Bilingualism at the core of the brain. Structural differences between bilinguals and monolinguals revealed by subcortical shape analysis

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Abstract

Naturally acquiring a language shapes the human brain through a long-lasting learning and practice process. This is supported by previous studies showing that managing more than one language from early childhood has an impact on brain structure and function. However, to what extent bilingual individuals present neuroanatomical peculiarities at the subcortical level with respect to monolinguals is yet not well understood, despite the key role of subcortical gray matter for a number of language functions, including monitoring of speech production and language control –two processes especially solicited by bilinguals. Here we addressed this issue by performing a subcortical surface-based analysis in a sample of monolinguals and simultaneous bilinguals (N=88) that only differed in their language experience from birth. This analysis allowed us to study with great anatomical precision the potential differences in morphology of key subcortical structures, namely, the caudate, accumbens, putamen, globus pallidus and thalamus. Vertexwise analyses revealed significantly expanded subcortical structures for bilinguals compared to monolinguals, localized in bilateral putamen and thalamus, as well as in the left globus pallidus and right caudate nucleus. A topographical interpretation of our results suggests that a more complex phonological system in bilinguals may lead to a greater development of a subcortical brain network involved in monitoring articulatory processes.

Key Words: Basal Ganglia, Thalamus, Structural MRI, Neuroanatomy, Bilingualism

Introduction

The human brain displays a considerable degree of structural plasticity. Learning or practicing a given skill can trigger experience-dependent changes in dendrification, vascularization, glial support and axonal myelination and rearrangement that, in some cases, impact macroanatomical brain morphology as measured by magnetic resonance imaging (MRI) techniques (Zatorre, Fields, Johansen-Berg 2012). A particularly interesting capacity that naturally shapes the human brain is language (Li, Legault and Litcofsky 2014), one of the most important cognitive attributes of humans. In this context, the study of bilingualism has proved to be a powerful way to understand how this long-lasting language learning process affects brain morphology (Costa and Sebastian-Galles 2014; Li, Legault and Litcofsky 2014).

fMRI studies directly comparing bilinguals and monolinguals show that the former generally make increased activations of cortical areas traditionally related to language processing (mainly because of more demanding word retrieval and articulatory processes; Parker Jones et al. 2012) as well as of brain regions involved in cognitive control (relevant for language switching, error monitoring and language interference inhibition; Abutalebi 2008; Abutalebi and Green 2007; Indefrey 2006). Therefore, the morphology of structures involved in these processes is expected to reflect bilingual experience. Indeed, research on the neuroanatomical differences between bilinguals and monolinguals has observed increased cortical gray matter volume in bilinguals in areas relevant for vocabulary acquisition and low-level auditory processing, among other language functions. Some of those areas are left-lateralized, such as the left inferior parietal cortex (Mechelli et al. 2004; Abutalebi et al. 2015) and left anterior temporal pole (Abutalebi et al. 2014), whereas others show bilateral effects, e.g. inferior frontal gyrus (Klein et al. 2014), Heschl's gyrus (Ressel et al. 2012), anterior cingulate cortex (Abutalebi et al. 2012) and cerebellum (Pliatsikas et al. 2014). Moreover, at the

level of the underlying white matter connections, both integrity increases (Luk et al. 2011; Mohades et al. 2012; Pliatsikas et al. 2015) and decreases (Mohades et al. 2012; Gold, Johnson and Powell 2013) have been observed in bilinguals compared to monolinguals in a number of commisural (anterior corpus callosum) and association white matter tracts (e.g. inferior longitudinal and fronto-occipital fasciculus), with mainly bilateral, but also left-lateralized effects being reported. Furthermore, García-Pentón et al. (2014) recently reported that bilinguals display greater structural connectivity and network efficiency in two left-lateralized language-related subnetworks, at the expense of decreased global network efficiency.

Here we focused on the morphological peculiarities that bilinguals might show at the subcortical level, namely, the basal ganglia and thalamus. The basal ganglia have received increased attention regarding their functional role in a wide array of language-related processes, such as speech production (Binder et al. 2005; Bohland and Guenther 2006; Kuljic-Obradovic 2003; Riecker et al. 2002; Rosen et al. 2000; Sakurai et al. 1993), rule learning (De Diego-Balaguer et al. 2008), and phonological processing (Tettamanti et al. 2005; Tricomi et al. 2006; Watkins et al. 2002), among others. The basal ganglia are an important component of the procedural memory system, which underlies the extraction and computation of language regularities and rules (e.g., mental grammar) (Ullman, 2004). Similarly, the thalamus is itself a key structure for language function with a well-established role in language production and lexical decision (for a review of fMRI studies, see Llano 2013), articulation, prosody, semantic processing, and verbal memory (for a review of electrical stimulation studies, see Hebb and Ojemann 2013). Importantly to our current goals, fMRI studies specifically focused on bilingualism have tended to underscore the relevance of subcortical structures for managing two or more languages. In particular, different studies have reported increased activation of the caudate nucleus in language switching (Abutalebi et al. 2007a; Crinion et al. 2006; Garbin et al. 2011; Wang et al. 2007; Wang et al. 2009). Also, there is evidence of recruitment of the putamen during demanding articulatory and motor control

processes, generally observed in bilinguals (Abutalebi et al. 2013; Klein et al. 1994; Tettamanti et al. 2005). In this vein, bilingualism is hypothesized to train a gating system in the striatum that modulates prefrontal cortex activation for language control and application of language rules (Stocco et al. 2012). In spite of the substantial evidence, the literature is almost inexistent regarding the subcortical structural signature of bilingualism, with only two small-sized, whole-brain voxel-based morphometry (VBM) studies reporting subcortical gray matter differences between bilinguals and monolinguals: Zou et al. (2012) showed greater volume in the head of the left caudate nucleus in bimodal bilinguals, who use spoken and sign languages, compared to monolinguals. Also, Abutalebi et al. (2013) showed an increased volume in the left putamen of female multilinguals compared to a group of monolingual participants. These studies suggest that bilingualism may shape the morphology of subcortical brain regions involved in language switching and articulatory processes, respectively. However, their limitations in terms of sample size and other restrictions (e.g. only females, language bimodality), as well as the lack of specificity of VBM approaches to study subcortical morphology, may have well reduced their sensitivity to fully capture the effect of bilingualism on subcortical gray matter.

Recent advances in brain morphometry now allow investigating subcortical morphology in an anatomically meaningful fashion while boosting sensitivity for capturing potential effects. Whereas VBM has long been considered a standard approach in morphometric studies, it is acknowledged that it cannot differentiate between size, shape and/or positional effects (Zatorre, Fields, Johansen-Berg 2012). At the cortical level, surface-based morphometry techniques have addressed this issue by allowing the measurement of different aspects of the cortex (e.g., thickness and surface area) while providing a more accurate characterization of cortical anatomy. However, at the subcortical level, it was not until the advent of shape analysis techniques (e.g., Patenaude et al. 2011) that successfully estimating regional shape variations in subcortical structures with high anatomical precision was possible. This approach has been mainly applied to unveil

abnormal subcortical morphology in mental disorders or disease (Coscia et al. 2009; Harms et al. 2007; Kang et al. 2008; McKeown et al. 2008; Qiu et al. 2008; Xu et al. 2008) but recently also to understand the role of subcortical shape in high-order cognition in healthy populations (Burgaleta et al. 2013b).

In the present study we used the subcortical shape analysis approach to explore, for the first time, whether bilinguals display a distinctive morphology of the subcortical gray matter compared to monolinguals. This approach allowed us to robustly characterize the anatomical boundaries of subcortical structures for each participant and to test for potential morphological differences between groups at the vertex level. We recruited monolinguals (Spanish speakers) and simultaneous bilinguals (Catalan-Spanish speakers) who did not differ in average educational level, socioeconomic background and proficiency in other languages. Spanish and Catalan are two Romance languages that share a great amount of lexical cognates (words that share a common etymological origin and differ in their phonology) and differ mainly at the phonological level. All participants underwent MRI acquisition, and subsequent subcortical segmentation and surface reconstruction were performed for all striatal structures (caudate, accumbens, putamen, and globus pallidus) and thalamus. We then computed the perpendicular vertex displacements with respect to a sample-specific average surface, thus representing relative surface expansions or contractions at the regional level. Because bilinguals are hypothesized to more strongly recruit brain areas involved in articulatory and language switching processes, we expected to find a plasticity effect (expansion) primarily on the putamen (articulation) and the caudate nucleus (language switching) in bilinguals compared to monolinguals, as well as in the thalamus, given its key role in language functions. Nucleus accumbens was included under the assumption that, given its reduced volume as well as the low spatial resolution typically found in fMRI studies, its potential relevance for language might have been obscured by the structures in its vicinity. In addition to these analyses, and for the sake of completeness, we also applied voxel-based morphometry to address potential differences in cortical gray matter

between bilinguals and monolinguals. Based on our previous work on Catalan-Spanish bilinguals, we mainly expected significant differences favoring bilinguals in the auditory cortex (Heschl's gyrus, Ressel et al. 2012).

Methods

Participants

88 right-handed participants took part in the study. All participants were undergraduate students at the University Jaume I of Castellón de la Plana (Spain) so they had the same educational level. None of them reported known auditory or neurological deficits. Forty-six participants were monolingual Spanish speakers (26 females; mean age = 21.85 years, SD = 4.13) and 42 were simultaneous Catalan–Spanish bilinguals (22 females; mean age = 21.64 years, SD = 2.17). The study followed the ethical protocol of the University Jaume I. All the participants were paid for their participation.

Sample characteristics were similar to those in Ressel et al. (2012) regarding the languages spoken and proficiency level, although here we used a greater sample size and our bilingual participants acquired their two languages simultaneously. The bilingual participants learned both Catalan and Spanish from birth and used them daily. They all attended bilingual schools since age 5 at the latest as part of the official linguistic policy of the Castellón region (see Table 1 for further details on participants' self-reported linguistic background). Catalan and Spanish are two Romance languages that differ mainly at the lexical and phonological level. Catalan has a larger set of allophones, with 8 vowel sounds (compared to 5 in Spanish) and three affricate consonants (/dz/, /dZ/, /ts/) in addtition to the Spanish /tS/. The Spanish fricative unvoiced consonants /T/ and /x/ are substituted in Catalan by /S/ and /Z/, respectively. There are also differences in the realization of certain allophones (e.g. /j/, /l/, /w/). Other peculiarities of the Catalan language include the lack of diphthongization of Latin short ĕ, ŏ, the high prevalence of /ʎ/ and /ɲ/ at the end of words, and the presence of final obstruent devoicing –e.g. *amic*

('male friend') vs. *amiga* ('female friend'). Importantly, Spanish and Catalan have many cognate words (65-70%; Harris & Vincent 1988).

Monolingual participants were also university students that moved from other regions of Spain to Castellón to enroll in university courses. Focusing on university students minimizes potential group differences in nuisance (gross educational, cognitive and sociodemographic) factors while allowing for potential bilingualism-related differences in cognitive performance (e.g., executive functions, Bialystok & Craik 2010; Costa & Sebastián-Gallés 2014). All participants received formal education in English as part of the Spanish official educational system. Individuals with high proficiency in languages other than Catalan or Spanish were excluded from our study. Note, however, that we did not evaluate whether participants spoke additional languages with a very low proficiency, although given the social and educational similarities between the groups assessed here, we did not expect different distributions in that respect. Self-ratings of comprehension, reading, fluency, pronunciation, and writing skills in English and Spanish (on a four-point scale: 1 = perfect, 2 = good, 3 = sufficient, 4 = poor) were obtained for all participants. English proficiency was low in average for both groups (Table 1). No significant differences were found between bilinguals and monolinguals in any of the English or Spanish scales ($p > 0.1$).

Image acquisition

Structural MRI data were acquired with a 1.5T scanner (Siemens Symphony, Erlangen, Germany) with a standard quadrature head coil. Participants' heads were immobilized with cushions to reduce motion artifacts. A high-resolution structural T1-weighted MPRAGE sequence was acquired (TR/TE = 2200/3.8 ms, matrix = 256 x 256 x 160, voxel size = 1 x 1 x 1 mm).

Subcortical shape analyses

To study the subcortical morphology we applied the FIRST tool, part of FSL package (http://www.fmrib.ox.ac.uk/fsl/first/index.html) which implements the Bayesian

Appearance Model (Patenaude et al. 2011). This model combines probabilistic information about shape and intensity in order to segment the structures of interest. One advantage of this approach is that it is based solely on the geometry and location of the anatomical boundary of the structure (thus not requiring tissue classification and arbitrary smoothing, as in VBM methods).

Prior to image segmentation, the software implements a two-stage affine registration to standard space (MNI152 template). The first stage is a whole-brain, 12 d.o.f. registration. The second stage takes the resulting image and uses a subcortical weighting mask to perform a new 12 d.o.f. registration in order to achieve optimal registration of the subcortical structures. The modelled shape variance will be the residual variance resulting from the described affine registration process.

Following image registration, the Bayesian Active Appearance Model (AAM) is used to segment each subcortical structure, which is parameterized as a deformable surface mesh (similar to a tesselated sphere) consisting of sets of vertices connected by edges. Variability in deformations (vertex coordinates and intensities) is modelled by a multi-variate Gaussian distribution. Software developers applied this algorithm to a training dataset and eigenvectors of deformations were calculated, representing a wide range of possible brain shapes and sizes. Subcortical segmentation of new images is then performed by searching through eigenvectors in order to find the most probable shape instance. Mesh surfaces are deformed from the mean shape of their respective structure until optimal registration is achieved, and vertex coordinates are then recorded. This approach ensures that each vertex corresponds to the same anatomical location across subjects.

The current version of the software allows for the analysis of orthogonal vertex displacements only (which are assumed to be more easily interpreted from an anatomical standpoint), so that a single scalar will characterize the relative outward or inward position of a given vertex with respect to its corresponding average sample coordinates.

We used FIRST to automatically segment the caudate nucleus, the nucleus accumbens, the globus pallidus, the putamen, and the thalamus. Quality control of the subcortical segmentations was performed by an experienced researcher (M.B.). Five subjects (1 bilingual and 4 monolinguals) were discarded because of poor segmentation of one or more structures. A total sample size of N = 83 was therefore included in further steps.

Following a standard procedure, we performed a 6 parameters registration of the remaining subcortical surfaces generated by FIRST to a sample-specific average surface in native space in order to eliminate differences in orientation and location, while preserving sensitivity to shape and regional size. For each subject and structure of interest, vertex coordinates were projected onto the average surface, generating maps of vertex displacements (perpendicular to the surface) with respect to the average coordinates –so that positive values represent outward displacement (expansion) and negative values represent inward displacement (compression). These displacement values were submitted to statistical analysis. Additionally, we also computed the volume of each structure in order to test for potential global differences between bilinguals and monolinguals.

Voxel-based morphometry

To investigate the effects of structural differences in grey matter (GM), Voxel-based morphometry (VBM) was used. VBM was performed with the VBM8 toolbox (http://dbm.neuro.uni-jena.de/vbm/) for the SPM8 package (Wellcome Department of Imaging Neuroscience, London). The preprocessing procedure implemented in VBM8 is based on the New Segment Toolbox using the Tissue Probability Maps of SPM8. Images were segmented into gray matter (GM), white matter (WM) and cerebrospinal fluid (CSF), and registered by affine (12-parameter) transformations to a standard template provided by the International Consortium of Brain Mapping (ICBM). The GM and WM segments were input into DARTEL in order to create a customized DARTEL template of all subjects. Then the individual tissue segments were registered to the template obtaining the individual deformation fields, which were used to normalize each

participant's GM tissue maps. Voxel values were modulated by the nonlinear components derived from spatial normalization; thus, the volume variations resulting from normalization were corrected in the resulting GM volume maps. Modulation by linear components was not performed in order to account for individual differences in global brain size in the subsequent analyses, thus rendering correction for total intracranial volume of the individual unnecessary (Scorzin et al., 2008). Hence, inferences were made on local GM volume changes. Finally, images were smoothed with an 8 mm Gaussian kernel.

Statistical analysis

F statistics for the main effect of Group (Bilinguals vs. Monolinguals) were computed vertexwise while controlling for potential effects of age and gender. Subcortical analyses were carried out via permutation-based inference (Nichols and Holmes 2002), implemented using the randomise tool of the FSL package (FMRIB, Oxford, UK; http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Randomise). The Threshold-Free Cluster Enhancement algorithm (Smith and Nichols 2009) was applied to detect cluster-wise statistical signal while avoiding the setting of arbitrary cluster-forming thresholds. Resulting statistical maps were thresholded at $P < 0.05$ corrected for multiple comparisons (family-wise error rate below 5%). The same statistical design was implemented in our VBM analyses, where the statistical threshold for the spatial extent test at the cluster level was at $P < 0.05$, family-wise error (FWE) corrected for multiple comparisons with an underlying voxel level of $p < 0.005$ to a cluster-size criterion of at least $k = 347$ voxels.

Brain-behavior correlations

Based on the self-reported percentages of language use (Spanish and Catalan), we computed continuous indices of bilingual/monolingual language use by subtracting 50 from the percentage of use of the dominant language, and then computing the absolute value of such difference (so that values close to zero indicate similar use of the two

languages, and values departing from zero indicate preference for one of the two languages). We obtained two indices per subject: a 'bilingual production index' (based on his/her reported percentage of time speaking his/her dominant language) and a 'bilingual perception index' (based on his/her reported percentage of time listening to his/her dominant language). We then performed bivariate correlations (in the bilingual group only) between these indices and brain morphology at the peak vertices and voxels revealed by our between-groups FIRST and VBM analyses, respectively. We expected that more balanced individuals would present greater expansion/volume than those whose language use is less balanced.

Results

Subcortical shape analysis

At the subcortical level, we observed that bilinguals displayed bilateral expansion of putamen and thalamus with respect to monolinguals, as well as of the left globus pallidus and right caudate ($P < 0.05$, corrected for multiple comparisons)(Fig. 1). No other significant effects were observed for any other structure. Similarly, no significant expansions were observed for monolinguals with respect to bilinguals. Figure 2 displays density plots for the surface displacements in bilinguals and monolinguals at the peak vertices observed for each structure.

Putaminal effects were distributed in the left structure, with expansions observed along the anteroposterior axis, both in the external (lateral) and internal (medial) surface, as well as in the anterior pole. Conversely, the significant effect found for the right putamen was well localized in the anterior section of the external surface. With regard to the thalamus, the greater expansion observed in the bilinguals group was distributed across its surface bilaterally, suggesting a global effect rather than a regional one. The pallidal expansion, solely observed in the left hemisphere, took place in a well-defined area of its anteromedial surface. Finally, for the right caudate nucleus, a small cluster in

its dorsolateral surface was found to be more expanded in bilinguals compared to monolinguals.

The observed regional effects were accompanied by significant effects at the volumetric level. Bilinguals displayed greater total volumes of bilateral putamen (p < 0.05), bilateral thalamus (p < 0.01), and right caudate nucleus (p < 0.05). The left globus pallidus only showed a greater size in bilinguals at a trend level (p < 0.1). Nevertheless, none of these differences were still significant after applying a Bonferroni correction for multiple comparisons.

Voxel-based morphometry

Results for the VBM analysis are reported in Table 2. Bilinguals displayed greater gray matter volume in left- and right-sided areas of the frontal, temporal, and parietal lobes, as well as in the cerebellum. It is of note that we replicated our previous observation regarding increased volume of the left Heschl's gyrus in bilinguals (Ressel et al. 2012). Similarly, some of the areas detected here have been previously shown to be sensitive to bilingual experience, e.g., bilateral cerebellum (Pliatsikas et al. 2014) and bilateral inferior frontal gyrus (Klein et al. 2014). Conversely, monolinguals showed increased gray matter volume in the left middle and superior temporal gyrus.

Correlations between brain morphology and behavioral measures in bilinguals

Our bilingual perception index correlated significantly and in the expected direction with individual differences in the morphology of the left thalamus (r = -.357, p < .05, one-tailed), whereas our bilingual production index correlated with the right caudate nucleus (r = -.324, p < .05, one-tailed). Furthermore, at the cortical level we observed a significant correlation between our bilingual perception index and morphology of the left middle temporal gyrus (r = .365, p < .01, one-tailed). The direction of this association was also expected given that this area was found to be reduced in bilinguals compared to monolinguals.

Discussion

In the present study we addressed the question of whether monolinguals and bilinguals differ in the morphology of those subcortical structures typically involved in language processing. We investigated this issue by applying subcortical shape analysis for the first time in a large sample of monolinguals and simultaneous bilinguals, an approach that allowed us to unveil fine-grained regional differences between these two groups in the morphology of the basal ganglia and thalamus. Interestingly, we observed an expansion of bilateral putamen and thalamus, as well as of left pallidum and right caudate nucleus, in bilinguals compared to monolinguals. Our results suggest that extended usage of two languages simultaneously since early developmental stages may have an impact on brain morphology at the subcortical level.

One of the main results reported here was observed bilaterally in the putamen. This result is consistent with, and also expands, the recent report by Abutalebi et al. (2013) where increased gray matter density in the left putamen was observed for female multilinguals compared to monolinguals. Nevertheless, our greater sample size, the fact that we focused on simultaneous (instead of early) bilinguals, and the use of a more sensitive technique for the analysis of subcortical morphology, likely explain the larger extent and bilaterality of our results. The role of this striatal structure in language production and perception is well documented (Bohland and Guenther 2006; Gil Robles et al. 2005; Murdoch 2001; Oberhuber et al. 2013; Riecker et al. 2005; Seghier and Price 2010; Tettamanti et al. 2005), including the monitoring and programming of speech articulations (Chan et al. 2008; Dodel et al. 2005; Garbin et al. 2010; Klein et al. 1994, 1995; Riecker et al. 2002; Simmonds, Wise, Leech 2011) and the processing of phonological errors (Tettamanti et al. 2005; see also Bitan et al. 2005; Booth et al. 2002, 2007; Houk 2005). Given the wider range of speech sounds managed by Catalan-Spanish bilinguals compared to Spanish monolinguals, it is reasonable to expect that the

putamen will be more strongly recruited by the former group, which might have an effect at the structural level.

The other subcortical structure for which we observed a significant and highly distributed difference between groups was the thalamus. This structure is commonly activated during fMRI naming or word generation experiments (Indefrey and Levelt 2004), but also during lexical decision and reading tasks (Llano 2013). This wide-ranging functionality, along with the distributed effect of bilingualism over thalamic morphology reported here, makes it likely that the functional consequences (and sources) of a globally expanded thalamus are manifold. From a theoretical standpoint, coordinated thalamic and basal ganglia activity have been explicitly taken into consideration by some models of language production (e.g., the Response-Release Semantic Feedback Model, Crosson 1985, 1992; Murdoch and Whelan 2009; Murdoch 2001; see also the Lexical Selection Model, Mink 1996; Norris and McQueen 2008; Wallesch and Papagno 1988), in line with their profile of anatomical connectivity (Ford et al. 2013). The fact that we observed concurrent bilingualism effects in all these structures might be due to a greater need for speech output monitoring in bilinguals (Parker Jones et al. 2012). However, further research should address the impact of bilingualism over specific thalamic subnuclei, as they show specialized language functions (e.g., foci of activation for generative tasks tend to be found around its medial segments; naming tasks generally comprise left lateral foci; and active speech listening tasks are distributed bilaterally across the thalamus; Llano 2013).

Some of the aforementioned theoretical models also posit explicit language-related roles for the globus pallidus, a structure for which we observed a well-localized bilingualism effect in the anterocentral half of its medial surface. The Response-Release Semantic Feedback Model states that the GP plays a role in semantic monitoring of speech production (Crosson 1985). On the other hand, the Lexical Selection model (Wallesch and Papagno 1988; Wallesch 1990) proposed that the GP is relevant for

combining lexical and contextual information with temporal precision. In a more general manner, GP has been shown to be activated during speech production tasks (Klein et al. 2006; Riecker et al. 2000; Wise et al. 1999) and several studies have demonstrated that this structure is relevant for verbal fluency (Schmand et al. 2000; Whelan et al. 2004; York et al. 2003). In addition, abnormalities in activity and structure of GP have also been reported in language-related disorders, such as Developmental Language Disorder (Hwang et al. 2006; Lee, Nopoulos, Bruce Tomblin 2013; Ors et al. 2005) and children with speech sound errors (Preston et al. 2012). Therefore, the results observed here for the globus pallidus further support the possibility that morphological differences between bilinguals and monolinguals are related to an array of subcortical structures involved in language production, ranging from articulatory, low-level motor structures to regions involved in lexico-semantic monitoring.

Finally, we observed differences between bilinguals and monolinguals in a small dorsocentral region of the lateral surface of the right caudate nucleus. Right-lateralized activity in the caudate nucleus has been reported during a language switching task in Chinese-English bilinguals (Ma et al. 2014) and, in a meta-analysis of language switching studies, Luk et al. (2012) showed the implication of both right and left striatal structures. Simultaneous interpretation studies have also highlighted the role of right-lateralized caudate activity (Hervais-Adelman, Moser-Mercer and Golestani 2015; Hervais-Adelman et al. 2014) and morphology (Elmer et al., 2011), in line with studies using translation tasks (Abutalebi and Green, 2007; Price et al., 1999). Whereas other studies highlight the role of the left caudate nucleus in language control and language switching in bilinguals (Abutalebi et al. 2008; Abutalebi, Miozzo, Cappa 2000; Abutalebi et al. 2007b; Crinion et al. 2006; Garbin et al. 2010; Wang et al. 2007, 2009), it seems that left caudate is recruited mainly during initial stages of L2 acquisition (Abutalebi and Green 2007; Indefrey 2006) and when switching to the least proficient language (Abutalebi et al. 2013). Because our participants were highly proficient in both languages, it is possible that the left anterior caudate function was not as germane as in other populations

where language proficiency is less balanced. Alternatively, it is also possible that the observed effect on the right caudate nucleus is related instead to its role in speech production. For instance, Grogan et al. (2009) observed that L2 phonemic fluency was associated with gray matter density in bilateral areas of the caudate nucleus, and Crosson et al. (2003) observed significant activity in the right caudate nucleus during tasks requiring generation of words.

As a final comment, several considerations must be made regarding the sample used here. We studied a sizeable, rigorously selected sample of homogeneous monolingual and bilingual individuals. In particular, bilinguals did not differ in terms of the languages they spoke (i.e., only Spanish and Catalan), and age and language learning situation did not differ between monolinguals and bilinguals, as all languages were acquired in a naturalistic environment from birth. Also, all participants went through the same (Spanish) education system and had the same educational level, the only difference being that in the case of bilinguals, some courses were taught in Catalan and others in Spanish, while in the case of monolinguals all courses were taught in Spanish. Moreover, the fact that bilinguals learned their two languages simultaneously allows excluding the potential problems of self-selection effects that often make difficult to compare monolinguals and bilinguals. It remains to be tested whether other bilingual populations (e.g. early sequential, late immersed or non-immersed bilinguals) may present a similar pattern of neuroanatomical differences with respect to monolingual speakers.

Future research is necessary to better understand the cellular and functional implications of the macroanatomical differences observed here. On the one hand, the cellular underpinnings of basal ganglia morphology cannot be determined by means of structural MRI, and might include greater dendritic or axonal arborization, higher number of neurons, stronger glial support, and/or greater vascularization (Burgaleta et al. 2014). On the other hand, it should be addressed empirically which specific language (and non-language) functions are responsible for the observed subcortical differences

between bilinguals and monolinguals, as the purpose of our work was solely to capture global effects of bilingualism. Brain morphology was related here to self-reported measures of language use in bilinguals, although such associations were only observed for the left thalamus and right caudate nucleus, as well as for the left middle temporal gyrus. While these results provide additional support to our conclusions, extensive behavioral assessment of language functions should be included in future studies in order to better understand the functional implications of morphological differences between bilinguals and monolinguals. Similarly, potential group differences in general cognitive abilities (e.g., executive functions; Bialystok & Craik 2010; Costa & Sebastián-Gallés 2014) may also be controlled for if one is interested exclusively in language-specific effects of bilingualism.

Another important question to be answered in future works is whether the reported structural differences between bilinguals and monolinguals at the subcortical level can be generalized to other language pairs. Language-specific differences in bilingualism research have been already suggested (Klein et al. 2006; Perani et al. 1996; Price, Green, von Studnitz 1999). In the present study we investigated bilinguals in Spanish and Catalan, two Romance languages that share a great amount of lexical cognates and differ mainly at the phonological level. Because cognates are words that share a common etymological origin and differ in their phonology, they may be strongly taxing the phonological and articulatory processing in Spanish-Catalan bilinguals in a way that might not be observed in other language pairs. It has also been argued that a greater similarity between languages may lead to a more difficult conflict resolution and target selection during bilingual lexical access (Costa, Santesteban and Ivanova 2006). However, some evidence does not support, and even contradicts, this possibility. On the one hand, a cognate facilitation effect has been observed in multiple studies on bilingual (visual and auditory) word recognition and production (e.g., Marian & Spivey, 2003; Costa et al. 2000, Costa et al. 2005). Interestingly, in an fMRI study, Rodriguez-Fornells, De Diego and Münte (2006) reported that bilinguals showed decreased activation when processing cognates (versus noncognates) in the left dorsolateral prefrontal cortex and

anterior cingulate cortex, hence supporting the possibility that cognitive control is in fact reduced during cognate processing in bilinguals. Finallly, Costa, Santesteban and Ivanova (2006) demonstrated that language similarity did not affect switching cost in bilinguals during a picture-naming task. Therefore, it could be the case that Catalan-Spanish bilinguals present either equivalent or even reduced output monitoring needs compared to bilinguals speaking less similar language pairs.

Conclusion

How does lifelong experience in two languages affect subcortical morphology? Here we show that early bilinguals display localized expansions in the putamen, globus pallidus, caudate and thalamus. This pattern of results suggests that subcortical morphology may be affected by language use. Furthermore, our findings also highlight the role of subcortical structures in language and suggest that phonological and articulatory enrichment entails structural changes in striatal and thalamic structures primarily involved in monitoring speech production.

Acknowledgments

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Tables and Figures

Table 1. Linguistic background for monolingual and bilingual participants. The fluency scores used a four-point scale (1 = perfect, 2 = good, 3 = sufficient, 4 = poor).

	Monolinguals		Bilinguals		
	Mean	SD	Mean	SD	F (p value)
Onset of listening to Catalan (years)	-	-	0.36	0.96	-
Onset of speaking Catalan (years)	-	-	2.21	1.24	-
Onset of listening to Spanish (years)	0.26	0.85	0.2	0.56	0.18 (0.676)
Onset of speaking Spanish (years)	1.88	0.86	1.98	0.72	0.33 (0.565)
Proportion listening to Catalan (%)	8.76	9.84	42.5	13.76	177.32 (<.001)
Proportion speaking Catalan (%)	0.11	0.74	53.29	17.18	440.34 (<.001)
Proportion listening to Spanish (%)	85.59	13.83	53.1	11.99	137.46 (<.001)
Proportion speaking Spanish (%)	97.85	4.76	43.86	17.09	423.59 (<.001)
Pronunciation score in Catalan (1-4)	3.91	0.41	1.29	0.46	803.35 (<.001)
Pronunciation score in Spanish (1-4)	1.13	0.34	1.12	0.33	0.02 (0.874)
Pronunciation score in English (1-4)	2.87	0.83	2.88	0.77	0.01 (0.947)
Comprehension score in Catalan (1-4)	3.76	0.48	1.07	0.26	1038.12 (<.001)
Comprehension score in Spanish (1-4)	1.09	0.28	1.05	0.22	0.53 (0.470)
Comprehension score in English (1-4)	2.7	0.73	2.52	0.8	1.11 (0.295)
Fluency score in Catalan (1-4)	3.93	0.25	1.1	0.3	2370.04 (<.001)
Fluency score in Spanish (1-4)	1.04	0.21	1.07	0.26	0.31 (0.577)
Fluency score in English (1-4)	2.8	0.86	2.83	0.79	0.03 (0.870)

Table 2. Summary of results for the voxel-based morphometry analysis comparing gray matter volume between bilinguals and monolinguals.

AAL Region	Bilinguals > Monolinguals		
	Cluster	Z-value	MNI coordinates
R Inferior Temporal gyrus	829	4.58	65 -29 -29
L Frontal inferior orbitalis	1109	3.14	-29 26 -29
R Frontal inferior orbitalis	399	4.09	30 29 -27
L Cerebellum	1078	3.88	-15 -61 -65
L Heschl	388	3.73	-45 -12 7
R Cerebellum	1065	3.72	9 -67 -60
R Inferior Parietal Lobe	736	3.33	36 -25 43
	Monolinguals > Bilinguals		
L Middle Temporal Gyrus	458	4.09	-56 -51 6
L Superior Temporal Gyrus		3.89	-54 -43 15

Fig. 1. Significantly expanded subcortical areas (in blue; FWE-corrected *P* < .05) in bilinguals compared to monolinguals.
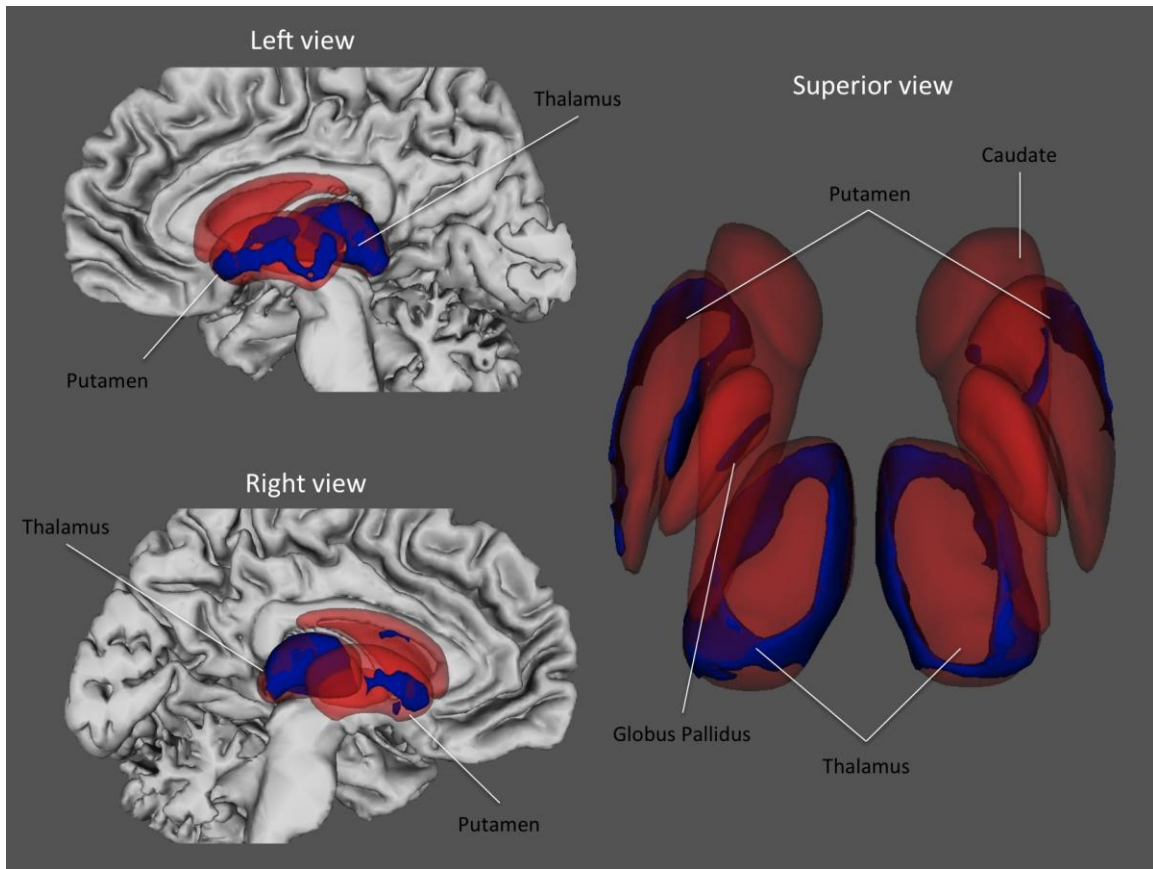
Fig. 2. Density plots for the surface displacements in bilinguals and monolinguals at the peak vertices for the maximum group difference observed at each structure. Surface displacements are in arbitrary units, with 0 representing no orthogonal displacement with respect to the total average surface. MNI coordinates (in mm) for the peak vertex are provided in brackets.