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# The Left, The Better: White-Matter Brain Integrity Predicts Foreign Language Imitation Ability

Lucía Vaquero[1,2], Antoni Rodríguez-Fornells[1,2,3], and Susanne M. Reiterer[4]

[1]Cognition and Brain Plasticity Unit, Bellvitge Research Biomedical Institute (IDIBELL), Hospital Duran i Reynals, 3d floor, Gran Via de l'Hospitalet, 199 (08908) L'Hospitalet de Llobregat, Barcelona, Spain, [2]Department of Basic Psychology, University of Barcelona, 171 (08035) Barcelona, Spain, [3]Catalan Institution for Research and Advanced Studies (ICREA), Passeig Lluís Companys, 23 (08010) Barcelona, Spain, and [4]Unit for Language and Teaching Research, Department of Linguistics, University of Vienna, Spitalgasse, 1090 – Vienna, Austria

Address correspondence to Susanne M. Reiterer, Department of Linguistics, University of Vienna, Unit for Language and Teaching Research, & Centre for Teacher Education: Spitalgasse, 2-4, court 8.3, 1090–Vienna, Austria. Email: susanne.reiterer@univie.ac.at.

## Abstract

Speech imitation is crucial for language acquisition and second-language learning. Interestingly, large individual differences regarding the ability in imitating foreign-language sounds have been observed. The origin of this interindividual diversity remains unknown, although it might be partially explained by structural predispositions. Here we correlated white-matter structural properties of the arcuate fasciculus (AF) with the performance of 52 German-speakers in a Hindi sentence- and word-imitation task. First, a manual reconstruction was performed, permitting us to extract the mean values along the three branches of the AF. We found that a larger lateralization of the AF volume toward the left hemisphere predicted the performance of our participants in the imitation task. Second, an automatic reconstruction was carried out, allowing us to localize the specific region within the AF that exhibited the largest correlation with foreign language imitation. Results of this reconstruction also showed a left lateralization trend: greater fractional anisotropy values in the anterior half of the left AF correlated with the performance in the Hindi-imitation task. From the best of our knowledge, this is the first time that foreign language imitation aptitude is tested using a more ecological imitation task and correlated with DTI tractography, using both a manual and an automatic method.

**Key words:** speech imitation, arcuate fasciculus, DTI, lateralization, language learning

Speech and voice imitation require the transformation of acoustic information into motor responses (Canevari et al. 2013). A striking phenomenon in this topic is the large individual variability in foreign language pronunciation ability, from very talented individuals possessing excellent mimicking capacities to very poor imitators (Golestani and Pallier 2007; Reiterer et al. 2011; Hu et al. 2013). This variability might depend on underlying functional-neuroanatomical individual differences (Reiterer et al. 2011; for a review, see Zatorre 2013). The neural network involved in speech imitation abilities, mainly reported on the left hemisphere, includes the inferior frontal gyrus (IFG), the superior temporal gyrus (STG), the Heschl's gyrus, the supramarginal gyrus (Catani et al. 2005; Kappes et al. 2010; Adank, 2012), as well as the insular and premotor cortices (Berthier et al. 2012; Hu et al. 2013). All these regions are connected via the three segments of the arcuate fasciculus (AF: long frontotemporal segment, anterior parietofrontal segment, and posterior parietotemporal segment) or, following an alternative classification, via the long and posterior segments of the AF and the ventral superior longitudinal fasciculus (SLF-III, Fernández-Miranda et al. 2015; Wang et al. 2016). Interestingly, individual differences in other domains of

language learning abilities have been already associated to microstructural variability in these pathways (Catani et al. 2007; López-Barroso et al. 2013; Ripollés et al. 2014).

Speech imitation has been defined as copying phonological parts of a linguistic stimulus (Kappes et al. 2010; Shuster et al. 2014), being an ability crucial for both language acquisition and second-language learning (Fitch 2010; Kappes et al. 2010; Shuster et al. 2014). Imitation tasks require the proper perception of the speech input-model and the ability to correctly produce a copy of that model, taking into account complex tonal features as well as subtle phonetic and contour changes (Jilka, 2009). When imitating speech materials from their native language, subjects focus overall on prosodic information (because the phonemic segmentation process in those languages has been already acquired). However, imitation of a completely new language—requiring accurate attention to the sounds and phonotactic structures that differ from the native language—involves phoneme-segmentation processes and relies on the ability to reproduce those new perceived sound patterns (Jilka 2009). Besides, there is an interesting phenomenon in which a speaker changes his/her own pronunciation to mimic a conversational partner, named "phonetic convergence" (also known as "chameleon effect") (Dell and Jacobs 2016). This phenomenon involves the imitation of speech features of the model such as voice intensity, fundamental frequency (the particular sound-wave elicited by the vibrations of the vocal cords), temporal and spectral information to segment the speech stream into phonemes (extracted, e.g., from the "percussive" onsets and/or silences preceding the pronunciation of some consonants), and the specific gestures that the model speaker is performing to pronounce each word or phrase (Garnier et al. 2013; Binder 2016; Blumstein and Baum 2016; Leonard and Chang 2016). In the present study, the term "speech imitation" will be used in a broad sense that may include some traits from the "phonetic convergence" phenomenon, such as the copy of prosodic traits.

A largely discussed issue is the lateralization of language-related functions and neural structures. As Corballis (2010) proposed, the dominant left representation of language could be the consequence of a bias introduced by the incorporation of an articulatory-vocalization neural loop (left-lateralized even in nonhuman species; Aboitiz 2012), or the resultant way of dealing with the complexity of manual skill and language itself. In a similar way, hemispheric lateralization has been recently proposed as a special case of functional specialization, a process that decomposes large brain functions into smaller processes to reduce the functional interference and improve the efficiency of the system (Gotts et al. 2013). Although the final explanation remains open, left-lateralized activity and better integrity in the left AF have been previously reported as related to speech tasks (Parker et al. 2005; Menenti et al. 2011; Adank et al. 2013; Saygin et al. 2013; Ocklenburg et al. 2014; Sreedharan et al. 2015), phonological awareness and phonological memory (Yeatman et al. 2011). Furthermore, it has been proposed that the left auditory cortex extracts information from short temporal windows, which contributes, for example, to the processing about place of articulation during a speech stream (information regarding where in the oral cavity and in which manner phonemes are pronounced, Idsardi and Monahan 2016). Hence, the left auditory structures have been suggested to be more important for speech discrimination than their right homologues (Zatorre et al. 2002; Poeppel 2003). The right auditory cortex might be preferentially involved in decoding the frequency content of the speech signal (see Poeppel

2003; and Giraud et al. 2007), and it has been more related to pitch and tonal discrimination (Zatorre et al. 1992; Zatorre et al. 2007) as well as prosody (Friederici and Alter, 2004; Sammler et al. 2015). Interestingly, higher volume of grey- and white-matter (WM) in the left auditory cortex, and better WM microstructural organization in the left temporoparietal region and IFG seem to be predictive of the ability to learn new words and articulate foreign language sounds (Golestani and Pallier 2007; Zatorre 2013). Overall, these results point to the left dorsal network as a crucial pathway for language learning (Scott and Wise 2004; Rodríguez-Fornells et al. 2009), but the issue regarding the specific neural correlates of foreign language imitation remains open. Besides, the large variability that exists in the lateralization of WM pathways (Catani and Bambini 2014) could be related to the large variance observed in speech imitation processes (Catani et al. 2007).

Only a few attempts to investigate the functional or structural neural correlates of foreign language imitation aptitude have been carried out recently (Reiterer et al. 2011). Based on the previous literature commented above, a better white matter microstructural organization in the left hemisphere is expected to be strongly related to the speech-imitation performance (Poeppel 2003; Zatorre et al. 2007); however, prosodic cues may play a role (as in L1 or L2 imitation tasks) and thus partial involvement of the right hemisphere could be found as well (Sammler et al. 2015). In the present investigation, we aimed to study for the first time, to which extent morphological variability and lateralization degree in the AF could predict speech imitation aptitude. With that aim, we used a more ecological task to test foreign language imitation (using sentences and words from a nonexperienced language, instead of the syllables, sounds, or words paradigms previously applied). Besides, WM tractography analysis of the AF was conducted using two different approaches (i.e., a deterministic-manual one, and an automatic one that combines a deterministic approach with corrections and refinement of the tract based on a probabilistic atlas). The manual-deterministic approach allowed us to dissect the AF in different segments (López-Barroso et al. 2013) and extract the mean diffusivity values for each branch. The automatic method, on the other hand, is based on the hypothesis that WM can present variations in the diffusivity values along each single tract; these variations have been previously described for the AF and could be due to intrinsic variability or the geometry of the tract, among other factors (Klingberg et al. 2000; Yeatman et al. 2011). This approach allowed us to extract 100 diffusivity values along the AF and, thus, investigate in more detail whether there is a specific region in this pathway specially correlating with the imitation abilities of our participants.

## Materials & Methods

### Participants

Fifty-two native German-speakers (25 females; age range: 19–43 years, mean age 26.33 ± 5.38) participated in this study, who were recruited via two universities' outreach (University of Tübingen and University of Stuttgart), community advertisements, and local media. All of them were students or young academics and reported no hearing (self-reported, verified by experimenter, but not audiometrically), neurological or psychiatric disorder. All participants reported to be right-handed, and all but two completed the Edinburgh handedness inventory (Oldfield 1971), which confirmed their right-handedness (group-mean score ($n = 50$) = 0.95 ± 0.096). None of them had previous

experience or training in Hindustani-derived languages. Furthermore, information about previous speech and musical training was obtained via self-report (online questionnaires), such as the number of musical instruments played (mean: 1.04 ± 0.99), number of German dialects (mean: 1.58 ± 1.73), and number of foreign languages (mean: 2.57 ± 1.64) spoken. Moreover, participants also completed the AMMA test (Advanced Measures of Music Audiation, Gordon 1989) in a web-based version using head-phones (mean score: 58.96 ± 7.99). Participants received financial remuneration for their participation after giving informed written consent to participate in the study. The study was approved by the local Ethics Committee and was in accordance with Helsinki's declaration.

## Behavioral Task

To characterize speech imitation aptitude, a behavioral language imitation task was carried out, consisting of *ad hoc* imitation of three polysyllabic (7–11 syllables) Hindi sentences and one trisyllabic Hindi word spoken by a model Hindi speaker (Reiterer et al. 2011). Hindi was selected to test "pure" imitation abilities as this was the first time that our participants were exposed and requested to imitate this language. Furthermore, we decided to use these stimuli, in which all natural levels of phonetics and prosody co-occur in time, because we were interested in the ability to imitate speech materials in a more ecological way, closer to a real-life situation. During the speech-imitation task, participants listened three times to each sentence (in a nonself-paced way) via Sennheiser headphones, and were instructed to imitate the sentence as accurately as they could immediately after the third time they listened to the stimuli. A pilot experiment showed that repetition after one listening trial was not feasible with unknown language stimuli. It was a direct imitation, without any practice or familiarization trials, and with no possibility to repair the response. We selected this simple task and instructions to capture an authentic and spontaneous first imitation of this new language. Speech production of each participant was recorded in a sound-proof room and later subjected to web-based native speaker judgements in India (30 raters, 15 females; age range: 20–55 years, mean age: 27.63 ± 6.6; inter-rater reliability, $r = 0.9$). The raters were naïve (no linguistic experts) and blind regarding the linguistic background of the participants and were instructed to score them based on their global impression of "sounding like a native Indian". The raters got financial remuneration, were recruited from our Indian cooperation partners (NCS, SR, VK) and came from different regions of India with Hindi as either their first or their second language (language backgrounds: Hindi (most raters), Bengali, Manipuri, Marathi, Telugu, Kannada). Most of the raters had a university or tertiary educational background (60%), only very few (around 20%) had linguistic expertise and none of them had explicit phonetic expertise. We deliberately chose to address naïve raters, because it is known from the literature (Bongaerts et al. 1995; Flege et al. 1995; Bongaerts 1999) and from prior research (Christiner and Reiterer 2013; Berken et al. 2015) that for the fields of speech and singing evaluation the performance of naïve raters is comparable to that of experts. To ensure that the raters understood their task correctly, we instructed them to think of characteristics such as word-stress, the rhythm of the language, intelligibility, and overall pronunciation. We used a Likert-based intuitive rating bar ranging from "10" to "0" (10 = maximum native-speaker-like, 0 = minimum native-speaker-like) and calculated the means of all sentences/all raters. To enhance

evaluation quality, recordings from 18 Hindi native speakers were randomly inserted into the Internet database. Speech samples were presented in a random order (for more details, see Jilka 2009; Reiterer et al. 2011).

## Imaging Acquisition and Analysis

Diffusion tensor imaging (DTI) and $T_1$-weigthed MDEFT (Modified Driven-Equilibrium Fourier Transform) data was obtained from a 1.5-T Siemens scanner (Erlangen, Germany). Diffusion tensor imaging parameters were: repetition time (TR) = 6700 ms, echo time (TE) = 82 ms; field-of-view (FOV) = 256 × 256 mm; matrix size = 128 × 128; slice thickness = 2.5 mm; no gap; 52 axial slices; voxel size was 2 × 2 × 2.5 mm. Diffusion was measured along 12 noncollinear directions, chosen according to Siemens DTI acquisition scheme using *a b* value of 800 s/mm$^2$, and including *a b* = 0 as the first volume of the acquisition (in addition to the other 12).

The $T_1$-weigthed image parameters were: TR = 7.92 ms; TE = 2.48 ms; inversion time (TI) = 910 ms; FOV = 176 × 256 × 256 mm; flip angle = 16°; voxel size = 1 × 1 × 1 mm; matrix = 256 × 256; 176 sagittal slices obtained with an eight-channel head coil.

## Manual Reconstruction of DTI Tracts

To preprocess the diffusion-weighted images, first, the brain was virtually separated from the rest of the head using FSL's Brain Extractor Tool (Smith 2002; Smith et al. 2004; Woolrich et al. 2009). Afterward, motion and eddy-current correction was performed using FMRIB's Diffusion Toolbox, part of the FMRIB Software Library (FSL 5.0.1 www.fmrib.ox.ac.uk/fsl/). The *b*-vectors gradient matrix was then rotated to take into account the corrections made at the previous stage, by using the fdt_rotate_bvecs software included in the FMRIB Software Library. The diffusion tensors were then reconstructed using Diffusion Toolkit's least-square estimation algorithm for each voxel, and Fractional Anisotropy (FA) was calculated (Ruopeng Wang, Van J. Wedeen, Martinos Center for Biomedical Imaging, Massachusetts General Hospital, www.trackvis.org).

Whole-brain deterministic tractography was performed in Diffusion Toolkit, using an interpolated streamlines algorithm, with a maximum curvature threshold of 35 degrees and a minimum FA threshold of 0.2. The fiber direction is assumed to correspond to the principal eigenvector (the eigenvector with the largest eigenvalue). This vector was color-coded (green for anterior–posterior, blue for superior–inferior, and red for left–right directions) to generate a color-coded FA map.

Dissections were carried out for each subject in the native space and in both hemispheres. The three segments of the AF were dissected on Trackvis software using three main manually defined regions of interest (ROIs) as described in previous studies (Catani et al. 2005, 2007; López-Barroso et al. 2013). The ROIs were defined on the FA and FA color-coded maps according to individual anatomical landmarks, instead of atlas-based constraints that neglect individual differences (López-Barroso et al. 2013). Specifically, a first ROI was delineated in the coronal view, anterior to the central sulcus, encompassing the fibers going to the IFG (including Broca's area; Brodmann's areas 44 and 45). Then, in the axial slice a second ROI was depicted covering the WM underlying the medial temporal gyrus (embracing the fibers traveling to Wernicke's territory; Brodmann's areas 22p, 41, and 42). Finally, a third ROI was drawn on the sagittal view, covering supramarginal and

angular gyri and encompassing the fibers traveling to Geschwind's territory (Brodmann's areas 39 and 40). These ROIs were combined to encompass the three rami of the AF: the long (between IFG-Broca's and Wernicke's areas), the anterior (linking IFG-Broca's and Geschwind's territories), and the posterior (uniting Wernicke's and Geschwind's territories) segments. Artefactual fibers were removed using exclusion ROIs.

We restricted our statistical analysis to FA and volume measures based on recent investigations that showed these WM parameters to be very sensitive to individual differences (Saygin et al. 2013; Ocklenburg et al. 2014; Sreedharan et al. 2015). We extracted the volume and the FA from each of the three segments of the bilateral AF, and the sum of the three segments of each hemisphere to obtain the values for Complete Left and Complete Right AF. A lateralization index was calculated for each parameter and segment [Lateralization Index = (values on the L − values on the R) / (values on the L + values on the R)] and included in the analysis to see whether the WM organization had a clear hemispheric preference in relation to imitation abilities. The lateralization index ranges from −1 to 1: negative values represent right lateralization, values around zero symmetrical distribution, and positive values left lateralization (López-Barroso et al. 2013). Pearson correlation between all these measurements and the Hindi-imitation score was performed. Significance of all the reported results was thresholded at a $P < 0.05$ corrected for multiple comparisons by means of False Discovery Rate (FDR), to control for the proportion of false positives relative to true positives (Benjamini and Hochberg 1995).

## Automatic Reconstruction of the Tracts

Variations in diffusivity values along each single WM tract, and specifically for the AF, have been previously described (Yeatman et al. 2011). These variations may be explained by (i) intrinsic variability of the tract, (ii) the geometry of the tract, and (iii) neighboring tracts (i.e., partial voluming due to crossing fibers problems) (Klingberg et al. 2000; Yeatman et al. 2011). Since a tract may possess different values of diffusivity in its trajectory, certain region(s) may show a stronger correlation with a given behavioral variable than the rest of the portions of the tract. Hence, to look for the exact portion of the AF which may be specifically involved in foreign language imitation abilities, we used another approach applying an open-source software for automated fiber-tract quantification (AFQ, Stanford University, described in Yeatman et al. 2012). AFQ automatically identifies major fiber tracts and quantifies WM properties along their trajectories. To apply the AFQ pipeline to our data, we first coregistered the brain extracted DTI raw-volumes and a $T_1$ image of each subject (with the $b_0$ as reference), realigning them to the AC–PC line afterwards (anterior commissure, posterior commissure). Then, we performed some preprocessing steps using mrDiffusion and specifically, dtiInit pipeline (VistaLab, Stanford University) on these images: $b$-vectors were rotated, eddy current correction was performed, DTI volumes and $T_1$-structural images were aligned, $b$-vectors were reoriented and aligned, and diffusion tensors were reconstructed using the simple least square fit. Finally, a file containing all the fiber and tensor information that the AFQ requires was built (a file called dt6).

Once the preprocessing was done, AFQ was applied in each subject, performing (i) a whole-brain tractography, (ii) the segmentation of 20 main fascicles (based on the Wakana et al. 2007 white-matter atlas, see Yeatman et al. 2012) using a 2-ROI approach and comparing and refining it by comparing each fiber in each fascicle with a probabilistic fiber tract atlas, (iii) a cleaning of outlier-fibers that deviate from the core of each fiber-group (the core of each tract is defined by creating a 3D Gaussian, removing afterwards those fibers importantly deviating from the center), followed by (iv) the calculation of diffusion measurements in 100 nodes along the trajectory of each fiber group, weighting each fiber's contribution to the measurement based on its distance from the tract core. Although within these measurements there is a value for volume of the tract, the authors of the original paper (Yeatman et al. 2012) strongly suggest not to take this parameter into account for analysis since it is considered a noisy and imperfect measure. Due to this fact, we decided to restrict the analysis to FA values. It is important to note that, since all the dissections are performed using a 2-ROI approach, in the specific case of the AF this means that the tract reconstructed corresponds only to the long segment in the manual-deterministic dissection (i.e., any measurement is restricted to the pathway linking inferior frontal and superior temporal regions, without taking into account the indirect segments that create a structural communication with the supramarginal and angular gyri).

Taking the FA measurements calculated for each node along the AF by the AFQ software, we calculated and extracted a lateralization index (in the same way than for the manually dissected data) for each node. Pearson correlations between the Hindi-imitation score and (i) the FA in each node on the one hand, and (ii) the lateralization index of FA in each node on the other hand were performed. For each correlation, the AFQ function for Multiple Comparisons was used to check for a FWE corrected P-value $< 0.05$ at the individual nodes and at a cluster level (this AFQ function returns, among other values, the minimum number of sequential nodes above the alpha threshold to consider that that particular group of nodes is corrected for multiple comparisons at the cluster level).

## Comparison Between Manual and Automatic Reconstructions

In addition, we were interested in performing a comparison between the manually and the AFQ dissected data and results. Hence, since the AFQ dissection limits the reconstruction to the long segment, a Pearson correlation between the mean FA values extracted for the long segment manually reconstructed and the mean of the 100 FA values calculated for the nodes obtained with AFQ was carried out.

## Results
### Behavioral Results

The Hindi-imitation task was extremely difficult: none of the participants ranged within the "native speaker" range in which the 18 inserted Hindi-native speakers' samples were scored (mean = 9.50 ± 0.60; range = 8.07–9.90 points), although none of them was at the lowest end of the scoring scale either (<2). The mean Hindi score for the full sample was 4.84 ± 1.11 (range = 2.65–7.74 points).

To control the influence of the musical and language experience of our subjects on the Hindi-imitation task, a Pearson correlation with the Hindi-imitation score was performed, but no significant result was obtained for number of instruments ($r = 0.251$, $P = 0.073$), AMMA test ($r = 0.238$, $P = 0.096$), number of German dialects ($r = 0.208$, $P = 0.140$), or foreign languages ($r = 0.081$, $P = 0.570$) spoken.

## Manual DTI Dissections: Correlations with Hindi-Imitation Score

Within the Right AF, a significant negative correlation between the Hindi-imitation score and the volume of the Complete AF was found ($r = -0.395$, $P < 0.005$, FDR corrected: see Fig. 1A and Table 1), meaning that the smaller the volume of the Right AF, the better the performance in the Hindi sentence-imitation task. No significant correlations were found for the left AF, neither for the long, anterior, or posterior segments, nor for the Complete AF, at a FDR-corrected $P < 0.05$.

We found a significant positive correlation between the Hindi-imitation score and the lateralization index for Complete AF volume ($r = 0.434$, $P < 0.005$, FDR corrected: see Fig. 1B and Table 1): the higher the lateralization of AF's volume to the left, the better the performance in the sentence-imitation task. See Figure 2 for some examples of the AF reconstructions and differences in lateralization across the best and worst participants.
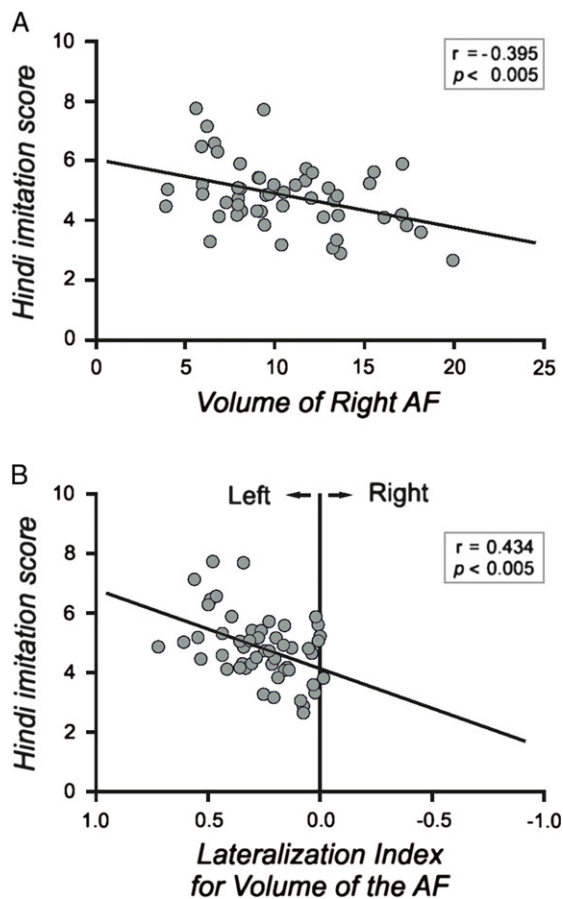


## Automatic DTI Dissections: Correlations with Hindi-Imitation Score

After applying the multiple comparisons function to the automatically dissected data, taking into account the individual 200 nodes conforming the left and the right AF, we found a significant area in the anterior half of the left tract that correlated significantly with the Hindi-imitation score (see Fig. 3A). As depicted in Figure 3B (black line), this significant area (FWE-corrected at cluster level) was formed by 21 contiguous nodes (the minimum number of nodes considered as corrected given by the Multiple Comparisons function was 18); specifically, it contained nodes 23–43 (both included). No significant nodes or clusters were found for the right AF (see magenta line in the graph in Fig. 3B). Furthermore, no significant results were found either for the correlation between the Hindi-imitation score and the lateralization index calculated for the FA values in each node.

## Comparing the Manual and the Automatic Reconstructions

As shown in Figure 3C, a significant correlation was found between the FA values extracted from the manually dissected left long segment and the mean of the 100 FA values calculated for the nodes obtained with AFQ for the left AF ($r = 0.762$, $P < 0.001$). In Figure 3D, four examples of the overlap between manual (in red) and automatic (in green) reconstruction can be observed.

**Table 1** Details of the correlations between DTI parameters extracted from the manual dissection and the Hindi-imitation score (means, standard deviation, and P values displayed)

| DTI parameters | Group mean (SD) | r (Pearson) | P value |
|---|---|---|---|
| FA L long segment | 0.48 (0.02) | 0.282 | 0.430 |
| Volume L long segment | 8.78 (3.14) | 0.157 | 0.267 |
| FA L anterior segment | 0.41 (0.14) | 0.142 | 0.316 |
| Volume L anterior segment | 3.50 (2.24) | 0.040 | 0.776 |
| FA L posterior segment | 0.45 (0.02) | −0.069 | 0.629 |
| Volume L posterior segment | 5.30 (1.79) | −0.048 | 0.737 |
| FA L complete AF | 1.34 (0.15) | 0.160 | 0.256 |
| Volume L complete AF | 17.57 (4.44) | 0.112 | 0.429 |
| FA R long segment | 0.32 (0.24) | −0.015 | 0.918 |
| Volume R long segment | 3.10 (3.23) | −0.204 | 0.147 |
| FA R anterior segment | 0.46 (0.03) | −0.056 | 0.695 |
| Volume R anterior segment | 3.91 (1.95) | −0.271 | 0.052 |
| FA R posterior segment | 0.45 (0.02) | 0.096 | 0.497 |
| Volume R posterior segment | 3.42 (1.26) | −0.253 | 0.069 |
| FA R complete AF | 1.23 (0.24) | −0.012 | 0.935 |
| **Volume R complete AF**[a] | **10.43 (3.82)** | **−0.395** | **0.004** |
| Lat Index for FA of complete AF | 0.05 (0.11) | 0.105 | 0.460 |
| **Lat. Index for volume of complete AF**[a] | **0.26 (0.18)** | **0.434** | **0.001** |
| *Other variables of interest* | | | |
| Number of musical instruments | 1.04 (0.99) | 0.251 | 0.073 |
| Gordon AMMA test | 58.96 (7.99) | 0.238 | 0.096 |
| Number of foreign languages | 2.57 (1.64) | 0.081 | 0.570 |
| Number of German dialects | 1.58 (1.73) | 0.208 | 0.140 |

*Notes*: Abbreviations: DTI, diffusion tensor imaging; SD, standard deviation; FA, fractional anisotropy; L, left; R, right; AF, arcuate fasciculus; Lat. Index, lateralization index; AMMA, Advanced Measures of Music Audiation.
[a]Significant correlations with Hindi-sentence imitation score, at a $P < 0.05$ corrected for multiple comparisons by means of False Discovery Rate (FDR).
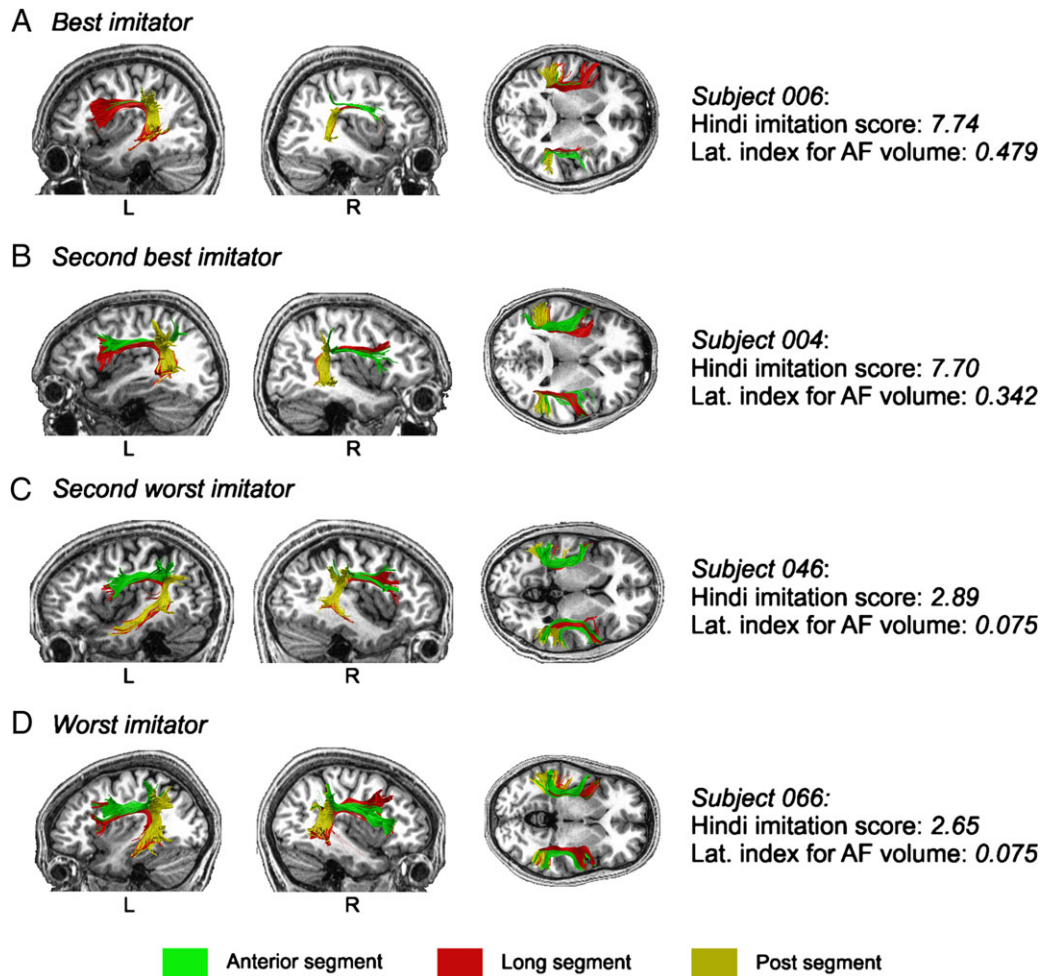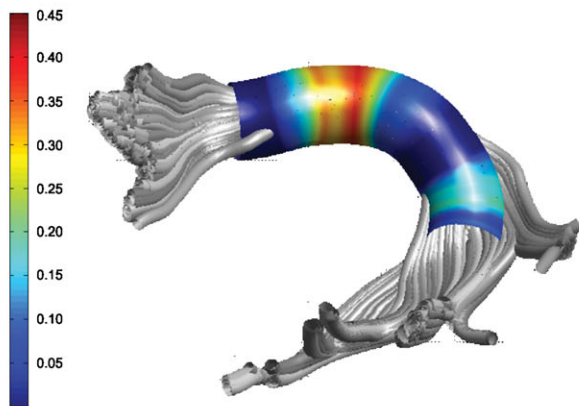
**Figure 1.** Relationship between DTI properties extracted from the manual reconstruction and performance in the Hindi-imitation task. Scatterplots show the Pearson correlation between AF volume and the Hindi-imitation score. (A) Negative correlation with the volume of the complete right AF. (B) Positive correlation with the lateralization index for volume of the complete AF. Lateralization index: values closer to 1 mean lateralization to the left, values around 0 represent symmetrical distribution, values closer to −1 mean lateralization to the right. These results evidence that the more lateralized to the left is the integrity of the AF, the better is the imitation of Hindi. Correlation index and P-values are displayed. Abbreviations: AF, Arcuate Fasciculus; DTI, Diffusion Tensor Imaging.

**Figure 2.** Examples of the manual AF reconstruction. Examples of AF reconstruction superimposed on the corresponding $T_1$ image of: (A) the most talented subject, (B) the second most talented subject, (C) the second less talented subject, and (D) the less talented subject. Individual Hindi-imitation scores and Lateralization indexes of the whole AF volume are displayed. The closer is the lateralization index to 1, the more lateralized is the AF volume to the left. Abbreviations: AF, Arcuate Fasciculus; Lat Index, Lateralization index.

## Discussion

In this study, a manual deterministic and an automatic (combining a deterministic approach with corrections based on a probabilistic atlas) tractography analyses of the AF were performed to investigate the relationship between foreign language imitation aptitude and the WM organization of this tract. On the one hand, we manually dissected the left and right AF (distinguishing three rami: long, anterior—or SLF-III—and posterior; Catani et al. 2005; Fernández-Miranda et al. 2015; Wang et al. 2016) in 52 native-German speakers who completed a Hindi sentence- and word-imitation task rated by Hindi native speakers. On the other hand, the same DTI data was fed into the open-source AFQ software to obtain an automatic dissection of the right and left AF, from which WM measurements were extracted from 100 nodes along the tracts. This method allowed a more fine-grained analysis of which region within the AF tract correlated most importantly with foreign language imitation scores. Our results showed that larger lateralization of the overall AF volume to the left, as well as better WM microstructural organization (FA) in the anterior portion of the left long segment of the AF, predicted better performance in the Hindi sentence- and word-imitation task.
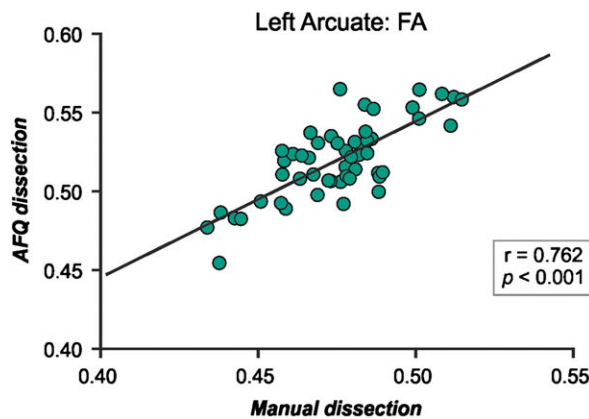
Imitation tasks require the correct perception of the input model and the ability to correctly reproduce the representation of that model (Jilka 2009). To imitate speech materials from their native tongue subjects focus mainly on prosodic patterns that they can understand and mimic, whereas imitation of a not-experienced language (i.e., Hindi in our case) requires a perceptive focus on the sounds and phonotactic structures that are not present in the native language, and the ability to articulate and pronounce the acoustic patterns as they have been perceived (Jilka 2009). Our more realistic task using a complete new language may request the reproduction of phonemes, as well as the copy of other characteristics such as the vocal intensity, the fundamental frequency, and some prosodic traits that may have helped participants to pronounce the speech-stream as the model speaker does. It is important to note the difficulty of our task: (i) the stimuli were sentences (which are long and more complex streams than single phonemes or words) and the exposure was limited to only three repetitions for each one; (ii) the language selected (Hindi) was completely new to our participants; and (iii) importantly, Hindi language contains phonemes that are uncommon across the languages of the world, making them difficult to perceive during the first exposures for listener of languages without these sounds
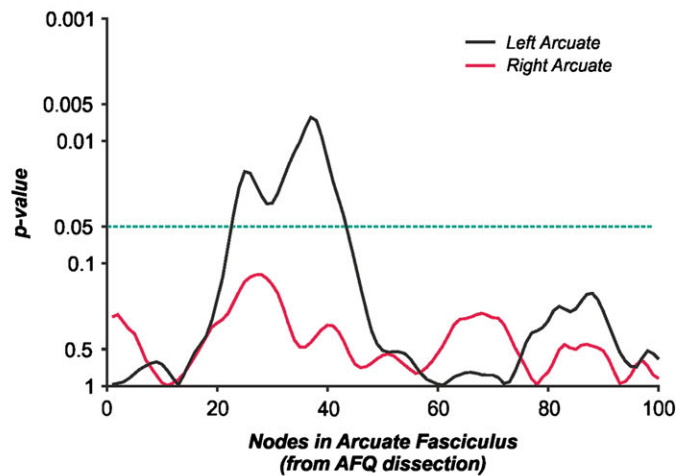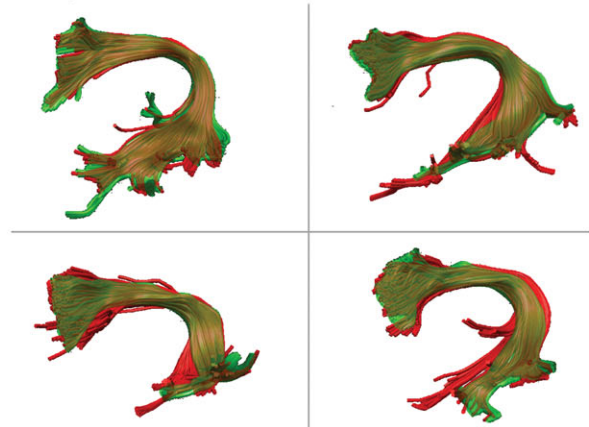
**Figure 3.** Results from the automatic fiber quantification analysis and the comparison with the manual reconstruction. (A) Correlation between Hindi-imitation score and the values of FA in the 100 nodes of left AF: *r*-values are projected on the left AF of one of our subjects, warm colors show the significant cluster between node 23 and node 43. (B) Graph showing the correlation between Hindi-imitation score and the FA values along the 100 nodes for the left AF (black line) and the right AF (magenta line); the green line represents the alpha threshold from which FWE corrected (at cluster-level) results are found. (C) Correlation between mean FA value for the left long segment extracted manually and the mean FA values from the 100 nodes reconstructed with AFQ for the left AF, in the 52 subjects. (D) Visual overlap between manual (in red-transparent) and automatic (in solid green) reconstruction of the left long segment—AF (4 different subjects shown as examples).

(Golestani and Zatorre 2004; Ventura-Campos et al. 2013). Furthermore, the task was purposely chosen to be as difficult as possible (few stimuli, little exposure) to elicit individual differences and to avoid a ceiling effect. Despite these difficult aspects, imitation was possible for all the participants: no one got the lowest score (between 0 and 2), and some participants even obtained moderately high scores (around 7). Besides, a previous investigation using the same task (Reiterer et al. 2011) reported a normal distribution for Hindi-imitation ability, which is in agreement with the Gaussian distribution that language aptitude has been described to adopt (Selinker 1972; Wells 1985).

The left bias in the lateralization of the AF in relation to foreign language imitation found by two different methods in the present study is in convergence with the predominant view that the left auditory cortex is more predisposed to process language stimuli than its right-hemisphere homologue (Zatorre et al. 2002; Poeppel 2003; Friederici and Alter 2004; Giraud et al. 2007). It has been proposed that, during auditory perception,

the left auditory areas extract information from rapid changes in timing and contour variables along the auditory stream. Such changes in the specific case of speech give the listener cues about the place of articulation; in other words, information about how the speaker is pronouncing the different phonemes (Poeppel 2003). Furthermore, previous reports have described two different types of listeners: (i) the fundamental listeners, who mainly decode the keynote or fundamental pitch of the stimuli and (ii) the spectral listeners, who focus on the lowest harmonic components of the sound signal (which nevertheless allow them to perceive the speech contour) (Schneider et al. 2005a, 2005b; Postma-Nilsenová and Postma 2013). Interestingly, Schneider and collaborators (2005a, 2005b) reported that fundamental listeners rely more on the left temporal cortex (i.e., present more GM and enhanced functional magnetoencephalography activity on the left Heschl's gyrus), while spectral listeners depend more on the right auditory cortex. Thus, although it is speculative at this point, this may suggest that the left-lateralized results found in this study could

be partially explained by a greater number of fundamental listeners among our participants.

Speech and voice imitation tasks require the existence of an auditory-to-motor mapping process in which the AF might be helping, allowing the repetition of phonological elements (Canevari et al. 2013) and perhaps other acoustic characteristics (such as prosodic patterns, Sammler et al. 2015). We hypothesized that our participants might have increased their attention to the articulatory information to transform the auditory input into the required motor patterns. Thus, participants might rely on fast feedforward/feedback auditory-(pre)motor loops that calibrate the articulatory representations of the new phonological sequences, recruiting the AF as well as attentional and phonetic-working memory networks (Cunillera et al. 2009; Rauschecker and Scott 2009; Rodríguez-Fornells et al. 2009; López-Barroso et al. 2013, 2015). In line with this idea, Zatorre and colleagues (1992) described that during phonetic judgement (i.e., discriminating final consonants between syllables) it is necessary to recruit neural circuits able to access articulatory representations, such as left IFG/BA6 and surrounding regions. The IFG and premotor cortices might transmit information on programmed articulatory sequences about to occur (feedforward) into the auditory and inferior parietal regions, which in parallel receive information about ongoing pronunciation (feedback) (Rauschecker 2012). This information would be compared with the auditory templates stored from previous exposures to the foreign language in the posterior STG (Warren et al. 2005). The template-matching algorithm might allow the detection of coincidences between the stored "phonological templates" and the new input (Warren et al. 2005), permitting the calibration and minimization of ongoing production errors (Rauschecker and Scott 2009), with the IFG and premotor regions acting as a top-down mechanism regulating this process.

In agreement with this idea, Foreign Accent Syndrome studies have highlighted the importance of certain structures involved also in speech monitoring and cognitive control (i.e., anterior insula, deep frontal operculum, anterior cingulate cortex) that may be important for pronunciation and foreign language imitation (Moreno-Torres et al. 2013). Similarly, several studies have shown that difficult speech processing relies on cortical regions in which comprehension and production overlap (Adank 2012). Specifically, vocal control and speech production have been described to involve the anterior cingulate area, supplementary motor area, basal ganglia (mainly the ventrolateral thalamus and the putamen), and the anterior insula for the initiation and sequencing of speech (Jürgens 2002; Guenther 2006). In addition, to carry out the sound production (perceiving the output and making corrections based on the auditory and proprioceptive feedback), it is necessary to activate the face area of the motor cortex (precentral gyrus, including Broca's region and the deep frontal operculum), the somatosensory cortex, the primary auditory cortex and the auditory association cortices (i.e., superior and middle temporal gyri), and the inferior parietal cortex (Jürgens 2002; Brown et al. 2006; Guenther 2006; Kleber et al. 2013; Zarate 2013).

In addition to these neural networks involved in the control of vocalization and speech production, previous fMRI studies have described a close relationship between functional activation and connectivity across the mentioned areas and language learning abilities. Specifically, Ventura-Campos and colleagues (2013) observed activations in the bilateral inferior frontal operculum/anterior insula, the bilateral STG, and the right middle frontal gyrus during a foreign-language phoneme identification task. After 2-week training in this phoneme identification paradigm, some other regions were added, such as the inferior parietal lobe bilaterally, bilateral caudate head, and right cingulate gyrus. The BOLD response in the left frontal operculum after training correlated positively with behavioral improvement in the discrimination task (Ventura-Campos et al. 2013). Furthermore, the talent for imitating words, sentences, and a text in English and Hindi/Tamil was previously found to be associated with the activation in the left perisylvian network, including the premotor cortex and the inferior parietal lobe (Reiterer et al. 2011). Performance in a word-learning task has also been previously found significantly correlated both with the microstructure of the left long segment of the AF and with the strength of the functional connectivity between left temporal regions (Wernicke's area) and left inferior frontal areas (Broca's territory, frontal operculum) (López-Barroso et al. 2013).

As these previous studies suggested (Reiterer et al. 2011; López-Barroso et al. 2013; Ventura-Campos et al. 2013), brain activity measured during in-scanner tasks or via resting-state functional connectivity parameters may be related to actual anatomical WM pathways. As a matter of fact, the AF is interconnecting these cortical regions: the inferior frontal region (with terminations that may arrive to pars opercularis, pars triangularis, ventral precentral gyrus, and the caudal part of the middle frontal gyrus), the inferior parietal lobe/supramarginal region, as well as primary and association auditory regions (which may involve STG, rostral and caudal middle temporal gyrus, and caudal inferior temporal gyrus) (Fernández-Miranda et al. 2015). Thus, the proper functioning of this auditory-motor system in foreign language imitation and learning might depend on the WM integrity and asymmetry of the AF, which, as proposed recently, has a general function in sensorimotor integration and control (Berthier et al. 2012; Rauschecker 2012).

This auditory-motor network has also been related to mirroring and production of informative actions, being a crucial system for social communication through the development of mimicking abilities (Catani and Bambini 2014). Evolutionarily, the expansion of auditory-motor connections through the AF (whose complexity increases along the phylogenetic scale) permitted humans to develop a system for auditory working memory critical for learning and imitating complex phonological sequences produced by conspecifics (Aboitiz 2012; López-Barroso et al. 2013). Ontogenetically, Perani and colleagues (2011) observed in newborns a WM connection between auditory cortex and premotor areas, but not the direct pathway connecting auditory cortex with IFG (Perani et al. 2011). Thus, the direct segment of the AF develops later during infancy compared with other WM tracts (such as the anterior segment of the AF, the inferior longitudinal fasciculus, or the frontal aslant tract), and its maturation has been described to continue until the age of 7 (Catani and Bambini 2014; Friederici 2015). Regarding the left-lateralization of language abilities, a cerebral dominance for vocalizations might originate from complex sequential motor patterns that could be more efficiently processed asymmetrically (Aboitiz 2012). Moreover, left lateralized activity during speech production (Menenti et al. 2011; Adank et al. 2013), greater left AF volume in relation to speech tasks (Parker et al. 2005; Saygin et al. 2013; Ocklenburg et al. 2014; Sreedharan et al. 2015), and better left AF microstructure related to phonological awareness and phonological memory (Yeatman et al. 2011) were previously reported. These ideas are in line with the widely extended view commented before, which assigns a particular acoustic preference to each

hemisphere: left temporal areas more prompted to process rapid temporal variations that have been associated with language stimuli (as the voice-onsets and silences preceding the pronunciation of some consonants); right temporal areas more related to the processing of spectral changes, such as melodic contour and prosody (Zatorre et al. 1992, 2002; Poeppel 2003; Friederici and Alter 2004; Giraud et al. 2007; Sammler et al. 2015). However, this theory is still under debate since speech stimuli also depend on spectral features and the left-hemisphere dominance for "temporal" processing has not been unambiguously proved, while the right-hemisphere preference for spectral processing seems to be quite consistent in the literature (McGettigan and Scott 2012). Hence, McGettigan and Scott (2012) proposed that the real asymmetry might consist in the right auditory cortex possessing genuine preferences for specific properties of the acoustic signal, while the left hemisphere could not show any preference at all. Another interesting view was recently proposed by Gotts and collaborators (2013). These authors observed that the left hemisphere shows a greater preference for cortico-cortical interactions that are constrained toward the left hemisphere, while the right hemisphere presents more bilateral, interhemispheric interactions (Gotts et al. 2013). These authors also observed a correlation between vocabulary scores and intrahemispheric functional connectivity in language- and communication-related areas, such as the IFG, posterior and middle superior temporal regions, medial frontal areas, and the fusiform gyrus. These results suggest that speech production and comprehension (functions that request fast sequential interactions) may be better represented in the left hemisphere since they may benefit from shorter synaptic delays granted by the described preferential intrahemispheric processing (Gotts et al. 2013).

Despite this open debate, our results highlight a clear relationship between the WM microstructural organization of the AF and speech imitation aptitude, with a left-lateralization bias. In aphasia research, it has been suggested that the existence of a well-structured AF, as well as preserved cortical language-related areas on the left hemisphere, might be predictive of a better language recovery (Fridriksson 2010; Marchina et al. 2011; but see also Forkel et al. 2014). Interestingly, in infant language-learning research, Bishop and coworkers (Bishop 2013; Bishop et al. 2014) have suggested that the amount of left-lateralization might depend on the learning of language skills, evolving as language competence improves. Although there is controversy regarding the need of a specific lateralization for language functions (Dyukova et al. 2010; Fridriksson 2010), a left-bias in the integrity of language-related pathways has frequently been described and reported as crucial for foreign language imitation and learning (López-Barroso et al. 2013; for a review, see Zatorre 2013).

Regardless of the lateralization, an interesting point to discuss is that our results from the manual dissection are found only for the complete AF volume (no significant results were found for the three branches separately), while the results from the automatic reconstruction are restricted to the long segment. Different roles in speech repetition for the different segments of the AF were previously suggested (Catani et al. 2005; Dick and Tremblay 2012), as well as their diverse involvement in language and nonlanguage processing (Berthier et al. 2012), but their specific functions are still under discussion. We hypothesized that the present task might have required the contribution of all three AF segments as a whole, due to its complexity (perceive and reproduce phonetic and some frequency- or contour-related characteristic of the stimuli) and

novelty. Actually, looking at the manually dissected results it seems the case that speech imitation might rely on the three branches of the AF (dorsal stream) to ensure communication between all the components of the auditory-perceptive, auditory-working-memory, and oromotor loop (Rauschecker 2012), which might have a crucial role for storage and learning of novel words, and thus, a new language (Schulze et al. 2012). However, when looking at specific differences inside the tract with the automatic method, the long segment seems to possess more weight than the indirect rami. In any case, future research might shed light on the specific functions of the three branches of the AF and their relative importance in speech perception and production.

The present investigation may comprise some limitations, mainly associated not only with the DTI tractography analyses selected but also with the resolution of the images acquired here. One of the most common systematic errors in the DTI modeling process is the inadequacy of the tensor model to characterize fiber orientation when there is more than one fiber population within a voxel, and in which the Gaussian tensor model assumes the principal eigenvector as the only fiber orientation in the voxel (Jones 2008). This has been called the "crossing fiber issue" and although some solutions have been described and applied in the last years to overcome it, these new methods (i.e., spherical harmonic decomposition, Q-ball imaging, etc.) usually need more processing time and higher resolution images than the ones obtained for the present study (Jones 2008; Salat et al. 2009; Seunarine and Alexander 2009). As a matter of fact, the resolution of the images acquired for the present study may have prevented us from finding distinct results depending on the different segments (in the manual reconstruction) and/or to observe a more homogeneous pattern of diffusivity values along the whole long segment (in the case of the automatic method). Regarding the automatic reconstruction using AFQ, although this method may be remarkably interesting for localizing specific regions within a fiber tract in which some plastic or predisposing effects can be particularly strong and that may be lost when looking only at the tract-mean, as the creators of the method sustain, one should consider that an automatic method could never adapt to large interindividual differences. Moreover, in the particular case of the present study, we have focused in the AF, a tract that shows large important variability among individuals (Catani et al. 2007) and for which the AFQ program presents some problems in reconstructing the right-hemisphere pathway (Yeatman et al. 2011). However, as shown in Figure 3C,D, it is important to note the high correlation found between the FA values for the left AF extracted both manually and automatically ($r = 0.762$, $P < 0.001$), and how well the outputs from both types of reconstruction match (visually).

## Conclusion

To conclude, based on previous reports (Catani et al. 2005; Berthier et al. 2012; López-Barroso et al. 2013; Zatorre 2013; Sreedharan et al. 2015) and our present results from both manual and automatic dissections, it emerges that the crucial characteristic underlying foreign language imitation skills is the integrity of the WM pathways whose function is the translation and mapping of perceived sounds into speech production. Furthermore, it seems that the direct pathway of the AF is the most crucial for these functions and capacities, especially a region in the anterior half of the left long segment. To the best of our knowledge, this is the first time in which imitation

abilities are directly related to DTI tractography results, based on two types of dissection approaches, and showing a clear relationship between the lateralization of the AF and individual differences in speech imitation/pronunciation aptitude.

## Funding

## Notes

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