# 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 3

# Cognitive demand modulates connectivity patterns of rostral inferior parietal cortex in cognitive control of language

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## Abstract

The inferior parietal cortex (IPC) is involved in different cognitive functions including language. In line with the correlated transmitter receptor-based organization of the IPC, this part of the brain is parcellated into the rostral, the middle and the caudal clusters; however, the tripartite organization of the IPC has not been addressed in studies with a focus on cognitive control of language. Using multiband EPI, in this study we investigated how the rostral IPC contributes to this executive function in bilinguals. In doing so, we focused on the functional connectivity patterns of this part of the cortex with other brain areas in a context characterized with language engagement and disengagement that recruits the neural mechanisms of cognitive control. We found that in switching to L2, which was cognitively less demanding, the right rostral IPC had positive functional connectivity with the anterior division of the cingulate gyrus and the precentral gyrus. However, in switching to L1, which was cognitively more demanding, the right IPC rostral cluster had negative functional coupling with the postcentral gyrus and the precuneus cortex and positive connectivity with the posterior lobe of the cerebellum. In this condition, the left IPC rostral cluster had negative functional coupling with the superior frontal gyrus and the precuneus cortex. Thus, the connectivity patterns of the rostral IPC was influenced by the cognitive demand in an asymmetrical and lateral manner during cognitive control of language.

## 3.1 Introduction

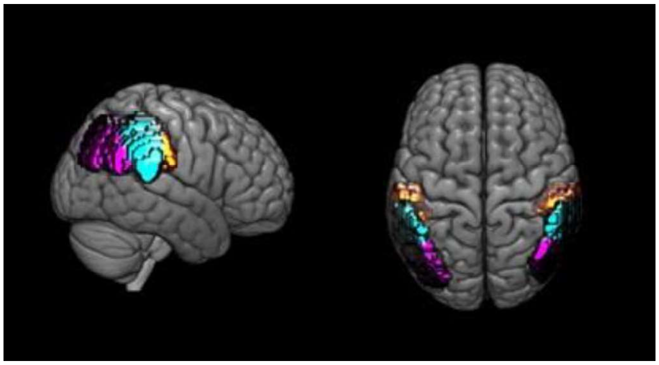
Cognitive control of language refers to the cognitive mechanisms that enable bilinguals to avoid interference from a non-target language when they utter a word in an intended language (Abutalebi & Green, 2007; Green & Abutalebi, 2013). Engaging brain areas involved in general aspects of cognitive control (Abutalebi & Green, 2007; Branzi, Della Rosa, Canini, Costa, & Abutalebi, 2016), cognitive control of language is characterized with language engagement and disengagement, to switch to another language and to stop speaking in one language accordingly (Abutalebi & Green, 2008; Kroll, Bobb, & Wodniecka, 2006). With regard to cognitive control of language, the inferior parietal cortex (IPC) is associated with a response selection system and its function is dependent upon the amount of inhibition which is needed, e.g., to avoid L1 (first language) lexical items when L2 (second language) lexical items are produced (Branzi et al., 2016). Such a function of the IPC in language task switching paradigms is mostly highlighted with regard to updating, shifting and inhibition, in particular (Abutalebi & Green, 2008; Price, Green, & von Studnitz, 1999; Sohn et al., 2000; Wager, Jonides, & Reading, 2004).

Thus far, only as a whole and irrespective of its tripartite organization, the IPC has been addressed either with regard to cognitive functions in broader terms - e.g., attention (Corbetta, Patel, & Shulman, 2008; Tomasi & Volkow, 2011), action-related functions (Caspers, Zilles, Laird, & Eickhoff, 2010; Keysers & Gazzola, 2009), self-perception (Ionta et al., 2011), memory (Martinelli, Sperduti, & Piolino, 2013), and social cognition (Molenberghs, Johnson, Henry, & Mattingley, 2016; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014) - or with a focus on cognitive control of language (Abutalebi & Green, 2007, 2008; Branzi et al., 2016).

With respect to structural parcellation of the human IPC, seven cytoarchitectonical areas are defined in this brain region, namely, PFt, PFop, PF, PFm, PFcm, PGa, and PGp, suggestive of functional differentiation in the IPC (Caspers et al., 2006, 2008). Based on the idea that characteristics of these cytoarchitectonically segregated brain regions should be reflected by receptor architectonics, Caspers et al. (2013) measured the density of fifteen different receptors in each part of the IPC and reported that with regard to a correlated transmitter receptor-based organization, this brain region consists of three clusters, that is, a rostral cluster covering areas PFop, PFt, PFcm, a middle cluster covering areas PF and PFm, and a caudal cluster covering areas PGa and PGp. Ruschel et al. (2014), in addition, via diffusion-weighted magnetic resonance imaging combined with probabilistic tractography, investigated the connectivity patterns of the human IPC, in order to parcellate this brain region. In line with parcellation of the IPC into rostral, middle and caudal clusters, based on a correlated transmitter receptor-based organization (Caspers et al., 2013), they also reported three subareas in the IPC akin to the above-mentioned clusters (see Figure 3.1).

**Figure 3.1**

*Lateral right and dorsal view of the IPC division to the rostral (yellow-red), the middle (cyan), and the caudal (violet) clusters*



The white matter connectivity as well as functional properties of the IPC is reported to be reflected by its structural division into cytoarchitectonically different areas (Caspers et al., 2013; Corbetta et al., 2008; Keysers & Gazzola, 2009). According to Caspers et al. (2011), the fiber tracks between subareas of the IPC and other brain areas do not show the same characteristics; while the caudal IPC has strong connections with the posterior parietal, the higher visual and temporal areas, the rostral IPC is more connected with the inferior frontal, motor, premotor, and somatosensory areas. The connectivity patterns of the middle IPC, however, show similarities with those of both caudal and rostral IPC, with major connections with the frontal, superior parietal, and intraparietal areas. In addition, some other earlier studies using Diffusion Tensor Imaging (DTI) had already pointed to such tripartition of the cortex in the IPC (Rushworth, Behrens, & Johansen-Berg, 2006; Tomassini et al., 2007).

Functional properties of the IPC confirm the tripartition of this part of the cortex. Shalom and Poeppel (2008) proposed that different aspects of language are processed in each of the three subareas of the IPC. According to this study, the caudal IPC areas process semantic content of words or sentences, while the rostral IPC areas are involved in sound and single phoneme processing. The middle IPC areas, in addition, process the underlying rules to assemble basic language components. The tripartite organization of IPC with respect to the functional properties of this part of cortex is not limited to language-related tasks; with regard to some other earlier studies, the middle IPC areas are involved in processing spatial or non-spatial attention tasks (Boorman, Behrens, Woolrich, & Rushworth, 2009; Caspers et al., 2011; Corbetta et al., 2008), and the caudal IPC areas are activated during moral decision making (for a review see Raine & Yang, 2006). The rostral IPC, however, seems to contribute to storing abstract somatosensory information (Binder et al., 2009). This part of the cortex is also activated during action observation and imitation (Caspers et al., 2010).

The reflection of functional properties of the IPC by its structural subdivisions, in particular in language-related tasks, also provides the rationale to focus on a network analysis approach in bilingual imaging studies with regard to the rostral, the middle and the caudal areas of this part of the cortex. Such an approach paves the way to map the functional connectivity of the IPC subdivisions, involved in bilingual cognitive control – as IPC is an important part of the language control network, mostly functioning in response selection in the face of a conflict (Abutalebi et al., 2013; Green & Abutalebi, 2013; Reverberi et al., 2015) – which thus far has not been addressed in the literature. Therefore, to address this gap in the related state-of-the-art research, we investigated the functional connectivity of the rostral, the middle and the caudal clusters of the IPC with regard to this executive function in bilinguals in a context characterized with language engagement and disengagement. However, delineating the connectivity profiles of all three subareas of the IPC with regard to cognitive control of language is far beyond the scope of this paper. This is because there is a massive amount of results from each part of the IPC and the related discussions for each part need detailed elaborations. Thus, we limited our report to the functional connectivity of the rostral IPC, and the way it is modulated by the task demand, defined in terms of switching to L1 and to L2.

The IPC, the presupplementary motor area (pre-SMA), the prefrontal, and the anterior cingulate cortices (Green & Abutalebi, 2013; Reverberi et al., 2015), in addition to the cerebellum are involved in language control network (Fabebro, Moretti, & Bava, 2000; Green & Abutalebi, 2013). This network supports language control operations, e.g., encoding, intending to use L1 and L2 languages, and resolving competition between languages (Reverberi et al., 2015). Regarding previous studies, the activation of brain areas involved in the language control network is more associated with L2 lexical production; L2 lexical production requires recruitment of more control processes in this network compared to L1 (Garbin et al., 2011; Reverberi et al., 2015); thus, as the IPC is part of the language control network and as L2 lexical production activates more brain areas in that network, our expectation was that in our language switching experiment, switching to L2 would involve stronger positive functional connectivity of the rostral IPC with other parts of the brain in language control network.

In this research, we have benefited from the multiband EPI technique, in which multiple slices are excited and acquired simultaneously. Such an imaging technique is associated with increased sensitivity of BOLD acquisitions (Kundu et al., 2012), the spatial and/or temporal resolution (Chen et al., 2015) and sensitivity in detecting brain functional connectivity (Liao et al., 2013; Preibisch, Castrillón, Bührer, & Riedl, 2015).

## 3.2 Methods

### 3.2.1 Participants

Fifty-two, healthy, right-handed students at Leiden University participated in this research. They were 18–27 years old and had normal or corrected-to-normal vision. Based on the information taken from a questionnaire about their language history, these participants were sequential Dutch-English bilinguals, who were not exposed to both Dutch and English from infancy – born to native Dutch parents – and started learning English in primary school. Participants also had regular contact with English because of their academic educations. We measured their English language proficiency by the quick placement test (University of Cambridge Local Examinations Syndicate 2001) (see Table 3.1).

Seven participants were later excluded from the research due to the excessive level of movements in the scanner. Participants gave their written informed consent prior to the experiment and they either were compensated with a small amount of money or received course credits for their participation in this study. The medical ethics committee of Leiden University Medical Center (LUMC) (Leiden, the Netherlands) approved the protocol of this experiment (NL61816.058.17).

**Table 3.1**

*Details of the participants included in the analysis*

| number of participants | male | female | average age | L2 level | means of measurement | mean score | SD |
|---|---|---|---|---|---|---|---|
| 45 | 11 | 34 | 21.7 | upper-inter | placement test | 44.17/60 | 2.23 |

### 3.2.2 Stimuli

Forty-eight pictures were selected from the International Picture Naming Project (IPNP- https://crl.ucsd.edu/experiments/ipnp/), based on the following variables in both Dutch and English languages: number of letters and syllables, RT (mean), H statistics which indicates response agreement by participants in naming a picture, initial fricative which indicates if a word starts with a consonant sound such as f or v especially since such words have longer naming latencies (see Bates et al., 2003) and word complexity (see Table 3.2 for a summary of each variable that the stimuli were matched on). We used both the CELEX lexical database and the database provided by IPNP as references for these variables, and we developed two sets of twenty-four stimuli (set A and set B), one set for each language (counterbalanced across participants) which were parallel in terms of all the above-mentioned variables in addition to word frequency, visual complexity and conceptual complexity (see Appendix 3.1 and Appendix 3.2 for further details). Visual complexity as the level of details in an image and conceptual complexity which refers to how many objects, animals or persons are depicted in each image (Snodgrass & Vanderwart, 1980) are the characteristics of images and are independent of a language; thus, these variables were not matched on L1 and L2 but on the two sets of twenty-four stimuli. These two sets were also parallel in terms of the number of cognates; there were nine cognates in each set. The reason that we did not use the same items in L1 and L2 was to avoid the influence of L1 naming on L2 naming and the other way around on the same items.

**Table 3.2**

*Summary of 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.

### 3.2.3 Procedure

The fMRI experiment included one run of 6 min and 46 s, in an event-related design, using 76 trials. During the experiment participants were required to carry out a language switching task, controlled by E-Prime Software, switching between Dutch (L1) and English (L2). There were two types of trials in four conditions; switch trials in which the cued language was different from the preceding trial (i.e. from Dutch to English or English to Dutch) and non-switch trials in which the language remained the same as the previous trial (i.e. Dutch to Dutch or English to English).

Each trial began with a visual cue for 250 ms, in the form of a red or blue frame (counterbalanced across participants) that preceded a picture and instructed participants which language to use to name the upcoming picture. It was then followed by a fixation cross for 500 ms and presentation of a picture for 2,010 ms.

Each trial ended with a jittered blank screen varying between 690 to 2,760 ms. Optseq program which schedules events in rapid-presentation event-related fMRI experiments was used to pseudo-randomize the order of pictures and to determine the length of each intertrial blank screen interval. In this experiment the switch rate was 50% and the maximum number of stay or switch trials in a row was four.

Before the fMRI data acquisition, participants underwent behavioral training. That included a) familiarization with pictures used in the experiment in which participants in two separate runs saw all pictures with their names one time in Dutch and one time in English, b) learning the association between the visual colored cue and the related language, c) familiarization with a task that was identical to the one used in the fMRI experiment in all respects, but not the target pictures. In order to avoid movement related artifacts, participants were instructed to name pictures with minimal jaw movement. After four weeks, participants attended a behavioral lab and performed the same task that they did inside the MRI scanner, and their responses were collected using an SRBOX. In line with previous research (e.g. Anderson et al., 2018; Grady, Luk, Craik, & Bialystok, 2015) we allowed a few weeks between the experiment in the scanner and the experiment in the behavioral lab to make sure that participants would not remember the stimuli from the first session. In the behavioral lab, E-Prime Software was used to control the presentation of pictures. We collected RTs in the behavioral lab and not in the scanner; however, to make sure that participants carry out the task in the scanner appropriately, they were told that their responses will be monitored by the researcher from the control room.

### 3.2.4 fMRI data acquisition

All data were acquired on a 3 Tesla Philips Achieva TX MRI scanner in Leiden University Medical Center, equipped with a SENSE-32 channel head coil. Prior to 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°, FOV = 250 x 195.83 × 170.5, 155 slices 1.1 × 1.1 × 1.1 mm. During the functional run, 555 T2*-weighted whole brain multiband gradient EPIs were acquired, including 6 dummy scans preceding each dynamic scan to allow for equilibration of T1 saturation effects. The scanning parameters regarding the functional run are as follows: TR = 690 ms, TE = 30 ms, multiband factor = 4, FA = 55°, FOV = 220 x 220 x 121, 44 slices 2.75 × 2.75 × 2.75 mm. A high quality BOLD screen 32, that was viewed through a mirror at the head and located at the end of the scanner, was used for visual stimulus presentation.

## 3.3 Data analysis

### 3.3.1 Behavioral data analysis

Behavioral data in terms of the reaction time (RT) in performing language switching task in both 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 the previous trial (i.e. Dutch to Dutch or English to English) were processed using SPSS software version 23. We used two (language: Dutch vs. English) by two (context: switch vs. non-switch) repeated-measures ANOVA with both subject and item factors – thus running two separate analyses – to see if both context and language would have a main effect with any possible interactions. In addition, we ran subsequent paired t-test to see if in a language switching task, switching to L1 and switching to L2 were significantly different.

### 3.3.2 Pre-processing of fMRI data

fMRI data were processed using FSL software version 5.0.10 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The following pre-statistics processing was applied: motion correction using MCFLIRT (Jenkinson, Bannister, Brady & Smith, 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 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 & Smith, 2001; Jenkinson et al., 2002).

### 3.3.3 Psychophysiological interaction (PPI) analysis

We did PPI analysis to examine the functional interaction between the IPC rostral cluster and the rest of the brain. Masks of the IPC rostral cluster right and left were made using the Jülich Histological Atlas. This atlas is implemented within FSLVIEW (www.fmrib.ox.ac.uk/fsl). The probabilistic maps of the right and the left IPC rostral clusters were binarised and thresholded at 50 percent. Then we transformed the masks into the functional space, projecting the ROI on the pre-processed functional images, and extracting the mean time series from the ROI using fslmeants. We did the PPI analyses for the IPC rostral cluster right and left separately using FEAT (FMRI Expert Analysis Tool) version 6.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The design matrix consisted of three regressors. The first regressor was the psychological variable, convolved with a double gamma hemodynamic response and the second regressor, the physiological variable, was the time series extracted from the ROI. The third regressor was the interaction between the psychological and physiological variables (PPI). In these analyses, we tested for significant linear increases and decreases in functional connectivity of the ROI with the rest of the brain during the language switching task with a focus on switch trials.

## 3.4 Results

### 3.4.1 Behavioral data

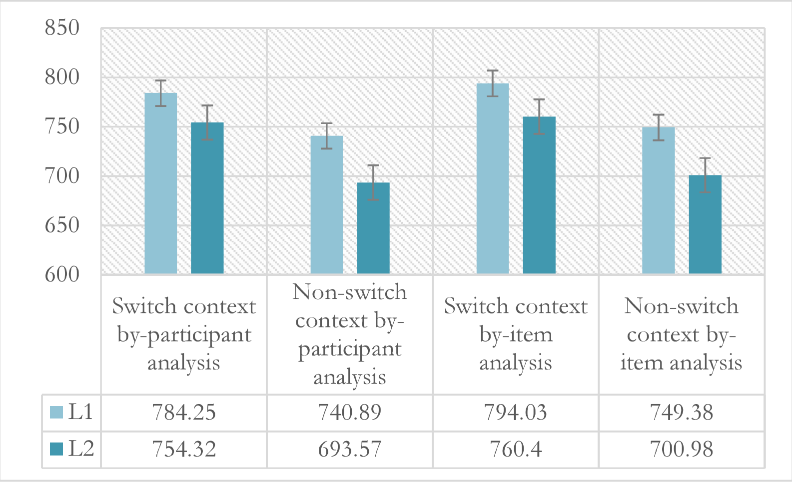
Data from 45 healthy volunteers were analyzed (see Fig. 3.2). Response latencies less than 350 ms and more than 1,500 ms were discarded. In total, the accuracy rate in doing this task - correct responses between 350 ms and 1,500 ms - was 93.8%. Repeated-measures ANOVA showed a significant main effect for context (switch & non-switch) in both by-participants analysis ($F1(1,44) = 75.63$, $P < 0.0001$, partial eta square = 0.63) and in by-item analysis ($F2(1,47) = 50.69$, $P < 0.0001$, partial eta square = 0.52). In the repeated-measures ANOVA the main effect of language (L1 & L2) was significant in both by-participant analysis ($F1(1,44) = 48.53$, $P < 0.0001$, partial eta square = 0.52) and in the by-item analysis ($F2(1,47) = 29.66$, $P < 0.0001$, partial eta square = 0.38). No interaction between language and context was observed ($F1(1,44) = 3.7$, $P = 0.061$, partial eta square = 0.07; $F2(1,47) = 1.18$, $P = 0.282$, partial eta square = 0.025), indicating symmetrical switch costs. These behavioral results are from the data collected four weeks after participants did the experiment inside the scanner.

As there is no interaction between the factors context and language, indicating symmetrical switch costs in Dutch and English, any possibility that the difference in participants' reaction times (RTs) between switch trials and non-switch trials in the stronger language (Dutch/L1) or the weaker language (English/L2) is differently influenced by the context can be ruled out. According to Fig. 3.2, the weaker language is quicker in both switch and non-switch trials. These results are in line with previous research (Christoffels, Firk & Schiller, 2007; Costa & Santesteban, 2004; Gollan & Ferreira, 2009; Verhoef, Roelofs, & Chwilla, 2009) and is presumably due to more suppression of the stronger language in language switching in order to speak in the weaker language - retrieving the more inhibited language is more effortful (for more details, see Green, 1998).

The subsequent paired *t*-test also showed that in the language switching task, switching to L1 was significantly slower than switching to L2 ($t1(44) = -3.859$, $P < 0.0001$; $t2(47) = -3.326$, $P < 0.002$). As number of letters and syllables, RT (mean), H statistics, initial fricative, morphological complexity, and word frequency were matched across stimuli in both languages, any possibility that a language might have suffered or benefited more than the other language due to more difficult or easier stimuli can also be ruled out.

**Figure 3.2**

*L1 and L2 RTs in millisecond in the switch and non-switch contexts in both the by-participants and the by-item analyses*



| | Switch context by-participant analysis | Non-switch context by-participant analysis | Switch context by-item analysis | Non-switch context by-item analysis |
|---|---|---|---|---|
| ■ L1 | 784.25 | 740.89 | 794.03 | 749.38 |
| ■ L2 | 754.32 | 693.57 | 760.4 | 700.98 |

*Note.* As shown in this figure, in both switch and non-switch contexts L2 lexical production is quicker than L1 lexical production, with symmetrical switch costs.

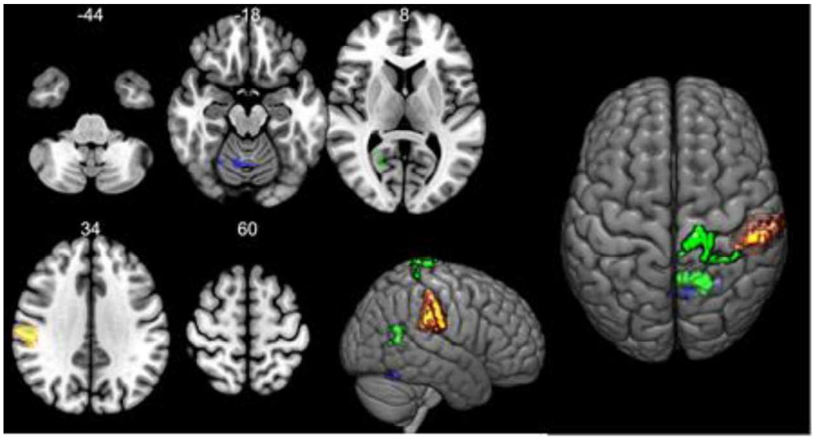
### 3.4.2 PPI results

#### 3.4.2.1 PPI results from switching to L1

Having created masks of the IPC rostral cluster right and left, we investigated the interaction between the psychological variable (time series associated with L1 switch trials, convolved with a double gamma hemodynamic response) and the physiological variable (time series extracted from the ROI).

**Figure 3.3**

*Showing clusters, that the right IPC rostral cluster has functional connectivity with, as a result of switching to L1.*

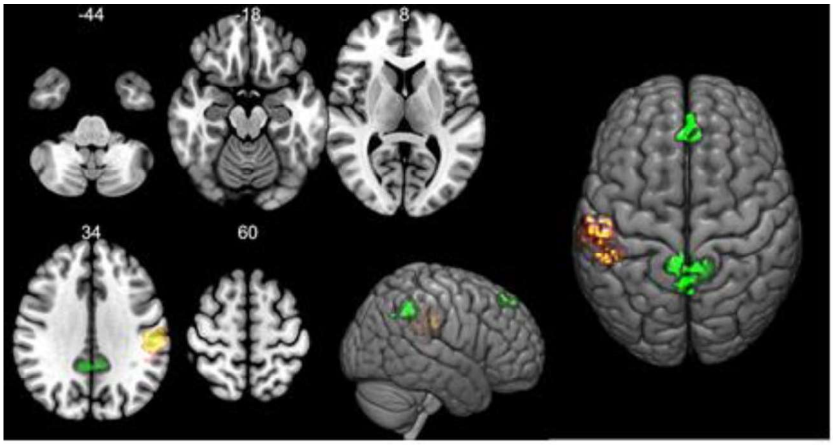


*Note.* In this figure, the location of the right IPC rostral cluster, as the seed region, is shown in yellow-red. The green color demonstrates brain areas, localized in the precuneus cortex and in the postcentral gyrus, that the right rostral IPC has negative functional connectivity with. The blue color shows a cluster localized in the cerebellum, posterior lobe, that the right rostral IPC has positive functional association with.

We tested for significant linear increases and decreases in the functional connectivity of the ROI with the rest of the brain. Z statistic images were thresholded non-parametrically using clusters determined by $Z > 3.1$ and a (corrected) cluster significance threshold of $P < 0.05$. Clusters with fewer than 10 active voxels were excluded. When participants switched to L1, there was a significant linear increase in the functional connectivity between a cluster localized in the right cerebellum, posterior lobe, declive, and the right IPC rostral cluster. In addition, we observed significant linear decreased coupling between the right IPC rostral cluster and two other clusters; one cluster was localized in the precuneus cortex and the other cluster was localized in the postcentral gyrus (see Table 3.3 and Fig. 3.3).

**Figure 3.4**

*Showing clusters, that the left IPC rostral cluster has functional connectivity with, as a result of switching to L1.*



*Note.* In this figure, the location of the left IPC rostral cluster, as the seed region, is shown in yellow-red. The green color demonstrates brain areas, localized in the precuneus cortex and the superior frontal gyrus, that the left rostral IPC has negative functional connectivity with.

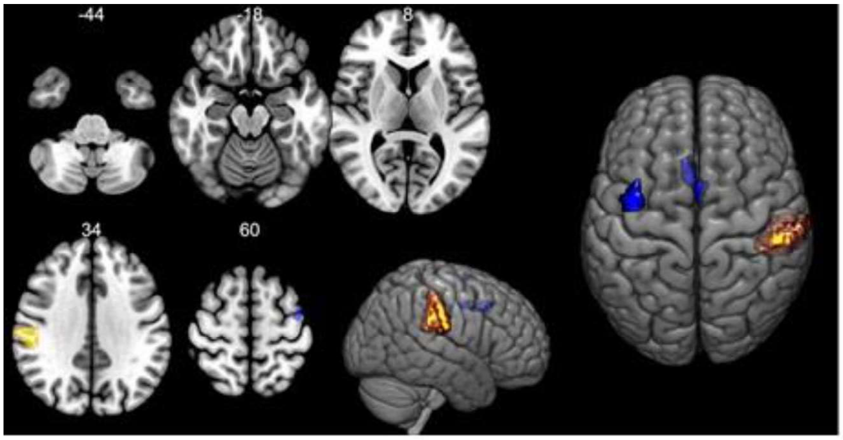
Regarding the functional associations between the left IPC rostral cluster and other parts of the brain under the effect of switching to L1, we observed no positive psychophysiological interactions; however, there were negative couplings between the left IPC rostral cluster and two clusters localized in the precuneus cortex and the superior frontal gyrus (see Table 3.3 and Fig. 3.4).

#### 3.4.2.2 PPI results from switching to L2

In a separate analysis, we also investigated the interaction between time series associated with L2 switch trials and the time series extracted from the ROI, to see if significant linear increases and decreases in the functional connectivity of the ROI and the rest of the brain could be detected. Z (Gaussianised T/F) statistic images were thresholded non-parametrically using clusters determined by $Z > 3.1$ and a (corrected) cluster significance threshold of $P < 0.05$. Clusters with fewer than 10 active voxels were excluded. Under the effect of switching to L2, positive correlation in the activity of the right IPC rostral cluster was observed with a cluster localized in the cingulate gyrus anterior division. In addition, in this condition we observed another positive coupling between the right IPC rostral cluster and a cluster localized in the precentral gyrus. No negative functional association between the ROI and any other cluster was detected in trials requiring participants to switch to L2 (see Table 3.3 and Fig. 3.5).

**Figure 3.5**

*Showing clusters, that the right IPC rostral cluster has functional connectivity with, as a result of switching to L2.*



*Note.* In this figure, the location of the right IPC rostral cluster, as the seed region, is shown in yellow-red. The blue color demonstrates brain areas, localized in the cingulate gyrus anterior division, and in the precentral gyrus, that the right rostral IPC has positive functional connectivity with.

Finally, we observed no positive or negative coupling between the left IPC rostral cluster and other brain areas under the effect of switching to L2.

**Table 3.3**

*Clusters that the rostral cluster IPC R/L has functional connectivity with, when switching to L1/L2.*

| Clusters | Switch L1/L2 | Voxels | Coupling | Z-Max | R/L Seed | Location (MNI) X Y Z |
|---|---|---|---|---|---|---|
| Cerebellum, posterior lobe | L1 | 125 | positive | 4.19 | R | 15.8, -60.8, -20.4 |
| Postcentral gyrus | L1 | 147 | negative | 4.13 | R | 20.5, -34.6, 76.5 |
| Precuneus cortex | L1 | 254 | negative | 5.18 | R | 15.8, -55.1, 17.7 |
| Superior frontal gyrus | L1 | 120 | negative | 4.05 | L | 2.44, 38.2, 48.3 |
| Precuneus cortex | L1 | 475 | negative | 4.6 | L | 4.28, -48.1, 39.9 |
| Cingulate gyrus, anterior division | L2 | 99 | positive | 3.91 | R | -2.01, 9.28, 40.7 |
| Precentral gyrus | L2 | 118 | positive | 4.3 | R | -39.5, -4.15, 63.7 |

## 3.5 Discussion

In this study, we focused on the functional connectivity of the rostral IPC with other parts of the brain with regard to cognitive control of language. For this reason, we used a language switching task paradigm, in which language engagement and disengagement in two contexts associated with higher cognitive demand (switching to L1) and lower cognitive demand (switching to L2) is a key factor. In a language switching paradigm, the stronger language (Dutch/L1) is more inhibited in order to speak in the weaker language (English/L2), and hence retrieving the more inhibited language is cognitively more demanding. We observed in our behavioral results that reaction times for L1 (across the board for switch and non-switch trials) were slower, in line with previous research (Christoffels et al., 2007; Costa & Santesteban, 2004; Ghafar Samar, Tabassi Mofrad, & Akbari, 2014; Gollan & Ferreira, 2009; Tabassi Mofrad, Ghafar Samar, & Akbari, 2015, 2017; Verhoef et al., 2009).

With regard to our fMRI findings, the functional associations of the rostral IPC did not follow the same patterns in switching to L1 and in switching to L2. That is, cognitive demand modulated the patterns of the functional connectivity of this part of the cortex – accompanied with laterality differences – with other brain areas. In the following we elaborate on the connectivity patterns of the rostral IPC in both switching to L1 and switching to L2, and how each functional association of this brain area is defined in these conditions with respect to the previous studies.

### 3.5.1 Switching to L1

In this research, we observed negative couplings, that is negative associations of both the right and the left IPC rostral clusters with the precuneus cortex in switching to L1. The precuneus cortex is part of default mode network (DMN) (Smith et al., 2009). This network is mostly reported to modulate executive functions via its reduced amount of functional connectivity (Dang, O'Neil, & Jagust, 2013). Moreover, according to Gilbert, Bird, Frith, and Burgess (2012), the more difficult a task is, defined in terms of more error rates and slower reaction times, the more suppression in the activity of the precuneus, the bilateral IPC as well as left middle frontal gyrus would be observed. The negative functional connectivity of both the right and the left IPC rostral clusters with precuneus cortex in the more cognitively demanding context, in our study, not only points to the previous accounts on the general function of the precuneus and the bilateral IPC in the face of a more difficult task, but also demonstrates the co-functioning of these parts of the cortex – the right and the left IPC rostral cluster with the precuneus – to meet task demands.

The other brain areas that the rostral IPC has functional connectivity with when switching to L1 are the superior frontal and the right postcentral gyri. The superior frontal is recognized to bring about a facilitating processing manner via its top-down bias mechanisms when irrelevant candidates compete with those representations which are related to a task (Miller & Cohen, 2001) and it has strong interconnections with the parietal cortex (Petrides & Pandya, 1984). Such a circuit has been reported to play a role when there is a need to select among competing responses, with the left parietal cortex engaged in activating responses which are possible, and the prefrontal cortex involved in selecting a response among competing candidates (Bunge et al., 2002). Results from our study corroborate the interconnections between the prefrontal cortex and the parietal cortex, however, in a more detailed way as we observed this interconnection between the superior frontal gyrus or rather the superior part of the prefrontal cortex and the left part of the rostral IPC. In our study both switching to L1 and switching to L2 necessitate selecting a response among competing candidates, however, the interconnection between the superior frontal gyrus and the left rostral IPC is only observed when switching to L1. Furthermore, this interconnection is defined in terms of the negative coupling between these two parts of the cortex. Therefore, it seems that this circuit is more evident when response selection is more challenging, however, the nature of such coupling involved in this circuit needs more research.

Regarding the postcentral gyrus, this part of the cortex is the location of the primary somatosensory cortex which is involved in executive functions (EFs). According to Reineberg et al. (2015) in individuals with better performance in EFs, when resting state functional connectivity is concerned, the fronto-parietal network in which the inferior parietal cortex is a major component, is more extended due to connectivity with nodes outside of this network, in particular with somatosensory regions. Tabassi Mofrad, Jahn and Schiller (2019), and Tabassi Mofrad and Schiller (2019), moreover, by investigating resting state networks involved in EFs reported the connectivity of the primary somatosensory cortex with the fronto-parietal network.

Research into brain functional connectivity architecture shows that there is a high correspondence between brain regions involved in both task-related and resting state functional connectivity (Fair et al., 2007) and that brain regions that work together to accomplish a particular task also fluctuate together when resting state functional connectivity is concerned (Cole et al., 2014; Smith et al., 2009). In fact, the intrinsic network architecture characterized during the resting state, shapes the architecture of brain functional networks involved in performing a task; hence, there is a strong association between the two (Cole et al., 2014), though the resting state functional associations have reverse activation during task-related brain functional connectivity. In our study, we observed the negative functional connectivity of the postcentral gyrus as the location of the primary somatosensory cortex, with the right IPC rostral cluster since this study concerns task-related functional associations. Moreover, as we observed such coupling only in switching to L1, we assume that this association is characterized with challenging conditions.

The other point in brain functional associations when switching to L1 regards the positive coupling the right IPC rostral cluster with the cerebellum, the posterior lobe, declive. The involvement of the cerebellum in EFs is not yet well understood and debated in the literature; however, it is emphasized that the cerebellum contributes to the higher order cognitive functions, though its contribution to EFs might be different from brain areas involved in the frontoparital network (Bellebaum & Daum, 2007). Moreover, it is also reported that the cerebellum is linked to the language control network regions, e.g. the inferior frontal cortex (Green & Abutalebi, 2013; Krienen & Buckner, 2009) to process morphosyntactic features in speech production (Marien, Engelborghs, Fabbro, & De Deyn, 2001) - For a review see Tyson, Lantrip, and Roth (2014). Although more research is needed to better understand the contribution of the cerebellum to EFs, we have at least shown its involvement in cognitive control of language via the positive coupling of the right IPC rostral cluster with this brain area when the context is cognitively more demanding.

### 3.5.2 Switching to L2

In the current research, we observed that the right IPC rostral cluster has positive functional connectivity with the ACC and the precentral gyrus when switching to L2. Generally, ACC contributes to response selection and it monitors conflicts between languages (Abutalebi et al., 2012). It is reported that in the process of response selection, ACC identifies the conflict among competing cues, then the prefrontal cortex via a signal received from ACC on the existence of a conflict, modulates control provided by the top-down regulatory mechanisms of the posterior cortex or the basal ganglia (MacDonald et al., 2000). In our study, switching to L2 is also associated with quicker responses, or rather shorter RTs; moreover, such positive association of the ACC and the right IPC rostral cluster is only observed in switching to L2. As the inferior parietal areas are also involved in response selection (Abutalebi et al., 2008), the positive coupling or rather the positive association of the right IPC rostral cluster with the ACC, in our study, indicates a strong response selection circuit involved in switching to L2, presumably responsible for shorter RTs in this context. Furthermore, as ACC is part of the language control network (Abutalebi & Green, 2008, 2016), that positive association points to our expectation of the research results.

Regarding the involvement of the precentral gyrus in switching to L2, the right part of the seed region has positive functional connectivity with this brain area. Precentral gyrus is generally reported to be involved in response inhibition (Bunge et al., 2002) and task RT (McGuire & Botvinick, 2010). In particular, in language studies, it is emphasized that the precentral gyrus contributes to language switching though the conditions of this task e.g. switching to L1 or switching to L2, in which this part of the cortex plays a role, is not differentiated (Hernandez, 2009; Luk, Anderson, Craik, Grady, & Bialystok, 2012). Moreover, without specifying the nature of the functional association of the precentral gyrus with other parts of the brain, it is reported that in language switching the fronto-parietal network is extended to precentral gyrus (Ma et al., 2014).

With respect to the results from our study, we elaborate that the right IPC rostral cluster, which is part of the fronto-parietal network, is extended to precentral gyrus via a positive functional coupling in language switching but only in switching to L2. As this condition is associated with shorter RTs, and as the precentral gyrus is also involved in response inhibition (Bunge et al., 2002) and task RT (McGuire & Botvinick, 2010), we assume that coupling of the right IPC rostral cluster, a sub area of the inferior parietal areas whose function in response selection have been repeatedly reported in the literature (Abutalebi et al., 2008; Branzi et al., 2016), with the precentral gyrus points to the underlying cognitive mechanisms with a facilitatory function in this language condition.

### 3.5.3 Laterality differences

According to the results of our research, not only task demand modulates the patterns of functional connectivity of the rostral IPC with other parts of the brain, but also it brings about the laterality differences of this part of the cortex. In switching to L2, only the right rostral IPC is involved in positive associations with ACC and the precentral gyrus. However, in switching to L1 the right and the left IPC rostral clusters showed negative functional coupling with the postcentral gyrus, and the precuneus cortex in the former and with the superior frontal gyrus and the precuneus cortex in the latter. The only positive functional connectivity in this condition regards the coupling of the right part of the rostral IPC with the cerebellum, the posterior lobe.

Regarding the laterality differences of the IPC as a whole, in previous research the left IPC is associated with language processing, in particular with semantic and phonological processing (Bzdok et al., 2016; Price, 2012; Vigneau et al., 2006). Moreover, in studies of bilingual aphasia damage to the left IPC is assumed to cause uncontrolled switching between languages (Fabbro, Skrap, & Aglioti, 2000; Khateb et al., 2007). The left IPC in healthy participants is also associated with language switching. According to Wang, Kuhl, Chunhui, and Dong (2009), language switching trials activated the left IPC, though the direction of the language switch was not differentiated in this comparison. The right IPC, however, is mostly reported to be involved in social cognition (Decety & Lamm, 2007; Koster-Hale, Saxe, Dungan, & Young, 2013), auditory spatial attention (Karhson, Mock, & Golob, 2015) and the presentation of deviant sounds (Schönwiesner et al., 2007). Although previous studies have not reported the involvement of the right IPC in language processing and in particular in language switching behavior, in the current study, by using a functional connectivity analysis, we have shown that both the right and the left IPC rostral clusters via positive or negative couplings with other parts of the cortex are involved in language switching. The nature of each coupling depending on switching to L1 and switching to L2 differentiated the functions of the right and the left IPC rostral clusters in this regard.

To recapitulate, with respect to the results of this research, switching to L1 requires bilateral recruitment of the rostral IPC, whereas in switching to L2 only the right IPC rostral cluster is involved. Consequently, we are of the opinion that recruiting more underlying neural processes in switching to L1, along with the function of connectivity patterns of the right and the left rostral IPC associated with this language condition, points to the more cognitively demanding nature of switching to L1. Consistent with this line of argument, the less cognitively demanding characteristic of switching to L2, marked with shorter RTs than those of L1, only necessitated the involvement of the right rostral IPC.

## 3.6 Conclusion

In this study, we focused on how the rostral IPC contributes to cognitive control of language, that is the cognitive mechanisms that enable bilinguals to avoid interference from a non-target language when they utter a word in an intended language (Abutalebi & Green, 2007; Green & Abutalebi, 2013). In doing so, we concentrated on how the rostral IPC adopts different functional connectivity patterns in a context characterized with language engagement and disengagement which recruits the neural mechanisms of cognitive control (Abutalebi & Green, 2008). In our study, we also focused on how cognitive demand - defined in terms of switching to L1 which is cognitively more demanding and switching to L2 which is cognitively less demanding - manipulates such brain functional connectivity in order to meet task demands. By mapping connectivity patterns of the rostral IPC involved in cognitive control of language, we have shown that this part of the cortex adopts asymmetrical patterns of functional connectivity when cognitive demand is concerned and how such functional associations contribute to cognitive control of language. Lastly, according to our research results in language switching behavior both the right and the left IPC rostral clusters are involved, with switching to L1 recruiting the bilateral rostral IPC and with switching to L2 requiring only the involvement of the right rostral IPC.

## References

Abutalebi, J., Annoni, J.M., Zimine, I., Pegna, A.J., Seghier, M.L., Lee-Jahnke, H., Lazeyras, F., Cappa, S., & Khateb, A. (2008). Language control and lexical competition in bilinguals: an event-related fMRI study. *Cerebral Cortex, 18*, 1496-1505.

Abutalebi, J., Della Rosa, P. A., Ding, G., Weekes, B., Costa, A., & Green, D. W. (2013). Language proficiency modulates the engagement of cognitive control areas in multilinguals. *Cortex, 49*(3), 905-911.

Abutalebi, J., Della Rosa, P. A., Green, D.W, Hernandez, M., Scifo, P., Keim, R., Cappa, S.F., & Costa A. (2012). Bilingualism tunes the anterior cingulate cortex for conflict monitoring. *Cerebral Cortex, 22*, 2076-2086.

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.

Abutalebi, J., & Green, D. W. (2016). Neuroimaging of language control in bilinguals: neural adaptation and reserve. *Bilingualism: Language and Cognition, 19* (4), 689–698.

Anderson, J.A.E., Chung-Fat-Yim, A., Bellana, B., Luk, G., & Bialystok, E. (2018). Language and cognitive control networks in bilinguals and monolinguals. *Neuropsychologia. 117*, 352–63.

Bates, E., D'Amico, S., Jacobsen, T., Székely, A., Andonova, E., Devescovi, A., Herron, D., Lu, C. C., Pechmann, T., Pléh, C., Wicha, N., Federmeier, K., Gerdjikova, I., Gutierrez, G., Hung, D., Hsu, J., Iyer, G., Kohnert, K., Mehotcheva, T., Orozco-Figueroa, A., … Tzeng, O. (2003). Timed picture naming in seven languages. *Psychonomic Bulletin & Review, 10*(2), 344-380.

Bellebaum, C., & Daum, I. (2007). Cerebellar involvement in executive control. *The Cerebellum, 6,* 184-192.

Binder, J.R., Desai, R.H., Graves, W.W., & Conant, L.L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19,* 2767-2796.

Boorman, E.D., Behrens, T.E., Woolrich, M.W., & Rushworth, M.F. (2009). How green is the grass on the other side? Frontopolar cortex and the evidence in favor of alternative courses of action. *Neuron, 62*(5), 733-743.

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.

Bunge, S. A., Hazeltine, E., Scanlon, M. D., Rosen, A. C., & Gabrieli, J. D. E. (2002). Dissociable contributions of prefrontal and parietal cortices to response selection. *NeuroImage, 17*, 1526-1571.

Bzdok, D., Hartwigsen, G., Reid, A., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2016). Left inferior parietal lobe engagement in social cognition and language. *Neuroscience and Biobehavioral Reviews, 68,* 319–334.

Caspers, S., Schleicher, A., Bacha-Trams, M., Palomero-Gallagher, N., Amunts, K., & Zilles, K. (2013). Organization of the human inferior parietal lobule based on receptor architectonics. *Cerebral cortex, 23*(3), 615–628.

Caspers, S., Eickhoff, S.B., Geyer, S., Scheperjans, F., Mohlberg, H., Zilles, K., & Amunts, K. (2008). The human inferior parietal lobule in stereotaxic space. *Brain Structure and Function*, *212*, 481- 495.

Caspers, S., Eickhoff, S.B., Rick, T., Von Kapri, A., Kuhlen, T., Huang, R., Shah, N.J., & Zilles, K. (2011). Probabilistic fibre tract analysis of cytoarchitectonically defined human inferior parietal lobule areas reveals similarities to macaques. *NeuroImage, 58*(2), 362-380.

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., & Zilles, K. (2006). The human inferior parietal cortex: cytoarchitectonic parcellation and interindividual variability. *NeuroImage*, *33*(2), 430-448.

Caspers, S., Heim, S., Lucas, M.G., Stephan, E., Fischer, L., Amunts, K., & Zilles, K. (2011). Moral concepts set decision strategies to abstract values. *PLoS One*. *6*(4), e18451.

Caspers, S., Zilles, K., Laird, A.R., & Eickhoff, S.B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage, 50*, 1148-1167.

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*, 238-251.

Corbetta, M., Patel, G., & Shulman, G.L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*, 306-324.

Costa, A., & Santesteban, M. (2004). Lexical access in bilingual speech production: Evidence from language switching in highly proficient bilinguals and L2 learners. *Journal of Memory and Language, 50*, 491–511.

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.

Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *Neuroscientist, 13*, 580–593.

Fabbro, F., Moretti, R., & Bava, A. (2000). Language impairments in patients with cerebellar lesions. *Journal of Neurolinguistics*, *13*, 173-188.

Fabbro, F., Skrap, M., & Aglioti, S. (2000). Pathological switching between languages after frontal lesions in a bilingual patient. *Journal of Neurology, Neurosurgery, and Psychiatry, 68*, 650–652.

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,* 396-405.

Fornito, A., Harrison, B. J., Zalesky, A., & Simons, J. S. (2012). Competitive and cooperative dynamics of large-scale brain functional networks supporting recollection. *Proceedings of the National Academy of Sciences, 109*(31), 12788-12793.

Garbin, G., Costa, A., Sanjuan, A., Forn, C., Rodriguez-Pujadas, A., Ventura, N., et al. (2011). Neural bases of language switching in high and early proficient bilinguals. *Brain and Language, 119* (3), 129–135.

Ghafar Samar, R., Tabassi Mofrad, F. & Akbari, R. (2014). Cognitive Differences in Picture Naming Speed among the Male and Female Persian-English Bilinguals. *Language Related Research, 5* (2), 161-178.

Gilbert, S., Bird, G., Frith, C. D., & Burgess, P. W. (2012). Does "task difficulty" explain "task-induced deactivation?" *Frontiers in Psychology, 3*, 1-12.

Gollan, T. H., & Ferreira, V. S. (2009). Should I stay or should I switch? A cost-benefit analysis of voluntary language switching in young and aging bilinguals. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35*, 640– 665.

Grady, C. L., Luk, G., Craik, F.I.M, & 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.

Hernandez, A.E. (2009). Language switching in the bilingual brain: What's next? *Brain and Language, 109*(2), 133-140.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved Optimization for the Robust and Accurate Linear Registration and Motion. *NeuroImage, 17*(2), 825-841.

Jenkinson, M., & Smith, S. (2001). A global optimization method for robust affine registration of brain images. *Medical Image Analysis, 5*(2), 143-156.

Karhson, D. S., Mock, J. R., & Golob, E. J. (2015). The Role of Right Inferior Parietal Cortex in Auditory Spatial Attention: A Repetitive Transcranial Magnetic Stimulation Study. *PLoS One*, *10*(12), e0144221.

Koster-Hale, J., Saxe, R., Dungan, J., & Young, L.L. (2013). Decoding moral judgments from neural representations of intentions. *Proceedings of the National Academy of Sciences of the United States of America, 110*, 5648–5653.

Keysers, C., & Gazzola, V. (2009). Expanding the mirror: vicarious activity for actions, emotions, and sensations. *Current Opinion in Neurobiology, 19*, 666-671.

Khateb, A., Abutalebi, J., Michel, C.M., Pegna, A.J., Hannelore, L.J., & Annoni, J.M. (2007). Language selection in bilinguals: a spatio-temporal analysis of electric brain activity. *International Journal of Psychophysiology, 65*, 201–213.

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*(02), 119-135.

Krienen, F. M., & Buckner, R. L. (2009). Segregated frontocerebellar circuits revealed by intrinsic functional connectivity. *Cerebral Cortex, 19*, 2485–2497.

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.

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., & Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron, 70*, 363-374.

Luk, G., Anderson, J. A. E., Craik, F. I. M., Grady, C., & Bialystok, E. (2012). Cognitive control for language switching in bilinguals: A quantitative meta-analysis of functional neuroimaging studies. *Language and Cognitive Processes, 27*(10), 1479-1488.

Ma, H., Hu, J., Xi, J., Shen, W., Ge, J., Geng, F., Wu, Y., Guo, J., & Yao, D. (2014). Bilingual cognitive control in language switching: an fMRI study of English-Chinese late bilinguals. *PLoS One*, *9*(9), e106468.

MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of dorsolateral prefrontal cortex and anterior cingulate cortex in cognitive control. *Science, 288,* 1835-1838.

Marien, P., Engelborghs, S., Fabbro, F., & De Deyn, P. P. (2001). The lateralized linguistic cerebellum: A review and a new hypothesis. *Brain and Language, 79*, 580–600.

McGuire, J. T., & Botvinick, M. M. (2010). Prefrontal cortex, cognitive control, and the registration of decision costs. *Proceedings of the National Academy of Sciences of the United States of America, 107*(17), 7922-6.

Martinelli, P., Sperduti, M., & Piolino, P. (2013). Neural substrates of the self-memory system: new insights from a meta-analysis. *Human Brain Mapping, 34*, 1515-1529.

Miller, E., & Cohen, J. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*, 167-202.

Molenberghs, P., Johnson, H., Henry, J.D., & Mattingley, J.B. (2016). Understanding the minds of others: a neuroimaging meta-analysis. *Neuroscience & Biobehavioral Reviews, 65*, 276-291.

Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the parietal region in the rhesus monkey. *Journal of Computational Neurology, 228*, 105-116.

Preibisch, C., Castrillón, J. G., Bührer, M., & Riedl, V. (2015). Evaluation of Multiband EPI Acquisitions for Resting State fMRI. *PLos One, 10* (9), 1-14.

Price, C. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage, 62*, 816-847.

Price, C. J., Green, D., & Von Studnitz, R. A. (1999). Functional imaging study of translation and language switching. *Brain, 122*, 2221-2236.

Raine, A., & Yang, Y. (2006). Neural foundations to moral reasoning and antisocial behaviour. *Social Cognitive and Affective Neuroscience, 1,* 203-213.

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.

Reverberi, C., Kuhlen, A., Abutalebi, J., Greulich, R. S., Costa, A., Seyed-Allaei, S., & Haynes, J. D., (2015). Language control in bilinguals: Intention to speak vs. execution of speech. *Brain & Language, 144*, 1-9.

Ruschel, M., et al. (2014). Connectivity architecture and subdivision of the human inferior parietal cortex revealed by diffusion MRI. *Cerebral Cortex, 24,* 2436-2448.

Rushworth, M.F., Behrens, T.E., & Johansen-Berg, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex, 16*, 1418-1430.

Schönwiesner, M., Novitski, N., Pakarinen, S., Carlson, S., Tervaniemi, M., & Näätänen, R. (2007). Heschl's gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the detection of acoustic changes. *Journal of Neurophysiology*, *97*(3), 2075-2082.

Sohn, M. H., Ursu, S., Anderson, J. R., Stenger, V. A., & Carter, C. S. (2000). The role of prefrontal cortex and posterior parietal cortex in task switching. *Proceedings of the National Academy of Sciences of the United States of America, 97*, 13448-13453.

Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neuroscience & Biobehavioral Reviews, 42*, 9-34.

Shalom, D.B., & Poeppel, D. (2008). Functional anatomic models of language: assembling the pieces. *Neuroscientist, 14*(1), 119-127.

Smith, S.M. (2002). Fast robust automated brain extraction. *Human Brain Mapping, 17* (3), 143–155.

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.

Snodgrass, J.G., & Vanderwart, M. (1980). A standardized set of 260 pictures. Norms for name agreement, image agreement, familiarity and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 174–215.

Tabassi Mofrad, F., Ghafar Samar, R., & Akbari, R. (2015). Nouns and Verb Processing in the First and Second Language: A Cognitive Investigation of Lexical Processing Levels in Persian English Bilinguals. *Linguistic Research, 6* (2), 57-69.

Tabassi Mofrad, F., Ghafar Samar, R., & Akbari, R. (2017). Differences in Contribution of Lexical Processing Levels in L2 Noun and Verb Retrieval and their Implications in English Language Teaching. *Journal of Language Studies, 9* (22), 147-162.

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.

Tomasi, D., & Volkow, N.D. (2011). Association between functional connectivity hubs and brain networks. *Cerebral Cortex, 21*, 2003-2013.

Tomassini, V., Jbabdi, S., Klein, J.C., Behrens, T.E., Pozzilli, C., Matthews, P.M., Rushworth, M.F.S., & Johansen-Berg, H. (2007). Diffusion-weighted imaging tractography-based parcellation of the human lateral premotor cortex identifies dorsal and ventral subregions with anatomical and functional specializations. *The Journal of Neuroscience, 27*, 10259-10269.

Tyson, B., Lantrip, A. C., & Roth, R. M. (2014). Cerebellar contributions to implicit learning and executive function. *Cognitive Sciences, 9,* 179–217.

Verhoef, K., Roelofs, A., & Chwilla, D. (2009). Role of inhibition in language switching: Evidence from event-related brain potentials in overt picture naming. *Cognition, 110*, 84–99.

Vigneau, M., Beaucousin, V., Herve, P.Y., Duffau, H., Crivello, F., Houde, O. et al. (2006). Meta analyzying left hemisphere language areas: phonology, semantics, and sentence processing. *NeuroImage, 30*, 1414-1432.

Wager, T. D., Jonides, J., & Reading, S. (2004). Neuroimaging studies of shifting attention: A meta- analysis. *NeuroImage, 22*, 1679-1693.

Wang, Y., Kuhl, P.K., Chunhui, C., & Dong, Q. (2009). Sustained and transient language control in the bilingual brain. *NeuroImage, 47*, 414-422.

## Appendix 3.1

*Summary of each variable that the stimuli were matched on in set A & B with regard to L1**

| Name of variable** | Mean Set A | Mean Set B | SD Set A | SD Set | t | P Value |
|---|---|---|---|---|---|---|
| Number of letters | 4.71 | 4.71 | 1.27 | 1.6 | 0.00 | 1.00 |
| Number of syllables | 1.25 | 1.33 | 0.44 | 0.48 | -0.62 | 0.54 |
| RT (mean) | 885.86 | 885.16 | 87.45 | 101.67 | 0.024 | 0.981 |
| H statistics | 0.23 | 0.23 | 0.17 | 0.2 | 0.004 | 0.997 |
| Initial fricative | 0.08 | 0.13 | 0.28 | 0.34 | -0.44 | 0.664 |
| Word frequency | 1.5 | 1.6 | 0.54 | 0.63 | -0.631 | 0.534 |
| Visual complexity | 17521.63 | 16857.21 | 7320.9 | 8299.79 | 0.27 | 0.79 |
| Conceptual complexity | 1.17 | 1.25 | 0.48 | 0.61 | -0.492 | 0.627 |
| Word complexity | 0.00 | 0.00 | 0.00 | 0.00 | *** | *** |

*Note*. *Set A and set B refer to the two sets of twenty-four stimuli.

**Visual complexity and conceptual complexity were matched on set A and B with respect to characteristics of the images and independent of L1.

***These values could not be computed because the standard deviations of both groups are 0.

## Appendix 3.2

*Summary of each variable that the stimuli were matched on in set A & B with regard to L2*

| Name of variable** | Mean Set A | Mean Set B | SD Set A | SD Set | t | P Value |
|---|---|---|---|---|---|---|
| Number of letters | 4.75 | 4.58 | 1.33 | 1.1 | 0.59 | 0.57 |
| Number of syllables | 1.38 | 1.3 | 0.58 | 0.46 | 0.62 | 0.54 |
| RT (mean) | 854.5 | 843.58 | 87.73 | 116.88 | 0.36 | 0.73 |
| H statistics | 0.27 | 0.18 | 0.4 | 0.23 | 0.93 | 0.36 |
| Initial fricative | 0.08 | 0.04 | 0.28 | 0.2 | 0.57 | 0.58 |
| Word frequency | 3.73 | 3.82 | 1.11 | 1.2 | -0.24 | 0.81 |
| Visual complexity | 17521.63 | 16857.21 | 7320.9 | 8299.79 | 0.27 | 0.79 |
| Conceptual complexity | 1.17 | 1.25 | 0.48 | 0.61 | -0.492 | 0.627 |
| Word complexity | 0.00 | 0.00 | 0.00 | 0.00 | ** | ** |

Note. *Visual complexity and conceptual complexity were matched on set A and B with respect to characteristics of the images and independent of L2.

** These values could not be computed because the standard deviations of both groups are 0.