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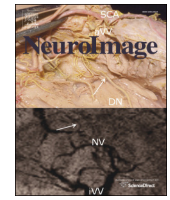

Bilingualism at the core of the brain. Structural differences between bilinguals and monolinguals revealed by subcortical shape analysis

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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.

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 et al., 2012). A particularly interesting capacity that naturally shapes the human brain is language (Li et al., 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 Sebastián-Gallés, 2014; Li et al., 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 et al., 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.

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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, 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 et al., 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 and 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