jernigan and others 1991; Plante and others 1991). More generally, there is evidence that variation in perisylvian anatomy accounts for variation in oral language ability (Rumsey and others 1997; Eckert and Leonard 2000; Eckert and others 2001). Lastly, there is evidence for WM microstructural abnormalities in temporoparietal regions in dyslexia (Klingberg and others 2000). Further, such abnormalities have been shown to vary continuously in relation to reading scores, even within the normal range, in adults (Klingberg and others 2000) and in children (Beaulieu and others 2005).

In the current study, we were interested in exploring systematic relationships between brain anatomy and normative individual differences in a measure of speech sound *learning*. We used the same stimuli and phonetic training procedures as

used previously (Golestani and others 2002) to train 65 native French speakers to distinguish the dental and retroflex sounds used in Hindi. We then selected the 11 fastest and 10 slowest learners and scanned them using high-resolution anatomical magnetic resonance imaging (MRI) and with diffusion tensor imaging (DTI) 3–4 months after training. We used optimized VBM to test for global as well as for more local anatomical differences such as the ones found previously between groups. We also compared aspects of sulcal and lobar anatomy using measures obtained from automatic segmentation of structures of interest, and we manually segmented regions of interest identified by VBM results. Finally, we tested for microstructural WM differences between the groups by comparing fractional anisotropy maps obtained from the DTI data.

Materials and Methods

Participants

Sixty-five native French speakers (33 men) were behaviorally trained to perceive the dental and retroflex sounds. Subjects had a homogeneous language background; all had learned a second language in school from the age of 11–18 years and a third language from the age of 13–18 years. None spoke a second or third language proficiently, and none had been regularly exposed to a language other than French before the age of 11. During training, the “fastest” learners were the ones who required the smallest number of training blocks to perform above the criterion level (80% correct) on the most similar sounds (stimuli 3 vs. 5, see below), and the “slowest learners” were the ones who could not reliably label the most different, prototypical dental and retroflex sounds (stimuli 1 vs. 7) even after 10 blocks of training. The 11 fastest (4 men) and the 10 slowest (2 men) learners were selected for MRI scanning. All subjects gave informed written consent to participate in the study, which was approved by the regional ethical committee.

Stimuli

Subjects were trained to perceive a synthetic version of the Hindi dental–retroflex contrast. There were 7 stimuli varying in equal steps in terms of the acoustic difference between adjacent items. Stimulus 1 corresponds to the dental voiced, unaspirated stop consonant prototype, and stimulus 7 corresponds to the retroflex prototype. All of the consonants were followed by the vowel /a/. The parameters that were manipulated to create the continuum are the frequency glides of the third formant (F3), as well as the center frequency of the initial noise burst. Details of stimulus synthesis and stimulus parameters have previously been reported (Golestani and others 2002).

Phonetic Training Paradigm

Training was administered in 20-trial blocks of identification with feedback where subjects heard one sound at a time, were asked to press one of two buttons corresponding to the presented sound, and received feedback on the computer as to the accuracy of their response. Training lasted approximately 15–20 min for each participant. We progressively reduced the acoustic difference between the stimuli to be identified as a function of successful performance by subjects. This “perceptual fading” training method adapts to subjects’ performance and allows them, if they are able to label the prototypical endpoint stimuli, to then try to distinguish dental and retroflex sounds that are a smaller step size apart. Subjects were initially asked to identify sounds 1 vs 7. If and when an individual achieved criterion performance, defined as 16/20 correct responses, on a given block, we administered stimuli 2 versus 6 during the next training block. Again, if and when criterion was reached with this slightly more difficult pair, we used stimuli 3 versus 5 for the next training block. Training was discontinued either once a subject achieved criterion on this last contrast or once they had completed a maximum of 200 trials (10 blocks).

MRI and DTI Acquisition and Analysis

Anatomical MRI and DTI scans were obtained on a 1.5-T Signa Horizon EchoSpeed MRI scanner (General Electric Medical Systems, Milwaukee,

WI). High-resolution anatomical T_1 -weighted images were acquired in the axial plane using a spoiled gradient echo sequence (128 slices, 1.2-mm thick, 2 number of excitations (NEX) [repetitions], time repetition [TR] = 10 ms, echo time = 2.2 ms, time to inversion = 600 ms, field of view [FOV] = 22 cm, $0.86 \times 0.86 \times 1.2$ -mm voxels). The diffusion tensor images were acquired using echo-planar imaging in the axial plain of the whole brain (DWSHFJ sequence parameters: 128 slices, 1 NEX, b value = 700, TR = 3000 ms, 41 directions, FOV = 22, $0.94 \times 0.94 \times 2$ -mm voxels).

We used VBM (Ashburner and Friston 2000), an exploratory, whole-brain technique, to search for relationships between brain morphology and phonetic learning. This method does not rely on the manual identification of anatomic boundaries and thus does not depend on arbitrary or conventional definitions of particular brain structures. Senjem and others (2005) offer a description and comparison of different VBM techniques. We used the optimized VBM method, in which the anatomical images were processed in 3 steps: tissue segmentation, linear spatial normalization, and smoothing at 6 mm. We chose this smoothing kernel in order to be able to compare the VBM and the DTI results and also to increase the chance of detecting group differences in small brain structures. Given that we complemented VBM with morphometric analyses including manual and automatic volume and sulcus segmentation (see below), we did not modulate the images during preprocessing. We compared the smoothed GM and WM images between the faster and slower learners on a voxel-by-voxel basis using independent samples t -tests. We used an uncorrected voxelwise threshold of $P < 0.001$ rather than a family-wise error rate corrected threshold of 0.05 for the whole brain because in this study, we use VBM in an exploratory manner and have followed up on any VBM findings with other morphometric analyses.

Diffusion tensor images were first corrected for distortions. The diffusion tensor was then calculated on a pixel-by-pixel basis using Brainvisa (Cointepas and others 2001, 2003). The fractional anisotropy (FA) images were normalized using a linear transformation calculated on the anatomical images and then smoothed at 5 mm. Finally, independent sample t -tests were performed to compare FA maps between faster and slower learners.

We obtained parietal lobe GM and WM volumes using an automatic segmentation technique that relies on the ANIMAL and INSECT programs. We used this method because it is the one that was previously used (Golestani and others 2002) to obtain the findings that we were attempting to replicate. This method involves combining automatic tissue classification with nonlinear registration to a template brain for which brain regions have been manually defined (Collins and others 1995, 1999; Collins and Evans 1997).

We also used Brainvisa (<http://brainvisa.info/>) to automatically segment and identify sulci of interest in the anatomical images. This method results in occasional labeling errors that were manually corrected. We performed statistical analyses on sulcal measures using the DataMind statistical toolbox (Duchesnay and others 2004). Lastly, in order to facilitate the interpretation of the voxel-based analyses, we performed regional morphometric analyses using Anatomist (<http://brainvisa.info/>) on a structure of interest (Heschl’s gyrus [HG]) identified by the VBM results. This software allows simultaneous real-time viewing and voxel labeling on sagittal, coronal, and horizontal planes.

Results

VBM and DTI

The results of VBM on WM and GM tissue-classified maps are listed in Tables 1–4, respectively. VBM on WM tissue-classified maps showed higher WM density in left Heschl’s gyrus (LHG) in faster compared with slower learners (t -score = 4.39, $P < 0.001$, Fig. 1 and Table 1), suggesting that there is a higher probability of WM existing in this region in the former compared with the latter group. This same comparison also revealed higher WM density in the former compared with the latter group in regions including the lingual gyri bilaterally (Table 1). Given that this result was obtained using linear normalization of the WM tissue-classified maps and that this could make it more likely

Table 1

VBM WM findings: faster minus slower learners

Structure	Talairach coordinates			t-value	Cluster size
	x	y	z		
LHG	-44	-21	9	4.39	81
Right precentral gyrus, WM	47	-10	29	4.96	165
Left lingual gyrus	-4	-73	3	5.14	317
Right lingual gyrus	13	-71	6	4.54	157

Note: VBM results are listed at $P < 0.001$.**Table 2**

VBM WM findings: slower minus faster learners

Structure	Talairach coordinates			t-value	Cluster size
	x	y	z		
WM anterior to left parietooccipital sulcus	-28	-66	21	6.36	206
WM anterior to right parietooccipital sulcus	31	-63	19	4.16	21
Right middle temporal lobe, WM	52	-2	-16	5.11	144
Right insula	39	-9	21	3.98	55

Note: VBM results are listed at $P < 0.001$.

that brain size or shape differences might be driving this result, we repeated the group comparison while this time including brain volume measures as a regressor of noninterest. The lingual gyrus results are still significant in this new analysis. (Talairach coordinates—left: -5, -74, 2, $t = 5.31$, $P < 0.001$, $k = 274$; right: 13, -71, 6, $t = 4.33$, $k = 91$). Comparison of WM maps of slower versus faster learners revealed a difference anterior to the left parietooccipital sulcus, in a region similar to the one previously detected (Golestani and others 2002) (location in Talairach space: -28, -66, 21). There was a finding in a similar region in the right hemisphere (Table 2). There was also a difference at the same left hemispheric location when comparing GM maps of faster versus slower learners (Table 3). Inverse relationships between GM and WM are typically found in brain regions in which GM and WM tissues are in close proximity, and when found near a sulcus, and can be due to a positional displacement of this latter between groups or conditions (cf., Golestani and others 2002). Results of tests on the location of the parietooccipital sulcus, which lies posterior to the reported VBM findings, are reported below. Lastly, VBM comparing GM tissue-classified maps of faster compared with slower learners yielded a result just superior to the right insula (at location: 39, -9, 22, see Table 3). There was a finding in the same region when comparing WM maps of slower with faster learners (Table 2), also suggesting a displacement in the position of this structure across groups. Results of tests on the location of the right insula across groups are also presented below.

DTI results are presented in Table 5. A t -test comparing the FA maps of slower with faster learners revealed a difference in the right insula, at a location similar to that obtained in the VBM results. There was also a bilateral trend in the region anterior to the parietooccipital sulcus, again at locations similar to those obtained in the VBM results. The opposite subtraction (faster vs. slower learners) yielded no significant results. The fact that the DTI findings are at similar locations to the VBM ones and that they are located in brain regions that are at or near GM/WM borders suggests that they reflect differences in the relative presence of GM versus WM such as might be detected with VBM, rather than differences in myelination or in WM anatomical connectivity per se.

Table 3

VBM GM findings: faster minus slower learners

Structure	Talairach coordinates			t-value	Cluster size
	x	y	z		
WM anterior to left parietooccipital sulcus	-28	-66	21	6.21	151
Right insula	39	-9	22	4.83	216

Note: VBM results are listed at $P < 0.001$.**Table 4**

VBM GM findings: slower minus faster learners

Structure	Talairach coordinates			t-value	Cluster size
	x	y	z		
Right parietal lobe	36	-30	37	4.52	161
Right cingulate gyrus	17	-4	42	4.46	216

Note: VBM results are listed at $P < 0.001$.

In order to test whether or not the lack of finding in LHG in the previous study (Golestani and others 2002) might have been due to the use of a different VBM methodology between studies (i.e., optimized VBM using a 6-mm smoothing kernel in the present study vs. standard VBM using a 12-mm smoothing kernel in the original study), we performed 1) standard VBM on the present data set using the same (6 mm) smoothing kernel, 2) standard VBM using a 6-mm smoothing kernel on the previous data set, and 3) optimized VBM using a 6-mm smoothing kernel on the previous data set. Neither standard VBM analyses on the present data set nor standard VBM on the original data set using a 6-mm smoothing kernel revealed WM density group differences in LHG. Optimized VBM using a 6-mm smoothing kernel on the previous data set, however, successfully replicated the finding of higher WM density in LHG in faster compared with slower phonetic learners ($t_{19} = 3.94$, $P < 0.001$, location in Talairach space: -48, -22, 6).

Segmentation of Parietal Lobes

We wanted to compare the relative contribution of GM and WM in the left and right parietal lobes in the 2 groups and see if results replicate the previous finding of a greater contribution of WM compared with GM in left compared with the right hemisphere only in faster learners. We therefore obtained automatically segmented parietal lobe GM and WM volumes and performed 2-way (hemisphere: left vs. right and tissue type: gray vs. white) repeated-measures analysis of variance (ANOVA) for faster and slower learners separately. For faster learners, there was a main effect of hemisphere, indicating larger parietal lobe volumes in the left compared with the right hemisphere ($F_{1,9} = 4.78$, $P < 0.05$, 1.6% difference in volume). There was also a main effect of tissue type, reflecting more GM compared with WM ($F_{1,9} = 42.0$, $P < 0.001$). The hemisphere by tissue type interaction was not significant. For slower learners, we found only a main effect of tissue type, again reflecting more GM compared with WM ($F_{1,9} = 46.8$, $P < 0.001$).

Sulcal Analyses

In order to test for a possible anterior-posterior displacement of the parietooccipital sulcus between groups, we performed tests on measures of the y axis position of the sulcus extremity between groups and between hemispheres. A 2-way (group by hemisphere) repeated-measures ANOVA revealed a main effect

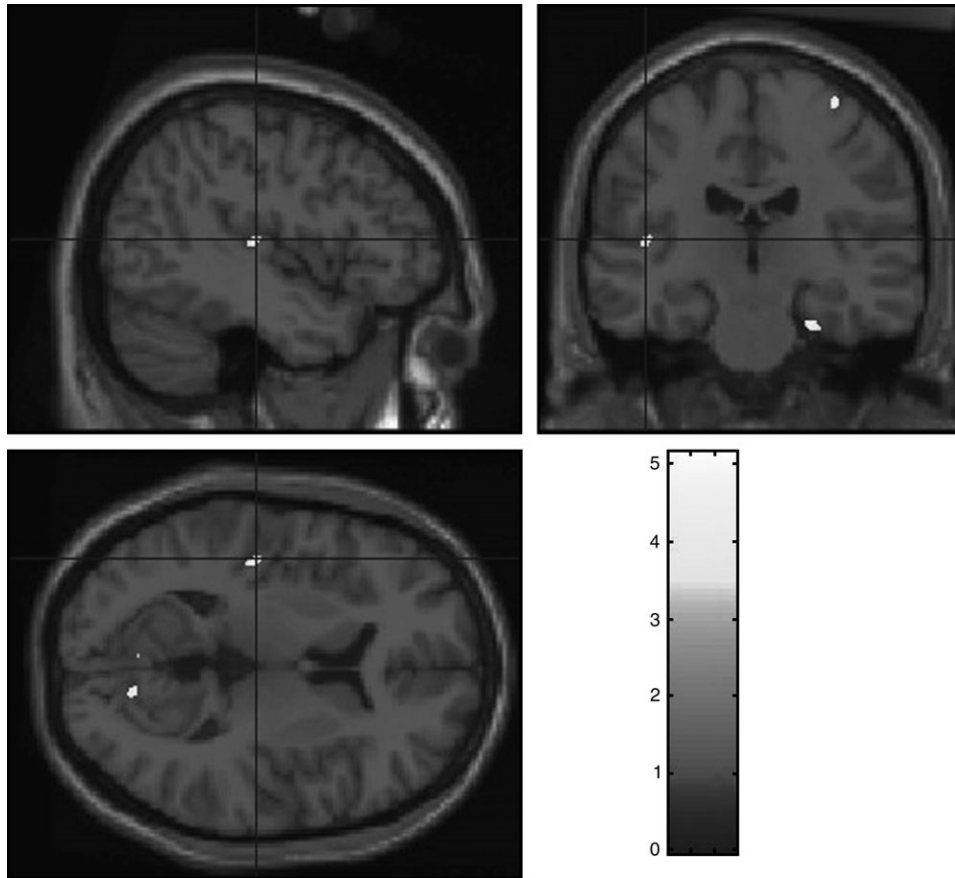


Figure 1. Anatomical difference in LHG: statistical parametric maps showing greater WM density in faster compared with slower learners (location: $x = -44$, $y = -21$, and $z = 9$). The images are presented in the neurological convention (the left hemisphere is on the left side of the image).

Table 5

DTI, FA: slower minus faster learners

Structure	Talairach coordinates			t-value	Cluster size
	x	y	z		
Right insula	44	-6	22	6.73	433
WM anterior to left parietooccipital sulcus	-30	-62	22	4.51	37 ^a
WM anterior to right parietooccipital sulcus	33	-56	21	5.27	30 ^a

Note: DTI results are listed at $P < 0.001$, corrected for multiple comparisons.

^aIndicates a trend, where the cluster extent is not significant.

of hemisphere ($F_{1,19} = 151.4$, $P < 0.001$, mean y axis displacement between hemispheres: 19 mm), indicating that the sulcus is more posteriorly located in the left compared with the right hemisphere, and of group ($F_{1,19} = 11.1$, $P < 0.005$, mean y axis displacement between groups: 6 mm), indicating that the sulcus is more posteriorly located in the faster compared with the slower learners (Fig. 2). The hemisphere by group interaction was not significant ($F_{1,19} = 3.2$, $P > 0.01$). Similarly, in order to test for a possible displacement of the right insula between groups, we performed tests on the x , y , and z axis positions of the center of gravity of this automatically segmented structure in both hemispheres. The only significant result was a difference in the z axis position of the right insula ($t_{19} = -3.81$, $P < 0.001$, mean displacement: 3 mm), revealing that the right insula is more superiorly located in slower compared with faster learners.

Segmentation of HG

In order to better characterize the VBM result in HG, we manually labeled (segmented) the left and right HG of the 21 subjects on anatomically normalized images using previously defined criteria (Penhune and others 1996). In cases where there were multiple transverse gyri, or when there was a single gyrus divided by a sulcus intermedius (SI) that extended to at least half of the length of HG, we included only the most anterior gyrus or gyral subregion, respectively, regions most likely to encompass the primary auditory cortex (Rademacher and others 2001). The rater was blind to group (faster vs. slower) and hemisphere, and the labeling was performed twice. HG volumes were significantly correlated across labelizations (left: $r = 0.81$, $P < 0.001$, $P < 0.001$, right: $r = 0.78$), providing evidence for labelization reliability. We found that the left but not the right HG is larger in faster compared with slower learners (left: $t_{19} = 2.13$, $P < 0.05$, 1-tailed, right: $t_{19} = 0.87$, $P > 0.05$, 1-tailed, Fig. 3*a,d*). A similar result was found for native (nonnormalized) HG volumes (left: $t_{19} = 1.93$, $P < 0.05$, 1-tailed, right: $t_{19} = 1.15$, $P > 0.05$, 1-tailed). We replicated this result in an independent sample of subjects, these being the 10 fastest and 10 slowest phonetic learners from the previous study (Golestani and others 2002) (LHG volume: $t_{18} = 3.79$, $P < 0.001$, 1-tailed). Further, we used automatically segmented GM and WM T_1 maps as masks to obtain GM and WM volumes of HG and found that the LHG group difference, in the current sample, is due to WM and not GM volume differences (GM: $t_{19} = 1.37$, $P > 0.05$, 1-tailed, Fig. 3*b*, WM: $t_{19} = 2.44$, $P < 0.05$, 1-tailed, Fig. 3*c*).

From Figure 3c, it appears that an outlier might be driving the WM group difference; however, this difference remains significant after the exclusion of the individual with the largest WM volume ($t_{18} = 2.52, P < 0.05$). Again, this pattern was also found

for native HG volumes (GM: $t_{19} = 1.21, P > 0.05$, 1-tailed, WM: $t_{19} = 2.34, P < 0.05$, 1-tailed). A linear discriminant analysis on WM volumes correctly classifies 76% (16/21) of the subjects.

An index of asymmetry, $\Delta = (R - L)/(R + L)/2$, was calculated for the total as well as for the WM and GM volumes of HG for the faster and slower learners (cf., Penhune and others 1996). An index value is considered asymmetric when $\Delta \geq 0.10$, and a negative value indicates leftward asymmetry. The mean asymmetry indices on normalized volumes for the 2 groups were the following—overall HG volumes: faster learners $\Delta = -0.08$ and slower learners $\Delta = -0.05$, HG GM volume: faster learners $\Delta = -0.07$ and slower learners $\Delta = -0.05$, and HG WM volume: faster learners $\Delta = -0.12$ and slower learners $\Delta = -0.005$. Independent sample *t*-tests revealed a significant group difference in the asymmetry index for WM volumes only, both for normalized ($t_{19} = -1.73, P < 0.05$) and for native ($t_{19} = -1.73, P < 0.05$) volumes, indicating a greater leftward asymmetry in HG WM volumes in the faster compared with the slower learners.

In order to test for differences between groups in the position of HG, we performed independent samples *t*-tests on the *x*, *y*, and *z* coordinates of the center of gravity of left and right HG. The only significant result was a group difference in the *z* axis coordinates of right HG, indicating that this structure

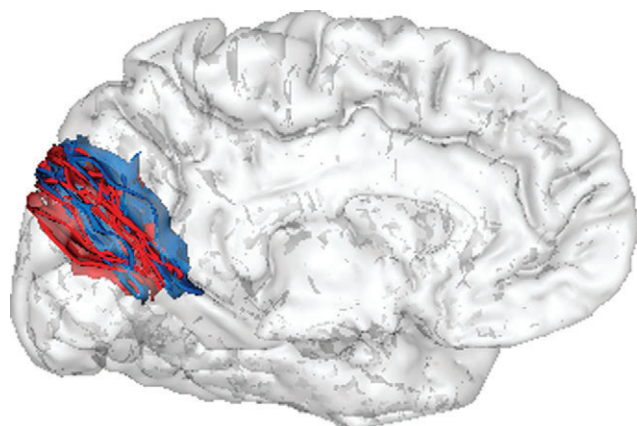


Figure 2. Medial view of parietooccipital sulcus in faster (red) and in slower (blue) learners shown on a transparent 3-dimensional brain (left hemisphere).

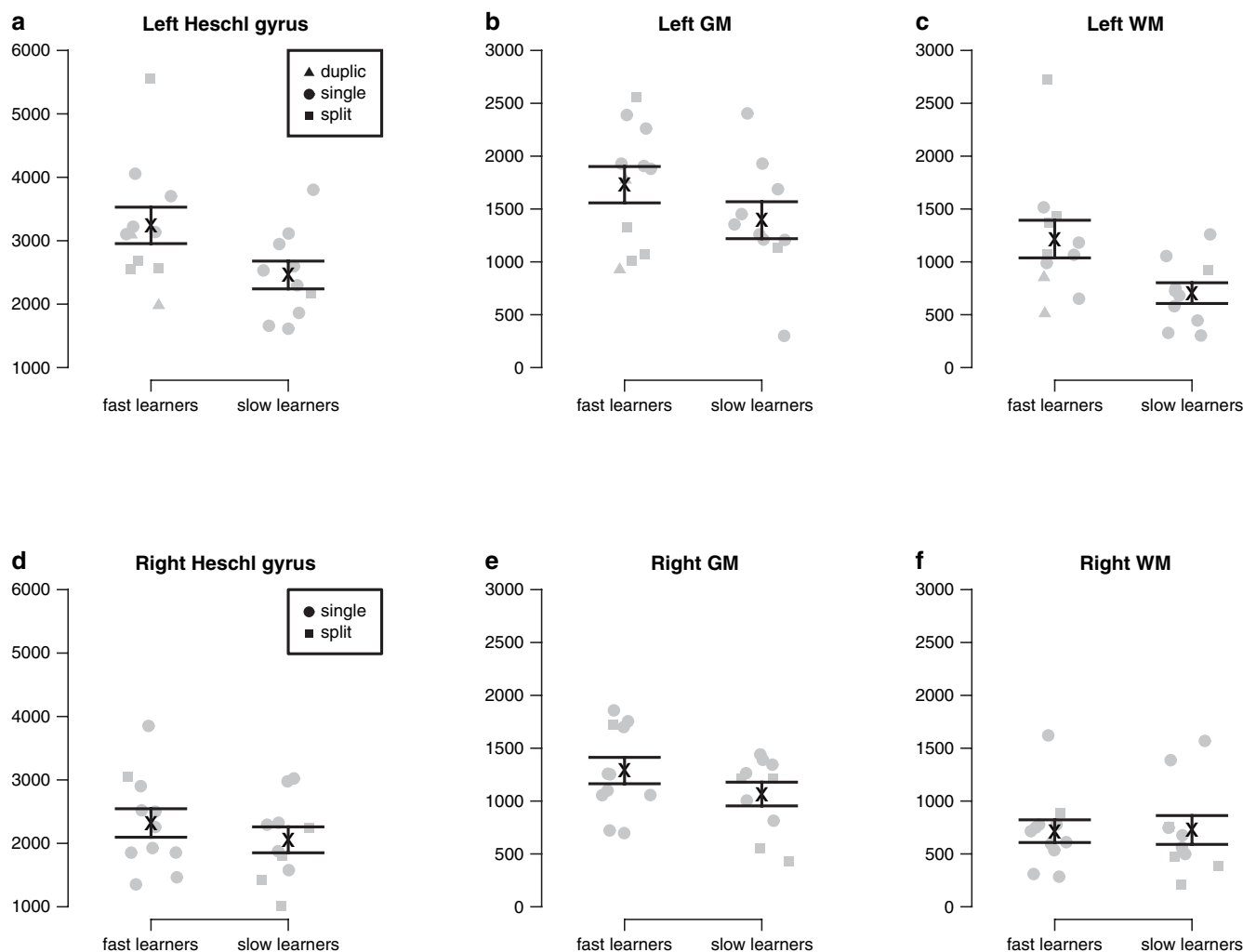


Figure 3. HG volumes for faster and slower learners and for (a) LHG, (b) LHG GM volume, (c) LHG WM volume, (d) right HG volume, (e) right HG GM volume, and (f) right HG WM. Bars represent one standard error above and below the mean.

is more superiorly located in slower compared with faster learners ($t_{19} = -2.13$, $P < 0.05$, mean displacement: 2.5 mm).

Finally, we explored group differences in the gross morphology of LHG by examining the frequency of duplication or splitting of HG in the left hemisphere in slower and faster learners. We found that in the group of faster learners, 6/11 individuals had either a duplicate or a split LHG, whereas in the group of slower learners, only 1/10 individuals had duplicate or split LHG. Figure 3a presents a scatter plot in which the frequency of these patterns can be seen in the 2 groups (symbols represent a single, split, or duplicate transverse gyrus). The odds ratio for having either a duplicate or a split LHG is therefore over 5-fold if one is a faster learner, and conversely, it is at least 5 times more likely that one is a faster learner if one has a duplicate or a split LHG. As described above, HG labeling criteria involved including only the more anterior transverse gyrus in the case that there was either duplicate transverse gyri or a SI which extended at least half the length of HG (see Materials and Methods). We therefore also tested for group differences in HG volumes when excluding the subjects who had either a duplicate or a split LHG. In other words, we tested for group differences in HG volumes that are less influenced by gross morphometric features. Tests revealed a group difference in LHG volume when including only the 14 subjects that did not have a split or a duplicate LHG ($t_{12} = 2.66$, $P < 0.05$, 1-tailed). In addition, WM volumes were also significantly larger in faster compared with slower learners in this subgroup ($t_{12} = 2.26$, $P < 0.05$).

Discussion

We found a number of anatomical differences between people who are faster and slower at learning to hear foreign speech sounds. These include differences not only in auditory regions such as LHG but also in components of a more general “language network” and its right hemisphere counterparts such as the parietal lobe and the right insula. Note that the use of a small smoothing kernel and a liberal statistical threshold in the VBM analyses increases the likelihood of obtaining false-positive results. However, as noted above (see Materials and Methods), we consider VBM to be an exploratory tool in this study, and have used other complimentary methods to better understand all but one of the results arising from the VBM analyses discussed below. Group comparisons of FA maps obtained from diffusion tensor images did not yield results over and above those found using VBM. We will discuss the different results below and explore possible implications of these with respect to what is known about the functional anatomy of these regions. We will also explore some of the clinical implications of these results by comparing them with previous anatomical and functional findings in individuals with language impairments.

VBM and manual labeling revealed higher WM density and larger volumes, respectively, of LHG in faster compared with slower phonetic learners, both in the present sample and in an independent sample of subjects, these being the participants of the previous study (Golestani and others 2002). In the present sample, this difference was due to WM rather than GM volume differences. We also found a leftward asymmetry of HG WM volumes in faster but not in slower learners. Our findings are relevant to work showing that normative anatomical asymmetries in the primary (Penhune and others 1996) and secondary (Anderson and others 1999) auditory cortex arise from WM volume differences. Differences in WM volume can be due to

greater myelination and/or a greater number of WM fibers connecting HG to regions such as the secondary auditory cortex, as well as to other brain regions involved in speech and speech sound processing, such as the parietal and frontal cortices. If the differences are due to greater myelination, this would allow faster conduction of neural signals, resulting in more efficient neural processing, which is likely critical for the successful processing and learning of certain speech sounds that involve very rapid acoustic change. Our findings, as well as the above-mentioned normative ones, support the idea that left auditory cortex is specialized for processing rapidly changing information (Zatorre and Belin 2001; Zatorre and others 2002). Further, our results suggest that normative variation in auditory cortex WM anatomy and in its degree of left/right asymmetry is predictive of an aspect of language learning, which relies on efficient temporal processing. More generally, our finding of greater asymmetry in the WM volume of HG in faster phonetic learners may constitute an extension of the above-mentioned findings of abnormal symmetry or reversed asymmetry of the planum temporale (PT) in people with poor verbal ability (Rumsey and others 1997; Eckert and Leonard 2000; Eckert and others 2001) in that we show that *more pronounced* asymmetry in regions including the primary auditory cortex in part predicts “above-average” performance during speech sound learning.

Interestingly, larger GM volumes of HG have been found bilaterally in musicians compared with nonmusicians (Schneider and others 2002), and further, it has been shown that these volumes correlate with musician status (i.e., professional musicians, amateur musicians, nonmusicians) (Gaser and Schlaug 2003) and musical aptitude (Schneider and others 2002). It remains for future work to examine the mechanisms whereby certain cognitive/behavioral measures are predictive of auditory cortex WM anatomy and others of auditory cortex GM anatomy. It can be speculated, however, that WM anatomy, which may be more important in determining temporal processing efficiency, is predictive of measures that rely more heavily on accurate processing of information changing on a timescale of 30–50 ms (e.g., processing of certain speech sounds) and that GM anatomy is predictive of auditory processing that does not depend as critically on temporal distinctions that are on such a small timescale (e.g., musical processing).

We also found that gross morphological features of the auditory cortex in part predict phonetic learning. Specifically, we found that faster phonetic learners are over 5 times more likely to have either a split or a duplicate LHG than are slower learners (see Fig. 3a). The gross morphology of HG and of the surrounding cortex is very variable between individuals and between hemispheres. For example, there can be from 1 to 3 gyri per hemisphere, and the number of gyri can differ between hemispheres. As previously noted, cytoarchitectonic studies show that the primary auditory cortex encompasses the most medial two-thirds of the most anterior HG. Taken together, our results suggest that both the gross morphology of LHG, which may be less directly related to cytoarchitecture, as well as volume differences based on morphometric landmarks which tend to favor the inclusion of primary auditory cortex, predict phonetic learning. The former suggests that even when examining features which include regions more likely to encompass secondary auditory cortices (e.g., in the case of HG duplication), one can in part predict speech sound learning. This in turn suggests that anatomical features predictive of phonetic learning

are not limited to primary auditory cortex but may extend to the PT and/or to other secondary auditory regions.

We replicated a previous finding of a more posterior parietooccipital sulcus in faster compared with slower learners and more posterior parietooccipital sulcus in the left compared with the right hemisphere. We did not replicate the hemisphere by group interaction reported previously (Golestani and others 2002), possibly because of the use of different methodologies across studies. Specifically, in the previous work, the parietooccipital sulcus was manually labeled, whereas in the present study, it was automatically labeled, possibly resulting in more noisy measures and thereby making it more difficult to detect a possible interaction. We found greater parietal lobe asymmetry (left > right) in faster compared with slower phonetic learners. In contrast to our previous findings (Golestani and others 2002), the group difference was not found to be limited to WM. The hemisphere and group differences in the position of the parietooccipital sulcus reported above could arise from differences in the volume or shape of the parietal lobes. Specifically, it is possible that larger left parietal lobe volumes in faster learners result in a posterior positional shifting of the sulcus in the left compared with the right hemisphere and/or in faster compared with slower learners. Greater parietal lobe asymmetry in faster compared with slower learners may be related to the known functional asymmetry for speech-related functions in the temporoparietal regions. Functional activation studies have repeatedly shown left parietotemporal involvement during phonetic processing tasks (Petersen and others 1989; Démonet and others 1992, 1994; Zatorre and others 1992, 1996; Paulesu and others 1993), and this region is thought of by some as the location of the phonological store in verbal working memory (Paulesu and others 1993; Jonides and others 1998; Henson and others 2000; Honey and others 2000). Interestingly, as mentioned above, it has been shown that bilingual individuals have a higher GM "density" in the left inferior parietal cortex compared with monolingual individuals and that the amount of structural difference in this region is modulated by proficiency and age of acquisition (Mechelli and others 2004). Taken together, these findings as well as ours suggest that individual differences in phonetic learning and also in more general aspects of second language proficiency attainment may be in part predictable by left parietal lobe anatomy.

The finding of larger WM volumes in LHG in faster compared with slower learners and differences across groups in parietal lobe asymmetry may be related. Specifically, it is possible that differences in connectivity between the left auditory cortex and left inferior parietal language regions are predictive of speech sound learning. This hypothesis will be tested by quantifying and comparing WM fiber-tracking results on DTI data obtained in the present sample. Interestingly, related to this hypothesis, there is evidence for disrupted functional connectivity between the left angular and temporal regions in dyslexic individuals (Horwitz and others 1998). More generally, it appears that anatomical differences in a network of regions in part predict an aspect of language learning. This network includes the left auditory cortex and parietal cortices, as well as regions that are not typically associated with language processing. For instance, we found higher WM density in the lingual gyri bilaterally in faster compared with slower learners, suggesting that the anatomy of certain visual brain regions, possibly including the shape of this or adjacent regions, may in part predict phonetic learning. There is evidence for right lingual gyrus involvement

during visual phonological processing (Burton and others 2005), and thus, it is possible that anatomical differences in regions thought to be involved in visual imagery and/or visual phonological processing also in part predict speech sound learning. Lastly, we found anatomical differences in right hemisphere structures between faster and slower learners: the right insula and right HG appear to be located more superiorly in slower compared with faster learners, suggesting a global displacement of certain right hemisphere structures between groups. These findings could be due to group differences in the degree of anatomical asymmetry of these components of a language network, which in turn could be related to the degree of functional lateralization for speech across groups, an idea to be tested in future studies.

Taken together, our results suggest that anatomical differences and possibly connectivity differences in a whole functional network predict an aspect of language learning. Further, it is possible that individuals with a particular type of cortical response to speech sounds, which arise from a particular pattern of anatomical connectivity, can learn to hear new speech sounds more quickly. More generally, WM anatomy may be different in some individuals compared with others as a result of experience driven by other anatomical particularities and functional network properties. For example, anatomical and functional differences in regions involved in visual phonological processing could facilitate phonetic perception for some individuals over others, and resulting qualitative differences in experience with speech sounds could in turn result in anatomical or anatomical connectivity changes in auditory or parietal regions. Avenues for future research include using very recent developments in the use of MRI in infants (Dehaene-Lambertz and others 2002) to determine whether very early anatomical differences might predict early or later behavioral abilities and/or the development of brain anatomy later in life (Paus 2005).

Notes

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Address correspondence to Narly Golestani, Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK. Email: n.golestani@ucl.ac.uk

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