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

Tabassi Mofrad, F.

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Chapter 4

Mapping caudal inferior parietal cortex supports the hypothesis about a modulating cortical area

This chapter is based on:

Abstract

The cytoarchitectonically tripartite organization of the inferior parietal cortex (IPC) into the rostral, the middle and the caudal clusters has been generally ignored when associating different functions to this part of the cortex, resulting in inconsistencies about how IPC is understood. In this study, we investigated the patterns of functional connectivity of the caudal IPC in a task requiring cognitive control, using multiband EPI. This part of the cortex demonstrated functional connectivity patterns dissimilar to a cognitive control area and at the same time the caudal IPC showed negative functional associations with both task-related brain areas and the precuneus cortex, which is active during resting state. We found evidence suggesting that the traditional categorization of different brain areas into either task-related or resting state-related networks cannot accommodate the functions of the caudal IPC. This underlies the hypothesis about a new brain functional category as a modulating cortical area proposing that its involvement in task performance, in a modulating manner, is marked by deactivation in the patterns of functional associations with parts of the brain that are recognized to be involved in doing a task, proportionate to task difficulty; however, its patterns of functional connectivity in some other respects do not correspond to the resting state-related parts of the cortex.

4.1   Introduction

The inferior parietal cortex (IPC) has long been reported to be involved in action-related functions (Keysers & Gazzola, 2009; Caspers et al., 2010), detection of visual target and novelty (Gur et al. 2007), flexible reconfiguration of behavior (Singh-Curry & Husain, 2009) and in particular in cognitive control of language which engages parts of the cortex involved in general aspects of cognitive control (Abutalebi & Green, 2007, 2008; Branzi et al., 2016). The IPC is in fact considered part of the language control network (Fabbro, Moretti, & Bava, 2000; Green & Abutalebi, 2013) that supports language control functions such as resolving competition between languages (Reverberi et al., 2015) and switching between languages (Abutalebi & Green, 2008; Kroll et al., 2006).

Based on the structural parcellation of the human IPC, this part of the cortex consists of three clusters, namely the rostral, the middle and the caudal (Caspers et al., 2013). The white matter connectivity of the IPC as well as the functional differentiations of this part of the cortex also point to the IPC's cytoarchitectonically different areas (Caspers et al., 2013; Corbetta et al., 2008; Keysers & Gazzola, 2009). Regarding the fiber tracks between the IPC clusters and other parts of the cortex, Caspers et al. (2011) reported that the IPC rostral cluster has connections with the somatosensory areas, motor and premotor cortex as well as with the inferior frontal cortex. The IPC caudal cluster is connected with the temporal and the higher visual areas in addition to the posterior parietal cortex. The IPC middle cluster, however, has strong connections with the superior parietal cortex, the intraparietal areas and with the frontal cortex, demonstrating similarities in white matter connectivity with both those of the rostral and the caudal IPC. Having said that, in delineating the contribution of the IPC to different cognitive functions, in particular to cognitive control including response selection (Branzi et al., 2016) updating, shifting and inhibition (Abutalebi & Green, 2008; Wager, Jonides, & Reading, 2004), attention (Corbetta, Patel & Shulman, 2008;

Tomasi & Volkow, 2011) and memory (Martinelli et al., 2013), the IPC is considered as a whole, regardless of its tripartite organization into the rostral, the middle and the caudal clusters. In other words, in reporting the involvement of the IPC in cognitive control and the importance of this part of the cortex in frontoparietal network (for a review see Dajani & Uddin, 2015), the literature has ignored the fact that every part of the tripartite section of the IPC has some functional characteristics related to its structural organization and depending on the type of task, the rostral, the middle and the caudal IPC can have different functional associations with other parts of the brain. Thus, it is possible that it is not the whole IPC that contributes to cognitive control but one or two parts of its tripartite organization, or if all three parts of the IPC contribute to cognitive control, they might not have the same activity and functional connectivity patterns.

As part of our comprehensive project to map the functional connectivity patterns of the IPC clusters, we have already reported the involvement of the rostral IPC in cognitive control of language and have highlighted that cognitive demand modulates connectivity patterns of this part of the cortex (Tabassi Mofrad & Schiller, 2020). In mapping the connectivity patterns of the caudal IPC, we followed an exploratory approach since to our knowledge there are no previous studies in which functional connectivity patterns of the caudal IPC in task performance are addressed, based on which one could formulate a hypothesis in the context of the related literature.

Regarding the activation (but not the connectivity patterns) of the angular gyrus, Wu et al. (2009) reported that this part of the cortex was strongly deactivated in performing the mental arithmetic tasks with Arabic and Roman numerals. The angular gyrus, which is subdivided into the two subregions, namely, PGa and PGp is identical to the caudal IPC when using correlated transmitter receptor-based organization of the IPC (Caspers et al. 2006, 2008 & 2013). In some other studies the angular gyrus is implicated in numerous tasks and processes (for a review see Seghier, 2013; Ramanan & Bellana 2019). The IPC is also questionably considered part of the resting state network e.g. Shehzad et al. (2009) reported that

the IPC is a task-deactivated area though the involvement of the IPC in different cognitive functions cannot be ignored.

As mentioned earlier, the inconsistencies in reporting the functions of the IPC are by far due to considering this part of the cortex as a whole and attributing functions of different IPC sub-areas to the whole IPC. Such contradictory reports gave us the hint of a possibility that the caudal IPC might show connectivity patterns different from what could be expected from the general behavior of the IPC as a whole, when task involvement is concerned.

In this project, we benefited from the multiband EPI technique (multiband factor = 4) with one of the quickest repetition time (TR = 690 ms) in image acquisition, resulting in increasing the sensitivity in mapping brain functional connectivity (Liao et al., 2013; Preibisch et al., 2015), increasing the temporal and the spatial resolution (Chen et al., 2015), and increasing the sensitivity of BOLD acquisitions (Kundu et al., 2012).

4.2   Methods
4.2.1   Participants

Fifty-two students from Leiden University aged 18-27 years took part in this study. They were Dutch-English bilinguals with upper-intermediate proficiency in English, healthy and right-handed with normal or corrected-to-normal vision. We did not use the data from seven participants because of their excessive movements in the scanner, so the final composition of the participants was 34 females and 11 males. Participants gave their written informed consent before taking part in the experiment and they were either remunerated or received course credits for their participation. We received the approval of the medical ethics committee of Leiden University Medical Center (LUMC) (Leiden, the Netherlands) for the protocol of this experiment (NL61816.058.17).

4.2.2   Stimuli

We selected forty-eight pictures from the International Picture Naming Project (IPNP- https://crl.ucsd.edu/experiments/ipnp/) based on the following variables in both Dutch and English: RT (mean), number of letters and syllables, initial fricative, H statistics, and word complexity (see Table 4.1 for a summary of the variables).

Table 4.1

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.

Both CELEX lexical database as well as the IPNP database were used as references for the variables summarized in Table 4.1. We developed two parallel sets of twenty-four stimuli, namely, set A and set B, which we counterbalanced across participants, having considered all the variables in Table 4.1 in addition to visual complexity, conceptual complexity and word frequency (see Table 4.2 and Table 4.3 for further details).

Table 4.2

Summary of each variable that the stimuli were matched on in sets 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

Table 4.3

Summary of each variable that the stimuli were matched on in sets 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.

4.2.3   Procedure

We used a language switching task, which requires cognitive control, with two levels of cognitive demand (switching to the first language (L1) is cognitively more demanding than switching to the second language (L2)) to map the functional connectivity of the caudal IPC. During the experiment, participants were required to do a language switching task that we controlled by the E-Prime Software, and they switched between Dutch (L1) and English (L2). The experiment included two types of trials in four conditions. There were either switch trials in which the response language

was different from the preceding trial (i.e. from Dutch to English or English to Dutch) or non-switch trials in which the response language remained the same as the previous trial (i.e. Dutch to Dutch or English to English). The fMRI experiment included one run of 6 min and 46 s, in an event-related design. Each trial began with a visual cue for 250 ms, in the form of a red (for Dutch) or blue frame (for English), which was counterbalanced across participants, and preceded a picture to instruct participants which language to use to name the upcoming picture. The cue was followed by a fixation cross for 500 ms and then by presentation of a picture for 2,010 ms, the order of which was pseudo-randomized. Each trial ended with a jittered blank screen varying between 690 to 2,760 ms.

Participants first underwent a behavioral training before the fMRI data acquisition. During the training, participants were familiarized with pictures used in the experiment, learned the association between the color cue and the response language and did a small scale of a language switching task in which the target pictures were not used. We instructed participants to name pictures with minimal jaw movement to avoid movement-related artifacts. Four weeks after the fMRI data acquisition session, participants attended the behavioral lab and did the same task that they performed inside the MRI scanner. We collected their responses using an SRBOX, in line with previous studies (e.g. Anderson et al., 2018; Grady et al., 2015).

4.2.4   fMRI data acquisition

We acquired all the data on a 3 Tesla Philips Achieva TX MRI scanner in the Leiden University Medical Center, which was equipped with a SENSE-32 channel head coil. First, we collected the high-resolution anatomical images for co-registration with the functional ones, before the functional images were acquired. The high-resolution anatomical images 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 x 170.5, 155 slices $1.1 \times 1.1 \times 1.1$ mm^3. We also acquired 555 T2*-weighted whole brain multiband gradient EPIs, preceded by 6 dummy scans 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 mm³. To present visual stimuli, we used a high-quality BOLD screen 32 located at the end of the scanner that participants viewed through a mirror at their head.

4.3   Data analysis
4.3.1   Behavioral data analysis

We processed the behavioral data by using SPSS software version 23. Behavioral data included the reaction time (RT) in doing the language task switching - the switch trials (i.e. from Dutch to English or from English to Dutch) and non-switch trials (i.e. Dutch to Dutch or English to English). A two (language: Dutch vs. English) by two (context: switch vs. non-switch) repeated-measures ANOVA was used to analyze the effect of both context and language, followed by paired t-test to examine whether in a language switching task, switching to L1 and switching to L2 were significantly different.

4.3.2   Pre-processing of fMRI data

We processed the fMRI data using FSL software version 5.0.10 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) and we applied the following pre-statistics processing: motion correction using MCFLIRT (Jenkinson et al., 2002), spatial smoothing using a Gaussian kernel of FWHM 5 mm, non-brain removal using BET (Smith, 2002), 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). We registered the functional images to MNI-152 standard space (T1-standard brain averaged over 152 subjects; Montreal Neurological Institute, Montreal, QC, Canada) by 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. We carried out the registration of

functional images to MNI-152 standard space by using FLIRT (Jenkinson & Smith, 2001; Jenkinson et al., 2002).

4.3.3   Psychophysiological interaction (PPI) analysis

To examine the functional connectivity of the caudal IPC with other parts of the brain, we did PPI analyses. In doing so, we created masks of the right and the left IPC caudal cluster by using the Jülich Histological Atlas, implemented in FSL. We binarised the probabilistic maps of the right and the left IPC caudal cluster and thresholded them at 50 percent. Masks were then transformed into the functional space and we projected the ROI on the pre-processed functional images and extracted the mean time series from the ROI by using fslmeants. We did separate PPI analyses for the right and left IPC caudal clusters using FEAT (FMRI Expert Analysis Tool) version 6.00. Our design matrix included three regressors. One of the regressors was the physiological variable which was the time series that we extracted from the ROI. The other regressor was the psychological variable convolved with a double gamma hemodynamic response. The third regressor was the interaction between the physiological and the psychological variables (PPI). By doing PPI analyses, we tested for the significant linear decreases and increases in functional connectivity of the right and the left caudal IPC with other parts of the brain when participants switched to L1 and to L2. We also did separate PPI analyses using the fMRI data from only female participants as sensitivity analyses, to test to what extent the results could be affected.

4.4   Results
4.4.1   Behavioral data

After having discarded RTs of less than 350 ms and more than 1,500 ms, repeated-measures ANOVA demonstrated a significant main effect for language (L1 & L2) ($F1(1,44) = 48.53$, $P < 0.0001$, partial eta square = 0.52) and for context (switch & non-switch) ($F1(1,44) = 75.63$, $P < 0.0001$, partial eta square = 0.63), with no interaction between language and

context ($F1$(1,44) = 3.7, P = 0.061, partial eta square = 0.07) which indicated symmetrical switch costs (see Fig. 4.1 for a summary of the behavioral data).

Figure 4.1

L1 and L2 RTs in millisecond in switch and non-switch contexts
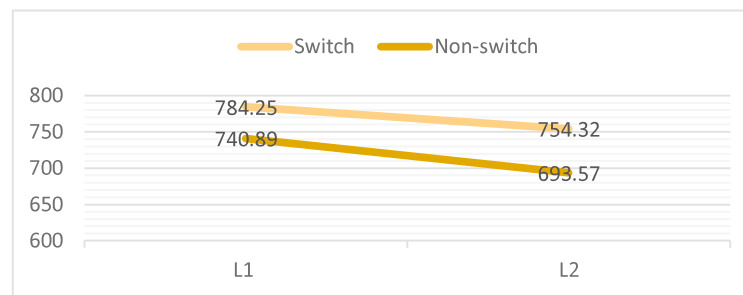
Note. As shown in this figure, in both switch and non-switch contexts L2 lexical production is quicker than L1 lexical production.

Due to suppression of the stronger language (L1) in language switching task in order to speak in the weaker language (L2), and since retrieving the more inhibited language is more effortful (Green, 1998), the stronger language is slower in both switch and non-switch trials, in line with previous studies (Christoffels, Firk & Schiller, 2007; Ghafar Samar, Tabassi Mofrad, & Akbari, 2014; Gollan & Ferreira, 2009; Tabassi Mofrad, Ghafar Samar, & Akbari, 2015, 2017). The paired t-test also demonstrated that switching to L1 was significantly slower than switching to L2 ($t1$(44) = -3.859, P < 0.0001; $t2$(47) = -3.326, P < 0.002), and that highlights the more cognitively demanding nature of retrieving the lexicons of the stronger language, in a language switching context.

4.4.2   PPI results

4.4.2.1   PPI results from switching to L1

Based on the masks that we created of the IPC caudal cluster the left and the right, the interaction between the psychological variable or rather the time series associated with L1 switch trials, convolved with a double gamma hemodynamic response and the physiological variable which is time series extracted from the ROI was investigated. In doing so, we looked for the functional connectivity of the ROI and the rest of the brain in the form of significant linear increases and decreases. We thresholded the Z (Gaussianised T/F) statistic images in a non-parametric manner and used the clusters that were determined by $Z > 3.1$ and a corrected cluster significance threshold of $P < 0.05$. According to our results, when participants switched to L1, there was a significant linear decrease in the functional connectivity of the left IPC caudal cluster with multiple clusters which are as follows: two clusters in the precuneus cortex, one cluster in the lateral occipital cortex, the inferior division, one cluster in the frontal pole, one cluster in the cingulate gyrus, anterior division, one cluster in the temporal occipital fusiform cortex, the posterior division, and one cluster in the lingual gyrus. The left IPC caudal cluster also showed a significant linear increase in its functional connectivity with a cluster located in the left side of the IPC in PGa (see Figure 4.2 A).

Figure 4.2

Demonstration of the seed regions, the left and the right IPC caudal clusters, and brain areas that the seed regions have functional connectivity with, when switching to L1.
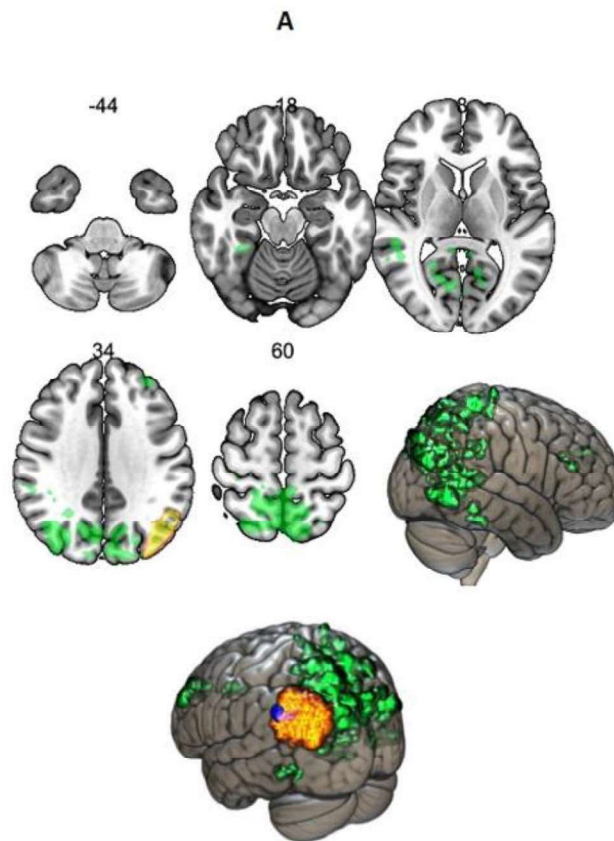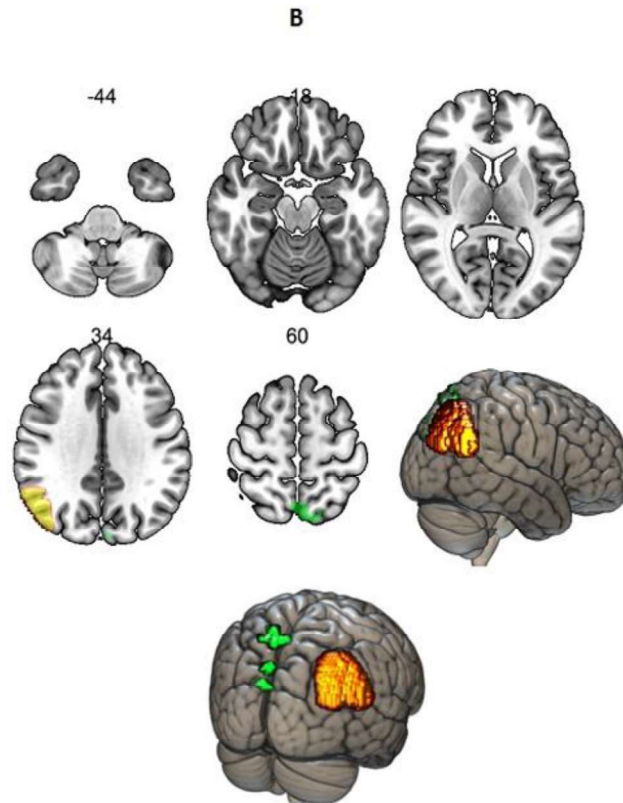
Note. The yellow-red color marks the seed regions, the green color and the blue color demonstrate clusters that the seed regions have negative and positive functional connectivity with, respectively. Panel A regards the left caudal IPC and its coupling when switching to L1 and Panel B relates to the right IPC caudal cluster and its functional associations under the same experimental condition.

The right IPC caudal cluster showed a different pattern of functional connectivity with other parts of brain compared with the left IPC caudal cluster, when participants switched to L1. We observed a significant linear decrease in the functional connectivity between the right IPC caudal cluster and a cluster localized in the cuneal cortex; the right IPC caudal cluster did not have any positive functional association with other parts of the brain (see Figure 4.2 B and Table 4.4).

4.4.2.2   PPI results from switching to L2

When participants switched to L2, we observed a significant linear decrease in functional connectivity of the left IPC caudal cluster with two clusters localized in the lateral occipital cortex inferior division, two clusters localized in the lateral occipital cortex superior division, and one cluster localized in the frontal pole. The right IPC caudal cluster did not show any significant linear increases or decreases in functional connectivity with other parts of the brain when switching to the L2 (see Figure 4.3 and Table 4.4).

Figure 4.3

Demonstration of the seed region, the left IPC caudal cluster, and brain a reas that the seed region has functional connectivity with, when switching to L2.
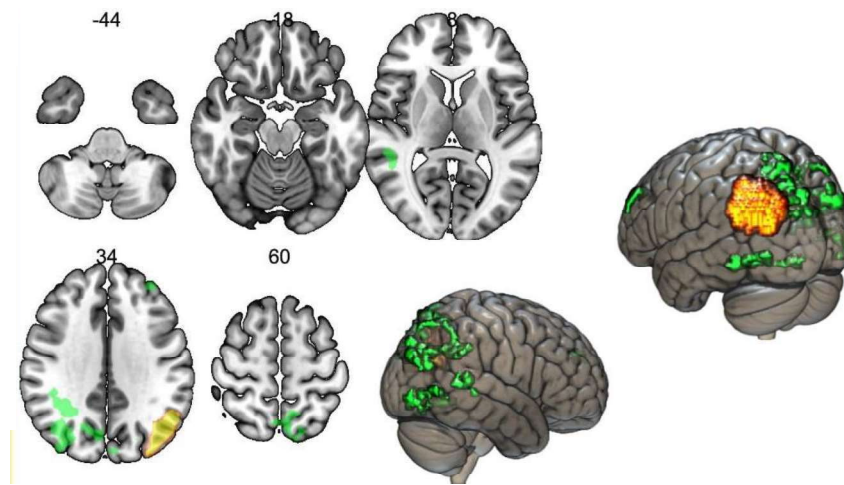
Note. The yellow-red color shows the seed region and the green color demonstrate clusters that the seed region has negative functional connectivity with, when switching to L2.

Table 4.4

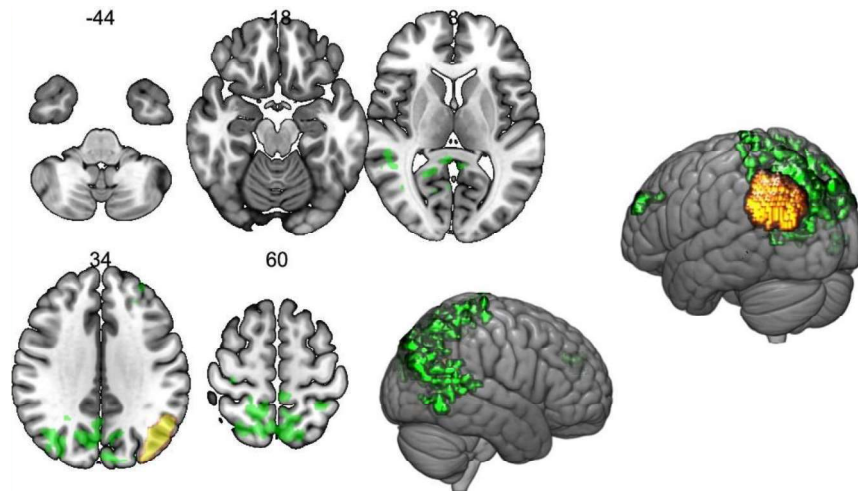*Clusters that the R/L IPC caudal cluster has functional connectivity with, when switching to L1/L2*

Clusters	Switch L1/L2	Voxels	Coupling	Z-Max	R/L Seed	Location (Z-COG)		
						X	Y	Z
Precuneus cortex	L1	6599	Negative	5.51	L	7.25, -66.1, 43.2		
Precuneus cortex	L1	421	Negative	4.32	L	14, -56.1, 9.87		
Lateral occipital cortex inferior division	L1	367	Negative	4.87	L	52.3, -63.3, -3.82		
Frontal pole	L1	259	Negative	5.2	L	-35.7, 46.2, 26.9		
Cingulate gyrus anterior division	L1	192	Negative	4.06	L	-5.47, 31.7, 23.1		
Temporal occipital fusiform posterior division	L1	153	Negative	4.01	L	29.7, -39.4, -17.2		
Lingual gyrus	L1	151	Negative	4.04	L	-12.5, -60.6, 4.32		
IPC caudal cluster left (PGa)	L1	129	Positive	3.92	L	-51.5, -62.7, 38.6		
Cuneal cortex	L1	101	Negative	4.34	R	-3.57, -84.6, 36.1		
Lateral occipital cortex inferior division	L2	305	Negative	4.68	L	-46.3, -65.3, -4.61		
Lateral occipital cortex inferior division	L2	215	Negative	4.43	L	49.7, -71.4, -2.68		
Lateral occipital cortex superior division	L2	242	Negative	4.43	L	-11.3, -64.3, 61.2		
Lateral occipital cortex superior division	L2	140	Negative	4.06	L	-21.1, -80, 43		
Frontal pole	L2	142	Negative	5.03	L	-35.1, 49.1, 29		

4.4.2.3   Sensitivity analyses of PPI results from switching to L1

According to our results, when female participants switched to L1, there were a significant linear decrease in functional connectivity of the left IPC caudal cluster with four clusters; the first cluster was localized in the precuneus cortex and the second cluster was localized in the frontal pole.

Figure 4.4

Demonstration of the seed region, the left IPC caudal cluster, and brain areas that the seed region has functional connectivity with, when switching to L1 in females.

Note. The yellow-red color marks the seed region and the green color demonstrate clusters that the left IPC caudal cluster has negative functional connectivity with.

The third and the fourth cluster were localized in the lateral occipital cortex, the inferior division and in the superior partial lobule (7PCL) (see Figure 4.4). The right IPC caudal cluster did not demonstrate any significant linear increases or decreases in functional connectivity with other parts of the brain when females switched to the L1 (see Table 4.5).

4.4.2.4   Sensitivity analyses of PPI results from switching to L2

There was a significant linear decrease in the functional connectivity patterns of the left IPC caudal cluster with three clusters when female participants switched to L2. One cluster was localized in the lateral occipital cortex, superior division, and the other cluster was localized in the precuneus cortex; the third cluster was in the frontal pole (see Figure 4.5). The right IPC caudal cluster did not show any significant linear increases or decreases in functional connectivity with other parts of the brain when females switched to the L2 (see Table 4.5).

Figure 4.5

Demonstration of the seed region, the left IPC caudal cluster, and brain areas that the seed region has functional connectivity with, when switching to L2 in females
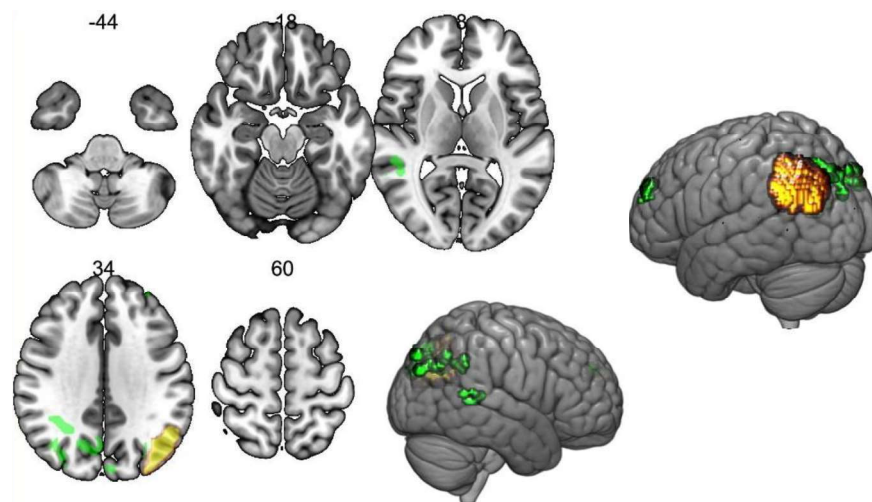
Note. The yellow-red color marks the seed region and the green color demonstrate clusters that the left IPC caudal cluster has negative functional connectivity with.

Table 4.5

Clusters that the R/L IPC caudal cluster has functional connectivity with, when females switched to L1/L2

Clusters	Switch L1/L2	Voxels	Coupling	Z-Max	R/L Seed	Location (Z-COG) X Y Z
Precuneus cortex	L1	6324	Negative	5	L	8.47, -65.4, 38.6
Frontal pole	L1	209	Negative	4.84	L	-34.4, 46, 28.3
Lateral occipital cortex inferior division	L1	138	Negative	4.16	L	54.1, -62.2, -4.39
Superior parietal lobule (7PCL)	L1	134	Negative	4	L	-33.2, -44.4, 57
Lateral occipital cortex superior division	L2	290	Negative	44	L	30.6, -79.5, 34.8
Precuneus cortex	L2	204	Negative	3.89	L	8.88, -66.1, 35.7
Frontal pole	L2	139	Negative	4.67	L	-35.8, 50, 28.1

4.5   Discussion

Using multiband EPI technique, the present study aimed to comprehensively investigate the functional connectivity patterns of the caudal IPC in a task requiring cognitive control, with two levels of cognitive demand. In doing so, we detected highly lateralized functional connectivity patterns in the caudal IPC which have both similarities and differences in the more demanding context (switching to L1) and in the

less demanding context (switching to L2) that we elaborate on in the following (see Table 4.4 for a summary).

4.5.1   The highly lateralized functional connectivity of the caudal IPC

The fMRI findings showed that the functional connectivity of the caudal IPC is very lateralized, with the left caudal IPC having five functional connectivity spots in switching to L2 and eight functional connectivity areas in switching to L1 compared with only one functional connectivity area of the right caudal IPC when switching to L1. Although the higher cognitive demand involved in switching to L1 and the lower cognitive demand associated with switching to L2 have made a difference in the number of functional coupling of the caudal IPC with other parts of the brain, the cognitive demand has not played a major role in the laterality of the caudal IPC functional connectivity, with switching to L2 being entirely (left) lateralized and with switching to L1 being heavily (left) lateralized.

The lateralized function of the caudal IPC is different from the laterality difference in the rostral IPC under the same task conditions in that task demand modulates the patterns of functional connectivity of the rostral IPC with other parts of the brain. In fact, switching to L1 is characterized with bilateral recruitment of the rostral IPC, whereas switching to L2 is marked by the involvement of the right IPC rostral cluster (Tabassi Mofrad & Schiller, 2020). While the rostral IPC is well involved in cognitive control of language, we observed that the caudal IPC has no involvement in task performance under the same experimental conditions. That is, the caudal IPC is marked by its negative functional connectivity with some parts of the cortex that are active in cognitive control, in particular. Moreover, the sensitivity analyses of the PPI results from switching to L1 and to L2 similarly demonstrated the lateralized functional connectivity of the caudal IPC.

4.5.2   Similar caudal IPC functional connectivity in switching to L1 and L2

In switching to both L1 and L2, the left caudal IPC has negative functional connectivity with the frontal pole or rather the most anterior part of the prefrontal cortex. This part of the cortex is involved in processing higher-order cognitive functions (Boorman et al., 2009; Hartogsveld et al., 2018) and its interactions meets the upcoming task demands (Sakai & Passingham, 2003). Contrary to our finding, the positive functional connectivity of the prefrontal cortex and the parietal cortex in frontoparietal network and the contribution of this network to cognitive control abilities (Dosenbach et al., 2008) and adjusting and initiating cognitive control (Cole et al., 2013; Zanto & Gazzaley, 2013) have been reported in the literature. The reason is that in reporting the contribution of the IPC to cognitive control behavior, the literature has considered this part of the cortex as a whole, regardless of its tripartite organization into the rostral, the middle and the caudal clusters (Caspers et al., 2013); the literature has ignored the fact that each of the tripartite sections of the IPC has specific functional characteristics with regard to the IPC's cytoarchitectonically different areas (Caspers et al., 2013; Corbetta et al., 2008; Keysers & Gazzola, 2009).

In the current study, we have shown that in switching to both L1 and L2, the caudal IPC has negative functional connectivity with the frontal pole and that points to the fact that this is not the whole part of the IPC that contributes to cognitive control behavior in the frontoparietal network, in its traditional definition. In line with this argument, in mapping the functional associations of the rostral IPC we reported that the right side of this part of the cortex has positive functional associations with the cingulate gyrus, anterior division (Tabassi Mofrad & Schiller, 2020) when switching to L2, indicating a strong response selection circuit in that language condition, which contributes to shorter reaction times in producing L2 words in a language switching context. Thus, comparatively, while the right rostral IPC proves to be the contributing part of the IPC to cognitive control, in the frontoparietal network when switching to L2,

the caudal IPC does not demonstrate to be part of a strong circuit in that network in the same language condition nor in switching to L1, in the absence of positive functional associations with other brain areas involved in cognitive control, in particular with the prefrontal cortex.

The lateral occipital cortex, the inferior division, is the other part of the cortex that in switching to both L1 and L2, the left caudal IPC has negative functional connectivity with. According to previous studies, positive functional connectivity between brain areas in the frontoparietal network and the visual regions results in better performance in cognitive abilities such as generating verbs as well as automatic word recognition (Twait & Horowitz-Kraus, 2019) and increased behavioral scores for word reading (Horowitz-Kraus & Holland, 2015). Better performance in such cognitive functions is in fact due to the increased visualization of the stimuli which via the positive functional connectivity of the visual regions with the brain areas involved in cognitive control brings about enhanced cognitive performance. In the current study, however, the negative functional associations of the left caudal IPC with the lateral occipital cortex in switching to L1 and to L2 points to the absence of the effect reported in the literature under a positive functional connectivity between brain areas involved in cognitive control and visual regions (i.e. enhanced cognitive performance) due to the deactivation of the caudal IPC in task performance.

With regard to the sensitivity analyses of the PPI results from switching to L1 and to L2, likewise the left caudal IPC has negative functional associations with both the frontal pole (as part of the frontoparietal network) and the lateral occipital cortex. Besides, when the PPI analyses are only done on the fMRI data from female participants, this is just the superior part of the lateral occipital cortex that the left caudal IPC has functional connectivity with, in switching to L2. This points to the gender-based differences in brain functional connectivity which has already been reported in the literature (Zhang et al., 2018; Zhang et al., 2020).

4.5.3   Different caudal IPC functional connectivity in switching to L1 and L2

In general, in switching to L1 which is cognitively a more demanding condition, the left caudal IPC has more negative functional associations with other parts of the brain compared with the functional connectivity patterns of the seed in switching to L2. Regarding the dissimilar patterns, when switching to L2 is concerned, the negative functional connectivity of the left caudal IPC with the lateral occipital cortex, the superior division, is prominent. However, in switching to L1, the left seed is characterized with negative functional associations with the cingulate gyrus, anterior division, the precuneus cortex, the temporal occipital fusiform, the posterior division, and the lingual gyrus. The cuneal cortex is the only part of the brain that the right caudal IPC has negative functional connectivity with in switching to L1. Besides, the only positive functional association of the caudal IPC is between the left seed and the PGa in the left caudal IPC.

We previously suggested that the co-activation of the brain areas in the frontoparietal network and the visual cortex improves some cognitive abilities (Horowitz-Kraus & Holland, 2015; Twait & Horowitz-Kraus, 2019). However, this has not been extensively addressed in the literature and thus it is not known whether the functional associations between the frontoparietal areas and different parts of the visual cortex would highlight any different behavioral effects. That is, it is not yet understood if e.g. the functional connectivity of brain areas in frontoparietal network with the lateral occipital cortex, the superior division and the lateral occipital cortex, the inferior division could differently contribute to cognitive abilities. Consequently, it cannot be concluded what different behavioral effects could be expected when such functional associations do not exist.

In the current study, when the dissimilar patterns in switching to L1 and in switching to L2 are concerned, we observed that in switching to L1, the left caudal IPC has negative functional connectivity with different parts of the visual cortex, namely, temporal occipital fusiform, the posterior division, the cuneal cortex and the lingual gyrus which are part

of the occipital lobe, and in switching to L2, the left caudal IPC has negative functional connectivity with the lateral occipital cortex, the superior division. While further research is needed to map the patterns of the co-activations between brain areas involved in the frontoparietal network and different parts of the visual cortex and to address what behavioral effects would be observed, what is evident in the current study is that, in general, the more cognitively demanding context is characterized with more negative functional associations of the caudal IPC with the visual areas.

One tangible explanation is that the caudal IPC, though part of the frontoparietal network, is not part of brain areas involved in cognitive control. This further strengthens the idea that this is not the whole part of the IPC that contributes to cognitive control but one or two parts of its tripartite organization, given the fact that the IPC's cytoarchitectonically different areas as the rostral, the middle and the caudal clusters have different white matter connectivity and different functional characteristics (Caspers et al., 2013; Corbetta et al., 2008; Keysers & Gazzola, 2009).

Besides, the left caudal IPC has negative functional connectivity with the cingulate gyrus, the anterior division. Generally, this part of the cortex, as part of the language control network (Abutalebi & Green, 2008, 2016) monitors conflicts between languages and it contributes to response selection (Abutalebi et al., 2012). In mapping the functional connectivity patterns of the rostral IPC, we showed that the positive functional associations of the ACC and the right IPC rostral cluster, by forming a strong response selection circuit involved in switching to L2, contribute to shorter RTs in this context (Tabassi Mofrad & Schiller, 2020). However, the negative connectivity pattern between the IPC caudal cluster and the ACC further bolsters the idea that this part of the cortex is not involved in cognitive control.

The fact that the left caudal IPC has also negative functional associations with the precuneus cortex, which is active during the resting state (Smith et al., 2009) confirms that the caudal IPC is not related to the resting state condition either. Interestingly, clusters located in the precuneus cortex with which the left caudal IPC has negative functional

connectivity, have the highest number of voxels compared with any other clusters that the left caudal IPC is negatively connected.

In switching to L1, the left caudal IPC has positive functional connectivity with the PGa which is itself part of the IPC caudal cluster. To address the general function of the angular gyrus in mental arithmetic tasks performed with Arabic and Roman numerals, Wu et al. (2009) reported that this part of the cortex was strongly deactivated in performing the task. Since the angular gyrus is identical to the caudal IPC when the correlated transmitter receptor-based organization of the IPC is concerned (Caspers et al. 2006, 2008 & 2013), our findings corroborate the research result of Wu et al. (2009) in the sense that the left caudal IPC has negative functional connectivity with the frontal pole and different parts of the visual cortex that are active during task performance, suggesting that the left caudal IPC is deactivated in performing the task. At the same time, the positive functional connectivity of the left caudal IPC with one of its own parts, namely PGa, highlights strong deactivation of PGa in switching to L1. Another interesting finding is that strong deactivation of PGa which has resulted in the positive functional association of the left caudal IPC with PGa is observed in the more demanding context and only in the left part of the cortex. However, we cannot associate the function of the caudal IPC with those of brain areas related to the resting state, as the left caudal IPC has negative functional connectivity with precuneus cortex in switching to L1.

The sensitivity analyses of the PPI results also demonstrated more negative functional associations of the left caudal IPC with other parts of the brain in the more cognitively demanding condition compared with the functional connectivity patterns of the seed in switching to L2. Moreover, the sensitivity analyses also showed the similar results for the negative functional connectivity of the seed with the lateral occipital cortex, the inferior division in switching to L1 and the negative functional connectivity of the left caudal IPC with the lateral occipital cortex, the superior division in switching to L2. While the negative functional connectivity of the left caudal IPC with the occipital cortex is preserved in the sensitivity analyses, the absence of the functional connectivity of the

seed with other parts of the occipital lobe i.e. temporal occipital fusiform, the posterior division, the cuneal cortex and the lingual gyrus signals the gender-based differences in brain functional connectivity.

4.5.4   Modulating function of the caudal IPC

According to Fair et al. (2007), there is a high correspondence between parts of the cortex involved in the task-related and the resting state functional connectivity in the way that they fluctuate together (Smith et al., 2009; Cole et al., 2014); that means brain areas that are active during resting state are deactivated in doing a task, and those parts of the cortex that are active in task performance are deactivated during resting state, an example of which is the connectivity of somatosensory cortex with some parts of the cortex in the frontoparietal network (see Tabassi Mofrad & Schiller, 2019; Tabassi Mofrad, Jahn & Schiller, 2020). Thus, when in performing the language switching task, the IPC caudal cluster has negative functional connectivity with the precuneus cortex, the caudal IPC cluster cannot be associated with the resting state despite the fact that this part of the cortex has also negative functional connectivity with other parts of the brain such as different parts of the visual cortex, that are active not necessarily in cognitive control but generally in doing a task. It is noteworthy that the negative functional connectivity of the left caudal IPC with the precuneus cortex, the frontal pole and different parts the visual cortex are preserved in the sensitivity analyses of the PPI results.

Regarding our research findings, there is evidence to believe that the traditional categorization of different brain areas into either task-related, i.e. active when the brain is busy with performing a task, or resting state-related networks, i.e. active when the brain is not processing external stimuli cannot accommodate the function of caudal IPC. Thus, we hypothesize that this part of the cortex functions in a modulating manner; while it is not necessarily associated with the resting state condition - its deactivations, proportionate to task difficulty, contribute to task performance. To elaborate more, when the caudal IPC has negative association with the precuneus cortex that is the evidence that the caudal

IPC and the precuneus cortex are not fluctuating together. While the precuneus cortex is recognized as a resting-state related part of the cortex, thus, the caudal IPC is not resting-state related. Since the caudal IPC has negative connectivity with some parts of the frontoparietal network, the caudal IPC is not part of the control network. As the caudal IPC also has negative functional connectivity with parts of the cortex that are involved in very general cognitive functions e.g. different parts of the visual cortex, therefore, the caudal IPC does not show task-related activity. That is, the caudal IPC deactivations contribute to task performance; the higher the cognitive demand, the more deactivations and the more the negative functional associations. Because the number of negative functional connectivity of the caudal IPC with other parts of the cortex changes with the cognitive demand, as a result the caudal IPC has a modulating role.

Although in the current study we used a language task to map the functional connectivity of the caudal IPC, the general connectivity behavior of this part of the cortex that we have reported should not be considered as limited to a language task. For one thing, the left lateralized function of the caudal IPC is the result of the negative functional connectivity of this part of the cortex with other parts of the brain. However, the left lateral function of the brain in processing language, reported in the literature, is the result of the positive brain activations and associations. Moreover, as mentioned earlier, the general connectivity patterns of the caudal IPC correspond to neither the resting-state related nor to the task based-related parts of the cortex, by which a new brain functional category that we have referred to as modulating is hypothesized and that is highly unlikely to be task dependent.

4.6   Conclusion

For long, the functions of the IPC in cognitive control have been considered regardless of its tripartite organization into the rostral, the middle and the caudal clusters (Caspers et al., 2013). That has resulted in poor understanding of the functions of the IPC subsections and forming general characteristics for this part of the cortex which are not

representative of the IPC's constituents. Mapping the functional connectivity of the caudal IPC has revealed that this brain area does not show functions that have characteristically been reported about the IPC as a whole. Besides, our research findings have demonstrated that functional associations of the caudal IPC are neither typical of resting state-related nor task-related parts of the brain. These results support the hypothesis about a modulating cortical area that its involvement in task performance, in a modulating manner, is marked by deactivation in the patterns of functional connectivity, proportionate to task difficulty, with parts of the brain that are involved in doing a task; however, its connectivity in some other respects does not correspond to the resting state-related parts of the cortex.

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