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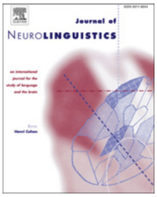

Neuroanatomical markers of individual differences in native and non-native vowel perception

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ABSTRACT

Although most human beings experience no difficulty in perceiving their native language, strong individual differences are observed for certain foreign phonemic contrasts. Diaz, Baus, Escera, Costa, and Sebastian-Galles (2008, Brain potentials to native phoneme discrimination reveal the origin of individual differences in learning the sounds of a second language. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 16083–16088) reported a correlation between event-related potential (ERP) responses to native and non-native vowels in a group of early and highly-skilled bilinguals. In the present study, we compared the brain morphology of two groups of bilinguals who were equally proficient in their second language but differed in their perception of both native and non-native vowels. A whole brain, voxel-based morphometry analysis (VBM) revealed larger white matter volume in the right insulo/fronto-opercular region in individuals who exhibited poorer perceptual discrimination of native and non-native vowels. As the volume of

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the left Heschl's gyri has previously been shown to correlate with the ability to perceive foreign phonemic contrasts (between consonants), we also measured the white and grey matter volumes of Heschl's gyri in our subjects. We did not observe any significant relation between these volumes and vowel discrimination capabilities. This result allows the identification of anatomical brain differences related to individual differences in vowel perception. The present results add to the relatively unexplored area of the relationship between brain structure and language function in adult healthy population.

1. Introduction

Most speakers learn the phonological repertoire of their first language effortlessly and with great success. However, as with any other perceptual or cognitive ability, speech perception is subject to individual differences. The present study explores the brain morphology correlates of individual differences in the perception of both native and non-native speech sounds. Although very little is known about individual differences in normal adult language processing for the native language, insights can be gained from research conducted in the field of second language acquisition.

Perhaps the most striking individual differences associated with speech perception concern the variability observed when learning a second language. Some second language (L2) learners rapidly manage to master the sounds of foreign languages, while others, even in the case of early and intensive exposure, show poor knowledge. Indeed, even when factors such as age of acquisition, amount of exposure to L2 and motivation are controlled for, there are important individual differences left unaccounted for (Flege, Bohn, & Jang, 1997; Flege, Munro, & MacKay, 1995; Moyer, 1999; Sebastian-Galles & Baus, 2005).

Crucially for the present study, individual differences in the perception of L2 phonology are correlated with the perception of native speech sounds. In Diaz, Baus, Escera, Costa, & Sebastian-Galles (2008) early and highly-skilled bilinguals, with life-long exposure to L2, were classified into two groups according to their performance on different behavioural tasks, exploring their capacity to perceive a non-native vowel contrast (see Sebastian-Galles & Baus, 2005, for a complete description of the selection procedure). Participants were classified as good perceivers (GP) if their responses systematically fell within the range of native listeners for all tasks, or as poor perceivers (PP) if they failed to fall within the range of native listeners for all tasks (participants falling within the range of natives for some, but not all, tasks were not studied). For the two groups of participants, event-related potentials (ERPs) in response to acoustic and speech changes were recorded. Specifically, both groups were compared as regards their mismatch negativity (MMN), an electrophysiological response to involuntary auditory change detection, whose amplitude is directly related to discrimination accuracy. The results showed that the two groups did not differ in the MMN elicited by acoustic changes. However, when speech material was presented (native and non-native vowels) there were differences between the two groups of participants in the amplitude of the MMN. Diaz et al. (2008) analysed the topographical location of the MMN differences in order to functionally interpret the origin of the differences between the two groups of participants. Given that the MMN is claimed to be sustained by temporal and frontal generators which are functionally dissociated (Deouell, 2007; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Rosburg et al., 2005; Shalgi & Deouell, 2007) and whose activity can be inferred from the amplitude and latency of the MMN, the MMN response to speech stimuli was further analysed for frontal (F3, F4) and temporal (LM, RM) electrodes. MMN differences between the two groups were only present at frontal electrodes (no traces of differences were observed at temporal electrodes), leading the authors to conclude that good and poor perceivers differed in the way speech sounds were processed at the MMN frontal generator.

The temporal generator has been associated with sensory processing and the comparison of information with memory representation. The neural substrate of the temporal MMN generator is the primary auditory cortex bilaterally (Alho, Huotilainen, & Naatanen, 1995; Giard et al., 1995; Opitz et al., 2002), an area where anatomical differences correlating with speed of acquisition of a foreign phonetic contrast have also been described (Golestani, Molko, Dehaene, LeBihan, & Pallier, 2007; Wong et al., 2008). However, the role and location of the frontal generator is a bit more controversial (see for a review Deouell, 2007). Different functional MRI studies indicate that fronto-opercular areas (a possible site of the frontal MMN generator) are involved in perceptually challenging situations, both for auditory perception and for speech perception. First, Opitz et al. (2002) observed that the frontal MMN generator, located in right fronto-opercular areas, is related to an automatic contrast or amplification mechanism that tunes the auditory change detection system. Accordingly, activation of this frontal contrast enhancement system would be triggered by decreased distinctiveness of sound input. Second, Golestani and Zatorre (2004) observed that the successful learning of a difficult non-native phonetic contrast resulted in the recruitment of different frontal areas (insular/frontal operculum and inferior frontal gyrus) in addition to temporal ones (the left superior temporal gyrus). Specifically, they observed that the right frontal operculum/insula was recruited after (but not before) training to hear a non-native speech contrast. Therefore, given these studies and the pattern of results obtained in Diaz et al. (2008), behavioural and electrophysiological differences between good and poor vowel perceivers may be paralleled by anatomical differences in right insulo/fronto-opercular areas.

In this article, we assess the morphological differences in brain associated with individual differences in the perception of (native and non-native) speech vowels, by means of voxel-based morphometry technique (VBM).

Several VBM studies have identified regional differences in brain anatomy (grey and/or white matter density) associated with the use of specific knowledge (or skills). These studies assume that the location of structural brain differences is related to regions that are also functionally active during tasks that engage these skills. One set of studies has established a direct relationship between experience (usually extensive) and modifications in brain structure. For instance, the work of Maguire et al. (2000) who reported increased grey matter density in the posterior hippocampi of taxi drivers, or the pioneering work of Amunts et al. (1997) who reported structural adaptations in the human motor cortex in professional musicians performing complicated bimanual movements (see for recent reviews about the relationship between experience and brain structure: Jäncke, 2009; and Pascual-Leone, Amedi, Fregni, Meraber, 2005). A second set of studies have analysed the anatomical basis of individual differences in task performance that are not associated with extensive practice; as, for example, individual differences in executive function (see for a recent review Braver, Cole, & Yarkoni, 2010). In this context, and central to our research goals there seems to be a relationship between brain anatomy and individual differences in the ability to learn foreign speech sounds. Golestani et al. (2007) reported a correlation between the volume of the left Heschl's gyrus and the speed of learning to distinguish two Hindi consonants (differing by the dental-retroflex contrast). Similarly, Wong et al. (2008) observed that the ability to learn to distinguish words differing on their pitch pattern also correlated with the volume of the left Heschl gyrus. In particular, differences have been reported in white matter volume (Golestani et al., 2007) and grey matter volume (Wong et al., 2008) of the left Heschl's gyrus (HG), where the left auditory cortex is located, along with differences in parietal areas (Golestani, Paus, & Zatorre, 2002). Therefore, these two studies reveal that anatomical correlates in the left auditory cortex (in particular in the Heschl's gyrus) predict individual differences in the speed of acquisition of non-native speech contrasts. The individual differences observed in these studies cannot be attributed to past experience with the specific speech sounds that participants had to learn, as they had no previous experience with those sounds. In the current research, we aim at contributing to our understanding of how anatomical differences correlate with individual differences in the ability to perceive vowel sounds. To do so, we explore the differences between two groups of participants that had extensive experience with their non-native language, but that vary in their ability to perceive some specific vowels. Importantly, the two groups of participants are balanced in all other aspects of non-native speech perception. Furthermore, the fact that the performance in non-native vowel perception correlated with native vowel perception (as shown by Diaz et al., 2008) supports the assumption that our good and poor vowel perceivers did not have significant disparities in language exposure.

Summing up, from the study by Diaz et al. (2008), one may expect differences between good and poor perceivers (for both native and non-native vowels) in frontal areas, while the predictions for the temporal ones are less clear. Indeed, as mentioned, temporal areas are fundamental to speech

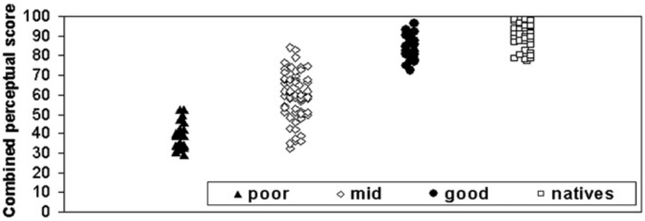

Fig. 1. Performance of Good and Poor Perceivers in the three behavioural tasks. Each individual score for each task was linearly transformed to a scale ranging from 0 to 100 (100 perfect performance). A global performance score was obtained by averaging the three tasks. For the sake of comparability, data of a group of Catalan natives are included in the plot, as well as data of early Spanish–Catalan participants who were not finally selected (*mid* group).

processing, however, the negative findings of Diaz et al. (2008) indicate that individuals differing in their capacity to perceive native and non-native vowels may not diverge at these specific brain sites (as differences between them were observed at the frontal generator of the MMN but not at the temporal one). In this context the present study explores voxel-wise structural differences between good perceiver (GP) and poor perceivers (PP) (from the same population tested in Diaz et al., 2008). This whole brain analysis was complemented by a region-of-interest (ROI) study as a further test of the potential negative results predicted by the previous absence of between-group differences in the temporal MMN generator.

2. Methods

2.1. Participants

Two groups of highly-proficient early bilinguals (the same participants tested in Diaz et al., 2008) who had learned their second language in a natural environment and with equivalent language experience were included in the study. They were raised as Spanish monolinguals until the age of four at the latest (when mandatory schooling started). All participants had received bilingual education and claimed to be very fluent in the two languages (Spanish and Catalan) in both listening and reading. These bilinguals were assigned to the two groups according to their ability to perceive a difficult vowel contrast in their second language. Participants were selected by testing a large population ($n = 126$) of highly-skilled, very early Spanish–Catalan bilinguals (from the very same population). Previous research has shown that in a comprehension task these Spanish–Catalan bilinguals show equivalent scores and patterns of brain activity to Catalan natives (Perani et al., 1998). Participants performed three speech perception tasks involving the Catalan-specific/e-ɛ/contrast which, Spanish natives find difficult to perceive (for a review, see Sebastian-Galles, 2005).[1] The tasks used were a categorization task, a gating task and a lexical decision task (respectively described in Pallier, Bosch, & Sebastian-Galles, 1997; Sebastian-Galles & Soto-Faraco, 1999; Sebastian-Galles, Echeverria, & Bosch, 2005). Participants were included in the final sample only if they performed within the range of Catalan natives or outside this range in all three tasks. Each individual score for each task was linearly transformed onto a scale of 0–100 (100 perfect performance; see Dupoux, Peperkamp, & Sebastian-Galles, 2010, for a similar composite index measure). The group of bilinguals considered as “good perceivers” attained native-level performance on all three tasks, while the group considered as “poor perceivers” were below natives on all three tasks. Because some of the participants in the study by Diaz et al. (2008) could not take part in the present study (they either refused to come back or could not be contacted), the sample was reduced to 14 poor perceivers and 13 good perceivers. To increase the statistical power, 6 additional poor perceivers and 7 additional good perceivers from the same population described above were also scanned (these participants were randomly selected

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[1] Catalan and Spanish are two Romance languages differing in their phonetic repertoires. Specifically, Spanish has only five vowels, while Catalan has eight vowels.

from the initial sample of 126 participants). Thus, the final sample comprised 20 poor perceivers and 20 good perceivers (see Fig. 1). These participants did not differ from those studied by Diaz et al. (2008) in any relevant aspect (specifically, the selection criteria). The combined perceptual score for the poor perceivers in Diaz et al. (2008) was 38.7, while that for the additional (new) ones was 38.5. The combined perceptual scores for the original and additional good perceivers were 83.4 and 80.3, respectively. None of the differences approached significance levels.

In the present study, the group of so-called *good perceivers* (GP) comprised 20 participants (15 females) with a mean age of 20.26 ($SD = 1.89$), while the group of so-called *poor perceivers* (PP) included 20 participants (18 females) with a mean age of 20.55 ($SD = 2.3$). All the participants were right-handed (the one left-handed participant in Diaz et al., 2008 was not included here) and none of them had received formal musical training or played professionally a musical instrument.

The experiment was approved by the local ethical committee and it was in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Written consent was obtained from each subject prior to the experiment. All participants were paid at the end of the experiment for their participation.

2.2. *MRI acquisition and analysis*

Structural MRI images were acquired on a 1.5-T magnet (Signa; GE Medical Systems, Milwaukee, Wis). A 60-slice, 3-dimensional, spoiled gradient-recalled acquisition sequence was obtained in the sagittal plane, with the following acquisition parameters: $TR = 40$ ms, $TE = 4$ ms, pulse angle = 30 degrees, field of view = 26 cm^2, matrix size = 256×192 pixels, in-plane resolution = 1.02 mm^2, and slice thickness = 2.6 mm (with no interslice gap). Acquisition time was 8 min 13 s (Pujol et al., 2002).

Imaging data were processed and normalized using a technical computing software program (MATLAB 6.5; The MathWorks Inc, Natick, Mass) and Statistical Parametric Mapping software (SPM2 and SPM5; The Wellcome Department of Imaging Neuroscience, London, England). All images were checked for artefacts before preparing MRIs for voxel-by-voxel analyses. At this point, one participant (female) from the poor perceivers group was excluded from the data analysis due to excessive movement during the MRI acquisition.

2.2.1. *Voxel-based morphometry*

Image pre-processing was based on the optimised procedure for structural data proposed by Good et al. (2001) and performed with the VBM2 toolbox for SPM2 (http://dbm.neuro.uni-jena.de/vbm/). In short, this procedure involves several automated processes aimed at: (a) creating scanner- and tissue-specific templates using the MRIs obtained in the same scanner of a large cohort of 131 normal controls (49 males, 82 females; mean age + SD = 22.88 + 2.95; range 17–29 years) from the same socio-demographic environment (we used this larger cohort of subjects because the number of subjects included in the study prevented the creation of a study specific template); (b) segmenting whole brain images in native space into grey matter (GM), white matter (WM) and cerebrospinal fluid (CSF) segments; (c) optimally normalizing, with linear and non-linear transformations, grey and white matter 15 segments to their scanner- and tissue-specific template to transform the images into Montreal Neurological Institute (MNI) standard stereotactic space (during this process images were re-sliced to a final voxel size of 1 mm^3); (d) modulating voxel values by the Jacobian determinants derived from the normalization step to restore the volumetric information lost because of these spatial transformations (Gaser, Nenadic, Buchsbaum, Hazlett, & Buchsbaum, 2001); and (e) smoothing the images with a 12-mm full width at half maximum (FWHM) isotropic Gaussian kernel to render the data more normally distributed and to load each voxel with region information. Each image transformation step has been described in detail previously (Pujol et al., 2004).

SPM2 was used to map regionally-specific volume differences throughout the brain on a voxel-wise basis. All the analyses were conducted separately for grey and white matter segments. Global grey or white matter volume was introduced as a confounding covariate in the analyses to remove global volume differences among subjects. Group comparison generated two *t* statistic maps ($SPM_{\{t\}}$) corresponding to two opposite contrasts: volume decrease and increase. Regional differences were reported as significant at $P < 0.05$ after Family Wise Error (FWE) correction for multiple comparisons throughout the brain, although in figures, to facilitate anatomical localization of findings, we used a more lenient threshold of $P < 0.001$, uncorrected. Spatial coordinates from all the obtained maps were converted to standard Talairach coordinates using a non-linear transform (mni2tal, implemented in MATLAB: http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach) of MNI standard space to Talairach space (Talairach & Tournoux, 1988). Finally, to study the correlations between volumetric data and the MMN response to a native contrast obtained in Diaz et al. (2008), we extracted the first eigenvariate of the clusters where significant between-group differences (at $P < 0.05$, FWE corrected) were observed. This value was correlated against the early and the late components of the MMN response.

2.2.2. *Segmentation of Heschl's gyri (HG)*

Left and right HG were manually drawn on each individual anatomical image after normalization on the avg152 T1 template provided by SPM (The spatial normalization was performed with SPM5, using only linear registration). The ROIs were delineated using the Anatomist software (http://brainvisa.info), which allows the three brain planes (sagittal, axial and coronal) to be displayed simultaneously (see Table 1). The methodology was the same as in Golestani et al. (2007). HG was identified in the axial plane as the first transverse gyrus delimited by the first transverse sulcus anteriorly and Heschl's sulcus (Penhune, Zatorre, MacDonald, & Evans, 1996). The inferior boundary of HG was identified in the sagittal and coronal planes by drawing a line from the depth of the Heschl's sulcus to the first transverse sulcus in the base of HG, and the superior limit was defined by the visible ending of the gyrus. However, duplications of HG or split HG are frequently present. According to Rademacher et al. (2001), primary auditory areas are located in the most anterior gyri whenever there are multiple transverse gyri (i.e. duplications of HG gyrus). They may also be located in the most anterior gyral subregion in the event that a single gyrus is divided by a sulcus intermedius to at least half of its length (i.e. split HG). Therefore, when duplications of HG or split HG were present, only the most anterior gyri or gyral subregion were segmented. One author drew HG, without knowledge of the group (good vs. poor) and hemisphere (right vs. left). To check for reliability, a second rater performed a new set of measurements on a random sample of 10 HG. The correlation between both measurements was 0.98.

After manual labelling of HG, automatically segmented WM and GM maps (SPM5) were used as masks to calculate the specific WM and GM volumes of HG.

Table 1
Volumes of Heschl's gyri (in mm^3).

	Poor perceivers		Good perceivers	
	Left HG	Right HG	Left HG	Right HG
	2157	1434	3541	1884
	3420	1319	1571	1614
	4346	2330	3763	2299
	1215	1557	1835	2257
	1374	1904	1461	2151
	4245	3271	3878	2591
	2680	1179	3855	1706
	3519	3003	2453	1768
	2995	1490	2111	2025
	2039	2603	2939	2040
	1773	2243	1855	1706
	4334	1447	2635	2670
	2256	1392	921	1545
	2328	2078	1884	2454
	2069	1761	1680	1756
	1664	1980	4716	2232
	2368	1736	1861	1620
	4848	1776	4656	3890
	1326	1684	3400	2110
			2827	2709
Average (SD)	2682 (1131)	1905 (571)	2692 (1107)	2151(546)

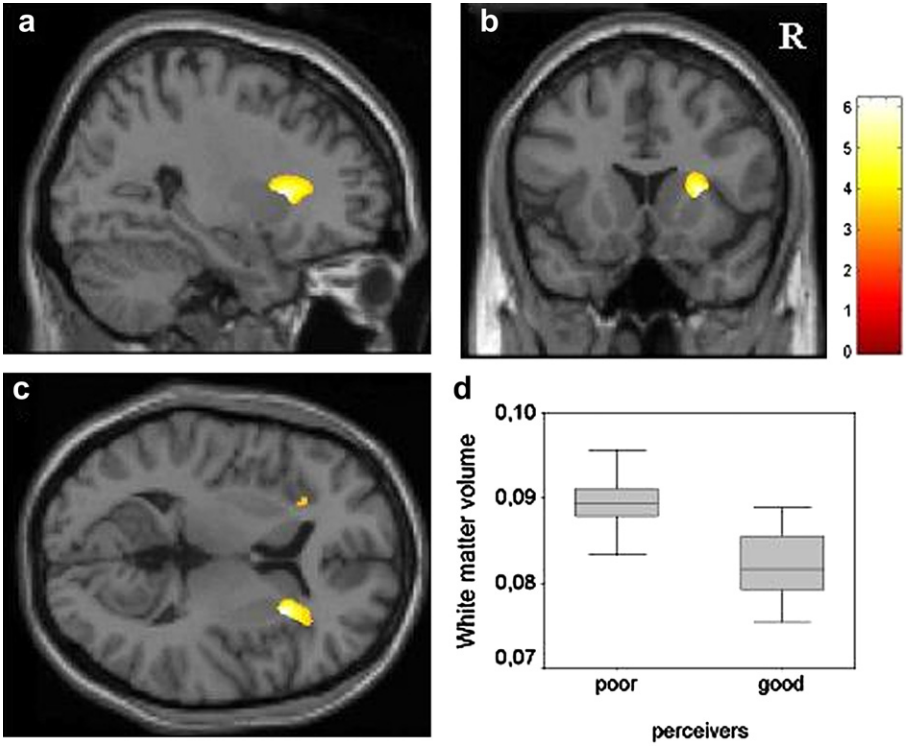

Fig. 2. White matter volume increases in Poor Perceivers. a–c, Statistical parametric maps superimposed on a normalized T1 image. a, Sagittal view; b, Coronal view; c, Axial view. *R* indicates the right hemisphere, and the colour bar represents the *t* score. Voxels showing uncorrected $p < 0.001$ are displayed. Significant voxels were found in the insulo/fronto-opercular region of the right hemisphere ($p < 0.05$, corrected). In the left hemisphere, a volume increase in the white matter of this same area, showing a tendency toward significance, is also displayed. d, White matter volume in the right insulo/fronto-opercular region, normalized to global white matter volume, for each group of participants.

3. Results

3.1. Voxel-based morphometry

Grey matter analyses revealed no significant differences between the good and poor perceivers groups. However, white matter analyses showed that poor perceivers had greater white matter volume in a cluster located in the right insulo/fronto-opercular region (see Fig. 2; peak coordinates: $x = 28$, $y = 16$, $z = 6$; $T = 6.21$, $p = 0.0025$, FWE corrected for multiple comparisons across the whole brain). There were no significant differences in the left hemisphere, although a tendency to increased white matter volume in poor perceivers was observed in a location similar to that reported for the right hemisphere, albeit in a more rostral position (peak coordinate: $x = -26$, $y = 26$, $z = 6$; $T = 3.62$, $p < 0.001$, uncorrected). White matter volumes in right and left clusters were similarly distributed in both the original participants tested in Diaz et al. (2008) and the additional participants scanned here (see Fig. 3).[2] No other significant differences in white matter volume were observed. Additionally, the analyses were repeated with

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[2] As in the analysis reported in the manuscript (with a 12 mm smoothing kernel), in all these new analyses the only significant between-group difference was located in the white matter of the right insulo/fronto-opercular region. The peak coordinates (x, y, z) in the analyses performed for 8 mm (28, 16, 6), 6 mm (27, 17, 7), and 4 mm (27, 17, 7) smoothing kernels had associated T values over 6.5 and P values (FWE corrected) below 0.005.

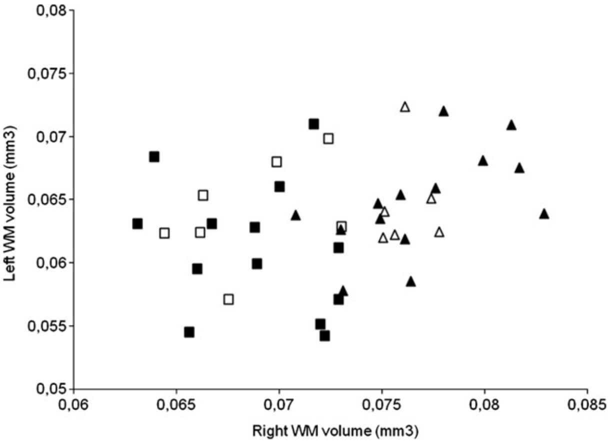

Fig. 3. White matter volume in right and left clusters located in the right and left fronto-opercular regions. Filled symbols (GP and PP) represent the original participants in Diaz et al. (2008), empty symbols represent the additional ones (nG and nP). Good perceivers are represented by squares and poor perceivers by diamonds.

different smoothing kernels (4 mm, 6 mm and 8 mm at FWHM) with no significant effects on the pattern of significances.[3]

3.2. Correlation with MMN values

A correlation analysis was performed to explore the relationship between WM volume in the right insulo/fronto-opercular cluster and the MMN response to a native contrast obtained in Diaz et al. (2008). For this analysis only the data of thirteen good perceivers and fourteen poor perceivers were available (as these were the participants who could participate and for whom valid data were obtained in both studies). Correlations were performed over the early and late components of the MMN response, as both components were identified in the Diaz et al. study. A significant correlation was observed between the early peak of the MMN response and WM ($r = 0.603$, $P < 0.001$, $P < 0.002$ Bonferroni correction for multiple comparisons). The correlation with the late peak of the MMN was also marginally significant ($r = 0.404$, $P < 0.05$ uncorrected, $P < 0.10$ corrected). Fig. 4 shows a plot of both correlations.

3.3. Segmentation of Heschl's gyri (HG)

The three different volume measures of the manually drawn HG (total, white matter (WM) and grey matter (GM)) were entered into separate split-plot ANOVAs with the within-subjects factor "Side" (left and right) and the between-subjects factor "Group" (good and poor perceivers).

The analysis revealed a leftward asymmetry of HG for all three HG volume measures (total volume: $F_{1,37} = 15.5$, $P < 0.001$; WM: $F_{1,37} = 24.2$, $P < 0.001$; GM: $F_{1,37} = 13.7$, $P < 0.001$). This asymmetry in HG has been previously reported (Dorsaint-Pierre et al., 2006; Penhune et al., 1996). In contrast, neither the factor "Group" ($F_{1,37} < 1$) nor the interaction "Group" × "Side" ($F_{1,37} < 1$) yielded significant results for any of the three measures (see Fig. 5).

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[3] An additional analysis was performed solely for the subset of participants tested in the study by Diaz et al. The pattern of results was practically identical to the one obtained with all the participants. Peak coordinates of the white matter volume located in the right hemisphere were: $x = 27$, $y = 19$, $z = 10$; $T = 4.79$, $p = 0.00004$, uncorrected for multiple comparisons. For the cluster located in the left hemisphere the coordinates were $x = -27$, $y = 25$, $z = 8$; $T = 4.78$, $p = 0.00004$, uncorrected for multiple comparisons.

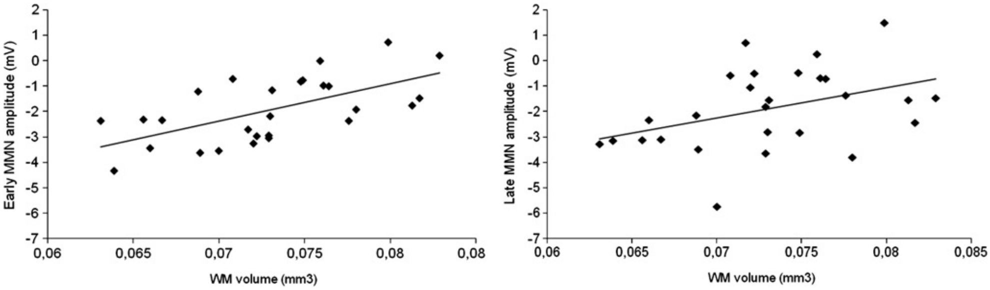

Fig. 4. Correlations between the WM volume of the right fronto-opercular region and the early MMN peak (left figure) and late MMN peak (right figure).

A further analysis tested whether the gross morphology of HG (single, split, duplicate or triplicate) differed between the two groups of bilinguals. The number of HG observed for each group was subjected to a χ^2 test for each hemisphere separately. The results showed no significant differences between good and poor perceivers in HG morphology for either the right ($\chi^2 = 2.53$, df = 3, $P > 0.05$) or the left hemispheres ($\chi^2 = 1.86$, df = 3, $P > 0.05$).

Even though the volume of HG did not differ between the groups of participants, HG volume might still correlate with performance on the behavioural tasks used to select the participants. Therefore,

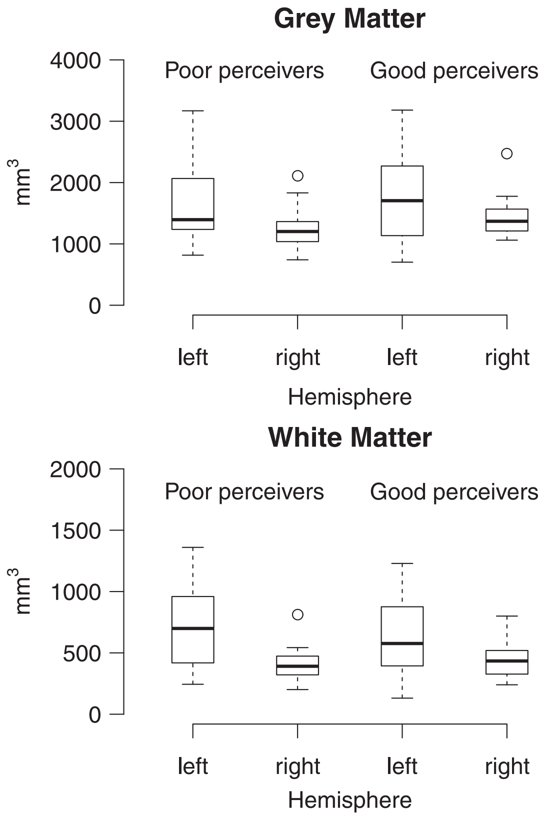

Fig. 5. Grey (top figure) and white (bottom figure) matter volumes of left and right Heschl's gyri for Poor and Good Perceivers.

correlations between right and left HG volumes and each of the three behavioural tasks were tested. None reached the $P < 0.05$ significance level (range of r correlations $= -0.14$ to 0.40).

4. Discussion

The aim of the present study was to explore the brain structural correlates of individual differences in vowel perception. We assessed whether structural differences in the right insulo/fronto-opercular areas do actually correlate with good and poor *native* vowel perception skills. The results of the voxel-based analysis showed that the only significant difference between the brain structures of good and poor perceivers concerned the white matter volume in a cluster located in the right insulo/fronto opercular area. Additional analyses focused on Heschl's gyri were also performed but showed no significant differences between the two groups of participants. These results are in line with the suggestion of Diaz et al. (2008) who did not find differences between good and poor perceivers at temporal electrodes but who found significant differences at frontal ones.

Several authors have proposed that the temporal structures (posterior STG and STS) are fundamental for the mapping from acoustic to phonetic information (Scott, Blank, Rosen, & Wise, 2000). Given the lack of differences between our two groups of participants in their MMN responses at temporal electrodes and in the structural analyses reported here, it seems that the individual differences between poor and good vowel perceivers are not related to differences in the ability to extract information from speech sounds. As Diaz et al. (2008) concluded, both groups would not significantly differ in their capacity to represent the phonetic auditory sensory information and to integrate this information into memory representations. However, both groups significantly differed in their anatomy at insulo/fronto-opercular areas. Frontal structures are engaged in the automatic triggering of attention (Deouell, 2007; Shalgi & Deouell, 2007; Stevens, Calhoun, & Kiehl, 2005). The differences at frontal electrodes between GP and PP lead Diaz et al. (2008) to propose that GP were "particularly good at making the deviant features of phonemes as salient information" (p. 16086). Our current data partially challenges that explanation. Most anatomical studies assume a direct relationship between increased myelination and efficient processing. Golestani et al. (2002, 2007) interpreted the difference in white matter between faster and slower learners as reflecting increased myelination, which, in turn, was assumed to underlie more efficient learning. However, the higher white matter volumes in our poor perceivers when compared with good perceivers indicate that insulo/fronto-opercular areas are more active in poor than in good perceivers. Yet, our results are compatible with the patterns of activity reported by several studies concerning the role of fronto-insulo/opercular areas and the successful processing of auditory stimuli. Golestani and Zatorre (2004) observed that although good and poor learners engaged frontal speech regions when learning a new foreign contrast, poor learners engaged these regions to a larger extend than good learners did. Platel et al. (1997) observed a negative relationship between learning of musical sequences and activity in bilateral insulo/fronto opercular areas. Opitz et al. (2002) reported greater activity in fronto-opercular areas when the stimuli were perceptually challenging. Although with the current data we cannot adjudicate a definitive account to our results, we favour the following explanation.

As mentioned, the greater white matter volumes in the right insulo/fronto opercular areas were observed in our poor perceivers. We believe this increase is indexing an augmented use of a compensatory mechanism for making specific vowel features salient during speech perception. The idea of interpreting increased activity as compensatory mechanisms is not new in speech-related pathologies. Increased frontal activation in neighbouring areas to the ones reported here have been observed in individuals suffering from developmental dyslexia (see Hoefta et al., 2011 for a recent proposal). The involvement of these areas would reflect the engagement of compensatory processes attempting to overcome less efficient processing in other cortical areas. These compensatory mechanisms raise the possibility that less skilled individuals overcome their difficulties by relying on an atypical involvement of cortical areas. In our study, the increased engagement of insulo/fronto-opercular areas would be enough to enable successful acquisition of the phonological system of L1, as poor perceivers (like good perceivers) did not report any trouble in native language (including reading) acquisition (all our participants were undergraduate and graduate university students, having effectively gone through all the educational system). It should be remembered, however, that differences in native language processing could be observed when fine-grained electrophysiological measures (the MMN) were taken. With regard to L2 processing, the increased use of a compensatory mechanism by poor perceivers was not enough to enable successful learning of difficult non-native vowel contrasts. Indeed, these individuals failed to notice the difference between the L2 (Catalan-specific) vowels even in a relatively easy behavioural categorization task, on which almost 70% of Spanish natives succeeded in perceiving it (Sebastian-Galles & Baus, 2005).[4]

The present study is the first to reveal a correlation between structural brain differences for healthy adults and native vowel perception. Interestingly, the present results depart significantly from those that have analysed structural differences between successful and less-successful non-native speech contrast learners. Golestani et al. (2002) observed that individuals who are faster at learning to hear a Hindi dental-retroflex contrast show a greater left $>$ right asymmetry in parietal lobe white matter volumes. In a subsequent study Golestani et al. (2007) also observed greater white matter volumes in the left Heschl's gyrus in faster learners compared with slow ones.[5] Wong et al. (2008) have also reported structural differences in HG between successful and less successful learners of picture-word associations of stimuli consisting of English pseudowords with pitch contours following the patterns of Mandarin tones. Unlike these studies, no difference in left Heschl's gyrus size was observed here between good and poor perceivers. Although there are substantial methodological differences between these studies, some of them related to the learning situation (natural vs. laboratory exposure), it is worth mentioning that in our study responses to both native and non-native vowels were analysed. Vowels are characterised by the relationship between steady-state frequency patterns. Golestani et al. (2002, 2007) used plosive consonants, involving rapid changes in the spectral domain. In this context, it should be noted that the processing of rapidly-changing acoustic information (consonants) is more lateralised to the left than is the processing of stable spectral information (vowels) (for reviews, see Poeppel, 2003; Zatorre & Gandour, 2008). The fact that we measured differences in vowel perception may have been responsible for a reduced role of temporal structures in favour of frontal ones in eliciting individual differences. However, the specific involvement of the right insulo/fronto-opercular area in non-native consonant contrasts observed by Golestani and Zatorre (2004) prevents us from considering that processing differences in basic acoustic parameters between consonants and vowels are solely responsible for the disparities between our results and previous ones.

The present results add to the relatively unexplored area of the relationship between brain structure and language function (for a review, see Richardson & Price, 2009). This approach has opened up promising avenues in several aspects of language processing (e.g., very early language development (Pujol et al., 2006), cross-linguistic research (Crinion et al., 2009) and acquisition of non-native phonemes (Golestani et al., 2002, 2007)). The specific contribution here is the identification of anatomical brain differences related to individual differences in vowel perception, since the two groups of participants differed in native and non-native perception (Diaz et al., 2008). These differences were present in a cluster located in the right insulo/fronto-opercular region, an area that previous functional studies have associated with auditory attention and non-native phoneme learning. The proposed interpretation of these findings is that the structural differences between good and poor perceivers reveal the use of a compensatory mechanism that enhances discrimination. Moreover, investigating the pattern of these structural differences over time in relation to improvements in linguistic skills may

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[4] Although our results are interpreted as indicating an increased (and compensatory) use of the right frontal opercular area in PPs, we acknowledge that with the present data it is impossible to determine if, in fact, the pattern observed by our PPs would coincide with the average population or whether the difference between the two groups is due to reduced white matter volume in GPs. These participants were also extremely good at perceiving the non-native sounds, as according to Sebastian-Galles and Baus (2005) less than 20% of the Spanish listeners fell within the range of Catalan natives for the most stringent behavioural task (an auditory lexical decision task (Sebastian-Galles et al., 2005; Sebastian-Galles, Rodriguez-Fornells, de Diego-Balaguer, & Diaz, 2006; Sebastian-Galles, Vera-Constan, Larsson, Costa, & Deco, 2009)). It could thus be argued that GPs are abnormally good in speech perception.

[5] It should be noted, however, that Golestani et al. (2007) also reported greater WM volumes in the right insula for slow learners compared with fast learners (although in a more posterior position than here). These authors interpreted the difference in WM volume as a displacement because the reverse contrast for GM was also detected (although the origin of this displacement was not clearly justified in the article).

provide an insight into brain regions supporting the process of compensation, which in turn may also influence remediation strategies and identify the most appropriate period for intervention.

However, we cannot rule out the possibility that the morphological brain differences between good and poor perceivers are the consequence of initial differences in brain myelination. Adjudicating between these two interpretations will require a longitudinal study.

5. Conclusion

In the present study we report very specific structural anatomical dissimilarities related to individual differences in the perception of difficult foreign vocalic contrasts. In particular, we have observed differences in white matter in the right frontal operculo-insular region in poor perceivers when compared with good ones. We propose that these differences reflect the differences in use of a compensatory mechanism that enhances auditory discrimination abilities.

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