FUNCTIONAL CONNECTIVITY BETWEEN LANGUAGE-RELATED AREAS AND ITS RELATION WITH AGE, L2 PROFICIENCY, AND GRAMMAR LEARNING ABILITY Merel Koning

Abstract

Functional connectivity patterns within the language network change from childhood to adulthood and have previously been associated with multiple language measures. In the current study, we investigated the relationship between age and functional connectivity between four language-related areas in the left hemisphere (i.e., the left inferior frontal gyrus (IFG), the posterior middle and superior temporal gyrus (pMTG/STG), the angular gyrus (AG), and the middle frontal gyrus (MFG)) by testing participants across a wide age range (9-29 years). Furthermore, we examined how functional connectivity between these regions relates to second language (L2) proficiency and grammar learning ability. Resting state data was acquired from 67 Dutch native speakers and their L2 (English) proficiency and grammar learning ability were assessed through multiple English proficiency tasks and an Icelandic grammar training respectively. We found that both left AG - left IFG connectivity and left IFG - left pMTG/STG connectivity were negatively related to age. Additionally, age was positively related to L2 proficiency, whereas grammar learning ability was not predicted by age. Furthermore, although connectivity between the four language regions was not significantly related to grammar learning ability, left IFG - left pMTG/STG connectivity was positively related to L2 proficiency. A positive relationship within these regions has previously been found for first language (L1) measures, which could suggest that stronger connectivity between these language regions subserves not only L1, but also L2 proficiency. Additionally, together with findings of previous studies, it suggests that a connection between these regions might be important in L2 learning.

Keywords: L2 proficiency, grammar learning ability, age effects, functional connectivity, resting state fMRI, language network

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Introduction

As the world becomes more and more interconnected, speaking multiple languages gets increasingly important in today's society. More than half of the EU's citizens (Eurobarometer, 2012), and maybe even half of the population in the world at large (Grosjean, 2010), learns or speaks a second language (L2). However, the proficiency that people ultimately attain in a second language can vary greatly between individuals (Golestani & Zatorre, 2009). One factor that appears to be important for L2 learning success is the age at which people start to acquire a second language; learning a second language is easier and more successful in childhood and becomes increasingly harder with age (e.g., Hartshorne et al., 2018; Johnson & Newport, 1989). Although many task-based fMRI studies have investigated how age of acquisition (AoA), L2 proficiency, and language learning ability affect brain activation patterns (e.g., Abutalebi, 2008; Abutalebi et al., 2001; Chee et al., 2001; Hernandez & Li, 2007; Perani & Abutalebi, 2005; Perani et al., 1998; Tatsuno & Sakai, 2005; Wartenburger et al., 2003), it is not clear yet how these factors are reflected in intrinsic brain activity. Therefore, the aim of the current study was to investigate how age, L2 proficiency, and grammar learning ability relate to intrinsic brain activity in language areas.

Task-based fMRI studies have shown that age and L2 proficiency affect brain activation patterns during L2 processing (Abutalebi, 2008; Abutalebi et al., 2001; Chee et al., 2001; Perani et al., 1998; Tatsuno & Sakai, 2005; Wartenburger et al., 2003). For example, Wartenburger et al. (2003) found that L2 proficiency had an effect on brain activity during semantic processing in Italian–German bilinguals, independently of age of acquisition. They found that late bilinguals with a low L2 proficiency level displayed decreased activation in the left middle frontal gyrus (MFG) and the right fusiform gyrus (FFG), and increased activation in the left inferior frontal gyrus (IFG) and right MFG compared to late bilinguals with a high L2 proficiency level. Another example is Tatsuno and Sakai (2005), who observed both L2 proficiency and age-related effects in brain activity. They compared L2 grammar processing in two age groups, 13 and 19 year olds, and found that activity in the left IFG was negatively correlated with L2 proficiency in the 19 year olds, but not in the 13 year olds. Thus, both age and L2 proficiency have been shown to modulate brain activity during L2 processing.

Although many task-based fMRI studies have provided insight into how age and L2 proficiency affect brain activation patterns during specific tasks, less is known about how these factors relate to intrinsic brain activity, measured using resting state MRI. Resting state MRI measures spontaneous fluctuations in the BOLD signal from different parts of the brain, in the absence of a task. The temporal correlation between these signals can provide information about the connectivity between brain regions; it is assumed that regions are functionally connected if their signals show similarities over time (Bijsterbosch et al., 2017). One way to investigate functional connectivity is to predefine multiple regions of interest (nodes) for which average timeseries of BOLD fluctuations are extracted. Then the connectivity between two nodes (edge) is determined by calculating Pearson's correlation coefficient between the timeseries of both nodes.

Correlation coefficients for all node pairs can then be combined in a network matrix (Bijsterbosch et al., 2017). This network matrix can be used to examine how connectivity patterns vary within the sample (e.g., in younger and older participants) or in relation to a behavioural measure (e.g., L2 proficiency). Using this resting state fMRI approach, studies have investigated functional connectivity patterns between language-related regions and how these connectivity patterns relate to L2 proficiency. For example, Gurunandan et al. (2019) found stronger functional connectivity between language control regions (i.e., the dorsolateral prefrontal cortex (dlPFC)) and language regions (i.e., the left superior temporal gyrus (STG) and the right IFG) in advanced L2-learners compared to intermediate L2-learners. Furthermore, functional connectivity has also been associated with first language (L1) and L2 reading abilities in both children and adults (Koyama et al., 2011; Zhang et al., 2014). In addition to L2 proficiency, studies have associated functional connectivity patterns with L2 learning ability (Chai et al., 2016), language analytical ability (Kepinska et al., 2017), and artificial grammar learning (Antonenko et al., 2012). Kepinska et al. (2018) investigated connectivity of the bilateral IFG during an artificial grammar learning task. They found that the ultimate rule knowledge of the artificial grammar was positively related to functional connectivity between the left IFG and the left MFG, which suggests that left IFG-MFG connectivity is related to the acquisition of rules of a new grammar.

Besides L2 proficiency and language learning ability, age has also been shown to have an effect on functional connectivity patterns (Berken et al., 2016; Koyama et al., 2011; Liu et al., 2017). Koyama et al. (2011) conducted one of the few studies that examined both children and adults to investigate age-related differences in the relationship between functional connectivity patterns and L1 reading competence. In both children and adults, a stronger functional coupling among classic language regions (i.e., the left IFG and left posterior STG) was associated with higher reading competence. However, the two age groups differed in that connectivity between the left IFG and left pSTG was significantly greater in adults than in children. Xiao et al. (2016) also looked at age effects by investigating functional connectivity between language-relevant regions of interest in 5 year old children and adults. They observed a significant correlation between the left IFG and left pSTS during rest in adults, but not in children. Additionally, they performed a seed-based analysis with a seed in the left IFG to explore how left IFG functional connectivity was related to behavioural performance in processing syntactically complex sentences. They found that functional connectivity strength between the left IFG and an area within the left pSTG/pSTS was related to syntactic language performance in children. The authors suggested that the first finding indicates that the left fronto-temporal functional network is not yet established in 5 year old children as it is in adults. However, functional connectivity seems to be already partly established at this age, since it correlated with the performance in processing syntactically complex sentences. Altogether, both studies showed that functional connectivity between language regions seems to be related to various L1 language measures and that these functional connectivity patterns change during development.

For the current study, we chose the left IFG, the left posterior middle and superior temporal gyrus (pMTG/STG), the left angular gyrus (AG), and the left MFG as regions of interest. These left hemisphere regions play a key role in neurobiological models of language processing (e.g., the Wernicke-Lichtheim-Geschwind (WLG) model (Geschwind, 1970) and the Memory-Unification-Control (MUC) model (Hagoort, 2013)), but more importantly, these regions have been shown to be involved during syntactic processing (Heim, 2008; Kepinska et al., 2018; Quiñones et al., 2018). Quiñones et al. (2018) found the left IFG, left posterior MTG/STG, and left AG to be involved during gender agreement computation between Spanish determiners and nouns. This finding supports Heim's (2008) neurocognitive model of syntactic gender processing in which these regions also play an important role. Moreover, the MFG seems to be involved in the acquisition of new grammar rules (Kepinska et al., 2018). For this reason, we chose these specific language-relevant regions as regions of interest. Based on the findings of the studies mentioned above and models of language processing, which predominantly contain left-hemispheric regions, we focused on these four regions of interest only in the left hemisphere.

Koyama et al. (2011) and Xiao et al. (2016) are one of the few studies that investigated functional connectivity between language-related regions in both children and adults. Moreover, they showed that this connectivity can be modulated by language measures such as L1 reading competence and syntactic language performance. However, these studies looked solely at L1 measures; thus far, no studies have investigated the correlation between functional connectivity patterns and L2 measures in children and adults across a wide age range. In the current study we aimed, therefore, to investigate how functional connectivity patterns between language-related regions (i.e., the left IFG, the left pMTG/STG, the left AG, and the left MFG) change with age by investigating both children and adults across a wide age range. In addition, we wanted to gain insight into how L2 (English) proficiency and grammar learning ability (separately) relate to functional connectivity between these language regions during rest.

Based on the literature, we expected to find a positive relationship between age and functional connectivity within the language network, especially between the IFG and the pMTG/STG (Koyama et al., 2011; Xiao et al., 2016). Furthermore, previous studies found that L1 language proficiency positively correlated with functional connectivity within the language network, specifically between the left IFG and left pSTG/STS (Gurunandan et al., 2019; Koyama et al., 2011; Zhang et al., 2014). Moreover, the left IFG and posterior temporal regions have also been associated with L2 learning (García-Pentón et al., 2014; Golestani & Zatorre, 2004; López-Barroso et al., 2013; Yang et al., 2015). Therefore, we expected to find a positive relationship between left IFG - left pMTG/STG connectivity and L2 proficiency. Finally, based on the findings of Chai et al. (2016) and Kepinska et al. (2017, 2018), who found that stronger functional connectivity between language areas was positively related to L2 learning ability and rule knowledge of an artificial grammar, we also expected to find a positive correlation between functional connectivity between language-related regions and grammar learning ability. In particular, evidence has been provided for a relation between left IFG - left MFG connectivity and knowledge of grammar rules (Kepinska et al., 2018). Therefore, we expected a positive relationship between left IFG - left MFG connectivity and grammar learning ability.

Methods

Participants

One hundred seventeen Dutch native speakers participated in the study. Fifty participants were excluded due to: excessive head movement (N = 12), failed brain extraction or registration (N = 12)25), or drop-out before the end of the whole study (N = 13). This resulted in an overall inclusion of 67 participants (aged 9.54-29.50 years, mean age = 18.87, SD = 5.07, 57 female and 10 male) (see Appendix A Figure A1 for the age distribution of the participants). Participants were righthanded, had normal or corrected-to-normal vision, and no hearing impairment or reading disorder. Other exclusion criteria included a bilingual upbringing, a history of neurological, psychiatric or cognitive disorders, or incompatibility with MRI. All participants learned English as a second language after the age of 4 (mean AoA = 9.46). Participants completed a language background questionnaire about English age of acquisition, English usage, and additional languages learned aside from Dutch and English. Most participants reported to have learned other languages in addition to English, among which the most commonly named were German and French, but only two participants reported to use these languages daily (see Appendix A Table A1 for background information about the participants). Written informed consent was obtained from all participants and their parents (if participant were younger than 18) before participation. Participants were compensated for their participation; adults received monetary compensation and children received a gift card for each session. The study was approved by the ethical committee (CMO region Arnhem-Nijmegen).

MRI Data Acquisition

Data was acquired on a 3T Siemens SKYRA MRI scanner using a 32-channel head coil at the Donders Institute for Brain, Cognition and Behaviour in Nijmegen. In order to obtain the resting state data, a multiband accelerated T2*-weighted EPI sequence was used with the following parameters: TR = 1000 ms; TE = 35.2 ms; multiband acceleration factor = 6; matrix size = 104x104; FOV = 213 mm; flip angle = 60°; voxel size = 2x2 mm; slice thickness = 2 mm, 66 axial slices covering the entire cerebrum. The duration of the scan was 8 min 10 s, in which 480 volumes were obtained. In order to minimize head movements, a small pillow was placed in the head coil to stabilize the participant's head and make them lie comfortably. Participants were instructed to relax, lie as still as possible, and remain awake. During the scan, lights were 50% dimmed and participants could either fixate on a white cross that was presented on a black screen in the scanner or they could keep their eyes closed (25 kept their eyes open, 26 closed, 7 alternated, 9 unknown). Additionally, fieldmap data (one phase difference image and two magnitude images at two different echo times) were acquired for distortion correction. For all participants, a structural T1-weighted image was acquired using a Magnetization Prepared Rapid Gradient Echo (MPRAGE) sequence, which served as anatomical reference (TR = 2000 ms; TE = 2.01 ms; matrix size = 256x256; FOV = 256 mm; flip angle = 8° ; voxel size = 1 mm; slice thickness = 1 mm, 192 sagittal slices covering the entire brain).

Data Preprocessing

The data was preprocessed using tools from the FMRIB's software library version 6.0.3 (Jenkinson et al., 2012). The following preprocessing steps were included: (1) discarding the first 5 EPI volumes of each scan, (2) motion correction using MCFLIRT (Jenkinson et al., 2002), (3) spatial smoothing (5 mm FWHM Gaussian kernel), and (4) high pass temporal filtering (100 s cut-off period). Finally, functional images were registered to the anatomical T1 and standard space in two steps; functional images were first registered to the MPRAGE structural image by computing a 12 DOF linear affine transformation with FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001). Then, registration from structural to standard MNI152 space was carried out using FNIRT nonlinear registration (Andersson et al., 2010).

Nuisance Signal Regression

ICA-AROMA was used to remove noise resulting from head motion. This is a data-driven technique that identifies components in the data related to head motion, which are then automatically regressed out (Pruim et al., 2015). Furthermore, the anatomical image of each participant was segmented into white matter (WM), grey matter (GM), and cerebrospinal fluid (CSF). These masks were eroded, coregistered to functional space, and the average timeseries were extracted from the resulting masks. The WM and CSF extracted timeseries were regressed out of the preprocessed data by multiple regressions. The resulting 4D timeseries were used in subsequent analyses.

Procedure

The resting state data analysed in this study was acquired as part of a bigger project investigating the neural correlates of age-related and individual differences in grammar learning ability. As part of this study, participants, who were unfamiliar with the Icelandic language prior to the experiment, did an Icelandic grammar training in which they learned some Icelandic grammar rules (i.e., nominative singular (NOM-S), nominative plural (NOM-PL), and accusative singular (ACC-S) case marking). Since performance in this grammar training is analysed in the current study and related to the resting state data, the grammar training will be described in more detail below. Participants underwent three testing sessions: one behavioural session and two MRI sessions.

Behavioural Session

In the first session, participants underwent an extensive behavioural test battery in which Dutch proficiency, English proficiency, working memory, executive control, non-verbal IQ (WAIS for adults and WISC for children), and episodic memory were tested. The Peabody Picture Vocabulary Task (PPVT-4) (Dunn & Dunn, 2007), the Test for Reception of Grammar version 2 (TROG-2) (Bishop, 2003), and a word and category fluency task served as a measure for English (L2) proficiency in this current study. In the final part of the first session, participants learned 20 Icelandic words through an Icelandic word learning task: 10 masculine nouns (e.g., einn api 'one monkey') and 10 feminine nouns (e.g., ein blussa 'one blouse').

Participants saw a matrix of Icelandic words and pictures on the computer screen and had to match a highlighted word with the corresponding picture.

First MRI Session

Participants came back on another day for the first MRI session. They first repeated the Icelandic word learning task, which was then followed by a more extensive Icelandic grammar training. This training consisted of three blocks of 60 items in which participants could end up in one of three levels of difficulty according to their performance. These three levels ensured that the training was not too difficult for children or too easy for adults, with the goal to avoid ceiling and floor effects.

Icelandic Grammar Training

Before the first training block started, participants first learned three Icelandic sentences: 'her er' ('here is'), 'her eru' ('here are'), and 'her serdu' ('here you see'), which require a NOM-S, NOM-PL, or ACC-S noun respectively. In the first training block (level 1), these three sentences were combined with only 10 of the 20 learned words. This means that in the first level, participants learned NOM-S, NOM-PL, and ACC-S case marking for five feminine nouns and five masculine nouns. A block consisted of 44 practice items in which cartoons pointed at a picture and asked for the corresponding sentence or vice versa. These practice items were followed by a short interim grammaticality judgement task (GJT); 16 Icelandic sentences were shown sequentially and the participant had to indicate whether they were grammatical or ungrammatical and whether they were certain or uncertain about their answer. The correct answer appeared on the computer screen after each item as feedback. If at least 12 out of 16 test items were answered correctly, the participant continued in level 2 in the second block. Otherwise, they stayed in level 1 for the second block.

In level 2, the masculine nouns were combined with one adjective (i.e., yellow, green, black, or white), which means participants learned masculine NOM-S, NOM-PL, and ACC-S case marking for these adjectives. Again, 44 practice items were followed by 16 test items of which at least 12 had to be correct in order to continue in level 3 in the third block. Otherwise, the participant stayed in level 2 for the remaining block. In level 3, both the feminine and masculine nouns were combined with the four adjectives, so participants additionally learned feminine NOM-S, NOM-PL, and ACC-S case marking for these adjectives (see Appendix B for the full list of stimuli).

GJT in the Scanner.

Participants performed the GJT in the MRI scanner in the same level that was reached in the training. The GJT took 18 minutes in total and consisted of 264 stimuli: 66 words and 66 NOM-S, 66 NOM-PL, 66 ACC-S sentences. This time, all 20 learned Icelandic words (i.e., including the 10 untrained items) were used in the GJT sentences. Participants had to indicate with button press whether the sentences were grammatical (66%) or ungrammatical (33%).

Home Training

After the first MRI session, participants continued with the Icelandic grammar training at home. They did the home training for five days, 30 minutes per day, in the same level as the first MRI session. The home training consisted of three blocks, each block containing 30 practice items, followed by a GJT on 16 test items. On day 5 of the home training, participants additionally learned a second set of 10 new Icelandic words (five feminine and five masculine nouns).

Second MRI Session

A week after the first MRI session, participants came back for the second MRI session. First, for optimal consolidation, participants repeated the second word learning task for the 10 newly learned words. In the scanner, participants performed the GJT on 264 stimuli (66 words and 66 NOM-S, 66 NOM-PL, 66 ACC-S sentences) for a second time, which included all 30 words. Additionally, they had to indicate with button press after each trial whether they were certain or uncertain about their answer (see Figure 1). The last scan in this second MRI session was the resting state scan of which the data was analysed in the current study.

Assessment of L2 Proficiency and Grammar Learning Ability

L2 Proficiency

As mentioned in the previous section, L2 (English) proficiency was assessed with three tasks. The Peabody Picture Vocabulary Task (PPVT-4) (Dunn & Dunn, 2007) was used to test receptive vocabulary in English (maximum possible raw score: 228). The Test for Reception of Grammar version 2 (TROG-2) (Bishop, 2003) was used to test receptive grammar (maximum possible raw score: 80). The final task was a word and category fluency task in which participants had 1 minute to name as many English words as possible starting with a certain letter or belonging to a certain category (i.e., animals or fruit). From the scores of these three tasks a combined factor score was calculated for each participant with principal component analysis in SPSS. This factor score served as a measure of L2 proficiency.

Grammar Learning Ability

In order to assess grammar learning ability, d' scores were computed for the sentence trials in the GJT in the two MRI sessions. D' scores were calculated by determining the hit rate (the number of grammatical sentences correctly judged as grammatical) and false alarm rate (the number of ungrammatical sentences incorrectly judged as grammatical) for each participant. These raw numbers were converted to z-scores and subtracted: d' = z(hit) - z(false alarm). The d' score from the first MRI session was subtracted from the d' score from the second MRI session. The resulting d' score indicates how much participants improved in the GJT between MRI sessions and served as a measure of grammar learning ability. We will refer to this score as Δ GJT score.

Node Definition, Time Course Extraction, and Edge Calculation

Four regions of interest (ROIs) were defined in MNI space based on peak coordinates and cluster sizes found in previous studies: the left IFG (-48, 20, 10; Quiñones et al., 2018), defined as a 7 mm sphere, the left pMTG/STG (-62, -26, -2, and -62, -32, 2; Quiñones et al., 2018), defined as 8 mm spheres, the left AG (-52, -66, 38; Quiñones et al., 2018), defined as a 5 mm sphere, and the left MFG (-42, 14, 38; Kepinska et al., 2018), defined as a 8 mm sphere (see Figure 2). The ROIs differed in size in order to resemble the cluster sizes found in Quiñones et al. (2018) and Kepinska et al. (2018). For the pMTG/STG ROI, two spheres were combined in order to capture the extended region found in Quiñones et al. (2018). Masks for these ROIs were transformed into each participant's functional space and the average timeseries was extracted from each ROI by averaging across all voxels within the mask. The first eigenvariate was also taken from each ROI. Just like the average, this is a summary of the activity within a ROI, but it does not assume homogeneous activity within the ROI and has therefore been suggested as a more sensitive measure (Friston et al., 2006).

The analysis package FSLNets (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLNets) was used in Matlab to compute full correlations between the timeseries of the four ROIs. This resulted in six edges in total: AG-IFG, AG-pMTG/STG, AG-MFG, IFG-MFG, IFG-pMTG/STG, and MFG-pMTG/STG. The correlations were computed both for the mean extracted timeseries and the eigenvariates; all were converted from Pearson correlation r-values into z-statistics with Fisher's transformation. This resulted in two 4x4 network matrices for each participant; one with z-scores based on correlations between the mean extracted timeseries and one with z-scores based on the correlations between eigenvariates. The statistical analyses described below were performed on both z-scores. Since results were very similar for both z-scores, the results obtained from the mean extracted timeseries are reported and it is mentioned when these deviate from the results based on the eigenvariates.

Statistical Analyses

We checked for outliers, which were defined as values being outside the range of 3.29 standard deviations away from the mean. One outlier was identified in the L2 proficiency scores with a standardized residual of -4.22. Therefore, this case was not included in the analyses involving L2 proficiency. Furthermore, one participant had a negative Δ GJT score, indicating that this participant did not improve in the GJT between MRI sessions. However, given that this participant completed the home training correctly and that the Δ GJT score did not seem to have a major effect on the final model (Cook's distance was close to zero), we decided to include this participant in the analyses.

The relation between age and functional connectivity strength between the four ROIs was tested in multiple regression analyses in SPSS. This analysis included age as independent variable, the edge strength as the dependent variable, and IQ as covariate of no interest. Next, the relation between functional connectivity strength between the four ROIs and the language measures (i.e., L2 proficiency and the Δ GJT score) was assessed with separate multiple regression analyses.

This analysis included the language measure as independent variable, the edge strength as the dependent variable, and IQ and age as covariates of no interest. Bonferroni correction was used for multiple comparisons correction for all analyses. Correlations between age, the Δ GJT score, L2 proficiency, and IQ were tested with separate partial correlation analyses.

Results

Behavioural Results

Mean raw scores for the three tasks measuring L2 proficiency were as follows: PPVT-4 = 175.26 (SD = 24.59), TROG-2 = 76.47 (SD = 4.36), and Fluency = 43.98 (SD = 11.27). The L2 proficiency factor score that was computed from these three individual scores with principal component analysis explained 77.1% of the total variance. The three individual scores had a high loading on this factor score (PPVT-4 = .931, TROG-2 = .853, Fluency = .847). The mean \triangle GJT score calculated from the sentence trials was 1.48 (SD = 0.74) and ranged from -0.14 to 3.17, since all but one participant improved in the GJT after training.

Relationship Between Age and the Language Measures

Partial correlations were conducted between age and the language measures (i.e., L2 proficiency and Δ GJT score) with IQ as a control variable. Age correlated significantly with L2 proficiency (r(63) = .57, p < .001) and IQ (r(65) = .32, p = .008), which means that older participants had a higher L2 proficiency and performed better on the IQ test than younger participants. Age did not significantly correlate with the Δ GJT score (r(64) = -.03, p = .793).

Relationship Between Age and Functional Connectivity

Multiple regression analyses were conducted to see if age predicted functional connectivity between the four ROIs. We found that age significantly predicted left AG-IFG connectivity (b = -0.21, 95% CI [-0.34, -0.09], t(66) = -2.96, p = .003), which was still significant after Bonferroni correction for multiple comparisons (adjusted p-value = .008). The relationship between age and left AG-IFG functional connectivity was negative, indicating that connectivity between these regions decreases with age. Age explained a significant amount of variance in left AG-IFG connectivity when controlled for IQ(F(2.64) = 4.52, p = .015, R2 = .12) (see Table 1). No significant relationship was found between age and edge strength of the other five edges (see Appendix C Table C1).

Relationship Between the Language Measures and Functional Connectivity

Next, multiple regressions were conducted to investigate whether the two language measures (i.e., L2 proficiency and the \triangle GJT score) separately predicted functional connectivity between the four ROIs. For left IFG-pMTG/STG connectivity, the model was not significant when only L2 proficiency was included as a predictor (F(1,64) = 2.01, p = .161, R2 = .03). However, the model significantly improved when including age and IQ as covariates (\triangle R2 = .12, p = .017).

In contrast, the positive effect of L2 proficiency indicates that left IFG-pMTG/STG connectivity increases with L2 proficiency. Both effects were still significant after correcting for multiple comparisons. None of the other edges showed a significant correlation between L2 proficiency and edge strength (see Appendix C Table C2). Finally, none of the edges showed a significant relationship between Δ GJT score and edge strength (see Appendix C Table C3). Notably, results based on the eigenvariates (instead of the mean extracted timeseries) showed a significant relationship between left AG-IFG connectivity and the Δ GJT score (b = 1.13, 95% CI [0.03, 2.24], p = .045), but this effect did not survive Bonferroni correction (see Appendix C Table C4).

Discussion

In this study, we investigated the relationship between age and functional connectivity between four language-related areas (i.e., the left IFG, the left pMTG/STG, the left AG, and the left MFG) across a wide age range. Furthermore, we investigated how functional connectivity between these regions is related to two language measures, L2 proficiency and grammar learning ability. First, we found that left AG-IFG connectivity decreases with age. A negative relationship with age was also found for left IFG-pMTG/STG connectivity, but only when controlled for L2 proficiency. Second, we observed a positive relationship between age and L2 proficiency, whereas grammar learning ability was not significantly related to age. Regarding our second research question, we found a positive relationship between left IFG-pMTG/STG connectivity and L2 proficiency, indicating that connectivity between these regions gets stronger when L2 proficiency increases. Although no significant effects were found between grammar learning ability and functional connectivity strength between the four ROIs, there was a positive trend between left AG-IFG connectivity and grammar learning ability that failed to survive multiple comparisons correction.

Considering first the effect of age on our two language measures, the significant positive correlation between age and L2 proficiency was expected and in line with the amount of English education that participants had. The adult participants (> 18 years) reported to have had on average more years of English education (M = 7.97 years) compared to the younger participants (M = 4.77 years). Additionally, adults used English more in their daily life; they reported to be engaged in English speaking, reading, writing, and listening for 35 hours per week on average compared to 22 hours per week for children. In contrast to English proficiency, no effect of age was found on grammar learning ability. According to the literature, language learning is easier in childhood than in adulthood (Hartshorne et al., 2018; Johnson & Newport, 1989). Findings of Hartshorne et al. (2018) suggest that grammar learning ability is preserved until around 17.4 years and then declines. This means that young learners generally have an advantage when learning a new language, although adults progress faster in the initial stages of L2 learning (Johnson & Newport, 1989; Krashen et al., 1979). The Icelandic grammar training in the current study only lasted for 5 days, which might have been too short to find any age-related differences in grammar learning ability on the behavioural level.

Our main research question was whether an age effect would be observed in the brain. We expected a positive relationship between age and functional connectivity within the language network and in particular for left IFG-pMTG/STG connectivity. Contrary to our hypothesis, we observed a negative relationship between age and left IFG-pMTG/STG connectivity, but only when controlled for L2 proficiency. This is not in line with previous studies; Koyama et al. (2011) and Xiao et al. (2016) found that connectivity between the left IFG and left pSTG/STS was significantly stronger in adults than in children and they suggested that this reflects developmental changes in the language network. A possible explanation for not replicating these findings might be that previous studies looked at different age ranges. Xiao et al. (2016) compared two different developmental stages, 5-year-olds and adults, while we investigated age as a continuous variable in a broader age range. Left IFG-pMTG/STG connectivity might be less established in 5-year-olds than in the older participants in our study. Therefore, Xiao et al. (2016) might have found an increase in left IFG-pMTG/STG connectivity in adults, because they compared the adults with children in a very early developmental stage. A difference between Koyama et al. (2011) and the current study is that they did not control for language proficiency when they looked at the effect of age on left IFG-pSTG connectivity. In the current study, we only found an effect of age when L2 proficiency was also included in the model. The positive effect of age on left IFG-pSTG connectivity found by Koyama et al. (2011) might have been confounded by the positive effect of the participants' language proficiency.

Additionally, another unexpected effect of age was observed; age was negatively related to connectivity between the left AG and left IFG. A decrease in left AG connectivity has mostly been observed in older populations. For example, Bagarinao et al. (2020) found that the overall connection strength of the left AG showed a significant negative relationship with age in participants in the age range of 21-86 years. Furthermore, the left AG is involved in multiple functional networks (e.g., the default mode network (DMN) and the frontoparietal control network (FCN) (Igelström & Graziano, 2017; Seghier, 2013)) and a common finding is that functional connectivity is reduced within these networks in older age compared to young adults (Sala-Llonch et al., 2015). Thus, a decrease in left AG connectivity with age has been observed. However, given that this decrease is mostly found in older populations, these studies are not directly comparable to our study since we looked at a younger population. Studies that looked at developmental trajectories of functional connectivity in a more similar age range as in the current study do not support our results. These studies generally found that overall functional connectivity of resting state networks seems to be reduced in children compared to adults (Hoff et al., 2013). Moreover, some studies observed that long-range connections in the anteriorposterior direction, including frontoparietal connections, generally seem to strengthen between childhood and adulthood, whereas functional connectivity between proximate regions decreases. It has been suggested that this indicates a shift from a local to global functional organization during development (Dosenbach et al., 2010; Ernst et al., 2015; Grayson & Fair, 2017). Based on these studies that found increased functional connectivity in long-range frontoparietal connections over development, an increase in left AG-IFG connectivity would be expected with age.

Therefore, the decrease in left AG-IFG connectivity with age that we found seems to be at odds with findings in the brain development literature and might suggest that left AG-IFG connectivity does not follow the trajectory generally observed during brain development. However, which anatomical and physiological mechanisms would underlie this decrease in left AG-IFG connectivity remains to be elucidated.

Our second hypothesis focused on the relation between functional connectivity and L2 proficiency. Previous studies have shown that connectivity between the left IFG and left pSTG/ STS is positively related to various L1 language measures (i.e., reading competence and syntactic language performance) (Koyama et al., 2011; Xiao et al., 2016). Moreover, the left IFG and posterior temporal language regions seem to be involved in L2 learning (García-Pentón et al., 2014; Golestani & Zatorre, 2004; López-Barroso et al., 2013; Yang et al., 2015). Based on these findings, we expected a positive relationship between L2 proficiency and left IFG-pMTG/STG connectivity. This hypothesis was supported by the data and suggests that functional connectivity between these language regions is not only associated with language measures in the L₁, but it is also related to L₂ proficiency. This supports the idea that learning a L₂ is (partly) associated with the same neural correlates as the L1 (Perani & Abutalebi, 2005). Although our results are based on resting state data and do not allow to draw firm conclusions about the involvement of these regions in L2 processing or the language processes they subserve, they fit with previous structural and functional MRI studies. Previous studies found that an increase in anatomical connectivity between the left IFG and posterior temporal language regions is associated with L2 learning. Furthermore, these regions have been found to be involved in L2 sound and word learning (García-Pentón et al., 2014; Golestani & Zatorre, 2004; López-Barroso et al., 2013; Yang et al., 2015). Therefore, our result supports the idea that a connection between the left IFG and left pMTG/STG might be important in L2 learning.

Finally, we expected that functional connectivity between the left IFG and the left MFG would be positively related to grammar learning ability. Contrary to this hypothesis, left IFG-MFG connectivity, as well as functional connectivity strength of the other edges, was not related to grammar learning ability. This result is not in line with the findings of Kepinska et al. (2018) who found a positive relationship between rule knowledge of an artificial grammar and left IFG-MFG connectivity. A possible explanation for this discrepancy is that Kepinska et al. (2018) assessed connectivity during an artificial grammar learning task and not during rest as was the case for the current study. Since the MFG has been associated with aspects of executive control, attention, and working memory (Andersson et al., 2009; Miller, 2000), it is possible that the relation between grammar learning ability and left IFG-MFG connectivity is most apparent during task performance. The idea that the task can have a large influence on functional connectivity between language regions and language control regions is supported by the findings of Gurunandan et al. (2019). They found that left dlPFC - left STG functional connectivity and left dlPFC - right IFG functional connectivity correlated positively with L2 proficiency. However, this was only observed during a L2 reading task, and not during a L2 comprehension task. Therefore, the absence of task-based activation in the current study could be a possible explanation for not replicating the finding of Kepinska et al. (2018).

Lastly, we should keep a few limitations in mind when interpreting the findings from the current study. First, we used the PPVT-4 (Dunn & Dunn, 2007) as one of the tests to assess English proficiency. The PPVT-4 was originally designed to measure vocabulary knowledge of English native speakers, therefore, this test might not be optimal to test non-native English speakers with a low L2 proficiency (Goriot et al., 2018). Indeed, some of our youngest participants scored very low on this test, which led to the exclusion of one participant. If the PPVT-4 was not a reliable measure of English proficiency for the youngest participants, this might have caused an increase in the effect of age on L2 proficiency. A second limitation is that participants differed in whether they kept their eyes open or closed during the scan. Younger participants (< 18 years) kept their eyes open more frequently during the scan (53%) than adults (23%). It is possible that fixating on a fixation cross led to increased attentional processing in children compared to adults. However, differences between eyes open or eyes closed conditions seem to be small in general (Patriat et al., 2013), so it is not likely that this had a major effect on our results. Another limitation is that our resting state data was acquired in the final scan of the session, after the GJT task. Therefore, it is possible that there were carry-over effects from the task that might have led to small changes within the language network (Waites et al., 2005). For example, a task-related increase in functional connectivity might obscure connectivity patterns present in intrinsic brain activity at rest. Moreover, it is possible that participants were still thinking about the task during the resting state scan, even though they were instructed to think about nothing in particular. Lastly, most participants indicated that they learned other languages in addition to English (see Appendix A Table A1). Although most participants reported to only have a basic level in these additional languages, some of them reported to be more advanced in a third or even fourth language. Some studies found that multilinguals have a higher language aptitude than bilinguals (Huang et al., 2020). Moreover, participants who learned for example German or Latin were probably familiar with case marking, which was the focus of the Icelandic grammar training. These factors could have given the multilingual participants an advantage in the Icelandic grammar training. However, if and how multilingualism would affect functional connectivity patterns is not clear and would be an interesting direction for future research.

Future studies could also look into the relationship between functional connectivity patterns and grammar learning ability. In the current study, we did not obtain significant results after Bonferroni correction, but our ROI approach limited the findings. One possibility is to take a data-driven approach to see what networks emerge as a function of grammar learning ability. Alternatively, since the left IFG has been shown to play a key role in syntactic processing and more in particular in learning new grammar rules (Friederici, 2011), another possibility for future studies is to take the left IFG ROI as a seed to investigate in which regions connectivity with this seed varies as a function of grammar learning ability. Taking this last approach, it would be interesting to see if left AG-IFG connectivity would emerge in relation to grammar learning ability. In the current study, we found a trend between left AG-IFG connectivity and grammar learning ability, but this did not survive Bonferroni correction.

Previous studies have associated left AG-IFG activity with semantic processing (Seghier, 2013), reading (Segal & Petrides, 2013; Seghier, 2013), dyslexia (Horwitz et al., 1998), intelligible speech processing (Abrams et al., 2013), and speech comprehension (Obleser et al., 2007). Moreover, Heim (2008) and Quiñones et al. (2018) suggested a coupling between these regions when syntactic gender information is retrieved. However, a possible link between left AG-IFG connectivity and grammar learning ability has not been observed before and could be an interesting direction to explore further.

In conclusion, the current study shows that functional connectivity within the language network changes from childhood to adulthood. We investigated how functional connectivity patterns change with age by investigating a broad and continuous age range, which likely captures the developmental trajectory of functional connectivity patterns better than when age groups are compared in a more narrow age range as has been done before. First, we found that left IFGpMTG/STG connectivity decreases with age. This is inconsistent with previous findings which might be explained by the fact that previous studies compared age groups in a more narrow age range and looked at earlier developmental stages. Furthermore, the decrease in left AG-IFG connectivity with age that we observed also seems to be at odds with previous studies. This result might imply that this connection does not follow general developmental trajectories that have been reported in the brain development literature. Future studies should replicate this unexpected negative relation between age and left IFG-pMTG/STG and left AG-IFG connectivity and identify the underlying mechanisms that contribute to this decrease in connectivity during development. A second aim of this study was to examine how functional connectivity relates to L2 proficiency and grammar learning ability. Although no significant results were obtained for grammar learning ability, we found that left IFG-pMTG/STG connectivity correlated positively with L2 proficiency. Left IFG-pMTG/STG connectivity has been previously associated with L1 measures, but our study shows that this functional connection might also subserve L2 proficiency. Furthermore, together with previous studies, this finding could imply that a connection between the left IFG and left pMTG/STG is important in L2 learning. Altogether, our findings contribute to our understanding of how age and L2 proficiency shape functional connectivity in the brain during rest and provide new directions to explore in future research.

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Supplementary Material

Table Al

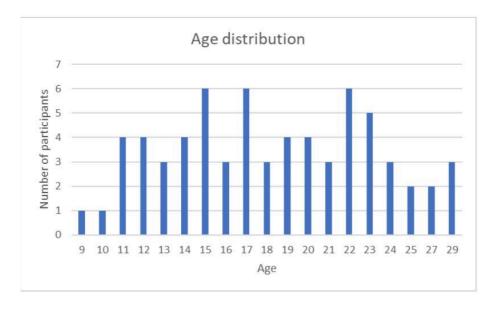
Demographics and Language Background of the Participants

Variable	Value
Sex (M/F)	10/57
Age (years) ^a	18.87 ± 5.07
Age range (years)	9.54-29.50
Language background	
L2 AoA (years)a	9.46 ± 1.93
L2 AoA range (years)	4–13
L2 education (years) ^a	6.44 ± 2.54
L2 engagement (hr/week) ^a	28.47 ± 23.10
L2 class (yes/no)	32/35
If yes, hr/week of English classa	1.36 ± 1.73
Learned L3 (yes/no)	59/8
Learned L4 (yes/no)	48/19
Learned L5 (yes/no)	18/49
Daily use L3/L4/L5 (yes/no)	2/65
Educational levelb	
MA	5
BA	7 4
HBO	4
VO	19

 $aM \pm SD$ reported

bEducational level shown for adults only

Figure A1Age Distribution of the Participants Included in the Analyses



Appendix B

Stimuli Icelandic Sentences Without Adjective

Masculine Words

	NOM-S	NOM-PL	ACC-S
1	her er einn api	her eru tveir apar	her serdu einn apa
2	her er einn jakki	her eru tveir jakkar	her serdu einn jakka
3	her er einn lampi	her eru tveir lampar	her serdu einn lampa
4	her er einn penni	her eru tveir pennar	her serdu einn penna
5	her er einn vasi	her eru tveir vasar	her serdu einn vasa
6	her er einn sofi	her eru tveir sofar	her serdu einn sofa
7	her er einn bolti	her eru tveir boltar	her serdu einn bolta
8	her er einn dreki	her eru tveir drekar	her serdu einn dreka
9	her er einn jeppi	her eru tveir jeppar	her serdu einn jeppa
10	her er einn mani	her eru tveir manar	her serdu einn mana
11	her er einn bursti	her eru tveir burstar	her serdu einn bursta
12	her er einn falki	her eru tveir falkar	her serdu einn falka
13	her er einn pakki	her eru tveir pakkar	her serdu einn pakka
14	her er einn safi	her eru tveir safar	her serdu einn safa
15	her er einn hani	her eru tveir hanar	her serdu einn hana

Feminine Words

	NOM-S	NOM-PL	ACC-S
1	her er ein blussa	her eru tvaer blussur	her serdu eina blussu
2	her er ein flauta	her eru tvaer flautur	her serdu eina flautu
3	her er ein krona	her eru tvaer kronur	her serdu eina kronu
4	her er ein panna	her eru tvaer pannur	her serdu eina pannu
5	her er ein sapa	her eru tvaer sapur	her serdu eina sapu
6	her er ein terta	her eru tvaer tertur	her serdu eina tertu
7	her er ein taska	her eru tvaer taskur	her serdu eina tasku
8	her er ein flaska	her eru tvaer flaskur	her serdu eina flasku
9	her er ein pumpa	her eru tvaer pumpur	her serdu eina pumpu
10	her er ein klukka	her eru tvaer klukkur	her serdu eina klukku
11	her er ein kirkja	her eru tvaer kirkjur	her serdu eina kirkju
12	her er ein pera	her eru tvaer perur	her serdu eina peru
13	her er ein tromma	her eru tvaer trommur	her serdu eina trommu
14	her er ein stjarna	her eru tvaer stjarnur	her serdu eina stjarnu
15	her er ein kista	her eru tvaer kistur	her serdu eina kistu

Stimuli Icelandic Sentences With the Adjective (Yellow as Example) Added

Masculine Words

	NOM-S	NOM-PL	ACC-S
1	her er einn gulur api	her eru tveir gulir apar	her serdu einn gulan apa
2	her er einn gulur jakki	her eru tveir gulir jakkar	her serdu einn gulan jakka
3	her er einn gulur lampi	her eru tveir gulir lampar	her serdu einn gulan lampa
4	her er einn gulur penni	her eru tveir gulir pennar	her serdu einn gulan penna
5	her er einn gulur vasi	her eru tveir gulir vasar	her serdu einn gulan vasa
6	her er einn gulur sofi	her eru tveir gulir sofar	her serdu einn gulan sofa
7	her er einn gulur bolti	her eru tveir gulir boltar	her serdu einn gulan bolta
8	her er einn gulur dreki	her eru tveir gulir drekar	her serdu einn gulan dreka
9	her er einn gulur jeppi	her eru tveir gulir jeppar	her serdu einn gulan jeppa
10	her er einn gulur mani	her eru tveir gulir manar	her serdu einn gulan mana
11	her er einn gulur bursti	her eru tveir gulir burstar	her serdu einn gulan bursta
12	her er einn gulur falki	her eru tveir gulir falkar	her serdu einn gulan falka
13	her er einn gulur pakki	her eru tveir gulir pakkar	her serdu einn gulan pakka
14	her er einn gulur safi	her eru tveir gulir safar	her serdu einn gulan safa
15	her er einn gulur hani	her eru tveir gulir hanar	her serdu einn gulan hana

Feminine Words

	NOM-S	NOM-PL	ACC-S
1	her er ein gul blussa	her eru tvaer gular blussur	her serdu eina gula blussu
2	her er ein gul flauta	her eru tvaer gular flautur	her serdu eina gula flautu
3	her er ein gul krona	her eru tvaer gular kronur	her serdu eina gula kronu
4	her er ein gul panna	her eru tvaer gular pannur	her serdu eina gula pannu
5	her er ein gul sapa	her eru tvaer gular sapur	her serdu eina gula sapu
6	her er ein gul terta	her eru tvaer gular tertur	her serdu eina gula tertu
7	her er ein gul taska	her eru tvaer gular taskur	her serdu eina gula tasku
8	her er ein gul flaska	her eru tvaer gular flaskur	her serdu eina gula flasku
9	her er ein gul pumpa	her eru tvaer gular pumpur	her serdu eina gula pumpu
10	her er ein gul klukka	her eru tvaer gular klukkur	her serdu eina gula klukku
11	her er ein gul kirkja	her eru tvaer gular kirkjur	her serdu eina gula kirkju
12	her er ein gul pera	her eru tvaer gular perur	her serdu eina gula peru
13	her er ein gul tromma	her eru tvaer gular trommur	her serdu eina gula trommu
14	her er ein gul stjarna	her eru tvaer gular stjarnur	her serdu eina gula stjarnu
15	her er ein gul kista	her eru tvaer gular kistur	her serdu eina gula kistu

Appendix C

Table C1

Summary of the Hierarchical Multiple Regression Analyses for Age Predicting Functional Connectivity
Between the Four ROIs in the Left Hemisphere

Edge	<u>b</u> ª	SE	Β β	p
AG-IFG	-0.21 (-0.3	4, -0.09) 0.0	37	.003*
AG-MFG	-0.07 (-0.2	2, 0.08) 0.0	13	.317
AG-pMTGSTG	-0.13 (-0.2	8, 0.04) 0.0	19	.134
IFG-MFG	-0.07 (-0.1	8, 0.05) 0.0	15	.222
IFG-pMTGSTG	-0.10 (-0.2	2, 0.03) 0.0	719	.123
MFG-pMTGSTG	-0.04 (-0.1	8, 0.10) 0.0	707	.622

Note. Age was the predictor variable. IQ was entered as covariate.

a 95% BCa CIs are reported in parentheses. CIs and SEs are based on 1000 bootstrap samples.

^{*}Results are significant below the adjusted p-value of .008.

Table C2Summary of the Hierarchical Multiple Regression Analyses for L2 proficiency Predicting Functional Connectivity Between the Four ROIs in the Left Hemisphere

Edge	ba		SE B	β	p
3 .					
AG-IFG	0.75	(-0.31, 1.78)	0.49	.21	.117
AG-MFG	-0.20	(-1.47, 0.98)	0.64	06	.753
AG-pMTGSTG	0.44	(-1.13, 1.65)	0.74	.11	.548
IFG-MFG	0.13	(-0.85, 0.97)	0.47	.04	.775
IFG-pMTGSTG	1.38	(0.54, 2.30)	0.46	.41	.003*
MFG-pMTGSTG	-0.12	(-1.48, 0.81)	0.61	04	.816

Note. L2 proficiency was the predictor variable. IQ and age were entered as covariates.

a 95% BCa CIs are reported in parentheses. CIs and SEs are based on 1000 bootstrap samples.

Table C3

Summary of the Hierarchical Multiple Regression Analyses for the ΔGJT Score Predicting Functional Connectivity Between the Four ROIs in the Left Hemisphere

Edge	ba		SE B	β	p
AG-IFG	0.93	(-0.08, 1.96)	0.52	.24	.084
AG-MFG	0.49	(-0.60, 1.62)	0.59	.13	.403
AG-pMTGSTG	-0.46	(-1.53, 0.48)	0.51	10	.341
IFG-MFG	-0.39	(-1.35, 0.46)	0.46	12	.378
IFG-pMTGSTG	0.12	(-0.93, 1.14)	0.48	.03	.794
MFG-pMTGSTG	-0.39	(-1.41, 0.53)	0.48	11	.400

Note. The Δ GJT score was the predictor variable. IQ and age were entered as covariates.

a 95% BCa CIs are reported in parentheses. CIs and SEs are based on 1000 bootstrap samples.

^{*}Results are significant below the adjusted p-value of .008.

^{*}Results are significant below the adjusted p-value of .008.

Table C4Summary of the Hierarchical Multiple Regression Analysis for the ΔGJT score Predicting Functional Connectivity Between the Left AG and Left IFG, Based on Eigenvariates

Variable	<u>b</u> a		SE B	β	p
Model 1					
Constant	0.33	(-1.35, 1.95)	0.86		.696
ΔGJT score	1.08	(0.09, 2.10)	0.51	.25	.036
Model 2					
Constant	4.14	(0.62, 7.49)	1.52		.010
ΔGJT score	1.13	(0.03, 2.24)	0.55	.26	.045
Age	-0.22	(-0.35, -0.12)	0.07	34	
.005*					
IQ	0.02	(-0.21, 0.23)	0.10	.02	.849

Note. R2 = .06 for model 1; Δ R2 = .11 for model 2 (p = .021).

a95% BCa CIs are reported in parentheses. CIs and SEs are based on 1000 bootstrap samples.

^{*}Results are significant below the adjusted p-value of .008.