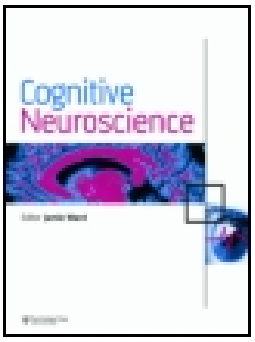

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Cognitive demand modulates connectivity patterns of rostral inferior parietal cortex in cognitive control of language

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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.

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Rostral inferior parietal cortex; cognitive demand; functional connectivity; cognitive control; bilingualism

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 which conveys the attentional resources 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 emphasized with regard to the stimulus-driven completion which necessitates updating, shifting and inhibition, in particular (Abutalebi & Green, 2008; Price, Green, & von Studnitz, 1999; Sohn, Ursu, Anderson, Stenger, & Carter, 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 commonalities of these cytoarchitectonically segregated brain regions should be reflected by receptor

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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 1).

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, Eickhoff, 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 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 also address the tripartition of this part of the cortex. Shalom and Poeppel (2008), by investigating functional anatomic models of language, proposed that different aspects of language are processed in each of the three subareas of the IPC. According to this study, 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. Of course, 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, Desai, Graves, & Conant, 2009). This part of the cortex is also activated during action observation and imitation (Caspers et al., 2010).

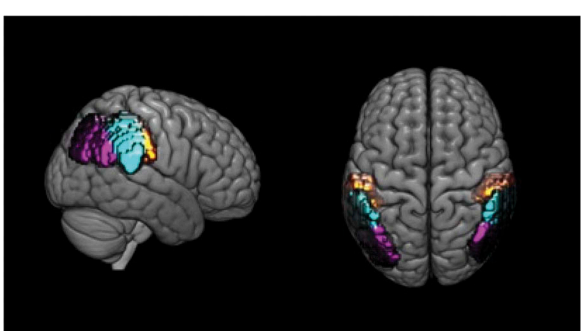

Figure 1. Right and superior display of the IPC division to rostral (yellow-red), middle (cyan), and caudal (violet) parts.

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, middle and 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, middle and caudal areas of the IPC with regard to this executive function in bilinguals in a context characterized with language engagement and disengagement. However, delineating the functional properties of all three IPC subareas and their contribution 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 was modulated by the task demands that are defined in terms of switching to L1 and 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 the previous studies, during bilingual lexical production the activation of brain areas involved in the language control network are more associated with L2 lexical production; therefore, 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 the language control 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 this 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 increasing the sensitivity of BOLD acquisitions (Kundu, Inati, Evans, Luh, & Bandettini, 2012), increasing the spatial and/or temporal resolution (Chen et al., 2015) and increasing the sensitivity in detecting brain functional connectivity (Liao et al., 2013; Preibisch, Castrillón, Bührer, & Riedl, 2015).

2. Methods

2.1. Participants

Fifty-two volunteer, 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 had started learning English via education from the 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), and the ones with upper-intermediate proficiency in English (Mean = 44.17/60, SD = 2.23) were invited to take part in this research (see Table 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). The data used in this study will be available upon request.

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 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 1 and Appendix 2 for

Table 1. Details of the participants included in the analysis.

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

Table 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

*For a detailed description on the identification of variables see: https://crl.ucsd.edu/experiments/ipnp/method/getdata/uspnovariables.html
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further details). Visual complexity as the level of detail 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 matched not 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.

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). There were 19 trials in each condition. 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 (available from [https://surfer.nmr.mgh.harvard.edu/optseq/]) 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. In addition, the randomization of trial sequence was done once and then it was kept constant for all participants.

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 by a voice key, using a SRBOX. In line with previous research (e.g. Anderson, Chung-Fat-Yim, Bellana, Luk, & Bialystok, 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.

2.4. fMRI data acquisition

All data were acquired on a 3 Tesla Philips Achieva TX MRI scanner (Best, The Netherlands) 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. Data analysis

3.1. Behavioral data analysis

Behavioral data in terms of the reaction time (RT) in performing language task switching 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.

3.2. 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. 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 defined using the Jülich Histological Atlas. This atlas is implemented within FSLVIEW, which is part of FSL (www.fmrib.ox.ac.uk/fsl). The probabilistic maps of the right and the left IPC rostral cluster 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 analysis 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 which was convolved with a double gamma hemodynamic response, and the second regressor was the physiological variable which was the time series extracted from the ROI. The third 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 and the rest of the brain during the language switching task with a focus on switch trials.

4. Results

4.1. Behavioral data

Data from 45 healthy volunteers were analyzed (see Figure 2). Response latencies less than 350 ms and more than 1,500 ms were discarded. In total, the accuracy rate of doing this task, that is 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 the by-

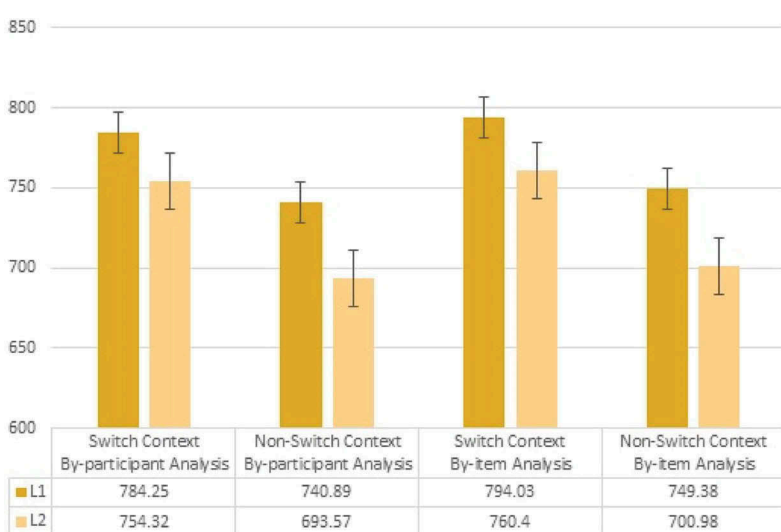

Figure 2. L1 and L2 RTs in millisecond in the switch and non-switch contexts in both the by-participants and the by-item analyses. As shown in this figure, in both switch and non-switch contexts L2 lexical production is quicker than L1 lexical production, with symmetrical switch costs. The error bars represent SEs.

participants analysis ($F1(1,44) = 75.63$, $P < 0.0001$, partial eta square = 0.63) and in the by-item analysis ($F2(1,47) = 50.69$, $P < 0.0001$, partial eta square = 0.52). Likewise, in the repeated-measures ANOVA the main effect of language (L1 & L2) was significant in both the by-participants 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 which were collected after four weeks that 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 either the stronger (Dutch/L1) or the weaker language (English/L2) is differently influenced by the context can be ruled out. According to Figure 2, the weaker language is quicker in both switch and non-switch trials and the stronger language is slower in both switch and non-switch trials in language switching. These results are also in line with other 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, and hence 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 slower than switching to L2 ($t1(44) = -3.859$, $P < 0.0001$; $t2(47) = -3.326$, $P < 0.002$), which in line with the above-mentioned studies points to the more cognitively demanding nature of retrieving the lexicons of the stronger language, in a language engagement and disengagement context.

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.

4.2. PPI results

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). Then, we tested for significant linear increases and decreases in the functional connectivity of the ROI and the rest of the brain. 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. In this section, we observed the correlation in the activity between the right and the left IPC rostral cluster with other parts of the brain when participants did the trials that required switching to L1. According to our results, 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 and Figure 3).

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 and Figure 4).

Table 3. Clusters exhibiting functional connectivity with the rostral IPC R/L seed as a result of switching to L1/L2.

						Location (MNI)		
Clusters	Switch L1/L2	Voxels	Coupling	Z-Max	R/L Seed	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 gyrusnegative	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

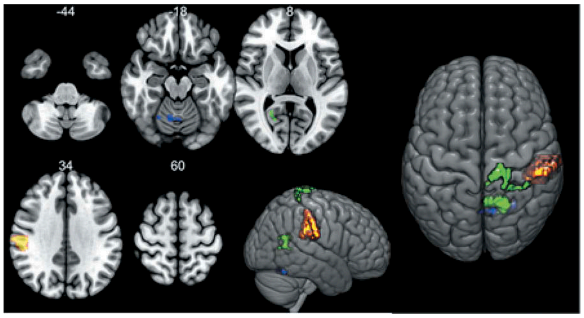

Figure 3. Showing clusters with positive and negative functional association with the right IPC rostral cluster as a result of switching to L1. In this figure, the location of the right IPC rostral cluster, as the seed region, is shown in yellow-red. Clusters with negative functional associations with the seed region, localized in the precuneus cortex and the postcentral gyrus are shown in green. A cluster localized in the cerebellum, posterior lobe, declive with positive functional association with the seed region is displayed in blue.

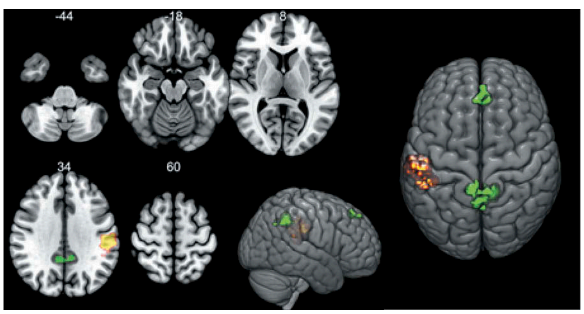

Figure 4. Showing clusters with negative functional association with the left IPC rostral cluster as a result of switching to L1. In this figure, the location of the left IPC rostral cluster, as the seed region, is shown in yellow-red. Clusters with negative functional associations with the seed region, localized in the precuneus cortex and the superior frontal gyrus are shown in green.

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

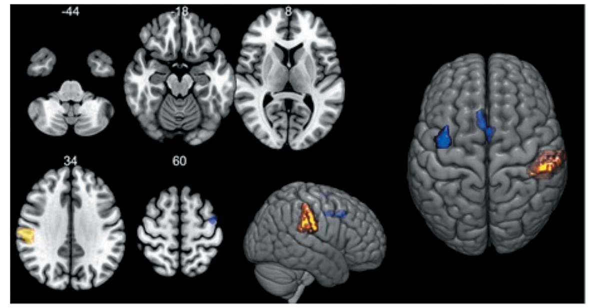

Figure 5. Showing clusters with positive functional association with the right IPC rostral cluster as a result of switching to L2. In this figure, the location of the right IPC rostral cluster, as the seed region, is shown in yellow-red. Clusters with positive functional associations with the seed region, localized in the cingulate gyrus anterior division, and localized in the precentral gyrus are shown in blue.

association between the ROI and any other cluster was detected in trials requiring participants to switch to L2 (see Table 3 and Figure 5).

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.

5. Discussion

In this study, we focused on how task demands, defined in terms of switching to L1 and switching to L2 would influence the functional connectivity of the rostral IPC, given a correlated transmitter receptor-based organization of the IPC (Caspers et al., 2013). For this reason, we used a language task switching paradigm, in which repetitive 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 more cognitively demanding. In fact, it is cognitively more demanding on a trial that requires switching back into L1 during a mixed-language task. This is what 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 clearly 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.

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 could 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 associated with negative functional connectivity with the rostral IPC when switching to L1 are the superior frontal and the right postcentral gyri. The superior frontal gyrus is located at the superior part of the prefrontal cortex. This part of the cortex 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, Hazeltine, Scanlon, Rosen, & Gabrieli, 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, Andrews-Hanna, Depue, Friedman, and Banich (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, Bassett, Power, Braver, & Petersen, 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 have 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 last point in brain functional associations when switching to L1 regards the positive coupling of the cerebellum, the posterior lobe, declive, and the right IPC rostral cluster. The mechanisms of the cerebellum involvement 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 fronto-parital 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 accounting on how the function of the cerebellum in EFs could be defined needs more research, we have at least shown its involvement in EFs via a positive coupling with the right IPC rostral cluster when the context is cognitively more demanding.

5.2. Switching to L2

In the current research, in line with previous studies, we observed the involvement of ACC and the precentral gyrus when switching to L2. These two parts of the cortex have positive functional connectivity with the right IPC rostral cluster. 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, Cohen, Stenger, & Carter, 2000). In our study, switching to L2 is also associated with quicker responses, or rather shorter RTs; moreover, such positive association of 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 ACC and the right IPC rostral cluster, 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), the positive association of the right IPC and ACC in switching to L2 points to our expectation of the research results.

Regarding the involvement of the precentral gyrus in switching to L2, this part of the cortex has positive functional connectivity with the right part of the seed region. 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 this part of the cortex with 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), points to the underlying cognitive mechanisms with a facilitatory function in this language condition.

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 show 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), compared with both Chinese and English stay trials, 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 the language switching. Of course, the nature of each coupling depending on switching to L1 and switching to L2 differentiates 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.

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.

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Appendix 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 B	*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	16,857.21	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	***	***

*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 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 B	*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	17,521.63	16,857.21	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	***	***

*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.