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Native language differences in the structural connectome of the human brain

Xuehu Wei*, Helyne Adamson, Matthias Schwendemann, Tomás Goucha, Angela D. Friederici, Alfred Anwander

Max Planck Institute for Human Cognitive and Brain Science, Department of Neuropsychology, Leipzig, Germany

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ABSTRACT

Is the neuroanatomy of the language structural connectome modulated by the life-long experience of speaking a specific language? The current study compared the brain white matter connections of the language and speech production network in a large cohort of 94 native speakers of two very different languages: an Indo-European morphosyntactically complex language (German) and a Semitic root-based language (Arabic). Using high-resolution diffusion-weighted MRI and tractography-based network statistics of the language connectome, we demonstrated that German native speakers exhibited stronger connectivity in an intra-hemispheric frontal to parietal/temporal dorsal language network, known to be associated with complex syntax processing. In comparison, Arabic native speakers showed stronger connectivity in the connections between semantic language regions, including the left temporo-parietal network, and stronger inter-hemispheric connections via the posterior corpus callosum connecting bilateral superior temporal and inferior parietal regions. The current study suggests that the structural language connectome develops and is modulated by environmental factors such as the characteristic processing demands of the native language.

1. Introduction

Over decades, neuroscientists have revealed an elaborate and extensive language processing system in the human brain (Friederici, 2011; Price, 2010). Numerous studies have identified syntactic (Friederici, 2011; Wilson et al., 2011) and semantic networks (Huth et al., 2016; Lau et al., 2008) which, together with a phonological network (Hartwigsen et al., 2010), appear to form the universal neural language network. However, languages in the world differ immensely from one another in the way they encode sound, syntax, and meaning (Evans and Levinson, 2009). Previous studies have shown that human brain functions are influenced by cross-cultural differences which are dominated by language diversity (Paulesu et al., 2000; Tang et al., 2006). However, it is still an open question whether the characteristics of a particular language itself have an impact on brain structure. The present study aimed to investigate the extent to which the attribute of a language modulates the structure of the universal language processing network.

The neural *language network* consists of a core system representing syntactic knowledge, the lexicon, and the relevant sounds of a language, called phonology. This network is complemented by brain structures that support language processing for speaking, the *speech network* (Catani et al., 2013; Finkl et al., 2020). Language use requires information exchange in those networks and their functionally specialized regions via a complex system of white matter connections (Friederici, 2011; Hagoort, 2019). As white matter connections are known to change as a function of use (Scholz et al., 2009; Wake et al., 2011), the language and speech structural connectome likely adapts to the specific processing requirements of a particular language.

The core language network consists of white matter fiber pathways connecting language-relevant brain regions in the left frontal and temporo-parietal cortices via dorsally and ventrally located pathways (Friederici, 2011). A dorsal language pathway connects the posterior part of Broca's area, Brodmann Area (BA) 44 in the inferior frontal gyrus (IFG), and the inferior frontal sulcus (IFS) with parts of Wernicke's area in the posterior superior temporal gyrus (pSTG), which is involved in syntax and grammatical relations (Friederici, 2011; Wilson et al., 2011). In this network, BA44 dominates syntactic processing while the IFS supports the processing of syntactic dependency relations in sentences (Friederici et al., 2006; Makuuchi et al., 2009). A ventral pathway connects the left temporal lobe to the left anterior IFG (BA45/47) and supports the analysis of semantic relations (Friederici, 2011). The superior temporal sulcus (STS) and the middle temporal gyrus (MTG) play an important role in lexical-semantic access and processing (Lau et al., 2008).

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* Corresponding author.
E-mail address: xuehuwei@cbs.mpg.de (X. Wei).

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In addition, language processing recruits the inferior parietal lobe (IPL), with its posterior area (angular gyrus, AG) supporting the integration of incoming information into current contextual and sentence representations (Seghier, 2013), while the anterior area (supramarginal gyrus, SMG) decodes phonological information (Hartwigsen et al., 2010). In addition to these left–hemispheric regions, language processing also involves the right hemisphere. Phonetic information is processed in auditory areas in both hemispheres, and suprasegmental information, i.e. prosody, is mainly processed in the right hemisphere (Friederici, 2011; Hickok and Poeppel, 2007). Thus, the corpus callosum (CC) allows the information transfer between hemispheres as the structural bridge (Friederici et al., 2007). The speech production network involves the frontal aslant tract (FAT), which connects the pre-supplementary motor area (pre-SMA) and supplementary motor area (SMA) with subregions in the IFG (Catani et al., 2013; Finkl et al., 2020), supports phoneme-level and syllable-level (Dick et al., 2020; Finkl et al., 2020) processing and is associated with speech fluency (Neef et al., 2018). This network for verbal language production can be segregated from the core language system responsible for semantic and syntactic processing (Finkl et al., 2020; Friederici, 2011). Taken together, the individual components reviewed above constitute the language system in the human brain.

However, languages in the world are diverse (Evans and Levinson, 2009). The brain is an adaptable organ and might be shaped by the particular language that is acquired. Previous functional studies have found systematic differences in brain activation patterns according to the language being processed (Bolger et al., 2005; Gandour et al., 2003; Paulesu et al., 2000; Tan et al., 2005) and significant differences in the functional brain connectivity between the different native speakers (Ge et al., 2015). These differences suggest that the organization of the functional nervous system is influenced by linguistic diversity during native language development. On the structural side, it has been shown that the gray and white matter of the brain adapts during language acquisition and development (Zatorre et al., 2012). The neural language system, which responds to different aspects of language processing, is established around the age of ten/eleven years (Skeide and Friederici, 2016). The particular processing demands of different languages during development and lifelong use may therefore be reflected and detectable in the language network in adults. Initial studies found localized structural brain differences between English and Chinese speakers in language processing areas that were attributed to the learned processing strategy (Crinion et al., 2009; Kochunov et al., 2003). In addition, the white matter language network has been shown to differ between native English, German, and Chinese speakers, reflecting the specific processing requirements of each language (Goucha, 2019).

Language-dependent structural white matter differences have also been found in cross-sectional studies comparing mono- and bilingual participants (Kuhl et al., 2016; Pliatsikas et al., 2015; Rossi et al., 2017), demonstrating neuroplasticity on a life-long scale. Similarly, several longitudinal studies of structural changes during second language learning (DeLuca et al., 2020; Legault et al., 2019; Mamiya et al., 2016; Schlegel et al., 2012; Xiang et al., 2015) showed changes in the gray and white matter of the brain during second language learning and brain structural correlates with language-learning aptitude and success (Novén et al., 2021; Sánchez et al., 2023). However, previous studies have shown that different brain areas and networks are involved in first and second language processing (Huang et al., 2012; Kim et al., 2016). These processing differences are also reflected in previous structural studies of second language acquisition in adults, which showed changes in the white and gray matter of the brain that extend to areas not involved in first language processing (Li et al., 2014). This suggests that a second language learned in adulthood is not processed in the native language system and may involve additional processing tasks such as language switching and cognitive control (Hervais-Adelman et al., 2011). These processing differences are found even in early bilinguals who learned the second language during childhood and the structural brain adaptation in first language acquisition during childhood differs from later second language learning (Liu and Cao, 2016; Perani and Abutalebi, 2005). Therefore, these comparisons are not specific to the native language network as they compare first and second language processing structures, and the shaping of the language system, and in particular the white matter network, by different native languages, remains an open question. The current study attempts to demonstrate the specialization of different native language and speech networks in the brain structural network by comparing two groups of participants with different native languages. We chose Arabic and German as they have very distinct linguistic characteristics.

In brief, Arabic and German are derived from two completely different language families: German is an Indo-European language, whereas Arabic is a Semitic language (Konig and der Auwera, 2013; Saiegh-Haddad and Joshi, 2014). German is a language with a complex grammatical system, its word order is rather flexible (Haider, 2010; Müller, 2015), and the amount of dependency relations of distant sentence elements is high (Liu et al., 2017). Indo-European languages, including German, use a dominant stem plus affix word formation process. Words and most derivations and inflections are typically formed by a linear and sequential concatenation of prefixes or suffixes to a base morpheme. Previous functional MRI studies of German language processing have shown activity in the left IFG, posterior STG/STS to support syntactic (Friederici et al., 2006; Raettig et al., 2010), phonological (Heim et al., 2003) and lexical-semantic processing (Friederici et al., 2000), respectively. In particular, left BA 44 is sensitive to the complex syntactic structure of German, which is dominated by word order changes (Embick et al., 2000; Friederici, 2011).

Arabic is a Semitic language that uses a “root-based” system in which most words are morphologically complex and are primarily characterized by a rich non-linear or non-concatenative morphological structure (Boudelaa and Marslen-Wilson, 2015; Saiegh-Haddad and Joshi, 2014). An Arabic word is derived from two independently unpronounceable bound morphemes: a root and a word-pattern. The root usually consists of three or four consonants (C) and provides the core semantic meaning or the semantic family, while the word-pattern is a fixed template primarily composed of vowels (V) with slots for consonants (Boudelaa and Marslen-Wilson, 2015, 2004). Such abstract patterns of consonants and vowels (CV skeleton) provide the phonological and morphosyntactic information of the word (McCarthy, 1981). The meaning of the word depends on the word patterns, which are composed of compound morphemes, grammatical information, and phonological structure. This rich and systematic morphology is an important feature that distinguishes Arabic words from Indo-European languages, including German. Until recently, there has been little research on the neural correlates of Arabic language processing, particularly using functional brain imaging. Two recent studies of picture naming in Arabic have shown activity in the language areas predominantly in the left hemisphere, including the IFG, STG, inferior temporal gyrus, IPL, SMA, and the anterior cingulate (Abou-Ghazaleh et al., 2018, 2020). This suggests that Arabic language processing is also driven by the core language systems built in the IFG, posterior temporal, and IPL regions. In addition, cross-linguistic electrophysiological comparisons of Arabic and Spanish (Al-Hamouri et al., 2005), as well as Arabic and English (Eviatar and Ibrahim, 2007) revealed language-specific brain activation patterns with stronger activations in semantic brain regions including posterior parts of the STG/MTG as well as the IPL. In particular, in Arabic language processing, these regions are activated in both hemispheres. This is in line with an earlier electrophysiological study in Arabic that revealed specific mismatch negativity in temporo-parietal regions in both hemispheres for processing Arabic word patterns and decoding Arabic word meanings (Boudelaa et al., 2010). The stronger activation associated with the Arabic root system of morphologically complex words may lead to stronger connectivity within the temporo-parietal semantic system in Arabic speakers compared to speakers of Indo-European languages.

The two languages also differ in their orthography and their writing system. While in Indo-European languages orthography consonants and vowels correspond to letters, Arabic orthography usually omits short vowels, such that the specific word meaning and pronunciation has to be retrieved from the context (Saiegh-Haddad and Joshi, 2014). The Arabic writing system also differs from that of the Indo-European languages in orthographic directionality, with Arabic script being written and read from right to left (Saiegh-Haddad and Joshi, 2014). These differences lead to distinct activation patterns in the brain, that is, while the right hemisphere reaches a similar activation level to the left side when reading in Arabic, this is not the case for Indo-European languages (Al-Hamouri et al., 2005; Eviatar and Ibrahim, 2007).

Our hypotheses are based on the notion that German and Arabic have unique processing demands. These processing demands, over time, shape the structural connectivity of the individual, which should be apparent in a group comparison and reflect the characteristic processing demands of each language. In the current study, we expect German native speakers to show higher connectivity within the core region (left posterior IFG) of syntax processing, as well as stronger structural connectivity along the dorsal language pathway involving this region. In contrast, for Arabic native speakers, we anticipate finding stronger inter-hemispheric connectivity, predominantly involving the bilateral semantic system, which supports the integration and decoding of Arabic words as well as stronger connectivity within the semantic system of each hemisphere. In addition, we expect stronger communication and connectivity between the two hemispheres in Arabic readers due to the specifics of Arabic orthography including the right-to-left writing system (Al-Hamouri et al., 2005; Eviatar and Ibrahim, 2007). This writing system may require additional transfer of information from the left visual field, which is processed in the right hemisphere, to the language-dominant left hemisphere.

To test these hypotheses, we acquired high-resolution diffusion MRI (magnetic resonance imaging) in a large cohort of 94 participants in two groups (47 subjects in each group) of young and healthy German and Arabic-speaking participants which were matched for age, gender, education, and handedness. The data were used to compute the white matter structural connectivity of the language network in each participant and to compare the network properties between the two groups using graph theoretical methods (Bullmore and Sporns, 2009). By comparing the connectivity strength of each region (expressed as the centrality of the network node) between the groups, we tested whether the particular processing demands in each language were reflected by a modulation of the importance of that node in the network. Additionally, we evaluated the group difference in network strength to identify particular connections between regions and subnetworks reflecting a modulation of specific pathways. Structural differences between the two language groups would help to identify brain areas and subnetworks that are particularly relevant for the specific processing demands in each of the two languages.

2. Materials and methods

2.1. Participants

For this study, we recruited 94 healthy young adult participants in two groups: 47 German native speakers (age 19–34 y, mean age 25.9 ± 4.1y, 12 females) and 47 Arabic native speakers (age 18–34, mean age 25.5 ± 4.3y, 12 females). Details of the MRI acquisition can be found in the *Supplementary Materials*. The distinct linguistic characteristics of the German and Arabic languages, along with some examples, are detailed in the *Supplementary Materials.* The groups were created to be large enough to detect differences in the language network (Ge et al., 2015).

The Arabic native speakers spoke the Levantine dialect of Arabic and had above average intelligence (non-verbal Raven's matrix test (Raven and Court, 1998), score 50.4 ± 6.7, ranging around the 90 percentile, subgroup $N = 32$). All participants, in both groups, were right-handed, spoke only one native language, and were matched for their education level. Participants with diagnosed neurological or psychiatric disorders were excluded from both groups. All native speakers of Arabic arrived in Germany 6–8 months before the start of the study and settled in Leipzig, Germany for a long-term stay and to learn German. A German test showed that the entire group had no to minimal knowledge of German, well below the beginner level A1. To exclude undiagnosed impairments triggered by the causes of migration to Germany, the Arabic-speaking participants were asked to complete two self-report questionnaires on symptoms of post-traumatic stress disorder (PTSD, https://www.ptsd.va.gov/professional/assessment). One is the PTSD Checklist for DSM-5 (PCL-5) which is a 20-item self-report measure that assesses the 20 DSM-5 symptoms of PTSD. The other test is the Trauma Screening Questionnaire (TSQ), a 10-item symptom screen that was designed for use with survivors of all types of traumatic stress. Only participants with no clear symptoms of mental health problems or PTSD were recruited for our study. The experiment was approved by the ethics committee of the University of Leipzig, and all participants provided written informed consent.

2.2. MRI data acquisition

We acquired structural and high-resolution diffusion-weighted MR images (dMRI, 1.3 mm isotropic resolution, b-value = 1000 s/mm^2, 60 directions and 7 b0, 3 repetitions to improve the SNR, TE = 75 ms, TR = 6 s, GRAPPA 2, CMRR-SMS 2, 2 b0 acquisitions with opposite phase encoding) on a 3-Tesla Prisma MR system (Siemens Healthineers, Erlangen, Germany) with a 32-channel head coil. The acquisition time for the dMRI protocol was 23 min. Structural images were acquired using a multiparameter mapping protocol with an isotropic resolution of 1 mm (Weiskopf et al., 2013).

2.3. Cortical parcellation of the language ROIs

To analyze the structural connectivity via probabilistic fiber tracking, we defined the cortical seed and target areas using the fine-grained atlas provided by the Human Connectome Project (HCP), in addition to a subdivision of the corpus callosum atlas (Fischl et al., 2002; Glasser et al., 2016). In each hemisphere, we selected language areas in the inferior frontal gyrus (IFG), the temporal lobe (TL), and the inferior parietal lobe (IPL) as core regions of the language network, which are connected via the dorsal and ventral language pathways, as defined previously (Friederici, 2011). Additionally, we included regions of the pre-SMA and SMA, which are connected with the IFG via the frontal aslant tract and which are particularly relevant for verbal language production (Finkl et al., 2020). To account for inter-hemispheric connections between the frontal and parieto-temporal regions respectively, we included white matter regions in the medial cross-section of the anterior and posterior corpus callosum (aCC and pCC) in both hemispheres (Fig. 1A). Details of all ROIs can be found in *Supplementary Materials* and Table S1.

2.4. Construction of the structural language connectome

After preprocessing (*see Supplementary Materials*), we used probabilistic diffusion MR tractography to construct the connectivity matrix between all regions in each hemisphere for each participant, according to the pipeline described in the *Supplementary Materials,* Fig. S1. First, we computed the structural connectivity between all regions in the language network, as described in the structural connectome analysis pipeline (steps 1 to 5 in the *Supplementary Materials)*. Second, we extended these connectivity profiles to include connections to non-language regions across the entire hemisphere. This allowed the additional characterization of the language regions by input, output, and association connections with non-language regions, as de-

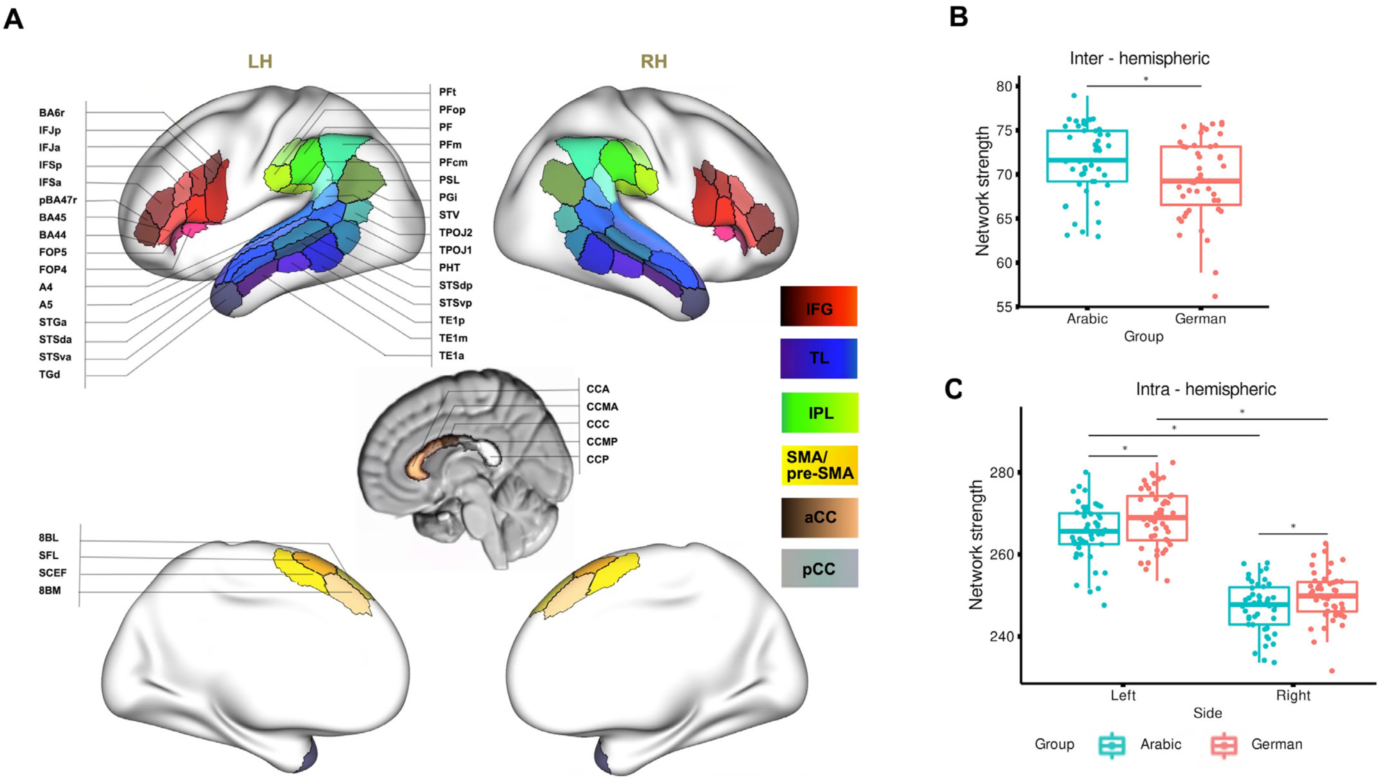

Fig. 1. Intra- and inter-hemispheric connectivity differences in the language network. (A) The language-related ROIs included sub-regions in the larger language areas IFG, TL, IPL, aCC, and pCC, color-coded in (A). The lower panels show the SMA/pre-SMA areas which are relevant in verbal language production. (B) Group difference of the inter-hemispheric connectivity. (C) Difference in intra-hemispheric connectivity between groups and hemispheres. * $p<0.05$, FDR corrected. LH: left hemisphere, RH: right hemisphere. IFG: inferior frontal gyrus, TL: temporal lobe, IPL: inferior parietal lobe, CC: corpus callosum, SMA: supplementary motor area. Detailed descriptions and labeling of the ROIs are provided in the *Supplementary Materials and Table S1*. In the boxplots, the values for interhemispheric connectivity range from 0 to 320 (all possible connectivity values = 1 without threshold), and the values within each hemisphere range from 0 to 992.

scribed in Step 6 in the *Supplementary Materials*. This connectivity matrix was based on 180 distinct cortical regions derived from the HCP atlas (Glasser et al., 2016) and five CC ROIs in each hemisphere computed using the FreeSurfer parcellation (Fischl et al., 2002). The entries in this matrix represent the normalized connectivity for each pair of regions. Using the CC regions to compute the connectivity with the cortical regions in each hemisphere was preferred to a full connectivity matrix including all connections in both hemispheres. This is because the CC is a bottleneck for inter-hemispheric connections, and the one-to-one connectivity between cortical regions cannot be robustly estimated by tractography. We also removed the weak connections (in the average matrix across all participants). In general, weak connections cannot be reliably estimated with tractography due to the limited sampling of the distribution. This may result in false-positive connections. To focus the analysis on strong and reliable connections, we removed false positive and noisy connections below a predefined threshold. This allowed us to remove connections that were not consistent with the major fiber pathways in the human brain (Maier-Hein et al., 2017). To do this, we increased the threshold to create seven networks with different densities. These networks ranged from the strongest 80% of connections to the strongest 20% (Buchanan et al., 2020), per hemisphere, increasing in 10% increments. A threshold of 40% was found to reliably remove anatomically implausible false-positive connections while retaining the major pathways for the network-based analysis. Finally, we constructed an extended language network that additionally included connections between the core language regions and the speech production regions in the SMA/pre-SMA and included 74 ROIs in each hemisphere. More details can be found in the *Supplementary Materials.*

2.5. *Network analysis*

The connectivity in the language network for each group was analyzed using the graph-theoretic method (Bullmore and Sporns, 2009; Rubinov and Sporns, 2010). At the global level, we computed the intra-hemispheric and inter-hemispheric network strength (sum of all weighted connections within and between each hemisphere). We considered all connections of the 74 language-related ROIs to represent the strength of the language connectome in the human brain. Additionally, we computed the global node centrality of all regions (the sum of all connections from the area to the entire cortex), as well as the local node centrality, which includes only the connectivity between the predefined language ROIs. We computed the global centrality of IFG, TL, IPL, aCC, and pCC to first test for differences in each of these larger language regions within the whole brain network. The local node centrality allows us to focus on the strength and potential for information exchange within the language network and is more sensitive to language-specific effects. We used node centrality as the most direct measure of connectivity, which is easier interpretable in the context of the structural language network than more complex graph-theory measures previously proposed (Rubinov and Sporns, 2010).

Furthermore, network-based statistics (NBS, Zalesky et al., 2010) was used to assess differences in specific connections and subnetworks. The connectivity of the superior frontal gyrus (areas in the SMA/pre-SMA) was analyzed separately. White matter connections with these areas form the speech production pathways of the extended language network. The node centrality of each seed region was defined by the connection from the seed area to all regions in the extended language network. Finally, the laterality index (LI) of the centrality of each region and each connection was calculated. Further details and all data used for the connectivity analysis can be found in the *Supplementary Materials*.

2.6. Statistics

We performed independent t-tests to examine possible group differences in network strength in the global node centrality of IFG, TL, IPL, aCC, and pCC. The centralities of each language region were computed as the sum of the centrality values of the smaller subdivisions. Next, we assessed the group difference in the global node centrality of each sub-region (ROI) and the fingerprints of each ROI. In this step, we focused on the ROIs located in the areas (IFG, TL, IPL, aCC, and pCC) where group differences emerged from the above analysis. Subsequent *post-hoc* t-tests allowed the identification of the sub-regions with group differences. To analyze group differences in the more specific local node centrality within the regions of the language network, we computed a two-way ANOVA and *post-hoc* t-tests.

Following nodal centrality, we analyzed differences in the connectivity between regions, represented as the edges of the graph (74 × 74 undirected connectivity matrices), using network-based statistics (NBS, Zalesky et al., 2010). NBS first identifies supra-threshold connectivity values between the two groups using a two-sample *t*-test (preselected T-threshold = 3.3). This is followed by a non-parametric permutation test ($K = 5000$ permutations) to assign a p-value to each connected component, controlling for the family-wise error (FWE, $p < 0.05$). Differences in the speech production connections were again compared using independent t-tests. Finally, we performed one-sample t-tests on the laterality index to examine the asymmetry of node centrality and each connection in this network. For each statistical group comparison, we controlled for the effects of age and gender on network properties using linear regression models. In all analysis steps, a false discovery rate (FDR) at a p-value of 0.05 was used to correct for multiple comparisons. This included the analysis of group differences in network strength, global node centrality of the five regions (IFG, TL, IPL, aCC, and pCC), post-hoc node centrality of each sub-region in the significant region, and for the extended language network properties.

3. Results

3.1. Intra- and inter-hemispheric differences in brain connectivity

We performed a 2 × 2 (Hemisphere x Group) ANOVA to test for differences in network strength between the hemisphere and the groups. We found a main effect for Hemisphere ($F = 376.3$ $p < 0.001$) and Group ($F = 10.57$, $p < 0.005$). The interaction effect between Hemisphere and Group was not significant ($F = 0.19$, $p = 0.67$). A *t*-test showed stronger connectivity in the left hemisphere compared to the right hemisphere reflecting the left hemispheric dominance of the language network in both groups (German: $t = 14.0$, $p<0.001$; Arabic: $t = 13.4$, $p<0.001$) (Fig. 1C). Comparing the groups, German speakers displayed stronger intra-hemispheric connectivity in both hemispheres than Arabic speakers (left: $t = 2.53$, $p<0.05$ FDR corrected; right: $t = 2.36$, $p<0.05$ FDR corrected, Fig. 1C), whereas Arabic speakers showed stronger inter-hemispheric connectivity ($t = 2.4$, $p<0.05$ FDR corrected, Fig. 1B).

3.2. Regional differences in global brain connectivity

After showing the group difference in Intra- and inter-hemispheric connectivity, we focused on the analysis of the connectivity of the larger language areas and the corpus callosum (IFG, TL, IPL, aCC, pCC) to identify areas with significant group differences in connectivity by testing the global node centrality. We found stronger global connectivity in German speakers than in the Arabic-speaking group in the left IFG ($t = 3.29$, p <0.05, FDR corrected) (Fig. 2A). To localize the sub-regions in the left

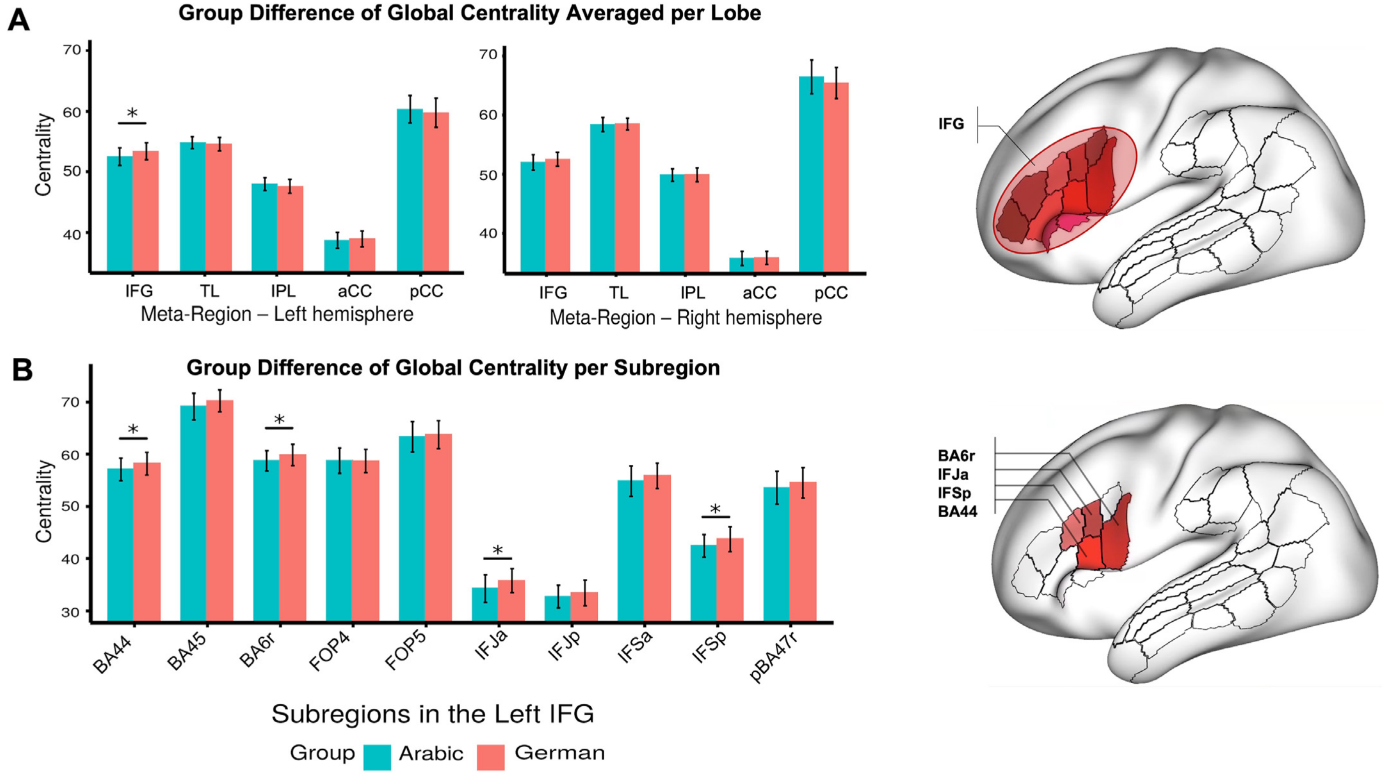

Fig. 2. Regional connectivity differences in the language network. (A) Average global node centrality of the language “meta” regions in both hemispheres. The left IFG showed significant group differences. (B) Group difference of global node centrality within the left IFG. * indicates significant differences, $p<0.05$, FDR corrected. Left: comparison between groups, right: locations of regions with differences. For labels see *Supplementary Materials and Table S1*. Centrality values for the meta-regions and the subregions range from 0 to 184 (all possible connectivity values = 1 without threshold).

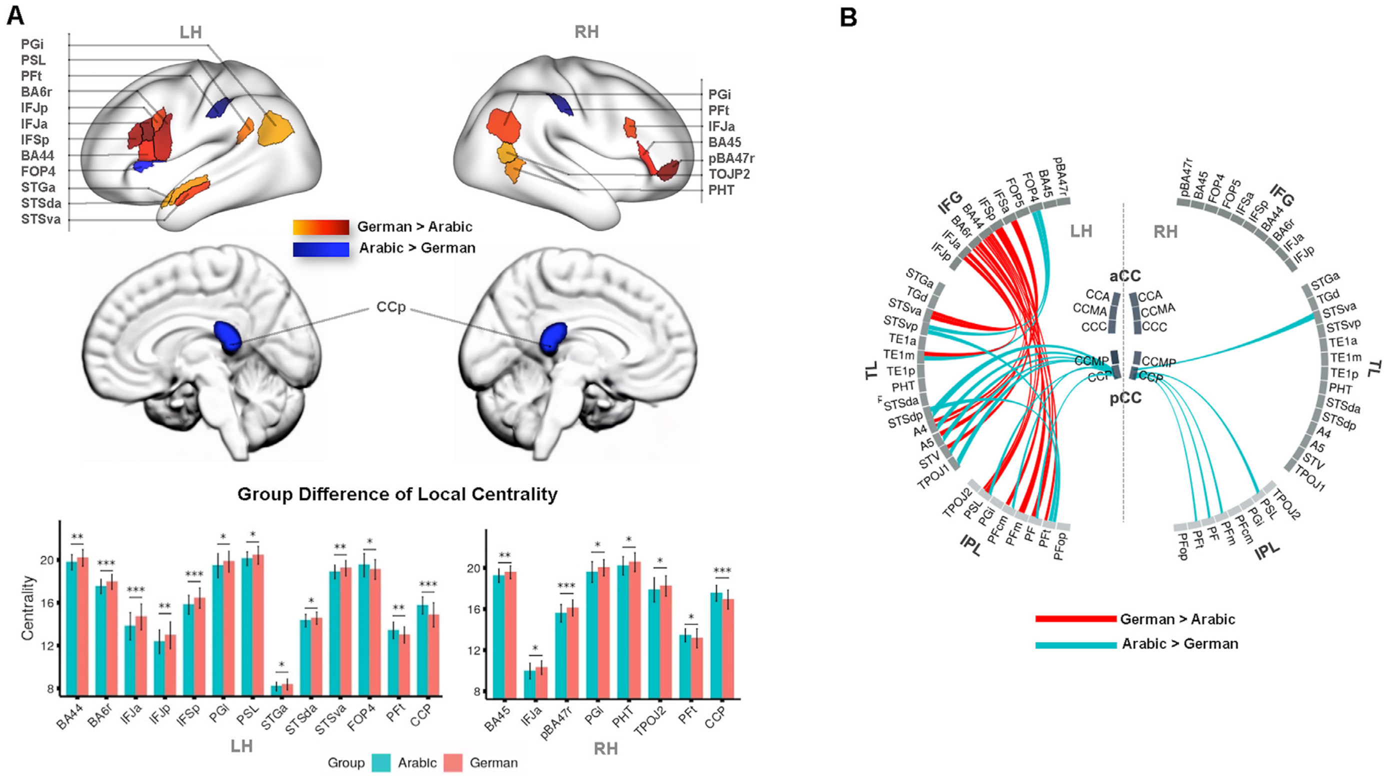

Fig. 3. Regional connectivity differences (local node centrality) and network-based differences in the connection strength. (A) Regions with significantly different local node centrality between groups (two-way ANOVA). The color indicates the result of the *post-hoc* t-test between groups. The bottom panel shows the comparison between groups. The local node centrality values for all regions range from 0 to 36 (all possible connectivity values = 1 without threshold). (B) Network-based statistical difference in connectivity within the language connectome between groups. Red: Edges of the network with significantly greater connectivity in the German group. Turquoise: Significantly stronger connectivity in the Arabic group. Regions grouped by language region, LH/RH: left/right hemisphere. Significance: *** $p < 0.005$, $^{**}p<0.01$, $^{*}p<0.05$.

IFG with significant group differences, we performed *post-hoc* t-tests. German speakers showed higher centrality than Arabic speakers in the following four sub-regions: left BA44 ($t = 2.53$,$p < 0.05$, FDR corrected; Cohen's d effect=0.52), left rostral BA6 (BA6r,$t = 2.96$, $p < 0.05$, FDR corrected; Cohen's d effect=0.61), left posterior inferior frontal sulcus (IFSp, $t = 2.75$, $p < 0.05$, FDR corrected; Cohen's d effect=0.57) and left anterior inferior frontal junction (IFJa, $t = 3.05$,$p < 0.05$, FDR corrected; Cohen's d effect=0.63) (see Fig. 2B).

3.3. Difference in connectivity patterns

In the previous section, a higher global node centrality was found for German-speaking participants compared to the Arabic group in the following four sub-regions of the IFG area: left BA44, BA6r, IFSp, and IFJa. We further examined whether the observed centrality difference could be explained by a distinction of these regions in their network fingerprint (connections to other language regions). Compared to Arabic, native German speakers were found to have higher connectivity between these four seed regions in the IFG and associated regions in the left STG and MTG, the left SMG, the perisylvian language area (PSL), as well as the temporal-parietal junction (*Supplementary Materials,* Fig. S2).

3.4. Regional differences in local brain connectivity

To estimate the potential for information exchange within the language network we analyzed the local node centrality. We performed a two-way ANOVA with the factor Group (German, Arabic) and the factor ROI (74 language ROIs) to analyze potential differences in local node centrality between German and Arabic speakers. We observed a significant main effect of ROI ($F = 2647.90$, $p < 0.001$), a significant main effect of Group ($F = 33.46$, $p < 0.001$), and an interaction between ROI and Group ($F = 2.36$, $p < 0.001$). The *post-hoc* t-tests revealed that native German speakers had higher node centrality than Arabic speakers in sub-regions of IFG (left: BA44, BA6r, IFJa, IFJp, IFSp; right: BA45, IFJa, pBA47r), TL (left: STSva, STSda; right: PHT), IPL (left: PSL, PGi; right: PGi, TOJP2) (Fig. 3A). The Arabic group had significantly higher local node centrality in the left frontal operculum (FOP4), bilateral anterior SMG (PFt), and the posterior subsections of the corpus callosum (Fig. 3A).

3.5. Network-based statistics (NBS)

To identify specific connections and subnetworks with significant differences in connectivity between German and Arabic speakers we computed network-based statistics (NBS) using the predefined language ROIs in both hemispheres. Statistical group comparison of connections (edges) revealed that the German group showed stronger connections in a left fronto-parietal/temporal network ($p<0.05$, NBS corrected, Fig. 3B). The Arabic group showed stronger inter-hemispheric connections between the bilateral STG and IPL, via the posterior CC, and stronger connections between the left frontal operculum (FOP4) and the left MTG (STSvp, TE1m) ($p < 0.05$, NBS corrected, Fig. 3B).

3.6. Difference in the language production pathways

The areas in the SMA/pre-SMA are part of the extended language network, which also includes aspects of speech production. Similar to the initial test of hemispheric differences, we first tested the connections

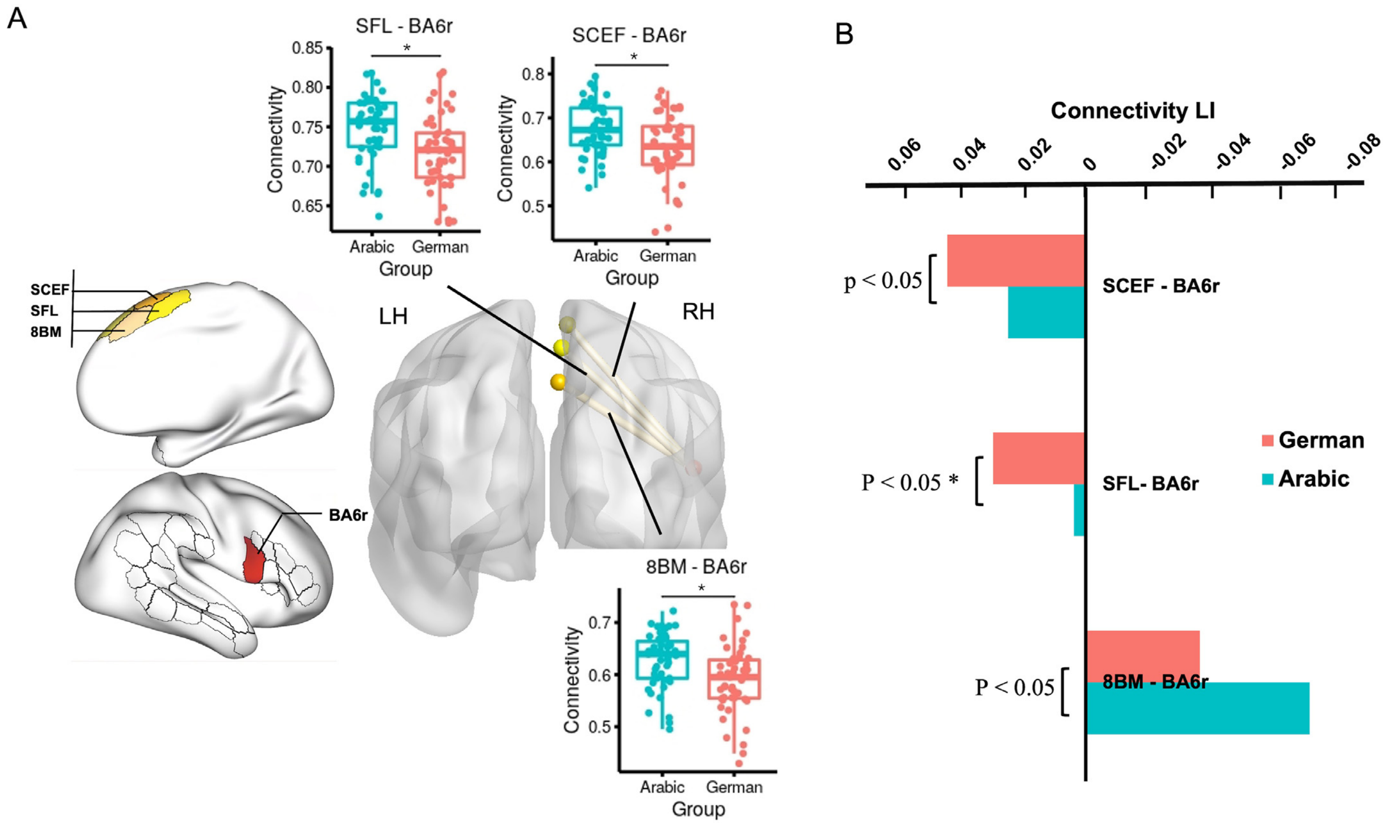

Fig. 4. Verbal language production regions: Differences in connectivity and lateralization. (A) Significant group differences in connectivity in the right hemisphere. Left: ROI location, right: connections and group comparison result. (B) Difference of the lateralization index (LI) of the connections. * p <0.05, FDR corrected.

with the SMA/pre-SMA for lateralization. Both, the German and Arabic native speakers showed consistent lateralization across different speech production areas (see *Supplementary Materials,* Fig. S3). There was no significant difference between the groups, neither in the node centrality nor in the lateralization index (LI) of each region. Interestingly, when comparing the connectivity between each seed region of the SMA/pre-SMA and each language target region, the Arabic group showed significantly stronger connections between the right SMA/pre-SMA and the posterior IFG following the frontal aslant tract (right SFL – BA6r: $t = 3.45$, $p<0.05$, FDR corrected; right SCEF- BA6r, $t = 3.1$, $p<0.05$, FDR corrected; right 8BM- BA6r, $t = 3.1$, $p<0.05$, FDR corrected, Fig. 4A). To investigate whether these differences were driven by an altered lateralization of the frontal aslant tract in the Arabic group compared to the German group, we calculated the mean LI of each speech pathway and compared the difference between the two groups (Fig. 4B). We observed that both, the German and Arabic group showed a trend in the leftward asymmetry of the connectivity of SCEF- BA6r, SFL- BA6r, and a rightward asymmetry in the connectivity of 8BM - BA6r. However, the Arabic group showed a lower LI in SFL-BA6r ($t = 3.4$, p <0.05, FDR corrected), SCEF-BA6r ($t = 2.1$, $p<0.05$), and 8BM-BA6r ($t = 2.3$, $p< 0.05$) than the German-speaking group.

4. Discussion

The present study provides new insights into the brain adaptation for cognitive processes, that is, the structural language connectome in the brain is shaped by one's native language. Previous behavioral studies have reported cross-linguistic differences in multiple aspects, concerning phonological, lexical, grammatical, and orthographic processing, etc. (Evans and Levinson, 2009). Each of these differences affected, for example, various brain activations during language processing (Paulesu et al., 2000; Tan et al., 2005), different aphasic symptoms in stroke patients (Bates et al., 1987), and diverse structural bases for developmental dyslexia (Paulesu et al., 2001; Siok et al., 2004). The fundamental effects of the cross-linguistic environment on the brains of first-language learners should be reflected not only in differences in functional activity, but also in structural organization. Using a graph-theoretic analysis of the language network, our results revealed significant differences in the language connectome between native speakers of two different languages: German and Arabic. Native speakers of German with complex syntactic dependencies show comparatively stronger network topological properties in the syntax-related system. Native speakers of Arabic, a language that is driven by its root system and where most words are morphologically complex, led to stronger network properties in the semantic and phonological neural system. This finding is consistent with previous studies that found localized brain structural differences between groups of native speakers (Crinion et al., 2009; Kochunov et al., 2003) and suggests that white matter plasticity in brain structure coincides with specific cognitive functions and processing demands of life-long use of a particular language. Thus, our findings contribute to our understanding of the mechanisms underlying experience-dependent white matter organization and adaptation in the human brain (Wake et al., 2011).

4.1. *Hemispheric specialization of the language network*

Analysis of intra-hemispheric and inter-hemispheric network strength revealed that both groups exhibited left lateralization (see Fig. 1C). This is consistent with the widely accepted theory that language processing exhibits left hemisphere dominance (Friederici, 2011; Price, 2010) and confirms the universality of the global properties of the language network. This is also reflected in a recent cross-language study of 45 different languages showing a consistent left lateralization of the native language processing areas (Malik-Moraleda et al., 2022). However, native German speakers showed higher intra-hemispheric network strength, whereas Arabic speakers showed higher inter-hemispheric connectivity. In the German group, the stronger connectivity appears to be related to higher connectivity as measured by local node centrality between the sub-regions within each hemisphere (Fig. 3A) and may reflect a more efficient signal transmission within each hemisphere. The higher inter-hemispheric connectivity of the Arabic group may be related to a stronger involvement of both hemispheres in Arabic language processing (Al-Hamouri et al., 2005; Eviatar and Ibrahim, 2007), with a reduced specialization of each hemisphere and stronger inter-hemispheric connections. Our study suggests that although the language network exhibits consistent global characteristics, that is, left lateralization, the local properties are shaped to adapt to the specific cognitive demands of a given language (Catani et al., 2007; Gandour et al., 2004).

4.2. The specific syntactic network of German native speakers

Previous electrophysiological studies comparing English and German language processing have shown that brain activity shows cross-linguistic grammatical differences related to word order properties (Bornkessel-Schlesewsky et al., 2011). While English has a rather rigid word order, German does not. Arabic also has a relatively rigid word order (Saiegh-Haddad and Joshi, 2014), which again differs from German, which is a langauge with a flexible word order. We found that native German speakers showed higher connectivity, as measured by global node centrality, than native Arabic speakers in the left IFG, particularly in the sub-regions BA44, IFSp, IFJa, and BA6r (Fig. 2). The additional comparison of local node centrality shows a consistent result that is even more specific to the characteristics of the language network. Higher centrality represents higher connectivity with the other regions in the language network and highlights the importance of the specific brain region for information integration (Bullmore and Sporns, 2009). Our findings may be related to the complex syntactic processing of German, due to the free word order (Haider, 2010; Müller, 2015) and higher dependency distance of sentence elements (Liu et al., 2017). Complex syntactic processing relies on the posterior IFG, especially left BA44 (Embick et al., 2000; Friederici, 2011). Previous studies using German sentences revealed that left BA44 is particularly sensitive to complex German syntactic structure which is dominated by word order changes (Friederici et al., 2006; Raettig et al., 2010). The left IFS is essential for processing long-distance dependencies in sentences because the integration of syntactic information over long distances requires additional working memory resources provided by the left IFS (Makuuchi et al., 2009). The IFJ and left ventral premotor cortex (BA6r) support information integration and local structural dependency processing, respectively (Friederici, 2011). Therefore, the higher node centrality of left sub-regions in the posterior IFG is advantageous for the efficient syntax processing in German.

In German, the free word order is accompanied by the morphological marking of syntactic information. This requires the anterior superior temporal gyrus (STG) to efficiently assign the heard word to a syntactic word category (Brennan et al., 2012; Friederici, 2011) and the perisylvian language area (PSL) to integrate syntactic information (Friederici, 2011). This may result in the observed higher local centrality of the sub-regions (STSva, STSda) of the left STG and PSL. In addition, syntactic complexity may recruit extra working-memory support in the right hemisphere (Meltzer et al., 2010), leading to higher local nodal centrality in the right hemisphere.

The observed stronger white matter network in the German-speaking group may facilitate efficient communication of the neural signal between regions. Consistent with our hypothesis, the language with complex syntax was associated with stronger structural connectivity along the dorsal language pathway, connecting sub-regions of the posterior IFG and the posterior temporal lobe (Fig. 3B). The dorsal language pathway, which connects the posterior IFG (BA 44/IFS) to the posterior STG via the IPL, is primarily involved in complex syntactic processing (Friederici, 2011; Wilson et al., 2011) and develops when the brain matures for complex language ability (Perani et al., 2011; Pujol et al., 2006). To adapt to the complex syntax of German during the development of the mother tongue, it is plausible that German native speakers develop stronger connectivity in the dorsal pathway. Along the language system, a second pathway connects the temporal cortex with the PMC (BA6r), which supports the mapping of auditory-to-articulatory representations for speaking (Friederici, 2011; Saur et al., 2008) and is already present at birth (Perani et al., 2011). Although the German sound system differs from Arabic articulation in several ways, for example, the absence of /p/, /g/, /ç/ and the addition of emphatic sounds /ħ/ and /ʕ/ in Arabic, it is unclear whether such auditory-motor differences in phonology lead to the observed differences in the brain, and further research is needed. However, compared to the syntactic structure of Arabic, which is mainly SVO (Subject–Verb–Object, Aoun et al., 2009), German has a more complex syntactic structure (Haider, 2010; Müller, 2015), which may have a direct effect on the dorsal pathways resulting in stronger connections. On the other hand, the stronger connectivity between the anterior temporal lobe and the posterior IFG might be related to local phrase formation in German sentences, which involves the left anterior STG/STS and the FOP and BA44 (Friederici, 2011). Our observations support the idea that the syntax-related white matter pathways reflect specific features of the mother tongue.

4.3. The specific semantic and phonology network of native Arabic speakers

The current research revealed that Arabic native speakers show stronger structural connectivity bilaterally in the IPL, posterior temporal lobe (STG/MTG), and left FOP. This may be related to the relatively complex semantic and phonological processing involved in Arabic word identification. Arabic word processing operates in a root-and-pattern unit. The root mainly provides the core semantic meaning, and word patterns express the phonological information, morphosyntactic information, and phonological structure of the surface form (Boudelaa and Marslen-Wilson, 2015; Saiegh-Haddad and Joshi, 2014). Hence, Arabic communication may require processes that facilitate the integration of these different aspects. Many views suggest that the cortex relevant to lexical processing includes the STG/STS, MTG, and SMG in the rostral IPL, as well as a ventral language pathway connecting the left temporal lobe and the pars triangularis in the IFG (Friederici, 2011; Hickok and Poeppel, 2007; Lau et al., 2008). These regions support word form and phonological decoding and morphosyntactic processing, lexical access, and lexical candidate selection, respectively. Recent studies have found that the lexical interface and phonological decoding are largely bilaterally organized (Hickok and Poeppel, 2007), suggesting that complex lexical processing relies more on the integration between the two hemispheres. Structurally, the left FOP is a "transit station" of the ventral pathway from the temporal lobe to the IFG. Together, efficient integration of Arabic lexical-related information requires stronger structural connections along the ventral semantic pathway and stronger inter-hemispheric connections that join the sub-regions of the STG and IPL (Fig. 3B). This would explain the higher local node centrality in the Arabic-speaking group, particularly in the left FOP, SMG, and posterior corpus callosum.

The stronger inter-hemispheric connection via the posterior corpus callosum also suggests a more complex integration of prosodic and syntactic information during language processing in Arabic. This is because in Arabic, the pattern of consonants (C) and vowels (V) (CV skeleton), as the abstract prosodic unit, is likely to contribute to general syntactic information. The corpus callosum is the structural bridge that supportsinterhemispheric communication of prosodic and syntactic information (Friederici et al., 2007). The complex integration of prosody and syntax in Arabic words may underlie the observed stronger connection along the corpus callosum.

On the other hand, unique features of the language network are associated with the orthographic characteristics of the specific writing systems in each language (Bolger et al., 2005; Siok et al., 2004). In our study, the stronger inter-hemispheric connections in Arabic speakers may be related to the adaptation of the specific orthography in written Arabic. Most Arabic texts lack short vowels, so the reader has to rely on context or prior linguistic knowledge to infer the meaning of the word (Saiegh-Haddad and Joshi, 2014). The right hemisphere has been reported to support semantic operations in complex reading, particularly for the integration of context, inference, and conceptual association (Vigneau et al., 2011). A previous study found that the MTG, AG, and SMG reached similar levels of activation in both hemispheres during Arabic reading (Al-Hamouri et al., 2005), which contrasts with the strong laterality observed during German processing as discussed in the review article (Friederici, 2011). The higher inter-hemispheric connectivity in native Arabic speakers may be the result of adaptation to reading Arabic texts in which short vowels are omitted.

In addition, there is a fundamental difference in reading and writing direction between Arabic and German. Previous neuropsychological studies have reported that reading direction habits of Indo-European and Semitic languages have led to differences in covert attention to the side where reading usually starts, even in non-language tasks (Eviatar, 1997). Moreover, previous studies have also suggested that the bilateral AG is involved in spatial cognition related to language (Seghier, 2013), particularly the left AG for Indo-European languages (Hirnstein et al., 2011). Native speakers of Semitic languages may rely more on regions for spatial cognition in the right hemisphere, which may have led to a strengthening of the inter-hemispheric connections between the bilateral AG to facilitate the transfer of spatial information, which is processed in the right hemisphere, to the left language areas.

4.4. Difference in speech pathways

Analysis of the extended language network, which includes speech processing pathways, showed that German and Arabic did not show significant differences in connectivity of the SMA/pre-SMA regions. However, Arabic native speakers had stronger connections along the right frontal aslant tract (FAT), which connects sub-regions of the SMA/pre-SMA and the sub-regions of the ventral premotor cortex (PMC). This difference may be related to the weaker left lateralization of this pathway in Arabic speakers compared to German participants. The right FAT plays a comparable role to the left FAT for speech production (Dick et al., 2020; Finkl et al., 2020) and is associated with speech fluency (Neef et al., 2018). In Arabic, the same word-pattern morphemes can have distinct phonological structures, depending on the type of root it combines with (Boudelaa and Marslen-Wilson, 2015). Therefore, Arabic speaking may involve more aspects of executive functions such as strategic search, switching, and selective inhibition, which are the essential cognitive processes for verbal fluency (Patterson, 2011). Therefore, fluent speech production in Arabic might recruit both hemispheres and especially involving the right FAT. This would lead to a stronger representation of the right connection and less left lateralization of the SMA-PMC pathway in the Arabic native speakers, as shown in this study.

5. Limitations

Using a graph-theoretic approach, our research has shown how cross-linguistic differences shape the complex structural neural language network. Although cross-language differences are a fundamental domain of cultural variation affecting brain organization, other variables such as educational level, social environment, genetic heritage, and nutritional status may also influence group differences. To minimize non-linguistic effects, the two groups of participants in our study were carefully matched for age, gender, health, and educational level. In particular, we recruited only healthy participants with normal weight and diet. All participants had at least a high school degree or equivalent, and most members of both groups had an educational experience in a university. The Arabic participants aimed to continue their academic education in Germany. All Arabic participants were screened with two questionnaires on trauma and symptoms of post-traumatic stress disorder (PTSD). Only individuals with normal scores on both questionaires were recruited for our study in order to minimize social and environmental influences on our results. In addition to spoken language and environmental factors, genetic factors have been reported to influence functional brain connectivity during brain development (Richmond et al., 2016). However, differences in the language network between genetically similar German and English populations (Goucha, 2019), as well as the previously reported white matter plasticity during second language learning (Schlegel et al., 2012), suggest that the language system may be primarily shaped by the particular characteristics of the spoken language. Additionally, social cognitive and affective processes and other non-linguistic factors may also lead to differences in the brain. In particular, cultural values such as individualism and collectivism have been shown to influence brain function. However, the influence was not in language areas, but in the medial prefrontal and posterior cingulate cortex (Chiao et al., 2009, 2010). Similarly, social cognitive and affective processes might particularly affect the ventromedial prefrontal cortex, amygdala, right somatosensory cortex, insula, and the cingulate cortex, which constitute the social cognition system in the brain (Adolphs, 1999; Mason and Morris, 2010). To minimize the influence of non-linguistic effects, we matched for age, gender, and education level and included only young and healthy participants with normal weight and diet. Furthermore, we focused our analysis on the core network of speech and language processing in the inferior frontal gyrus, temporal lobe, inferior parietal lobule, and (pre-)supplementary motor areas (Friederici, 2011; Hickok and Poeppel, 2007; Price, 2010), which do not overlap with the aforementioned system for social cognition. This language system may be primarily shaped by the specific characteristics of the mother tongue.

While the emergence of the white matter structural network of language, particularly the dorsal language pathway, associated with syntactic processing (Friederici, 2011), coincides with language development (Perani et al., 2011; Skeide and Friederici, 2016), many language factors might influence the rate and pattern of myelination in the brain. This strongly suggests that the current findings are indeed language-related. However, the lack of detailed individual language performance and functional data makes it impossible to directly quantify the relationship between language attributes and the structural language network. In addition, social, environmental, and genetic factors or other aspects of cultural differences may also contribute to differences in brain connectivity in language networks. Future studies incorporating functional brain data could help to specify the networks used for syntax, lexical morphology, and prosodic processing in German and Arabic participants. In addition, future investigations would benefit from detailed cross-linguistic semantic and syntactic behavioral assessments of individual language abilities. This would provide further evidence for the observed language-specific plasticity of the structural brain connectivity.

To obtain robust and reproducible results, we acquired high-resolution diffusion MR images of the highest quality on a 3-Tesla MR system. The structural connectivity network was constructed using a robust, probabilistic, crossing-fiber tractography method. Nonetheless, depending on the implementation, the fiber reconstruction may be prone to a certain number of false-positive and false-negative connections, which may limit the accuracy, even with high-quality data (Maier-Hein et al., 2017). Therefore, the results should be interpreted with some caution. To minimize false-positive connections in our probabilistic approach, we removed unreliable connections and retained only the 40% strongest connections (Bullmore and Sporns, 2009) in each hemisphere. Nevertheless, we cannot completely exclude false-positive and missing connections in our data.

In the current study, we analyzed the structural connectivity because we had a strong hypothesis about the differences in the white matter language network between speakers of the two different languages. However, we cannot exclude the possibility that the gray matter of the two groups also differs, and morphological cortical and sub-cortical parameters should be considered in future studies. Similarly, voxel-based microstructural parameters derived from diffusion measurements, such as fractional anisotropy or mean diffusivity, might reveal local differences in white matter. However, it may be difficult to relate them directly to specific white matter connections, so this analysis was not considered in this study.

6. Conclusion

Our study revealed stronger structural connectivity of the syntax network in a German-speaking group compared to matched Arabic-speaking participants. We suggest that this may reflect the more complex syntactic coding present in German. In contrast, the rich morphology of the Arabic language, which is involved in the lexical-semantic and phonological processes, may have led to the modulation of connections between the temporal and parietal lobes, as well as to the increased inter-hemispheric connectivity. Our results provide evidence for the modulation of the structural language network in the human brain by the demands of one's native language. In the cognitive domain, these findings are essential for our general understanding of the interaction of environment and behavior in shaping the human brain.

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Ethics statement

Informed consent was obtained from all participants before inclusion in the study. Ethical approval was obtained from the Ethics Committee of the Medical Faculty of the University of Leipzig, Germany.

Author contributions

XW, TG, AA, and ADF designed the study; XW, HA, and AA analyzed the data; and XW, HA, MS, TG, ADF, and AA wrote the paper.

Data and materials availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the *Supplementary Materials*.

Declaration of Competing Interest

The authors declare that they have no competing interests.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.119955.

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