Anatomical Correlates of Learning Novel Speech Sounds

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Summary

We examined the relationship between brain anatomy and the ability to learn nonnative speech sounds, as well as rapidly changing and steady-state nonlinguistic sounds, using voxel-based morphometry in 59 healthy adults. Faster phonetic learners appeared to have more white matter in parietal regions, especially in the left hemisphere. The pattern of results was similar for the rapidly changing but not for the steady-state nonlinguistic stimuli, suggesting that morphological correlates of phonetic learning are related to the ability to process rapid temporal variation. Greater asymmetry in the amount of white matter in faster learners may be related to greater myelination allowing more efficient neural processing, which is critical for the ability to process certain speech sounds.

Introduction

There are important individual differences in how well adults perform language-related tasks such as learning new speech sounds (Polka, 1991; Jenkins et al., 1995). The main goal of the present study was to examine whether such individual differences might be related to differences in brain anatomy. During development and starting as early as at 6 months of age, lack of experience with certain nonnative speech sounds results in a developmental shift from a language-general to a language-specific pattern of phonetic perception (Best et al., 1988; Polka and Werker, 1994; Werker and Tees, 1984a; Werker and Lalonde, 1988; Kuhl et al., 1992). In adulthood, most individuals cannot distinguish certain nonnative speech sounds from similar ones belonging to the native language. The results of laboratory studies aimed at improving nonnative phonetic perception have shown that some contrasts are more easily learned than others. Interestingly, even among adults with very similar language backgrounds, considerable individual differences exist in the ability to learn to perceive "difficult" nonnative speech sounds following phonetic training (Polka, 1991; Pruitt et al., 1990; Jenkins et al., 1995).

In the present study, we used voxel-based morphometry to investigate whether such individual differences might be predicted by differences in brain morphology. This method allows an exploratory search throughout the brain for relationships between a behavioral measure and brain morphology. It does not require subjective

identification of anatomic boundaries and, hence, the use of arbitrary or conventional definitions of particular brain structures. Furthermore, it allows examination of white matter morphology, which is otherwise difficult due to the lack of clear boundaries between adjacent white matter subregions. Voxel-based morphometry has been used by other investigators to demonstrate normative brain asymmetries (Watkins et al., 2001), maturation of white matter tracts (Paus et al., 1999), structural correlates of arithmetic abilities (Isaacs et al., 2001), and differences in brain morphology in normal versus clinical groups (Vargha-Khadem et al., 1998; Wright et al., 1995; Thompson et al., 2001).

We trained 59 healthy individuals to distinguish a phonetic contrast not present in their native language: the dental and retroflex sounds used in Hindi. Previous functional imaging work on phonetic perception has shown the involvement of several temporoparietal regions of the left hemisphere (Démonet et al., 1994; Zatorre et al., 1992, 1996; Binder et al., 1996, 1997; Petersen et al., 1988; Paulesu et al., 1993), the superior temporal gyri bilaterally (Binder et al., 1994; Mazoyer et al., 1993; Jäncke et al., 1998; Mummery et al., 1999), and left inferior frontal regions in and around Broca's area (Zatorre et al., 1992, 1996; Paulesu et al., 1993; Fiez et al., 1995; Burton et al., 2000). We predicted that phonetic learning measures would be correlated with differences in brain morphology in language-related cortical areas. In addition, we wanted to test the speech-specificity of any potential anatomical correlates of phonetic learning. It has been proposed that the ability to process certain consonant speech sounds depends on the ability to track rapidly changing acoustic information (Efron, 1963; Tallal et al., 1993; Benasich and Tallal, 1996) and that what has traditionally been thought of as dominant hemispheric specialization for speech may in effect be a more general and multimodal underlying specialization for the processing of rapidly changing information over time (Schwartz and Tallal, 1980; Belin et al., 1998; Zatorre and Belin, 2001). We therefore also trained subjects to perceive two other sets of nonlinguistic stimuli, consisting of rapidly changing sounds and steady-state tonal sounds, and examined associations and/or dissociations between the anatomical correlates of the three stimulus types (see Figures 1 and 2).

Synthetic seven-step continua were used for all three stimulus types, and testing and training procedures were identical for each of these. Subjects were tested using an identification task before and after training. Training involved one session of identification with feedback. For each stimulus type, we measured (1) pre-training identification slopes, reflecting initial performance; (2) post- minus pre-training identification slopes, reflecting the amount of improvement in performance resulting from training; and (3) L scores, a continuous variable developed to quantify learning rate during training. We correlated these measures with gray (GM) and white matter (WM) values from MRI scans using voxelwise analysis. This analysis was followed by regional morphometric analyses in areas revealed by the voxel-

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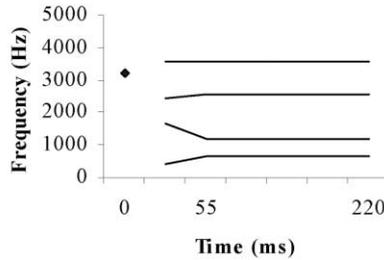
A: Dental CV
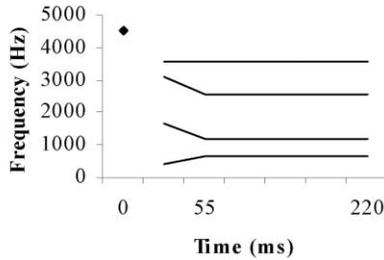
B: Retroflex CV

Figure 1. Hindi Stimuli

Schematized frequency versus time diagrams of the (A) dental and (B) retroflex synthetic consonant-vowel syllables. Each line represents the center frequency of a formant. The black dot indicates a noise burst.

based analysis. For the two nonlinguistic stimulus types, we only performed analyses that yielded significant results with the speech sounds, as the aim was to test the specificity of the effects.

Results

Behavioral Results
Identification

For each of the stimulus types, subjects were required to classify sounds from a seven-step stimulus continuum as belonging to one of two categories: "A" or "B." Figure 3 presents the mean percentage of "A" responses for each of the seven stimuli during pre- and post-training identification of the three stimulus types. For the Hindi stimuli, responses "A" and "B" correspond to the dental and retroflex sounds, respectively.

The slopes of individual subjects' identification curves and of identification curves averaged across subjects were calculated using a standard regression approach. Relatively steeper negative slopes reflect a relatively better ability to reliably identify the sounds in each stimulus set. A 2×3 two-way repeated measures ANOVA was performed on the identification slopes, with time (pre- versus post-training) and stimulus type (Hindi, nonlinguistic, and tonal) being the within-subjects variables. Results revealed a main effect of time [$F(1,58) = 62.49$, GG-corrected, $p < 0.001$], indicating that the post-train-

ing identification functions (mean slope, collapsed across stimulus type, was equal to -0.82) were steeper than the pre-training ones (mean slope $= -0.43$), reflecting improved performance after training. The effect of stimulus type was not significant. In addition, a significant interaction was found between time and stimulus type [$F(2, 116)$ (GG) $= 3.17$, $p < 0.05$]. We performed tests of simple main effects on the effect of training for each stimulus type in order to ensure that there was improvement in performance for all three stimulus types. Results revealed that performance was significantly better after, relative to before, training for all three stimulus types [Hindi: $F(1,58) = 8.47$, $p < 0.01$; nonlinguistic: $F(1,58) = 16.56$, $p < 0.01$; and tonal: $F(1,58) = 26.94$, $p < 0.01$]. Tests of simple main effects on the effect of stimulus type at pre- and at post-training revealed that identification performance was similar across the three stimulus types before training [$F(2,116) = 0.147$, $p > 0.05$]. After training, however, there was a significant difference in identification performance across the three stimulus types [$F(2,116) = 3.23$, $p < 0.05$]. Newman-Keuls post-hoc tests revealed that identification performance was significantly better on the tonal relative to the Hindi stimuli ($Q = 3.59$, $p < 0.05$).

Training

L scores were calculated for each subject, providing a measure of learning rate. Scores can range from 0 to 600, the higher scores indicating faster learning. There
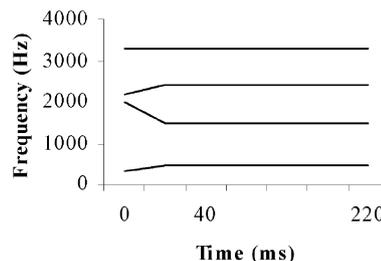
A: Stimulus 1
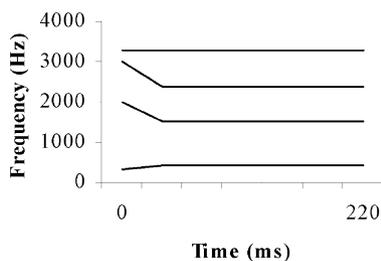
B: Stimulus 7

Figure 2. Nonlinguistic Stimuli

Schematized frequency versus time diagrams of (A) sound 1 and (B) sound 7 from the rapidly changing nonlinguistic stimulus continuum. Each line represents the center frequency of a formant.
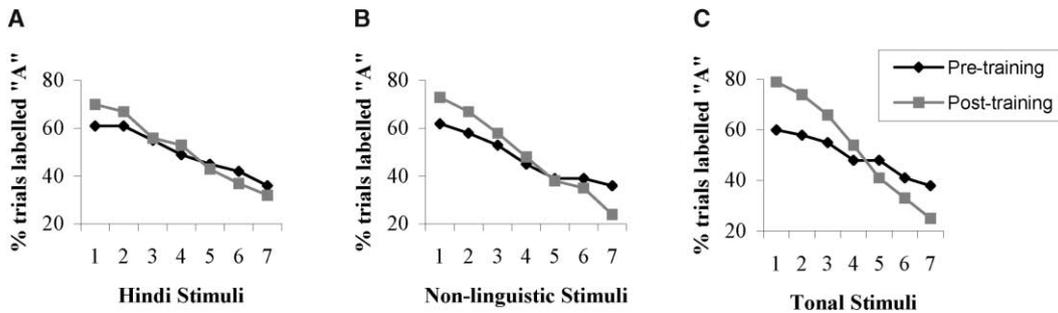
Figure 3. Behavioral Results

Pre-training and post-training identification functions for (A) Hindi stimuli, (B) nonlinguistic stimuli, and (C) tonal stimuli.

were large individual differences in learning rate across subjects; L scores ranged from 378 to 593.

Relationship between Pre-Test, Post-Test, and Training Measures

There was a significant relationship between pre-training and post-training identification slopes ($r = 0.50$, $p < 0.05$). There was no relationship between pre-training identification measures and L scores ($r = 0.13$, $p > 0.05$) nor between post- minus pre-training identification slopes and L scores ($r = 0.11$, $p > 0.05$) across subjects.

Imaging Results

Voxel-Based Correlations with Behavior

Refer to Table 1 for list of morphological analyses and main results. There was a positive correlation between L scores and the white matter density in a region just anterior to the parieto-occipital sulcus bilaterally (Figures 4A–4C and Table 2), suggesting that there is more white matter and/or less gray matter in these regions in faster relative to slower learners. As expected, the correlation with the gray matter maps yielded similar results with t values in the opposite direction (Table 2). The t value in the left hemisphere (Table 2) was just below the significance threshold; however, given that the shape of the signal is symmetrical and is found at highly similar, homologous locations in the two hemispheres, it is likely that this result represents a bilateral morphological correlation. The results did not change when a measure of linguistic experience was covaried out. We had predicted an association between measures of phonetic learning and gray or white matter density in primary speech regions of the brain; we did not, however, find such an association, even when lowering the threshold to 4.5. Correlations with pre-training and with post- minus pre-training identification performance for the Hindi stimuli did not yield any significant results. Similar analyses using L scores for learning nonlinguistic rapidly changing and tonal stimuli did not yield any significant findings.

Location and Volume of Parieto-Occipital Sulcus

The finding of a correlation between the Hindi L scores and gray/white matter density anterior to the parieto-occipital sulcus may be due to differences across subjects either in the location or in the gray matter volume of this sulcus. In order to distinguish between these two possibilities, we performed regional morphometric analyses of the parieto-occipital sulcus of 20 individuals

selected in the following manner. We chose ten of the fastest learners who also had the highest white matter density values and ten of the slowest learners who also had the lowest white matter density values at the following parieto-occipital location in the left hemisphere: $x = -14$, $y = -66$, $z = 39$, $t = 5.38$, $r = 0.57$ (Figure 5). These two groups constituted what we will from now on refer to as the faster and the slower learner groups. The groups did not differ in their final identification performance [$t(18) = 0.62$, $p > 0.05$].

We manually labeled the parieto-occipital sulcus in T1-weighted MR images of these 20 individuals. We averaged these labels separately for the faster and slower learners, thus creating probability maps for this sulcus (Figure 6). It can be seen from these images that the sulcus appears to be located more posteriorly in the faster learners as compared with the slower learners. In order to test this apparent location difference, we performed a mixed, two-factor analysis of variance on the y axis location of the center of gravity of the sulcus. The between-subjects variable was group (faster versus slower learners), and the within-subjects variable was hemisphere (right versus left). We found a main effect of group [$F(1,18) = 19.88$, $p < 0.001$], confirming that the sulcus is located more posteriorly in the faster relative to the slower learners, as well as main effect of hemisphere [$F(1,18) = 30.87$, $p < 0.001$], indicating that the sulcus is located more posteriorly in the left relative to the right hemisphere. There was also a significant group by hemisphere interaction [$F(1,18) = 5.10$, $p < 0.05$] (Figure 7A). Newman-Keuls post-hoc tests confirmed the two main effects and showed that the sulcus is located more posteriorly in the left relative to the right hemisphere for both faster [$Q = 7.81$, $Qc(2,18) = 2.97$, $p < 0.05$] and slower learners [$Q = 4.69$, $Qc(3,18) = 3.61$, $p < 0.05$] and that in both the left [$Q = 9.03$, $Qc(3,18) = 3.61$, $p < 0.05$] and the right [$Q = 4.69$, $Qc(3,18) = 3.61$, $p < 0.05$] hemispheres, the sulcus is located more posteriorly in faster relative to in slower learners. Results indicate that the significant group by hemisphere interaction (see Figure 7A) arises from a larger hemispheric difference in the location of the sulcus for the faster relative to the slower learners. In other words, there is a greater asymmetry (left more posterior than right) in the position of the sulcus in faster learners. We also performed a mixed, two-factor analysis of variance on the volume of the parieto-occipital sulcus. These volumes were obtained by summing across all labeled voxels for each subject.

Table 1. Morphometric Analyses

Analysis	Stimulus Type		
	Hindi	Rapidly Changing Nonlinguistic	Tonal
1. Voxel-based morphometry: correlation between three behavioral measures (pre-training identification slopes, L scores, and post- minus pre-training identification slopes) and GM and WM tissue classified maps.	*significant relationship between L scores and GM and WM signal in region anterior to parieto-occipital sulcus, bilaterally	ns	ns
2. Anova on position of parieto-occipital sulcus (measure: y axis location of center of gravity of sulcus). Factors: group (faster versus slower learners) and side (right versus left).	***more posterior in faster relative to slower learners ***more posterior in left relative to right hemisphere *greater asymmetry (L > R) in position in faster learners	(not performed)	(not performed)
3. Anova on volume of parieto-occipital sulcus. Factors: group and side.	ns	(not performed)	(not performed)
4. Correlation between corpus callosum (CC) cross-sectional areas and L scores.	ns trend in middle 3rd of CC (larger area in faster learners)	(not performed)	(not performed)
5. Anova on GM and WM volumes of the parietal lobe. Factors: goup, hemisphere, and tissue type (gray versus white).	**main effect of hemisphere: left > right *three-way interaction: faster learners have greater asymmetry (L > R) in WM volume relative to slower learners	(not performed)	(not performed)
6. Correlations between parietal GM/WM volumes and L scores	*left hemisphere: WM > GM in faster relative to in slower learners –right hemisphere: similar trend as in left (p = 0.06 and 0.07).	*left and right: WM > GM in faster relative to in slower learners, even when adjusting for performance with Hindi stimuli.	ns

"ns" indicates no significant findings. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

We found no difference in the volume of the sulcus between groups [$F_{(1,18)} = 0$, $p > 0.05$] nor between hemispheres [$F_{(1,18)} = 0.43$, $p > 0.05$].

Parietal Volumes

The difference in the location of the parieto-occipital sulcus across subjects may arise from differences in the volume or shape of the parietal lobes, which lie anterior to the sulcus. It is possible that larger parietal lobes in faster learners result in a posterior "positional shifting" of the sulcus relative to slower learners. In order to test this possibility, we performed a mixed factor analysis of variance on automatically segmented parietal lobe volumes. The between-subjects variable was group (faster versus slower learners), and the within-subject variables were hemisphere (right versus left) and tissue type (gray versus white matter). We found a main effect of hemisphere [$F_{(1, 18)} = 63.39$, $p < 0.001$], reflecting larger volumes in the left relative to the right hemisphere. There was a significant tissue by group interaction [$F_{(1,18)} = 5.44$, $p < 0.05$], as well as a significant tissue by hemisphere interaction [$F_{(1,18)} = 8.73$, $p < 0.01$]. Last, there was a significant three-way interaction between group, hemisphere, and tissue. Tests of simple interactions were performed for the two groups separately. Results revealed that for the faster learners, there was a two-way hemisphere by tissue interaction [$F_{(1,9)} = 18.00$, $p < 0.005$]. Newman-Keuls post-hoc tests showed that in both the left [$Q = 16.96$, $Qc(3,9) =$

3.95, $p < 0.05$] and right [$Q = 8.48$, $Qc(3,9) = 3.95$, $p < 0.05$] hemispheres, there is more white relative to gray matter. The hemisphere by tissue-type interaction for the faster learners arises from a greater difference in the amount of white relative to gray matter in the left relative to the right hemisphere (Figure 7B). Tests of simple interactions revealed that for slower learners, the hemisphere by tissue interaction was not significant.

Correlational analyses between the gray and white matter volumes of the left and right parietal regions with the rate of learning across the 20 subjects confirmed the above pattern of results. They revealed that in the left hemisphere, there is less gray matter ($r = -0.49$, $p < 0.05$) and more white matter ($r = 0.50$, $p < 0.05$) in the faster relative to the slower learners. There was a similar, marginally significant pattern of results for gray ($r = -0.43$, $p = 0.06$) and for white ($r = 0.41$, $p = 0.07$) matter volumes in the right parietal region. The same analysis across all 59 subjects revealed that there is significantly less gray matter in the left ($r = -0.31$, $p < 0.05$) and in the right ($r = -0.25$, $p < 0.05$) hemisphere as a function of L scores.

In order to determine whether a similar pattern of results exists for the nonlinguistic and for the tonal stimuli, we correlated gray and white matter volumes of the left and right parietal lobe with the rate of learning for these other two stimulus types across all 59 subjects. We found that there is more white matter in both the
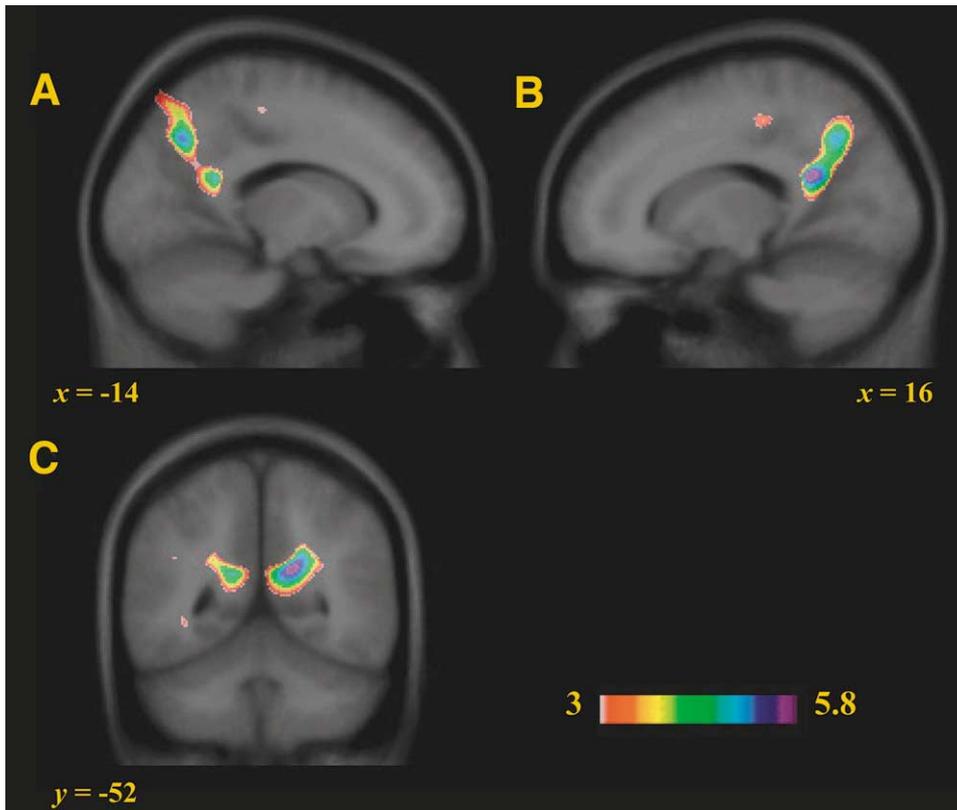
Figure 4. Voxel-Based Correlations

Voxel-wise correlation between behavioral Hindi L scores and white matter tissue classified maps (n = 59): (A) sagittal section through left hemisphere, (B) saggital section through right hemisphere, and (C) coronal view.

left (r = 0.25, p < 0.05) and in the right (r = 0.27, p < 0.05) hemisphere in individuals who learn the nonlinguistic stimuli more rapidly relative to those who learn these sounds more slowly. A test of part correlations revealed that in the right hemisphere, there is a significant amount of unique variation associated between performance on the nonlinguistic stimuli and white matter volume, even when adjusting for variation in performance associated with the Hindi stimuli (t = 2.00, p < 0.05). In the left hemisphere, white matter volumes can be predicted based on performance on the nonlinguistic stimuli even when adjusting for shared variation in performance on the Hindi stimuli with a p value of 0.07 (t = 1.87, p = 0.07). There was no association between parietal lobe volumes and performance on the tonal stimulus type.

Corpus Callosum Area

Visual inspection of the statistical parametric maps from the voxel-based analyses reveal that significant bilateral differences in morphology in the parieto-occipital region appear to lead inferiorly and medially to the corpus callo-

Table 2. Voxel-Based Morphometry: Correlations with Phonetic Learning

GM Maps Correlated with Hindi L Score

Talairach Coordinates			t Value	Structure
X	Y	Z		
16	−52	23	−5.73*	anterior to right parieto-occipital sulcus
18	−61	39	−5.05	anterior to right parieto-occipital sulcus
−14	−66	39	−5.38*	anterior to left parieto-occipital sulcus
−15	−49	20	−4.74	anterior to left parieto-occipital sulcus

WM Maps Correlated with Hindi L Score

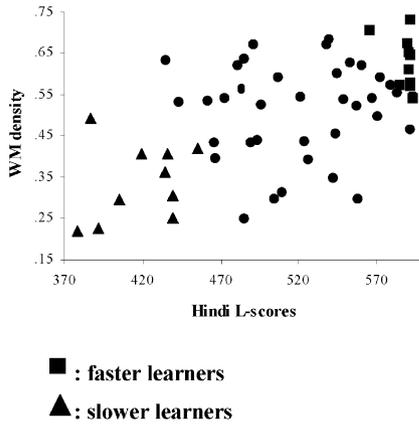| Talairach Coordinates			t value	Structure
X	Y	Z		
17	−50	23	5.84*	anterior to right parieto-occipital sulcus
−16	−64	38	5.09	anterior to left parieto-occipital sulcus

*p < 0.05.

Figure 5. White Matter Density versus Learning Rate

White matter density at peak t value location in the left hemisphere (−14, −66, 39) versus L scores (learning rate) across 59 subjects.

sum and extend into the opposite hemisphere (Figure 8). In order to test the possibility that the parieto-occipital finding is related to a difference across the groups in interhemispheric connectivity, we compared midsagittal area measurements of various subdivisions of the corpus callosum (CC) for the faster versus slower learner groups. Corpus callosum subdivisions included total CC, anterior, middle, and posterior third of the CC, and the splenium of the CC (Bermudez and Zatorre, 2001). None of the comparisons were significant; however, there was a nonsignificant trend [t(18) = 1.43, p = 0.09, one-tailed] indicating that faster learners tended to have a larger midsagittal area in the middle third of the CC relative to slower learners.

Discussion

We found a relationship between the rate of phonetic learning and the gray and white matter volumes in the parietal lobe in the left hemisphere, as well as a similar, marginally significant pattern of results in the right hemisphere. We also found a significant relationship between the speed of learning of novel speech sounds and the position of the parieto-occipital sulcus. Individuals who more quickly learn to distinguish the nonnative from the native sound have a more posterior position of this sulcus relative to slower learners. In both faster and slower learners, this sulcus is located more posteriorly in the left relative to the right hemisphere; however, there is a greater asymmetry in the location of the sulcus in the faster relative to the slower learners (Figure 7A). We did not find an association between measures of phonetic learning and gray or white matter density in primary speech regions of the brain, and this result did not change even when we lowered the statistical threshold in order to perform a directed search in regions of interest. The parieto-occipital finding was specific to the rate of learning; there was no association between the position of this sulcus and pre-training performance nor between its position and post- minus pre-training performance.

Behaviorally, there was a relationship between pre-training and post-training performance, suggesting that individuals who do well before training are also those likely to do well after training. There was no relationship between learning rate and pre-training performance nor between learning rate and post- minus pre-training measures. These behavioral results parallel the above reported dissociation between the morphological correlates of learning rate versus pre-training as well as post- minus pre-training measures. We suggest that pre-training performance provides a measure of phonetic processing that reflects aspects of *perception*, whereas post- minus pre-training measures reflect *improvement* in phonetic perception, and L scores indicate *learning rate*. The learning rate scores reflect performance over the course of training, whereas the post- minus pre-training improvement measures reflect performance during testing when no feedback is offered. These two measures are likely related to different cognitive processes. For instance, during training, feedback helps subjects to attend to features that are critical in distinguishing the dental and retroflex sounds, and this may result in more stable task performance than during later testing. It is also likely to improve motivation during the performance
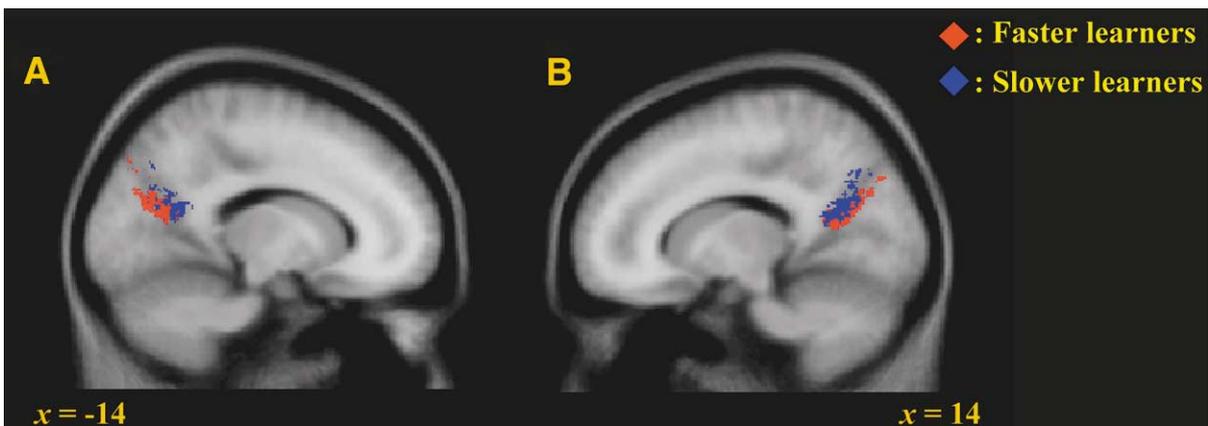

Figure 6. Parieto-Occipital Sulcus Probability Maps

Parieto-occipital sulcus 50% thresholded probability maps in (A) left hemisphere (x = −14) and (B) right hemisphere (x = 14) in faster (red) and in slower (blue) learners.
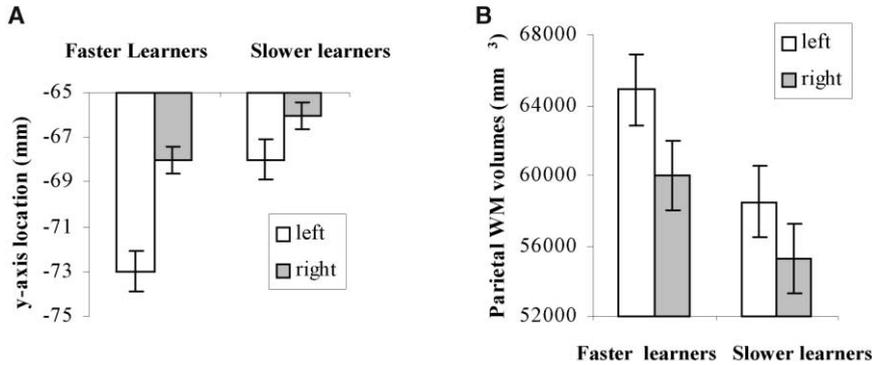
Figure 7. Group by Hemisphere Interactions

Group by hemisphere interactions for (A) *y* axis location of parieto-occipital sulcus and (B) white matter parietal lobe volumes.

of this difficult identification task because subjects have information that allows them to evaluate their performance. Taken together, the parallel behavioral and morphological dissociations suggest that morphological correlates of phonetic processing are specific to the rate of learning and not to pre-training perceptual processes nor to the amount of improvement in perception due to training.

Anatomical Factors Relating to Phonetic Learning

At least two nonexclusive possibilities exist to explain the parieto-occipital results. Anterior to the parieto-occipital sulcus are white matter tracts connecting several cortical regions both inter- and intrahemispherically (Talairach and Tournoux, 1993). The fibers connecting the temporal and parietal regions of the two hemispheres cross the caudal part of the corpus callosum (Waddington, 1984; de Lacoste et al., 1985). It is possible

that in fast learners, the more posterior position of the parieto-occipital sulcus is related to a greater number and/or thickness of interhemispheric fibers adjacent to the sulcus. This may suggest, in turn, that in faster learners, there is greater interhemispheric connectivity in temporal and temporo-parietal auditory-related brain regions.

We tested the hypothesis of greater interhemispheric connectivity in faster learners by examining possible relationships between area measurements of various subdivisions of the corpus callosum and learning measures. We did not find a relationship between phonetic learning ability and the area of the splenium or of the posterior third of the corpus callosum, although there was a trend in this direction in the middle third. It is possible that regional differences in the number of fibers in one region (e.g., caudal end) of the corpus callosum result in a positional shift of adjacent fibers. For this
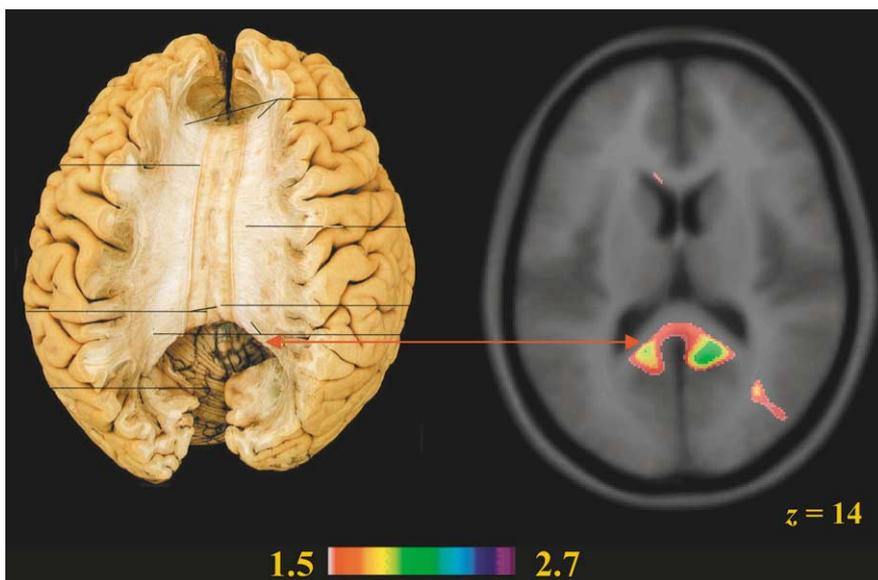

Figure 8. Shape of Voxel-wise Correlation at the Level of the Corpus Callosum

Voxel-wise correlation between Hindi L scores and white matter tissue classified maps (n = 59); horizontal slice illustrating shape of the correlation at the level of the corpus callosum. Note that in this region (z = 14) the result is not significant. Figure taken from Rohen and Yokochi (1983).

reason, area measurements of specific subdivisions of the CC may not be well suited to detect possible regional differences. It is also possible that existing differences between our groups in the number of interhemispheric fibers "funnel" together and are more densely packed at the midsagittal level, such that they do not result in a detectable overall difference in the area of the CC. Despite the nonsignificant CC area results, the possibility that there is greater interhemispheric connectivity in faster relative to slower learners may still hold. In support of this, Figure 8 shows that significant bilateral differences in morphology in the parieto-occipital region appear to lead inferiorly and medially to the corpus callosum and extend into the opposite hemisphere. The t statistic at the midsagittal level of the corpus callosum was not significant using a stringent correction for multiple comparisons; however, a t value of 2.73 at the location $x = 0$, $y = -41$, and $z = 14$ suggests that there tends to be more white matter at this location in faster relative to slower learners. These results are qualitatively nonetheless interesting and support the interhemispheric connectivity hypothesis.

The second interpretation, not exclusive with the first, for the more posterior position of the parieto-occipital sulcus in faster relative to slower learners is that it may indirectly result from differences in the size or shape of structures adjacent to this sulcus. The parietal lobe includes Brodmann's areas (BA) 39 and 40, which roughly correspond to the angular and supramarginal gyri, respectively, and it is posteriorly demarcated by the parieto-occipital sulcus. It is possible that in faster learners, the parietal lobes are larger or shaped differently than in slower learners, resulting in a relatively more posterior location of the parieto-occipital sulcus in the former relative to the latter group. In support of this, we found that, in the left hemisphere, there is a relationship between the rate of learning and amounts of parietal lobe gray and white matter such that there is less gray and more white matter in the faster relative to the slower learners. There was a similar, marginally significant pattern of results in the right parietal region. There was evidence for overall larger parietal volumes in the left relative to the right hemisphere in both faster and slower learners. Furthermore, we found evidence that, in faster learners, there is a more marked asymmetry (L > R) in the amount of white relative to gray matter (Figure 7B). Correlations between the y axis location of the parieto-occipital sulcus and the volumes of the left and right parietal lobes across the 20 learner and nonlearner subjects did not reveal the presence of a significant relationship in the left ($r = -0.21$, $p > 0.05$) nor in the right hemisphere ($r = 0.10$, $p > 0.05$).

These results, taken together, suggest a differential effect of both sulcal location and of white matter volume in the faster relative to the slower learners. The overall morphological asymmetry, as well as the differential degree of asymmetry when comparing faster to slower phonetic learners, may be related to the known functional asymmetry for speech-related functions in the temporo-parietal regions. Functional activation studies have often shown left-lateralized involvement of parieto-temporal regions in phonetic processing tasks (Paulesu et al., 1993; Petersen et al., 1989; Démonet et al., 1992, 1994; Zatorre et al., 1992, 1996). In the study by Paulesu and colleagues (1993), it was suggested that the left supramarginal gyrus is the substrate underlying the phonological store component of verbal working memory. They also, however, found weaker, nonsignificant activity in a symmetrical right supramarginal region, suggesting that this region in the nondominant hemisphere is also involved in some aspect of phonological processing. Our morphological results are also consistent with this latter finding in that we demonstrated that in faster learners, there are greater white matter volumes *bilaterally* relative to slower learners.

The finding of morphological differences in the parietal lobes bilaterally between faster versus slower phonetic learners parallel those of a functional magnetic resonance imaging (fMRI) study in which we examined changes in brain activation related to phonetic learning (N.G. and R.J.Z., submitted). Ten monolingual English-speaking subjects (not part of the present sample) were scanned while performing an identification task both before and after five sessions of training with a Hindi dental-retroflex nonnative contrast. There was a large range in training-related improvement in identification performance. We correlated a behavioral measure of improvement with the fMRI signal during the post-training phonetic comparison. Results revealed greater bilateral parietal lobe (BA 39, location in the left hemisphere: $x = -54$, $y = -66$, $z = 26$, and in the right hemisphere: $x = 44$, $y = -70$, $z = 34$) activation in the angular gyrus, a region adjacent and posterior to the supramarginal region found by Paulesu and colleagues (1993), in individuals who improved more relative to those who did not benefit from the training. This correlational finding supports the idea that "good learners" recruit these more posterior temporoparietal regions relatively more than do "poor learners" and that activity in this region is modulated by learning. This finding, as well as those of the present study, suggests that bilateral structural *and* functional differences in the parietal lobes can in part predict phonetic learning in normal individuals. Further, the results of these two studies taken together can suggest that, in individuals who learn new speech sounds rapidly or more proficiently, larger white matter volumes in the parietal lobes may be the anatomical feature that gives rise to greater functional activation in these regions during the performance of phonetic tasks.

Phonetic versus Auditory Processing
We found a similar pattern of results for the ability to learn rapidly changing nonlinguistic stimuli but not for the ability to learn steady-state tonal stimuli. Left and right parietal white matter volumes were larger in individuals who learned the nonlinguistic stimuli rapidly relative to those who learned them slowly, even when adjusting for performance on the Hindi stimuli. These results suggest that the morphological correlates of phonetic learning in parietal regions are not specific to learning speech sounds, but rather, that they are related to a more general, psychoacoustic ability to learn rapidly changing sounds. They are also consistent with behavioral results obtained in the same subjects, which showed an association between phonetic learning abilities and the ability to learn rapidly changing sounds but a weaker association with the ability to learn steady state sounds (N.G.

et al., submitted). It has been proposed that the ability to process some consonant speech sounds depends in part on the ability to track rapidly changing acoustic information (Tallal et al., 1993; Schwartz and Tallal, 1980; Benasich and Tallal, 1996; Belin et al., 1998; Johnsrude et al., 1997; Zatorre and Belin, 2001). Results of electrophysiological (Liégeois-Chauvel et al., 1999; Nicholls et al., 1999) and functional brain imaging (Belin et al., 1998; Zatorre and Belin, 2001) investigations have suggested better temporal resolution for the left auditory cortex. In contrast, findings from electrophysiological (Liégeois-Chauvel et al., 2001), lesion (Johnsrude et al., 2000; Robin et al., 1990), and functional imaging studies (Zatorre et al., 1994; see Zatorre, 2001; Zatorre et al., 2002) suggest that right auditory regions subserve aspects of pitch and spectral processing. Other studies have shown the involvement of left hemispheric regions outside of the temporal lobes during the processing of rapidly changing speech (Fiez et al., 1995) and nonspeech sounds (Temple et al., 2000; Fiez et al., 1995). Taken together, these results suggest that different functional substrates underlie temporal versus spectral processing. Our results extend these findings by demonstrating an association in brain *morphology* between phonetic learning ability and the ability to learn rapidly changing nonspeech sounds, together with a dissociation between the morphological correlates of these two stimulus types and those related to the ability to learn steady-state pitch differences.

Role of White Matter Asymmetries in Auditory Processes

The finding of more white matter in the left and right parietal region in faster relative to slower learners, as well as the finding of a greater asymmetry (left > right) in the amount of white matter relative to gray matter in faster learners, illustrates the importance of examining white matter morphology in relation to language-related behavior. In a study examining the white and gray matter volumes of Heschl's gyrus, Penhune and colleagues (1996) found that the left-greater-than-right asymmetry of the total volume of this gyrus can be explained by greater white but not gray matter volume in the left hemisphere. Marked asymmetries in white matter underlying left parietal, frontal, and temporal cortices have also been reported by Pujol et al. (2002). These results suggest that the well known left-hemisphere dominance for speech may be related to a larger volume of cortical connecting WM fibers rather than to differences in the size of speech-related GM structures. Several other investigations have also revealed interesting morphological findings in the white matter regions of language-related neural systems. Paus and colleagues (1999), using voxel-wise analysis of structural MRI, examined age-related increases in white matter density of fiber tracts in the human brain. They found age-related increases in white matter density along the arcuate fasciculus in the left hemisphere and suggested that these increases represent a structural component of the corticocortical pathway mediating sensory-motor interactions between the anterior and posterior speech regions. Differences in WM density or volume can be due to greater myelination and/or to a greater number of WM

fibers connection brain regions inter- or intrahemispherically. The former allows faster conduction of neural signals, resulting in greater efficiency of neural processing. Anderson and colleagues (1999) showed anatomical asymmetries of the posterior superior temporal lobes in postmortem data. They measured the thickness of myelination sheath and axon diameters with electron microscopy and found that the posterior superior temporal lobe white matter volume was greater on the left than on the right side. Furthermore, they found that this asymmetry appeared to be due to thicker axonal myelination in the left relative to the right hemisphere and not to an isolated proliferation of glia nor to the density of cortico-cortical projections of neurons in the overlying cortex. These findings suggest that an asymmetry of myelination may in part explain morphological and functional asymmetries in language-related temporal areas of the brain.

Processing of speech sounds depends in part on the ability to process sounds that change on the time scale of 30–50 ms. Rapid intra- or interhemispheric transfer of information between components of a language network would be critical for the processing of such rapidly changing sounds. Future studies can be designed to test the hypothesis of greater interhemispheric connectivity in individuals who are good relative to these who are poor at learning new, rapidly changing speech and nonspeech sounds. For example, diffusion tensor mapping techniques can be used to examine the relationship between aspects of behavior and the thickness and/or shape of white matter fiber tracts connecting brain regions inter- and intrahemispherically. Additionally, electrophysiological recordings can be combined with transcranial magnetic stimulation to measure differences in interhemispheric transfer time related to the ability to learn rapidly changing speech and nonspeech sounds across individuals.

Implications for Clinical Populations

Given the location (parietal lobes) and the laterality (favoring the left hemisphere) of the results, it is relevant to discuss some more broad implications of our results to clinical groups, such as to individuals with dyslexia. There is considerable evidence that a large proportion if not all of individuals diagnosed with dyslexia suffer from an impairment in segmenting and manipulating the phoneme constituents of speech (Rack et al., 1992). It has been proposed that the phonological difficulties experienced by dyslexic individuals may arise from difficulties in processing rapidly changing information (Temple et al., 2000; Tallal and Piercy, 1973; Tallal, 1980). Interestingly, functional imaging studies have shown abnormal functional activation of left temporoparietal regions in dyslexic relative to control subjects during phonological and during reading tasks (Rumsey et al., 1992, 1999). It has also been shown that normal functional connectivity between the left angular and temporal regions may be disrupted in dyslexic individuals (Horwitz et al., 1998). Abnormal morphology of left angular, parieto-occipital, and temporal regions has also been shown in dyslexia (Duara et al., 1991; Rumsey et al., 1986; Kushch et al., 1993; Larsen et al., 1990; Hynd et al., 1990) and in children with language disorders

(Jernigan et al., 1991; Plante et al., 1990), relative to normal control subjects.

Last, Klingberg and colleagues (2000) have observed, using diffusion tensor magnetic resonance imaging, that in adults with reading difficulty, there are bilateral micro-structural abnormalities in the white matter tracts of temporoparietal regions. In addition, they found that the degree of abnormality in the temporoparietal region of the left hemisphere was significantly correlated with reading scores within the reading-impaired adults *and* within the control group. The authors suggested that white matter "microstructure" may contribute to reading ability by determining the strength of communication between cortical areas involved in visual, auditory, and language processing. The results of Klingberg and colleagues' study support the idea that anatomical abnormalities seen in dyslexia may vary continuously in relation to language-related performance measures and, in addition, that they may extend into the normal range of performance and brain anatomy. Our results extend their finding of a relationship, within the normal range, between parietal lobe white matter microstructure and reading scores to a relationship between parietal white matter macrostructure and a measure of phonetic learning in normal individuals.

Conclusion

We have demonstrated that differences in white and gray matter morphology in the left and right parietal regions of the brain can in part predict the speed or facility of normal, healthy adults to learn rapidly changing speech and nonspeech sounds. This morphological correlate was specific to the rate of learning and was not found in relation to pre-training nor to final post-training abilities, suggesting that morphological differences in parietal white matter may help to predict the *ease* with which an individual may learn new speech sounds but not necessarily initial perceptual abilities nor final performance that may arise from more extensive training or experience. In other words, differences in morphology may in part explain how behavior is shaped across individuals due to preexisting differences in the amount of effort required to perform a task successfully, but such morphological differences do not determine behavioral limitations. This novel finding illustrates a morphological correlate of a continuous, speech-related behavioral ability which lies within the normal range. This finding raises interesting questions regarding whether such morphological differences exist at birth or whether there is some degree of experience-dependent structural plasticity during development. It is likely that a combination of both constitutional and experience-related factors are involved. These findings open exciting avenues for future research on morphological correlates of other aspects of human cognition and behavior.

Experimental Procedures

Subjects

Our subjects included 59 healthy right-handed adult volunteers, 33 male and 26 female. Ages ranged from 18 to 39 years (mean age 22). All subjects spoke English, and a subset also spoke one or more additional languages, none of which employ the retroflex sound. For each subject, audiometric testing revealed normal hearing.

Stimuli
Selection of the Nonnative Linguistic Stimulus
We selected the dental-retroflex place-of-articulation contrast that is used in languages of India, such as Hindi or Urdu. Retroflex consonants require a relatively complex articulation and are rare across languages; only 11% of the world's languages include a retroflex consonant, and they are unlikely to be pronounced allophonically in languages in which the contrast is phonetically irrelevant (Burnham, 1986). The nonnative perception of the retroflex sound is lost below the age of 1 year (Werker and Tees, 1983, 1984a; Tees and Werker, 1984). Perceptually, English listeners assimilate the dental-retroflex sounds such that they perceive both sounds as instances of the dental consonant (Polka, 1991; Werker and Lalonde, 1988).

Research aimed at training the nonnative perception of the dental and retroflex sounds in adults has shown that standard training approaches fail to improve performance (Werker and Tees, 1983, 1984a; Tees and Werker, 1984). Improvement has been reported under certain circumstances, including shorter interstimulus intervals (Werker and Tees, 1984b; Werker and Logan, 1985), truncated stimuli (Pruitt et al., 1990), and having had extensive experience with the contrast (Tees and Werker, 1984).

We selected this difficult nonnative retroflex consonant because we wanted to ensure that no individual would be able to distinguish this sound from the dental consonant before training and that we would find a considerable range in performance across subjects so that we could then correlate such individual differences with brain morphology. In a preliminary study (N.G. et al., submitted), we synthesized the retroflex consonant and showed that phonetic training resulted in overall improvement in the ability to identify this sound versus the native dental one in a large group of subjects. A considerable range in performance was observed across subjects.

Synthesis of Stimuli
Nonnative Hindi Contrast. Synthesis of the nonnative phonetic contrast was based on parameters reported by Stevens and Blumstein (1975) for the retroflex-dental place-of-articulation continuum. There were seven stimuli varying in equal steps in terms of acoustic difference between adjacent items. The set of four-formant stimuli was constructed with the use of the MITSYN (Henke, 1990) signal processing language software and the Klatt model synthesizer. Stimulus 1 corresponds to the dental voiced, unaspirated stop consonant prototype, and stimulus 7 to the retroflex prototype. All of the consonants were followed by the vowel /a/.

Stimuli began with an initial noise burst. 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 burst. The initial noise burst lasted 5 ms, and its center frequency decreased in equal step sizes of 217 Hz from 4500 Hz (stimulus 1) to 3198 Hz (stimulus 7). The voicing began 15 ms after the onset of the burst. Each stimulus lasted 220 ms in total, and formant transitions (FTs) lasted 40 ms. The fundamental frequency (F0) started at 130 Hz and decreased linearly to 125 Hz over the first 40 ms, remained steady-state at 125 Hz for 75 ms, and then gradually decreased to 90 Hz over the last 90 ms of the sound. The first formant (F1) rose from 400 Hz to 655 Hz during the transition and then remained steady-state during the remainder of the sound. The second formant (F2) decreased from 1650 Hz to 1185 Hz over the first 40 ms and then remained steady-state. The fourth formant (F4) remained steady-state at 3600 Hz throughout the entire sound. The starting frequency of the third formant (F3) varied in equal 111 Hz steps from 3080 Hz (stimulus 1) to 2414 Hz (stimulus 7), and the steady-state portion of this formant was always at 2585 Hz. Refer to Figure 1 for schematized frequency-time representations of the dental and retroflex consonant-vowel (CV) syllables.

Rapidly Changing Nonlinguistic Stimuli. Nonlinguistic stimuli were formant based and therefore had a voice-like quality yet did not represent phonemes from any existing language. The acoustics of the nonlinguistic stimuli were analogous to those of the speech syllables in that in both of these seven-step continua, the frequency glide of the third frequency band was manipulated. The nonlinguistic stimuli were different from the speech ones in that the frequencies of the "formants" were arbitrarily selected and in that there was no noise burst preceding the sounds. These sounds were created in a manner similar to those used by Belin and colleagues (1998). Our

stimuli were different from theirs in two respects: first, the direction and slopes of our glides were different, and second, their stimuli had frequency glides both at the beginning and at the end of the sounds, whereas ours only had glides at the beginning.

The acoustics of the nonlinguistic stimuli are the following. All of the stimuli lasted 220 Hz. The fundamental frequency (F0) was steady-state at 210 Hz. The first formant (F1) rose from 337.5 to 450 Hz during the first 40 ms and then remained steady-state. The second formant (F2) dropped from 2000 to 1500 Hz during the first 40 ms and then remained steady-state. The fourth formant (F4) remained steady-state at 3300 Hz throughout the entire sound. Finally, the starting frequency of the third formant (F3) decreased in equal 140 Hz steps from 3020 (stimulus 1) to 2180 (stimulus 7), and its steady-state frequency was 2400 Hz. Refer to Figure 2 for schematized frequency-time diagrams of stimuli 1 and 7.

Steady-State Tonal Stimuli. The steady-state stimuli consisted of pure tones with durations of 220 ms and had onset and offset times of 5 and 20 ms, respectively. The acoustic parameter that was manipulated was the frequency of the tones. The continuum consisted of seven tones at frequencies which differed in 7 Hz steps and ranged from 2007 Hz (stimulus 1) to 2042 Hz (stimulus 7). Stimuli can be heard at www.zlab.mcgill.ca.

Procedure

All subjects were scanned several months prior to behavioral testing and training. Linguistic and musical experience were evaluated with questionnaires before testing began. Identical testing and training procedures were followed for each of the three stimulus types, the order of which was counterbalanced across subjects. For each stimulus type, subjects were first familiarized with the sounds; they were then randomly presented with 20 instances of each of the two endpoint stimuli. As each stimulus was presented, subjects saw its corresponding label on the computer screen: "A" for one endpoint stimulus and "B" for the other. In the phonetic condition, "A" corresponded to the dental sound and "B" to the retroflex one. In this condition, subjects were then asked to describe what "A" and "B" sounded like to them. Typically, they produced the sound(s) that they heard and then used words to describe subtle qualitative differences which they may not have been able to produce accurately.

Pre-training identification testing was then conducted. Following this, subjects were trained, using the adaptive training procedure described below. Identification tests were readministered after training.

Identification Testing

During the identification task in the speech sound condition, subjects were encouraged to use the descriptions of "A" and "B" that they had provided during familiarization. In all three stimulus-type conditions, they were presented with one sound at a time from the seven-step stimulus continuum and asked to label each of these sounds by pressing either of two mouse buttons, each one corresponding to one of the two endpoint stimuli. Each of the seven stimuli was presented ten times in random sequence, for a total of 70 trials. Identification tests were again administered at the end of training.

Training

During the training phase of the experiment, we progressively reduced the acoustic difference between the endpoint sounds as a function of successful performance by subjects. This "perceptual fading" training method adapts to subjects' performance (Jamieson and Morosan, 1986; Morosan and Jamieson, 1986; Terrace, 1963). It allows them, if they do well using the endpoint stimuli, to try to distinguish dental and retroflex sounds which are a smaller step size apart. This training paradigm is likely to help individuals attend to the relevant acoustic differences between the dental and retroflex sounds. Training involved 20 trial identification training blocks. Subjects were presented with either sound 1 or sound 7 and were asked to press one of two mouse buttons corresponding to the presented sound. They received feedback on the computer as to whether their response was correct or incorrect. 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) and lasted approximately half an hour per stimulus type.

Psychophysical Analyses

Laboratory training studies using synthetic phonemes typically involve creating a continuum of sounds, such that the endpoint sounds are reliably perceived exemplars of the two contrasting phonemes in question and that there is an equal, controlled physical difference between each of the adjacent sounds in the series. Before training, the endpoint sounds are difficult to identify, and pairs of sounds from the series are difficult to discriminate. Identification is tested following training by presenting the sounds of the series one at a time, and successful training is reflected by the ability to reliably label one endpoint as one of the phonemes and the other endpoint as the other phoneme. A steeper identification function therefore indicates that individuals are better at reliably classifying the sounds at one end of the continuum as belonging to one category and the sounds at the other end as belonging to the second category.

We developed a continuous learning rate variable ("L scores") to quantify subjects' performance over the course of learning. This variable takes into account both the number of blocks at each level of difficulty and the accuracy of performance during each of the blocks. L scores were obtained by first weighing the number of incorrect responses in each block by a "difficulty" weight corresponding to that block. The three possible weights are 3, 2, and 1, for the easiest, intermediate, and hardest blocks, respectively. Resulting values were then subtracted from 600, which was the maximum possible value, yielding an L score. This learning can range from 0 (slowest possible learner) to 600 (fastest possible learner).

For each of the three stimulus types, we measured (1) pre-training identification slopes, reflecting initial performance; (2) post- minus pre-training slopes, reflecting the amount of improvement in the ability to classify the two sounds resulting from training; and (3) L scores, reflecting rate of learning. We correlated these three measures for the Hindi stimuli with brain morphology using a voxelwise analysis. This analysis was followed by regional morphometric analyses in brain areas detected by the voxel-based analysis.

Scanning Protocol and Morphometric Analyses

We used a voxel-based statistical analysis (Ashburner and Friston, 2000) in order to determine whether there is a systematic relationship between the behavioral measures of interest and regional amounts of gray matter or white matter. The following three MR sequences were used: T1-weighted (3D fast field echo scan with 140–160 slices, 1 mm isotropic resolution, TR = 18 ms, TE = 10 ms, flip angle = 30°), T2-weighted (2D multislice fast spin echo scan with 140–160 2 mm slices with a 1 mm overlap, TR = 3300 ms, TE = 35 ms), and proton density-weighted (as for T2 scan but with TE = 120 ms). Each of these image volumes underwent a nonuniformity correction (Sled et al., 1998) to remove variations in signal intensity related to radio frequency inhomogeneity. Each T1-weighted image volume was linearly transformed with an automatic image registration method (Collins et al., 1994) based on multiscale 3D cross-correlation with an average (n = 305) MR image aligned with the Talairach stereotaxic space (Talairach and Tournoux 1988). The transformed images were then classified into gray matter, white matter, and cerebrospinal fluid, using INSECT (Zijdenbos et al., 1998), an automatic tissue classification paradigm. The binary tissue-classified gray matter (GM) and white matter (WM) maps were then smoothed using a Gaussian smoothing kernel of 10 mm full-width at halfmaximum, resulting in three-dimensional (3D) maps of GM and WM "density." Smoothing serves the purpose of converting binary into continuous data, which is necessary for correlating the signal with a continuous behavioral measure. It also serves to weigh the signal at each voxel according to the signal in neighboring voxels, thereby reflecting the amount of gray or of white matter within the smoothing kernel (i.e., GM or WM regional "density").

The GM and WM maps were then correlated with the three measures of performance on a voxel-by-voxel basis using a linear regression model, yielding three GM and three WM maps. Inverse relationship between GM and WM is typically found in brain regions

in which GM and WM tissues are in close proximity, such as the cerebral cortex. This is primarily due to partial-volume effect induced by smoothing the images and is independent of total scaling induced by stereotaxic normalization. In our experience, the inverse relationship is less likely in relatively large GM (e.g., thalamus) and WM (e.g., centrum semiovale) structures; this reflects the lack of the partial-volume effect here. The three behavioral measures were pre-training identification slopes, post- minus pre-training identification slopes, and L scores. Thresholds for the t statistic of >5.3 for gray matter and of >5.4 for white matter were calculated (Worsley et al., 1996); these cut-off t values are based on 57 degrees of freedom, a voxel size of 1 mm^3, smoothness of 10 mm, a significance of p $<$ 0.05, and volumes of interest of 540 cm^3 for gray matter and of 810 cubic centimeters for white matter.

In order to facilitate the interpretation of the voxel-based analyses, we also performed regional morphometric analyses using DISPLAY (MacDonald et al., 1994). This manual segmentation software allows simultaneous real-time viewing and voxel labeling on sagittal, coronal, and horizontal planes. We also correlated measures of performance with existing midsagittal corpus callosum (CC) area measurements (Bermudez and Zatorre, 2001), as well as with the volumes of the gray and white matter in the left and right parietal lobes. The CC areas were acquired by manual segmentation using DISPLAY. The parietal volumes were measured using an approach to automatic segmentation that relies on the ANIMAL and INSECT programs. This technique involves combining automatic tissue classification (see above) with nonlinear registration to a template brain for which brain regions had been manually defined (Collins et al., 1995, 1999; Collins and Evans, 1997).

Acknowledgments

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