

Cortical contributions to cognitive control of language and beyond: evidence from functional connectivity profiles of the inferior parietal cortex and cognitive control-related resting state networks

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Chapter 2

Dual function of primary somatosensory cortex in cognitive control of language: evidence from resting state fMRI

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Abstract

Resting state functional connectivity can be leveraged to investigate bilingual individual differences in cognitive control of language; however, thus far no report is provided on how the connectivity profiles of brain functional networks at rest point to different language control behavior in bilinguals. In order to address this gap in state-of-the-art research we did a functional connectivity analysis on the resting state data acquired via multiband EPI to investigate three resting state networks of interest namely, the frontoparietal network, the salience network, and the default mode network, which are related to cognitive control, between two groups of Dutch-English bilinguals based on how they performed in a language switching task. Results demonstrated that there is the increased coupling of the left primary somatosensory cortex with the dorsolateral prefrontal cortex in the group with better performance in cognitive control of language and the increased coupling of the right primary somatosensory cortex with the inferior parietal cortex in the group with poorer performance in this executive function. As regards these results, we claim that the primary somatosensory cortex has a dual function in coupling with the dorsolateral prefrontal cortex and the inferior parietal cortex in the frontoparietal network, and in fact, in what characterizes bilingual individual differences in cognitive control of language in healthy participants. The results of this study provide a model for future research in cognitive control of language and may serve as a reference in clinical neuroscience when bilinguals are diagnosed with dysfunction in cognitive control.

2.1 Introduction

Resting state functional connectivity MRI provides the means to investigate brain intrinsic functional networks, by detecting similar patterns of functional activity shared between separated brain regions, when the brain is not processing external stimuli (Fox & Raichle, 2007). Among different brain intrinsic functional networks, three networks are recognized to be involved in cognitive control, of which language control is one component. One of these networks is the frontoparietal network (FPN) which includes the anterior prefrontal, the dorsolateral prefrontal, the dorsomedial superior frontal/anterior cingulate, the inferior parietal lobule, and the anterior insular cortex (Vincent et al., 2008). By controlling the involvement of other brain networks, this network plays an important role in meeting task demands involved in cognitive control (Cole et al., 2013; Spreng et al., 2013).

The other network related to cognitive control is the salience network (SN) which includes the anterior insula/inferior frontal area, the dorsal anterior cingulate and the supramarginal gyri (Seeley et al., 2007). This network is also a task-related network which is active in different aspects of cognitive control, for instance working memory and task switching (Luks et al., 2002; Owen et al., 2005, Dosenbach et al., 2007). The third network related to cognitive control is the default mode network (DMN) which includes the medial parietal (the precuneus and the posterior cingulate), the bilateral inferior parietal and the ventromedial frontal cortex (Smith et al., 2009). The DMN mostly modulates cognitive control by reducing its amount of activity when performing a task and the strength of functional connectivity within its nodes (Dang et al., 2013). This network is recognized as the posterior and the anterior DMNs (Laird et al., 2017).

Investigating brain functional connectivity in healthy participants with regard to the above-mentioned networks related to cognitive control has not been widely reported in the literature and among the few reported ones (Douw et al., 2016; Vatansever et al., 2016), no report is provided on how the functional connectivity of the FPN, the SN and the DMN at rest is responsible for bilingual individual differences in language control. This is in fact what we have addressed in this study by focusing on cognitive control of language which prevents production of words from an unintended language, when bilinguals speak in the target language (Abutalebi & Green, 2007; Green & Abutalebi, 2013). Such cognitive mechanisms which engage brain areas involved in cognitive control (Abutalebi & Green, 2007; Branzi et al., 2016) are characterized with switching to another language or rather language engagement and stopping to speak in the other language, recognized as language disengagement (Abutalebi & Green, 2008; Kroll et al., 2006).

In a few studies, the brain functional connectivity with respect to cognitive control has been investigated. This issue has partly been addressed by Douw et al. (2016), by investigating how the state-dependent variability of the dynamic functional connectivity (vdFC) is related to cognitive flexibility. They studied the brain functional connectivity during both the resting state and the task-based functional magnetic resonance imaging, using a block design Stroop task. According to this research, the state-dependent vdFC between the FPN and the DMN is related to cognitive flexibility, and that better performance in this executive function is characterized with a more dynamic connectivity between the FPN and the DMN when participants performed a cognitive flexibility task; however, the reverse association of the FPN-DMN vdFC was true in the resting state. In another study, Vatansever et al. (2016) conducted an experiment by using an intra/extradimensional set-shifting task (IED) outside the scanner to investigate a link between DMN connectivity and cognitive flexibility as an index of cognitive control. Associating fewer errors in doing different parts of the IED task with more of this executive function, they reported that stronger posterior cingulate cortex/precuneus functional association with the rest of the default mode region is indicative of more cognitive flexibility.

Considering a previously stated hypothesis that the language control behavior in bilinguals characterizes the brain connectivity profiles in cognitive control regions in bilinguals (Luk et al., 2011), Grady et al. (2015) by reporting stronger intrinsic functional associations in FPN and DMN in bilinguals also emphasized the role of these two networks in relation to cognitive control. Moreover, in some other studies, the interactions between DMN, the parahippocampal gyri, the angular gyri (Spreng et al., 2009) and FPN including inferior parietal regions, inferior frontal and dorsolateral regions (Spreng et al., 2013) in different aspects of cognitive control are reported.

With respect to studies on brain functional connectivity patterns, brain regions that fluctuate together to do a particular task, also work together during the resting state functional connectivity (Smith et al., 2009, Cole et al., 2014). Therefore, there is a high similarity between brain regions involved in the resting state and the task-related functional connectivity (Fair et al., 2007). Based on an assumption that an intrinsic functional connectivity architecture, characterized by the resting state functional connectivity, is present across brain regions (Fox & Raichle, 2007, Vincent et al., 2007) Cole et al. (2014) reported that the brain connectivity architecture related to doing a task is shaped by the architecture of the brain intrinsic networks and thus, between these two there is a strong association. These reports have also provided the bases for more research regarding individual differences in the resting state functional connectivity.

In previous studies the involvement of three resting state networks, namely the FPN, the SN, and the DMN in cognitive control has been pointed out, however, no elaborations have been provided on how these networks contribute to individual differences in different aspects of cognitive control. Moreover, as it is emphasized that brain's connectivity profiles in doing a task are formed by the resting state networks, this would provide the rationale to investigate how the intrinsic networks signal individual differences in the first place. Thus, focusing on our research question whether the individual differences in language control are reflected by the functional association of the resting state networks involved in cognitive control, we addressed the above-mentioned gap in previous studies, using a multiband EPI technique.

2.2 Experimental procedures

2.2.1 **Participants**

In this study fifty-two healthy (11 males and 41 females), right-handed psychology students at Leiden University took part. They had normal or corrected-to-normal vision and they were 18-27 years old. These participants were all sequential Dutch-English bilinguals, born to native Dutch parents. In order to measure the English language proficiency of the potential participants we used the quick placement test (University of Cambridge Local Examinations Syndicate 2001). We later excluded four participants from this study because they had excessive movements when we were doing resting state data acquisition.

When we recruited participants we excluded left-handed volunteers as they process language in a different way from right-handed people, and anyone who had any report and history of neurological or psychiatric problems. We asked final participants for their written informed consent before they could take part in the experiment and we compensated for their participation by giving them course credit or paying them a small amount of money. The medical ethics committee of Leiden University Medical Center (LUMC) (Leiden, the Netherlands) approved the protocol of this experiment.

2.2.2 Stimuli

International Picture Naming Project (IPNP https://crl.ucsd.edu/experiments/ipnp/) we selected forty-eight pictures and in doing so we took into account the following variables in both English and Dutch languages (see Table 2.1 for a summary): RT (mean), number of letters and syllables, H statistics which points to the rate of response agreement by participants when they name a picture, word complexity (we did not use any compound words as they increase RT) and initial fricative which specifies if a word begins with a consonant sound such as f or v because such words are associated with having longer naming latencies (see Bates et al., 2003).

Table 2.1 Summary of matching the variables of the stimuli. This summary provides details on each variable that the stimuli were matched on in L1 & L2 with t-test statistics

Name of variable*	Mean L1	Mean L2	SD L1	SD L2	t	P Value
Number of letters	4.71	4.67	1.43	1.21	0.154	0.878
Number of syllables	1.3	1.33	0.46	0.52	-0.42	0.678
RT (mean)	885.51	849.04	93.81	102.39	1.82	0.072
H statistics	0.23	0.22	1.86	3.28	1.33	0.894
Initial fricative	0.1	0.06	0.31	0.245	7.33	0.465
Word complexity	0.00	0.00	0.00	0.00	**	**

Note. *For a detailed description on the identification of variables see: https://crl.ucsd.edu/experiments/ipnp/method/getdata/uspnovariables.html **These values could not be computed because the standard deviations of both groups are 0. In fact, no complex words were used.

In this study we used both the database provided by IPNP and the CELEX lexical database as references for the variables and we created two sets of twenty-four stimuli which were counterbalanced across participants (set A and set B). These two sets were parallel with respect to the above-mentioned variables along with, visual complexity, word frequency and conceptual complexity. As the visual complexity which refers to the level of details in an image, and conceptual complexity which points to how many animals, objects and persons are shown in each image (Snodgrass & Vanderwart, 1980) are language-independent and in fact are features of images, we did not match these variables on L1 and L2, however, we matched these two variables on the two sets of twenty-four stimuli.

2.2.3 Language switching task

In this study we used a language switching task which is indicative of language control and we used E-Prime software to control this task. We presented the stimuli in the center of the screen and we asked participants to name them as quickly as possible following a cue which indicated in which language - Dutch (L1) or in English (L2) - the stimuli should be named. This experiment included two types of trials in four conditions, i.e. there were switch trials in which the cued language was different from the preceding trial (i.e. from Dutch to English or from English to Dutch) and non-switch trials in which the language remained the same as in the previous trial. At the beginning of each trial we showed a visual cue in the form of a red or blue frame for 250 ms and this was counterbalanced across participants. This visual cue also preceded a picture and instructed participants to name the upcoming picture either in Dutch or in English. The cue was then followed by a fixation cross for 500 ms and presentation of a picture for 2010 ms. The end of each trial was marked by presentation of a jittered blank screen which varied between 690 and 2760 ms. We used Optseq program in order to pseudo-randomize the order of stimuli and to determine the length of each intertrial blank screen interval.

Before acquiring the fMRI data, participants practiced the behavioral part of the experiment. That included (a) making participant familiarized with the pictures that we used in the experiment. In this section participants saw all the pictures with their Dutch and English names; (b) making participants familiarized with the association of the visual colored cue and the related language and the task procedure. In this section participants did a short scale of the task that was similar to the main task without using the target pictures. We collected participants' responses by using a voice key outside the MRI scanner.

2.2.4 Resting state fMRI acquisition

All resting state data were acquired on a 3 Tesla Philips Achieva TX MRI scanner at the Leiden University Medical Center, equipped with a SENSE- 32 channel head coil. Prior to resting state functional images, high-resolution anatomical images were collected for co-registration with the functional ones. These included a 3D gradient-echo T1-weighted sequence with the following parameters: TR = 7.9 ms, TE = 3.5 ms, $FA = 8^{\circ}$, $FOV = 250 \times 195.83 \times 170.5$, 155 slices $1.1 \times 1.1 \times 1.1 \text{ mm}3$. During the resting state fMRI acquisition, 700 T2*-weighted whole brain multiband EPIs were acquired, excluding 6 dummy scans preceding the dynamic ones. The scanning parameters in the resting state fMRI acquisition are as follows: TR = 690 ms, TE = 30 ms, multiband factor = 4, $FA = 55^{\circ}$, $FOV = 220 \times 220 \times 121$, 44 slices $2.75 \times 2.75 \times 2.75 \text{ mm}$.

2.3 Data analysis

2.3.1 Behavioral data analysis

We processed participants' reaction times (RTs) in doing the language switching task in switch and non-switch trials by using SPSS software version 23. We used a two (language: Dutch vs. English) by two (context: switch vs. non-switch) repeated-measures ANOVA and we looked into any main effects of the factors and any possible interactions. In addition, we ran subsequent paired *t*-tests to see if the language switching task produced statistically significant switch costs (RT switch – RT non-switch) in both L1 (Dutch) and L2 (English). In the following, we divided participants into two groups to investigate if individual differences in language control are influenced by the functional connectivity of the resting state networks involved in cognitive control.

We measured language control with regard to participants' L1 and L2 switch costs. We averaged the switch costs across L1 and L2, separately. Participants with switch costs less than the mean value in both L1 and L2 conditions were categorized as having better performance in the language switching task (indicating better language control) compared with the ones with switch costs more than the mean value in both L1 and L2 (indicating poorer language control). To make sure that these two groups were statistically different from each other, we used a one-way MANOVA (group with switch costs less than the mean value in both L1 and L2 vs.

group with switch costs more than the mean value in both L1 and L2) and a significance threshold of p < 0.05.

2.3.2 Pre-processing of resting state images

Resting state images were processed using FSL software Version 5.0.10 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components) Version 3.15, was used for pre-processing. The following pre-statistics processing was applied: motion correction using MCFLIRT (Jenkinson et al., 2002), non-brain removal using BET (Smith, 2002), spatial smoothing using a Gaussian kernel of FWHM 5 mm, grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = $50.0 \,\mathrm{s}$). The functional images were registered to MNI-152 standard space (T1-standard brain averaged over 152 subjects; Montreal Neurological Institute, Montreal, QC, Canada) using a three-step registration from functional to high-resolution images, which were registered to T1-weighted structural images, and then registered to the standard space of the MNI template. Registration was carried out using FLIRT (Jenkinson and Smith, 2001, Jenkinson et al., 2002).

2.3.3 Functional connectivity analyses

Multi-session temporal concatenation with 70 independent components (high dimensional ICA) and variance normalization was used to carry out group ICA as implemented in MELODIC Version 3.15, using FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) Version 5.010. Multi-session temporal concatenation performs a single ICA run on the concatenated data matrix to estimate group-level independent components in RSNs. Ten ICs were identified as anatomically and functionally classical RSNs of interest. We overlaid IC maps onto previously defined resting-state network templates (Smith et al., 2009; Laird et al., 2011) and we selected IC maps with the highest overlap for subsequent analyses. The rest of the ICs belonging to other networks or with majority of voxels in white matter, ventricular space, and outside of the brain were discarded.

The analysis for the individual differences in language control between groups was carried out using FSL dual regression technique that provides voxel-wise comparisons of the resting-state fMRI (Littow et al., 2010). First, for each participant, the group-average set of spatial maps was regressed (as spatial regressors in a multiple regression) into the participant's 4D space-time dataset. This resulted in a set of participantspecific time series, one per group-level spatial map. Next, those time series were regressed (as temporal regressors, again in a multiple regression) into the same 4D dataset, resulting in a set of participantspecific spatial maps, one per group-level spatial map (Filippini et al., 2009). We performed dual regression analysis with variance normalization. In order to correct data thresholded for p < 0.05 (Nichols & Holmes, 2002) and to test statistically significant voxel-wise differences between groups via threshold-free cluster enhancement(TFCE), and to correct for multiple comparisons across IC maps, the FSL randomize tool with 5,000 permutations (Filippini, et al., 2009) was used. In accordance with Reineberg et al. (2015), the permutation testing procedure was done for each set of participant-specific RSNs (one for each group-level RSN of interest).

2.4 Results

2.4.1 Behavioral data

Data from 48 healthy volunteers were analyzed (see Table 2.2). Repeated-measures ANOVA showed main effects for both context (switch & non-switch) $F_{1,47} = 76.3$, p < 0.0001 and language (L1 & L2) $F_{1,47} = 49.9$, p < 0.0001 with no interaction between these two factors $F_{1,47} = 3.1$, p < 0.085, indicating symmetrical switch costs and that the language switching task produced significant switch costs (RT switch – RT non-switch) in both L1 (Dutch) $t_{47} = 5.8$, p < 0.0001, and in L2 (English) $t_{47} = 8.7$, p < 0.0001.

Table 2.2 Summary of the behavioral data

Switching context	Mean RT (ms)	SD
Switch trials		
L1 to L2	764.14	112.88
L2 to L1	794.15	126.64
Non-Switch trials		
L1 to L1	747.22	110.68
L2 to L2	701.87	99.87
Switch cost in L1 condition	46.93	55.85
Switch cost in L2 condition	62.27	49.51

Note. The behavioral data regards the reaction time (RT) in performing language switching task in both L1 and L2.

Because there is no interaction between the factors language and context, there is no possibility that the difference in participants' reaction times (RTs) between non-switch trials and switch trials in either the weaker language (English/L2) or the stronger language (Dutch/L1) is influenced differently by the context. Furthermore, since we had matched RT (mean), H statistics, the number of letters and syllables, initial fricative, word frequency and morphological complexity across stimuli in L1 and L2, it is not possible that because of more difficult or easier stimuli, naming a picture in one language might have benefited or suffered more than naming a picture in the other language.

According to Table 2.2, in this language switching task L1 is slower than L2 in both switch and non-switch trials. Previous studies also reported such behavioral results (Christoffels et al. 2007; Costa & Santesteban, 2004; Gollan & Ferreira, 2009; Verhoef et al., 2009) and this is probably as a result of suppressing the stronger language more in a

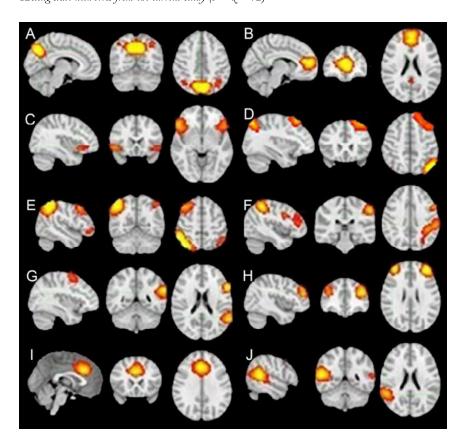
language switching context - which makes its retrieval also more effortful - in order for the bilinguals to speak in the weaker language (for more details, see Green, 1998).

In order to investigate how individual differences in cognitive control of language are influenced by the functional connectivity of the resting state networks involved in cognitive control we averaged the switch costs across L1 and across L2, separately. Participants with switch costs less than the mean value in both L1 and L2 conditions were categorized as having better performance in the language switching task, indicating better language control (mean age 20.25), and participants with switch costs more than the mean value in both L1 and L2 were categorized as having poorer performance in this task, indicating poorer language control (mean age 22.17). Processing the data based on grouping participants via a oneway MANOVA (group with switch costs less than the mean value in both L1 and L2 vs. group with switch costs more than the mean value in both L1 and L2) showed that there was a statistically significant difference between these two groups ($F_{2,21} = 29.97$, p < 0.0001; Wilks' Lambda = 0.26; partial eta squared = 0.74); in addition, considering the results for the dependent variables separately, a Bonferroni-adjusted alpha level of 0.025 showed that in both L1 switch cost ($F_{1,22} = 54.06$, p < 0.0001, partial eta squared = 0.71) and L2 switch cost ($F_{1,22}$ = 33.26, p < 0.0001, partial eta squared = 0.6) these two groups were also statistically different.

2.4.2 Independent components analysis

Ten RSN related IC maps of interest, namely, the DMN, the SN, and the FPN were identified in all participants (see Fig. 2.1). To identify these maps we overlaid the IC maps onto the previously defined resting state network templates (Smith et al., 2009; Laird et al., 2011) and we selected the IC maps with the highest overlap for subsequent analyses using fslcc. The rest of the ICs with majority of voxels in the white matter, in the ventricular space, and outside of the brain were discarded.

Figure 2.1 Resting state networks from the current study (5 < z < 12)



Note. Location (Z-COG) of the resting state networks: (A) IC 14 (8, -64, 44), (B) IC 18 (8, 46, 22), (C) IC 30 (37, 20, -6), (D) IC 1 (-35, 25, 48), (E) IC 5 (48, -57, 55), (F) IC 8 (-42, -30, 39), (G) IC 13 (-37, -50, 21), (H) IC 35 (42, 38, 26), (I) IC 42 (-1, 23, 32), (J) IC 63 (54, -49, 23). In this figure, the right side of the brain is on the left side of the images.

According to Laird et al. (2017), the FPN is composed of many constituent sub-networks by having high level of fractionation on the right side and medium level of fractionation on the left side, due to inter-lobal communication within this network. In this study, we also report such fractionation and sub-networks in the FPN - which includes the anterior prefrontal, the dorsolateral prefrontal, the dorsomedial superior frontal/anterior cingulate, the inferior parietal lobule, and the anterior insular cortex (Vincent et al., 2008) - with respect to IC 1 (the left inferior parietal lobule, and the superior frontal gyrus), IC 5 (mostly covering the right part of the FPN), IC 8 (the middle frontal gyrus, and the left inferior parietal lobule), IC 13 (the inferior frontal gyrus, the middle frontal gyrus, and the left inferior parietal lobule), IC 35 (the dorsolateral prefrontal cortex), IC 42 (the cingulate gyrus, anterior division), IC 63 (the inferior parietal lobule). We also report the DMN in terms of the anterior DMN (IC 18) and the posterior DMN (IC 14). IC 30 pertains to the SN.

2.4.3 Dual regression

We investigated between-group differences in the voxel-wise spatial distribution of the functional connectivity maps on ten ICs. Between-group differences were revealed in two ICs, namely, IC 35 and IC 63 due to their different functional connectivity between groups. In group with better performance in language task switching, there was increased coupling of the left primary somatosensory cortex (BA1) with IC 35, a subcomponent of the FPN including dorsolateral prefrontal cortex (DLPC).

Table 2.3 Dual regression summary

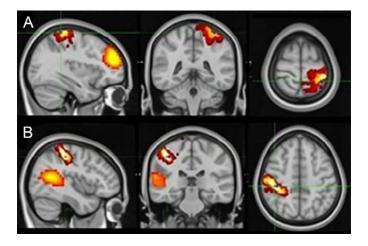
Network	IC	Voxels	Coordinates	P value (corrected)
Subcomponent of FPN (dorsolateral prefrontal cortex)	35	3569	-34,-42,68	0.0134
Subcomponent of FPN (Inferior parietal cortex)	63	5751	42,-30,48	0.0176

Note. This summary provides further specifications about IC 35 (DLPC) and IC 63 (inferior parietal cortex) that characterize between group differences with regard to the shape of these two ICs.

In group with poorer performance in the language switching, there was increased coupling of the right primary somatosensory cortex (BA2) with IC 63, a subcomponent of the FPN including the inferior parietal cortex (see Fig. 2.2 and Table 2.3).

Figure 2.2

Results of the dual regression analyses



Note. These results reveal between-group differences in the shape of IC 35 (DLPC) and IC 63 (inferior parietal cortex). In panel A between-group difference – group with better performance in language control > group with poor performance in language control – is overlaid on (left) BA1 and then overlaid on IC 35. In panel B between-group difference – group with poor performance in language control > group with better performance in language control – is overlaid on (right) BA2 and then overlaid on IC 63.

2.5 Discussion

In this study, we investigated how individual differences in language control are influenced by the functional connectivity of the resting state networks involved in cognitive control, given the fact that brain regions that fluctuate together to do a particular task, also work together during

the resting state functional connectivity (Cole et al., 2014; Smith et al., 2009). Moreover, the intrinsic network architecture which is present across brain regions has strong associations with brain's functional networks involved in performing a task (Fox & Raichle, 2007; Vincent et al., 2007). We benefitted from the multiband EPI in which the sensitivity of BOLD acquisitions (Kundu et al., 2012), the spatial and/or temporal resolution (Chen et al., 2015) and the sensitivity of detecting brain functional connectivity (Liao et al., 2013; Preibisch et al., 2015) are increased.

For our research purpose, we used a language switching task outside the scanner room, in which language engagement and disengagement, e.g. switching to L1 and switching to L2 is a key factor. We divided the participants into two groups based on their L1 and L2 switch costs. Better language control is characterized with better performance in language switching task and poorer language control is associated with higher switch costs in this task. In this study, we focused on three resting state networks of interest namely the FPN, the SN and the DMN as the networks which are related to cognitive control (Seeley et al., 2007; Smith et al., 2009; Vincent et al., 2008). Language control engages areas involved in cognitive control, and also similar mechanisms are reported to be at work in both language control and cognitive control (Abutalebi & Green, 2007; Branzi et al., 2016).

Regarding the relation of the resting-state networks of interest in the current research with functions which require cognitive control, the FPN has an important role in meeting task demands involved in cognitive control (Cole et al., 2013; Spreng et al., 2013) and the SN has repeatedly been reported to be active in different aspects of cognitive control, such as working memory and task switching (Dosenbach et al., 2007; Luks et al., 2002; Owen et al., 2005). Besides, the DMN modulates cognitive control by reducing the strength of the functional connectivity within nodes of this network when the brain is busy with different functions requiring cognitive control (Dang et al., 2013). In total, we detected ten ICs maps of interest related to the FPN, the SN and the DMN and we carried out FSL dual regression technique that provides voxel-wise

comparisons of the resting state fMRI (Littow et al., 2010) to investigate the association between better and poorer language control with the patterns of the functional connectivity of the resting state networks of interest.

In our study, we observed the increased coupling of the left primary somatosensory cortex (BA1) with IC 35, a subcomponent of the FPN including DLPC in the group with better performance in the language switching task. Moreover, we detected the increased coupling of the right primary somatosensory cortex (BA2) with IC 63, a subcomponent of the FPN including the inferior parietal cortex in the group with poorer performance in this task.

Investigating the brain resting state functional connectivity related to the functions requiring cognitive control in healthy participants has not been widely reported in the literature and among the few reported studies we found the one by Reineberg et al. (2015) more relevant to our study. They investigated how resting state networks reveal individual differences in both common and specific aspects of cognitive control such as response inhibition, task set shifting and working memory updating. Based on this study, it is reported that individuals with better task performance involving cognitive control may have more expanded resting state networks, with regard to the FPN. In fact, having better performance in functions that require cognitive control is characterized with the FPN being more extended due to the connectivity with the nodes in particular with somatosensory regions (Tabassi Mofrad & Schiller, 2019). The FPN has an important role in meeting task demands involved in cognitive control (Cole et al., 2013; Spreng et al., 2013); thus, better task performance in functions requiring cognitive control is directly reflected by the patterns of the functional connectivity of this network at rest. This is of course in accordance with the previously stated idea that the intrinsic network architecture which is present across brain regions has strong associations with the brain's functional network involved in performing a task (Fox & Raichle, 2007; Vincent et al., 2007).

Results from the current research with respect to the functional connectivity of the FPN in the groups with better and poorer performance

in language switching task to some extent replicate the results from Reineberg et al. (2015). Better performance in the language switching task, indicative of better language control, is associated with the coupling of the FPN with the somatosensory cortex at rest, and the somatosensory regions are involved in stimulus-response mappings when performing a task. Therefore, the increased coupling of the FPN at rest with the regions involved in stimulus-response mapping in individuals with better performance in the language switching task is indicative of better linking the stimuli and the response when doing the task. However, what the current study adds to the previous literature is that connectivity patters of the left somatosensory cortex, but not the right side of this part of the cortex is associated with better task performance in language switching. In fact, we demonstrated that the primary somatosensory cortex has a dual function in coupling with the FPN. We further elaborated that the (left) BA1 and the (right) BA2 couple with different parts of this network, the DLPFC and the IPC, respectively, to characterize individual differences in cognitive control of language. That is, the increased coupling of the left primary somatosensory cortex (BA1) with the DLPC is associated with better language control and the increased coupling of the right primary somatosensory cortex (BA2) with the IPC is linked with poorer language control in healthy bilingual participants.

With regard to studies on human motor cortex, it is emphasized that this part of the brain plays an important role in mental rotation (Cona et al., 2017; Tomasino et al., 2005), and in fact it is the left side of the motor cortex that controls mental rotation in right-handed individuals (Tomasino et al., 2005). As somatosensory cortex converges to the motor cortex circuitry (for a review see Hooks, 2017), and in our study only righthanded volunteers participated, so the left somatosensory cortex appears to be linked to cognitive control or language switching, as if one is manually switching between languages. Thus, it seems that participants, with better performance in language switching task, use the left motor cortex circuitry in a network fashion to switch between languages; However, the involvement of the right sensorimotor cortex in participants

with poorer performance in language task switching is indicative of less efficiently connected regions involved in motor cortex circuitry.

Regarding the parietal regions as well as DLPFC, which are parts of the FPN, the activities of these parts of the cortex in some functions requiring cognitive control, in particular in task switching have already been reported in the literature (Collette et al., 2005; Derrfuss et al., 2005; Esterman et al., 2009; Tabassi Mofrad & Schiller, 2019; Tabassi Mofrad & Schiller, 2020; Wager et al., 2004). Based on our research results, we suggest that BA1 and BA2 in the right and left part of this cortex, with regard to their patterns of the functional connectivity with the FPN at rest, seem to have other secondary connectivity outside of the control network. However, further research is needed to investigate how the primary somatosensory cortex adopts different functions in BA1 and BA2 in the right and left part of this brain area, in particular, with regard to the stimulus-response mapping as coupling these regions within the somatosensory cortex with the DLPFC and the IPC, in our study, has characterized better and poorer language control in individuals.

In this study, by dividing participants into two groups, we investigated whether individual differences in language control are influenced by the functional connectivity of the resting state networks involved in cognitive control, but we could not match these two groups with regard to their IQ as this variable was not part of the including criteria in participant recruitment. We suggest that in future research participants' IQ be also considered as an including criteria to see how this might influence task takers language control behavior. Besides, in this study we did not have access to MRI compatible microphone, thus participants did the language switching task also outside the scanner. This would count as a limitation in our study.

As mentioned earlier in this discussion, in language control - marked with language engagement and disengagement (Abutalebi & Green, 2008; Kroll et al., 2006) - and in cognitive control similar brain areas are at work (Abutalebi & Green, 2007; Branzi et al., 2016). Therefore, the results of this study will have broader implications especially for clinical neuroscience in bilingual populations. Autism spectrum disorder,

attention deficit hyperactivity disorder, and obsessive-compulsive disorder are all characterized by dysfunction in cognitive control (Corbett et al., 2009; Sergeant et al., 2002; Willcutt et al., 2005; Zandt et al., 2009). However, research into the neurobiology of cognitive control deficits is not well reported in the literature. By addressing what characterizes individual differences in cognitive control of language in healthy bilingual participants in terms of the functional connectivity of the brain networks related to cognitive control at rest, the current study provides a possible model for future research and may serve as a reference in clinical neuroscience when bilinguals are diagnosed with the above-mentioned disorders.

References

- Abutalebi, J., & Green, D.W. (2007). Bilingual language production: The neurocognition of language representation and control. *Journal of* Neurolinguistics, 20, 242-275.
- Abutalebi, J., & Green, D.W. (2008). Control mechanisms in bilingual language production: Neural evidence from language switching studies. Language and Cognitive Processes, 23(4), 557-582.
- Beckmann, C. F., DeLuca, M., Devlin, J. T., & Smith, S. M. (2005). Investigations into resting-state connectivity using independent component analysis. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 360(1457), 1001–1013.
- Beckmann, C.F., & Smith, S.M. (2004). Probabilistic independent component analysis for functional magnetic resonance imaging. IEEE Transactions on Medical Imaging, 23, 137-152.
- Boubela, R.N., Kalcher, K., Huf, W., Kronnerwetter, C., Filzmoser, P., & Moser, E. (2013). Beyond noise: using temporal ICA to extract meaningful information from high-frequency fMRI signal fluctuations during rest. Frontiers in Neuroscience, 7, 168.
- Boyacioglu, R., Schulz, J., Muller, N.C., Koopmans, P.J., Barth, M., & Norris, D.G. (2014). Whole brain, high resolution multiband spinecho EPI fMRI at 7 T: a comparison with gradient-echo EPI using a color-word Stroop task. NeuroImage, 97, 142-50.
- Branzi, F.M., Della Rosa, P.A., Canini, M., Costa, A., & Abutalebi, J. (2016). Language Control in Bilinguals: Monitoring and Response Selection. Cerebral Cortex, 26, 2367–2380.
- Byers-Heinlein, K., Esposito, A. G., Winsler, A., Marian, V., Castro, D. C., & Luk, G. (2019). The Case for Measuring and Reporting Bilingualism in Developmental Research. Collabra. Psychology, 5(1), 37.
- Chen, L., Vu, A.T., Xu, J., Ugurbil, M.K., Yacoub, E., & Feinberg, D.A. (2015). Evaluation of highly accelerated simultaneous

- multi-slice EPI for fMRI. NeuroImage, 104, 452-459.
- Christoffels, I. K., Firk, C., & Schiller, N. O. (2007). Bilingual language control: an event-related brain potential study. Brain Research, 1147, 192-208.
- Cole, M. W., Bassett, D. S., Power, J. D., Braver, T. S., & Petersen, S. E. (2014). Intrinsic and task-evoked network architectures of the human brain. Neuron, 83(1), 238-251.
- Cole, M. W., Reynolds, J. R., Power, J. D., Repovs, G., Anticevic, A., & Braver, T. S. (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. Nature Neuroscience, 16(9), 1348–1355.
- Collette, F., Van der Linden, M., Laureys, S., Delfiore, G., Degueldre, C., Luxen, A., & Salmon, E. (2005). Exploring the unity and diversity of the neural substrates of executive functioning. Human Brain Mapping, 25(4), 409-423.
- Cona, G., Marino, G., & Semenza, C. (2017). TMS of supplementary motor area (SMA) facilitates mental rotation performance: Evidence for sequence processing in SMA. NeuroImage, 146, 770-
- Corbett, B. A., Constantine, L. J., Hendren, R., Rocke, D., & Ozonoff, S. (2009). Examining executive functioning in children with autism spectrum disorder, attention deficit hyperactivity disorder and typical development. Psychiatry Research, 166(2-3), 210-222.
- Crone, E. A., Ridderinkhof, K. R., Worm, M., Somsen, R. J., & Van Der Molen, M. W. (2004). Switching between spatial stimulus-response mappings: developmental study cognitive flexibility. Developmental Science, 7(4), 443–455.
- Dang, L. C., O'Neil, J. P., & Jagust, W. J. (2013). Genetic effects on behavior are mediated by neurotransmitters and large-scale neural networks. NeuroImage, 66, 203-214.
- Derrfuss, J., Brass, M., Neumann, J., & von Cramon, D. Y. (2005). Involvement of the inferior frontal junction in cognitive control: meta-analyses of switching and Stroop studies. Human Brain Mapping, 25(1), 22-34.

- Dosenbach, N. U. F., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A., et al. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 11073–11078.
- Douw, L., Wakeman, D. G., Tanaka, N., Liu, H., & Stufflebeam, S. M. (2016). State-dependent variability of dynamic functional connectivity between frontoparietal and default networks relates to cognitive flexibility. *Neuroscience*, 339, 12–21.
- Esterman, M., Chiu, Y. C., Tamber-Rosenau, B. J., & Yantis, S. (2009). Decoding cognitive control in human parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 106(42), 17974-17979.
- Fair, D. A., Schlaggar, B. L., Cohen, A. L., Miezin, F. M., Dosenbach, N. U., Wenger, K. K., Fox, M. D., Snyder, A. Z., Raichle, M. E., & Petersen, S. E. (2007). A method for using blocked and event-related fMRI data to study "resting state" functional connectivity. *NeuroImage*, 35(1), 396-405.
- Filippini, N., MacIntosh, B. J., Hough, M. G., Goodwin, G. M., Frisoni, G. B., Smith, S. M., Matthews, P. M., Beckmann, C. F., & Mackay, C. E. (2009). Distinct patterns of brain activity in young carriers of the APOE-epsilon4 allele. *Proceedings of the National Academy of Sciences of the United States of America*, 106(17), 7209–7214.
- Fox, M. D., & Raichle, M. E. (2007). Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nature Reviews Neuroscience*, 8(9), 700–711.
- Grady, C. L., Luk, G., Craik, F. I., & Bialystok, E. (2015). Brain network activity in monolingual and bilingual older adults. *Neuropsychologia*, 66, 170–181.
- Green, D.W. (1998). Mental control of the bilingual lexico-semantic system. *Bilingualism: Language and Cognition*, 1, 67–81.
- Green, D. W., & Abutalebi, J. (2013). Language control in bilinguals: The adaptive control hypothesis. *Journal of Cognitive Psychology*, 25(5), 515–530.

- Hooks B. M. (2017). Sensorimotor Convergence in Circuitry of the Motor Cortex. The Neuroscientist, 23(3), 251–263.
- Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. NeuroImage, 17(2), 825-841.
- Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. Medical Image Analysis, 5(2), 143–156.
- Kroll, J. F., Bobb, S.C., Wodniecka, Z. (2006). Language selectivity is the exception, not the rule: Arguments against a fixed locus of language selection in bilingual speech. Bilingualism: Language and Cognition, 9(2), 119-135.
- Kundu, P., Inati, S. J., Evans, J. W., Luh, W. M., & Bandettini, P. A. (2012). Differentiating BOLD and non-BOLD signals in fMRI time series using multi-echo EPI. NeuroImage, 60(3), 1759-1770.
- Liao, X. H., Xia, M. R., Xu, T., Dai, Z. J., Cao, X. Y., Niu, H. J., Zuo, X. N., Zang, Y. F., & He, Y. (2013). Functional brain hubs and their test-retest reliability: a multiband resting-state functional MRI study. NeuroImage, 83, 969-982.
- Laird, A. R., Fox, P. M., Eickhoff, S. B., Turner, J. A., Ray, K. L., McKay, D. R., Glahn, D. C., Beckmann, C. F., Smith, S. M., & Fox, P. T. (2011). Behavioral interpretations of intrinsic connectivity networks. Journal of Cognitive Neuroscience, 23(12), 4022–4037.
- Laird, A. R., Riedel, M. C., Okoe, M., Jianu, R., Ray, K. L., Eickhoff, S. B., Smith, S. M., Fox, P. T., & Sutherland, M. T. (2017). Heterogeneous fractionation profiles of meta-analytic coactivation networks. NeuroImage, 149, 424-435.
- Littow, H., Elseoud, A. A., Haapea, M., Isohanni, M., Moilanen, I., Mankinen, K., Nikkinen, J., Rahko, J., Rantala, H., Remes, J., Starck, T., Tervonen, O., Veijola, J., Beckmann, C., & Kiviniemi, V. J. (2010). Age-Related Differences in Functional Nodes of the Brain Cortex - A High Model Order Group ICA Study. Frontiers in Systems Neuroscience, 4, 32.

- Luk, G., Green, D. W., Abutalebi, J., & Grady, C. (2011). Cognitive control for language switching in bilinguals: A quantitative metaanalysis of functional neuroimaging studies. Language and Cognitive Processes, 27(10), 1479-1488.
- Luks, T. L., Simpson, G. V., Feiwell, R. J., & Miller, W. L. (2002). Evidence for anterior cingulate cortex involvement in monitoring preparatory attentional set. NeuroImage, 17(2), 792-802.
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: a primer with examples. Human Brain Mapping, 15(1), 1–25.
- Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). Nback working memory paradigm: a meta-analysis of normative functional neuroimaging studies. Human Brain Mapping, 25(1), 46-59.
- Preibisch, C., Castrillón G, J. G., Bührer, M., & Riedl, V. (2015). Evaluation of Multiband EPI Acquisitions for Resting State fMRI. PLoS One, 10(9), e0136961.
- Reineberg, A. E., Andrews-Hanna, J. R., Depue, B. E., Friedman, N. P., & Banich, M. T. (2015). Resting-state networks predict individual differences in common and specific aspects of executive function. NeuroImage, 104, 69-78.
- Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. The Journal of Neuroscience, 27(9), 2349–2356.
- Smith S. M. (2002). Fast robust automated brain extraction. Human Brain Mapping, 17(3), 143–155.
- Sergeant, J. A., Geurts, H., & Oosterlaan, J. (2002). How specific is a deficit of executive functioning for attention-deficit/hyperactivity disorder? Behavioural Brain Research, 130(1-2), 3-28.
- Smith, S.M., Fox, P.T., Miller, K.L., Glahn, D.C., Fox, P.M., Mackay, C.E., Filippini, N., Watkins, K.E., Toro, R., Laird, A.R., & Beckmann, C.F. (2009) Correspondence of the brain's functional architecture

- during activation and rest. Proceedings of the National Academy of Sciences of the United States of America, 106, 13040-13045.
- Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. Journal of Cognitive Neuroscience, 21(3), 489–510.
- Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. Journal of Cognitive Neuroscience, 25(1), 74–86.
- Tabassi Mofrad, F., & Schiller, N.O. (2019, February). Resting connectivity patterns between somatosensory cortex and frontoparietal network predict individual differences in language control. Poster presented at LIBC Day, Leiden, The Netherlands.
- Tabassi Mofrad, F., & Schiller, N. O. (2020). Cognitive demand modulates connectivity patterns of rostral inferior parietal cortex in cognitive control of language. Cognitive Neuroscience, 11(4), 181–193.
- Tomasino, B., Borroni, P., Isaja, A., & Rumiati, R. I. (2005). The role of the primary motor cortex in mental rotation: a TMS study. Cognitive Neuropsychology, 22(3), 348-363.
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. Journal of Neurophysiology, 100(6), 3328-3342.
- Vincent, J.L., Patel, G.H., Fox, M.D., Snyder, A.Z., Baker, J.T., Van Essen, D.C., Zempel, J.M., Snyder, L.H., Corbetta, M., & Raichle, M.E. (2007). Intrinsic functional architecture in the anaesthetized monkey brain. Nature, 447, 83-86.
- Wager, T. D., Jonides, J., & Reading, S. (2004). Neuroimaging studies of shifting attention: a meta-analysis. NeuroImage, 22(4), 1679-1693.
- Willcutt, E. G., Doyle, A. E., Nigg, J. T., Faraone, S. V., & Pennington, B. F. (2005). Validity of the executive function theory of attentiondeficit/hyperactivity disorder: a meta-analytic review. Biological Psychiatry, 57(11), 1336-1346.

Zandt, F., Prior, M., & Kyrios, M. (2009). Similarities and differences between children and adolescents with autism spectrum disorder and those with obsessive compulsive disorder: executive functioning and repetitive behaviour. Autism, 13(1), 43–57.