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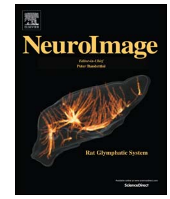

Bilingualism modulates the white matter structure of language-related pathways

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ABSTRACT

Learning and speaking a second language (L2) may result in profound changes in the human brain. Here, we investigated local structural differences along two language-related white matter trajectories, the arcuate fasciculus and the inferior fronto-occipital fasciculus (IFOF), between early simultaneous bilinguals and late sequential bilinguals. We also examined whether early exposure to two languages might lead to a more bilateral structural organization of the arcuate fasciculus. Fractional anisotropy, mean and radial diffusivities (FA, MD, and RD respectively) were extracted to analyse tract-specific changes. Additionally, global voxel-wise effects were investigated with Tract-Based Spatial Statistics (TBSS). We found that relative to late exposure, early exposure to L2 leads to increased FA along a phonology-related segment of the arcuate fasciculus, but induces no modulations along the IFOF, associated to semantic processing. Late sequential bilingualism, however, was associated with decreased MD along the bilateral IFOF. Our results suggest that early vs. late bilingualism may lead to qualitatively different kind of changes in the structural language-related network. Furthermore, we show that early bilingualism contributes to the structural laterality of the arcuate fasciculus, leading to a more bilateral organization of these perisylvian language-related tracts.

1. Introduction

Learning is rooted in the brain's ability to reorganize itself in response to changing demands (Lövdén et al., 2010) and each new skill is, by and large, reflected as changes in neural connections. Learning and speaking a second language (L2) is a sustained experience, which may have a profound impact on the brain. Speaking multiple languages has been shown to lead to a variety of functional changes, and evidence of specific brain activation patterns related to bilingual language processing is abundant (for a recent review, see e.g. Costa and Sebastián-Gallés, 2014). While functional adaptations in response to L2 experience have been extensively investigated, there are fewer studies on L2-induced structural changes. However, a growing body of research has shown that bilingualism-induced functional changes are, in fact, often accompanied by anatomical changes in the brain structure (for reviews, see e.g., Li et al., 2014; Stein et al., 2014). Bilingualism has been associated with structural modulations in e.g., the left inferior parietal lobule (Mechelli et al., 2004), left inferior frontal gyrus (Stein et al., 2012), anterior temporal pole (Abutalebi et al., 2014) and the cerebellum (Pliatsikas et al., 2014), measured, for instance, as changes in grey matter density. The extent of these modulations has been found to be sensitive to L2 proficiency and the age of L2 acquisition (Stein et al., 2014). Similar age of acquisition and proficiency effects (e.g. Perani et al., 2003; Li et al., 2014) have also been reported in functional activation studies on L2 processing, particularly for the left inferior parietal and frontal areas.

Recent diffusion weighted magnetic resonance imaging (MRI) studies have also began to investigate the possible structural white matter changes related to bilingualism. Diffusion tensor (DT) derived measures such as fractional anisotropy (FA) or radial and mean diffusivities (RD and MD respectively) have been used to describe the underlying microstructure and fibre organizations of the tracts. FA is a scalar measure between zero and one that describes the degree of anisotropy within a voxel. Values close to one indicate that the diffusion

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is highly restricted and only occurs along one orientation, while values near zero signify unrestricted diffusion, i.e., diffusion can occur in all orientations. Higher FA values are typically observed in regions where axons are densely packed and run parallel to each other, as water molecules cannot move across the axonal walls but are free to diffuse along them (Van Hecke et al., 2016). FA is highly sensitive to changes in the microstructural architecture, without providing insight about the specific type of change (Alexander et al., 2007). Factors that can modulate the FA include, but are not limited to, the degree of axonal myelination, axonal packing density, membrane permeability, the organizational coherence of the axons, and measurement technical details (Jones et al., 2013; Sairanen et al., 2017). In general, high FA values have been taken to indicate higher white matter integrity (Smith et al., 2006), although this interpretation has received considerable criticism of its vagueness (see e.g. Jones et al. 2013). RD and MD convey information about the diffusion magnitude and they are inherently related to FA, although both offer slightly different information: increased RD values have been linked to de- or dysmyelination of axons (Song et al., 2002), while MD is an inverse measure of the membrane density (Alexander et al., 2007). Furthermore, decreased MD in particular with increased FA has been suggested to reflect increasingly dense and ordered packing of the fibre tracts (Takahashi et al. 2000; Schmithorst et al. 2002).

Most DT studies on bilingualism have looked for global differences at the whole-brain level by utilizing Tract-Based Spatial Statistics (TBSS). This approach allows for comparing FA values, or any other tensor-derived values, with voxel-wise statistics at the centres of tracts common to all participants (Smith et al., 2004, 2006). These TBSS studies have reported a variety of sites responding to bilingualism, e.g., superior longitudinal fasciculus (Luk et al., 2011; Pliatsikas et al., 2015), inferior longitudinal fasciculus (Luk et al., 2011) and uncinate fasciculus (Luk et al., 2011). However, the two regions most consistently showing bilingualism-induced changes are the corpus callosum (CC) (Coggins et al., 2004; Luk et al., 2011; Mohades et al., 2012; Schlegel et al., 2012) and the inferior occipito-frontal fasciculus (IFOF) (Cummine and Boliek, 2013; Gold et al., 2013; Mohades et al., 2012). The IFOF is a long trajectory connecting the inferolateral and dorsolateral frontal cortex with the posterior temporal and occipital lobe (Catani et al., 2002; Jellison et al., 2004). It has been suggested to be relevant in semantic aspects of language processing (e.g. Duffau et al. 2005; Leclercq et al. 2010). Despite consistently reported differences for bilinguals vs. monolinguals at these locations, the directionality of the effect has varied. While some studies have shown increased FA for bilinguals in both locations (Luk et al., 2011; Pliatsikas et al., 2015), others have reported an opposite pattern of decreased FA for bilinguals (Cummine and Boliek, 2013; Gold et al., 2013; Kuhl et al., 2016). Due to contradictories in the findings, the exact effects of bilingualism on the IFOF remain ambiguous.

While analysis at the whole-brain level gives important information about the global effects of bilingualism, there are some restrictions related to this approach. First, the bilingual brain appears to be functionally less lateralized and more bilaterally balanced (Hull and Vaid, 2007) than the monolingual brain (but see e.g. Paradis, 1990). Since the CC is crucial in mediating information exchange between the two hemispheres, the reported changes in the CC fit well in line with the assumed more bilateral configuration of the bilingual brain. However, the salience of this effect might obscure smaller and more local tract-specific effects. Second, one step in the TBSS analysis pipeline involves skeletonizing the FA maps, a procedure aimed at improving comparability of the diffusion data across participants and between groups. This step leads to losing detailed participant-wise information about individual tracts and in some extreme cases can lead to entirely ill-posed comparisons if the projection of participant-wise tracts fails (Bach et al., 2014). Furthermore, the TBSS skeleton projection has been shown to be particularly vulnerable to distortions and misalignment in regions where pathways merge or the tract structure is circular in form (like e.g. the uncinate fasciculus) (Bach et al., 2014).

One important language-related tract that might suffer from the TBSS skeletonization procedure due to its complex structure and circular form, is the arcuate fasciculus. It is a pathway connecting temporal, parietal and frontal language regions via one direct and two indirect trajectories between Broca's and Wernicke's regions (Catani et al., 2005). These three separable segments have been suggested to have designated functions of their own: the left direct segment, for instance, has been related to phonological language functions (Catani et al., 2005; Forkel et al., 2014; López-Barroso et al., 2013), while left indirect trajectories (specifically the posterior part) have been suggested to underlie semantic language functions (Binder and Desai, 2011; Catani et al., 2005). So far, only one (longitudinal) study (Mohades et al., 2015, 2012) has used a tract of interest (TOI) approach to locally compare FA values between groups of mono- and bilingual children. They investigated changes in four preselected TOIs associated with language processing and communication, among them the left arcuate fasciculus/superior longitudinal fasciculus and the left IFOF. They reported increased FA values for simultaneous bilinguals only along the left IFOF, but found no effects of bilingualism on the arcuate fasciculus in these child participants.

Considering the important role of the arcuate fasciculus in conveying information between two major language-related sites, the processing demands entailed by bilingualism might modulate the lateralization of this structure. In the right-handed population, the speech and language functions have been shown to demonstrate notable leftward asymmetries (e.g., Cabeza and Nyberg 2000), along with leftward structural lateralization patterns of the perisylvian language-related tracts (Glasser and Rilling, 2008; Nucifora et al., 2005). However, the degree of structural lateralization has been shown to vary between individuals from an extreme left lateralization to a relatively bilateral configuration (Catani et al., 2007). Furthermore, higher symmetry in the structure of the arcuate fasciculus has been found to predict better performance in verbal recall task (Catani et al., 2007). As bilinguals tend to exhibit more bilateral functional activations in linguistic tasks in general (for review, see e.g. Hull and Vaid, 2007), this functional symmetry might also be reflected in the underlying structural organization. However, to the best of our knowledge, there are no studies on the structural correlates of the bilingual functional language lateralization.

Here, we examined a) how early bilingualism affects local white matter structures along two major language trajectories and b) whether there are bilingualism-related structural lateralization differences in the arcuate fasciculus. More specifically, structural properties (FA, RD and MD values) of the IFOF and the three segments of the arcuate fasciculus (presented in Fig. 2A) were assessed bilaterally between early simultaneous bilinguals and late sequential bilinguals. These specific fibre bundles were chosen due to their strong links to language processing. Furthermore, the arcuate fasciculus connects the inferior parietal and frontal regions, which have been linked to bilingualism-induced grey matter changes. Additionally, as the arcuate fasciculus has been shown to reflect the degree of language lateralization, focusing on this structure enables comparisons of structural lateralization patterns between groups with differing bilingualism status.

2. Materials and methods

2.1. Participants

30 young right-handed adults (15 early Finnish-Swedish bilinguals; 15 late English second language speakers, Finnish as a native language), recruited via university mailing lists and matched for age (early bilinguals: M=26.86 years, SD=5.67, late bilinguals: M=29.21 years, SD=4.54) and gender (early bilinguals: 47% males, late bilinguals: 67% males) participated in the study. The early bilinguals had learned their