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

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Chapter 5

Connectivity profile of middle inferior parietal cortex confirms the hypothesis about modulating cortical areas

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Abstract

According to the correlated transmitter-receptor based structure of the inferior parietal cortex (IPC), this brain area is divided into three clusters, namely, the caudal, the middle and the rostral. Nevertheless, in associating different cognitive functions to the IPC, previous studies considered this part of the cortex as a whole and thus inconsistent results have been reported. Using multiband EPI, we investigated the connectivity profile of the middle IPC while forty-five participants performed a task requiring cognitive control. The middle IPC demonstrated functional associations which do not have similarities to a contributing part in the frontoparietal network, in processing cognitive control. At the same time, this cortical area showed negative functional connectivity with both the precuneus cortex, which is resting- state related, and brain areas related to general cognitive functions. That is, the functions of the middle IPC are not accommodated by the traditional categorization of different brain areas i.e. resting state-related or task-related networks and this advanced our hypothesis about modulating cortical areas. Such brain areas are characterized by their negative functional connectivity with parts of the cortex involved in task performance, proportional to the difficulty of the task; yet, their functional associations are inconsistent with the resting state-related cortical areas.

5.1 Introduction

Based on the correlated transmitter-receptor based organization of the inferior parietal cortex (IPC), this cortical area has a tripartite structure, including the caudal, the middle and the rostral clusters (Caspers et al., 2006, 2008). The cytoarchitectonically different subareas of the IPC have also been reflected by the white matter connectivity of this part of the cortex (Caspers et al., 2013) as well as diffusion-weighted magnetic resonance imaging along with probabilistic tractography (Ruschel et al., 2014).

Despite the tripartite organization of the IPC, previous studies considered this brain area as a whole and associated the IPC with different executive functions, for instance, language control (Branzi et al., 2016), in particular language switching (Abutalebi & Green, 2008), memory functions (Martinelli et al., 2013), adaptation of behavior (Singh-Curry & Husain, 2009), attention (Tomasi & Volkow, 2011), and action observation (Apps et al., 2016). In fact, in reporting the importance of the IPC in the fronto-parietal network and the way this brain area contributes to cognitive control (Dajani & Uddin, 2015) it was ignored that the functions of the subsections of the IPC do not represent the whole IPC. The functional characteristics of the caudal, the middle and the rostral IPC are relative to their structural organization, and thus the patterns of their functional associations with other cortical areas do not constitute a unified representation of the IPC.

Until the time we reported the functional connectivity profiles of the rostral and the caudal IPC in a task which required cognitive control (Tabassi Mofrad & Schiller, 2020; 2022), in previous studies the functional associations of the clusters of the IPC with other parts of the brain had never been investigated. Examining the fiber tracks between the IPC's subareas and other parts of the cortex has made it clear that while the rostral IPC has connectivity with the motor, the inferior frontal, the somatosensory and the premotor areas, the caudal IPC has strong associations with the temporal, the visual and the posterior parietal areas. The middle IPC, however, has similarity with the caudal and the rostral IPC, in terms of white matter connectivity, by being associated with the intraparietal, the superior and the frontal areas (Caspers et al., 2011). Nonetheless, the fiber tracks reflect brain white matter connectivity, and they do not necessarily point to brain functional connectivity. That is, at the same time that cytoarchitectonically different subareas of the IPC have been differentiated and their fiber tracks have been detected, the functional connectivity profile of the middle IPC has yet remained a gap in the literature. According to the traditional definition of the IPC, this brain area is believed to process cognitive control; however, when the subareas of the IPC are concerned, the contribution of the middle IPC to cognitive control is still unknown.

In our previous study (Tabassi Mofrad & Schiller, 2020), we elaborated on the functions of the rostral IPC; this brain area, by having positive functional associations with the anterior cingulate cortex, is the contributing part of the IPC in the frontoparietal network to cognitive control. Besides, the rostral IPC forms a strong response selection circuit in cognitive control of language. However, the caudal IPC has different functional connectivity patterns and dissimilar functions to those of the rostral IPC. Mapping the connectivity profile of the caudal IPC demonstrated that this part of the brain does not contribute to cognitive control and its connectivity patterns are neither typical of the task-related nor the resting state-related brain areas - according to which we proposed the hypothesis about modulating cortical areas (Tabassi Mofrad & Schiller, 2022). By that hypothesis we delineated that the involvement of the modulating cortical areas in task performance is characterized by negative functional connectivity with task-related brain areas, proportional to task difficulty. At the same time, functional associations of the modulating cortical areas are not similar to those of the resting state-related parts of the cortex.

Having mapped the functional connectivity of the caudal and the rostral IPC in doing a task which required cognitive control, as part of our wide-ranging project to map the functional associations of the clusters of the IPC, in this study we addressed the functional connectivity profile of the middle IPC mostly via an exploratory approach, as to the knowledge of the researchers, the functional associations of the middle IPC are not reported in previous studies – according to which a logical hypothesis could be formed. Having said that, we expected that the patterns of functional connectivity that the middle IPC would demonstrate might be dissimilar to the general functional couplings of the IPC as a whole, when task involvement is concerned, due to structural differences of the clusters of the IPC. In mapping the functional connectivity profile of the middle IPC, we used multiband EPI (factor = 4). This technique provided us with one of the fastest repetition times (TR = 690 ms) in MRI image acquisition, which resulted in increased sensitivity in detecting functional associations of cortical areas (Liao et al., 2013; Preibisch et al., 2015), increased sensitivity of BOLD acquisition (Kundu et al., 2012), and increased temporal and spatial resolution (Chen et al., 2015).

5.2 Methods

5.2.1 Participants

Bilingual Dutch-English psychology students at Leiden University (fifty-two volunteers, healthy, aged 18-27, right-handed, with corrected-to-normal or normal vision) took part in this study. Due to excessive movements in the scanner (movement exceeding ~1–2 mm; see Wylie et al., 2014), we did not include the data from seven participants in the analyses. Thus 34 females and 11 males remained in the final set of participants. Participants were well informed about all stages of the experiment, and they submitted their consent to take part in this research. Participants received either course credits or a small financial compensation for their participation. The medical ethics committee of the Leiden University Medical Center (Leiden, The Netherlands) approved the research protocol (application no. NL61816.058.17).

5.2.2 Stimuli

The stimuli included 48 pictures taken from the International Picture Naming Project (IPNP). In selecting the pictures, we considered some variables in both Dutch and English which are as follows: H statistics, onset sound, number of letters and syllables, RT (mean) and word complexity; both the IPNP and CELEX lexical database were used as references. Moreover, we also considered word frequency, conceptual complexity, and visual complexity to make two sets of twenty-four stimuli – set A and set B – that were parallel and counterbalanced across participants.

5.2.3 Procedure

Participants performed a language-switching experiment which was controlled by the E-Prime software. The experiment had four conditions and they switched between English (L2) and Dutch (L1). Trials were either switch ones - the language in the preceding trial was different from the language in the following trial - or non-switch trials, that is, the language in the preceding trial and the following trial was the same. The fMRI experiment was event-related and consisted of one run of 6 min and 46s. Each trial began with a visual cue - a blue or red frame - for 250 ms, which was counterbalanced. The visual cue instructed the participant whether to use Dutch or English to name the demonstrated picture in that trial. The visual cue was followed by a fixation cross and the presentation of a picture, for 500 ms and 2,010 ms, respectively. There was a jittered blank screen with a duration varying between 690 and 2,760 ms, at the end of each trial; the presentation of trials was pseudo-randomized. Before conducting the experiment inside the MRI scanner, participants took part in a small scale of the task to familiarize them with the pictures that we used in the experiment. That also facilitated learning the association between the target language and the color cue. Participants were instructed to move their jaws minimally when naming the target pictures to avoid movement related artifacts.

5.2.4 fMRI data acquisition

The neuroimaging data were acquired in the Leiden University Medical Center, using a 3 Tesla Philips Achieva TX MRI scanner which was equipped with a SENSE-32 channel head coil. First the high-resolution anatomical images were acquired including 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 mm3, 155 slices 1.1×1.1×1.1 mm3. Then 555 T2*-weighted whole brain multiband gradient EPIs were collected with the following scanning parameters: TR = 690 ms, TE = 30 ms, multiband factor = 4, FA = 55°, FOV = 220 x 220 x 121 mm3, 44 slices 2.75 × 2.75 × 2.75 mm3. A high-quality MRI-safe HD 32" LCD monitor was located at the end of the scanner for displaying the visual stimuli. Participants viewed the stimuli through a mirror which was attached to the head coil.

5.3 Data analysis

5.3.1 Behavioral data analysis

SPSS software version 23 was used to process the behavioral data which were the reaction time (RT) in doing the language switching experiment. A two (language: English vs. Dutch) by two (context: non-switch vs. switch) repeated-measures ANOVA was used to examine the effects of language and context. Then paired t-tests were done to examine whether RTs in L1 and L2 switch trials were statistically different.

5.3.2 Pre-processing of fMRI data

FSL software version 5.0.10 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) was used to analyze the fMRI data with the following pre-statistics processing: spatial smoothing (Gaussian kernel of FWHM 5 mm), motion correction by using MCFLIRT (Jenkinson et al., 2002), non-brain removal by using BET (Smith, 2002), high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma

= 50.0s) and grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor. The functional images were registered to the MNI-152 standard space. The registration was done using a three-step procedure i.e. functional to high-resolution images, then to T1-weighted structural images, and finally to the standard space of the MNI template, using FLIRT (Jenkinson & Smith, 2001; Jenkinson et al., 2002).

5.3.3 Psychophysiological interaction (PPI) analysis

PPI analyses were conducted to analyze the functional connectivity of the middle IPC with other cortical areas. Using the Jülich Histological Atlas, masks of the right and the left middle IPC were created. The probabilistic maps of the left and the right IPC middle cluster were binarised and then thresholded at 50 percent, before transforming them into the functional space. The ROI was projected on the functional images that were already pre-processed, and by using fslmeants, the mean time series from the ROI was extracted. For the right and left IPC middle clusters, separate PPI analyses were carried out by using FEAT (FMRI Expert Analysis Tool) version 6.00. The design matrix had three regressors which are as follows: the physiological variable i.e. the time series that were extracted from the ROI, the psychological variable, convolved with a double gamma hemodynamic response, and the interaction between the physiological and the psychological variables (PPI). The significant linear increases and decreases in functional couplings of the right and left middle IPC with other cortical areas when participants did the language switching experiment were the main focus of the PPI analyses. To correct for multiple comparisons, cluster correction was employed as the most popular correction method in fMRI data analysis (see Woo et al., 2014). The cluster-defining threshold was set by considering a z-value of 3.1.

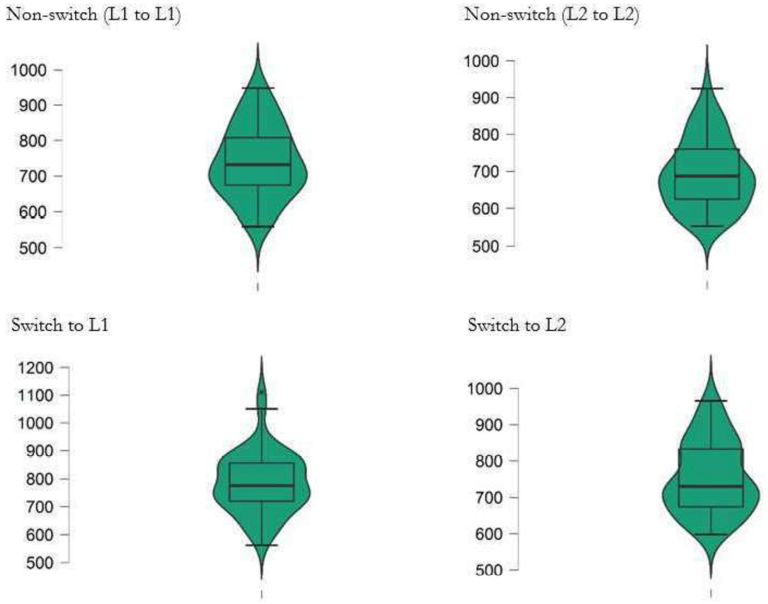
5.4 Results

5.4.1 Behavioral data

Results from repeated-measures ANOVA revealed a significant main effect for context ($F1(1, 44) = 75.63$, $P < 0.0001$, partial eta square = 0.63) as well as language ($F1(1, 44) = 48.53$, $P < 0.0001$, partial eta square = 0.52). However, we did not observe any interaction between context and language ($F1(1, 44) = 3.7$, $P = 0.061$, partial eta square = 0.07).

Figure 5.1

Visualization of the distribution of the behavioral results (in RTs) in all four conditions of the experiment.



Note. In both contexts, L2 lexical production was faster than that of L1.

In order for the bilinguals to speak in the non-dominant language (L2), the dominant language (L1) is suppressed, and because retrieving the language that is more inhibited is also more demanding (Green, 1998) the stronger language has longer RTs in both non-switch and switch trials; hence, the reversed language effect (Christoffels et al., 2016; Ghafar Samar et al., 2014; Tabassi Mofrad et al., 2015; 2017). According to the results from the paired t-test, switching to the L1 was significantly slower than switching to the L2 (t1(44) = -3.859, L1 Mean RT = 784.25, L2 Mean RT = 754.32, P < 0.0001; t2(47) = -3.326, P < 0.002) (see Figure 5.1). Thus, that underlines the fact that in language-switching, retrieving items from the lexicon of the more dominant language is cognitively more demanding.

5.4.2 PPI results

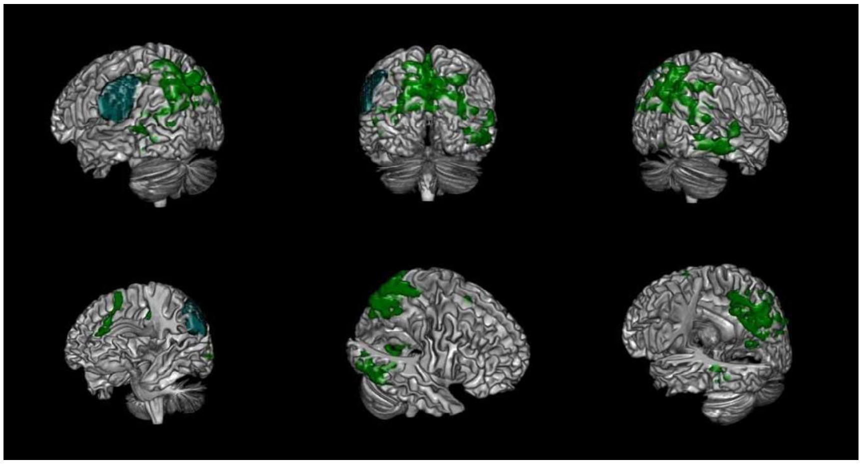
5.4.2.1 PPI results from switching to L1

The interaction between the time series related to L1 switch trials or rather the psychological variable, and the physiological variable was investigated using the masks created of the right and the left middle IPC. The Z (Gaussianised T/F) statistic images were thresholded in a non-parametric way, and we used clusters that were determined by Z>3.1. We investigated the functional association of the ROI with other cortical areas by considering significant linear decreases and increases. Based on our results, when switching to L1, there was significant linear decrease in the functional association between the left middle IPC and some other clusters, namely, two clusters in the lateral occipital cortex inferior division, one cluster in the precuneus cortex, one cluster in the cingulate gyrus, anterior division, one cluster in the lingual gyrus and one cluster in the occipital fusiform gyrus (see Figure 5.2 Panel A).

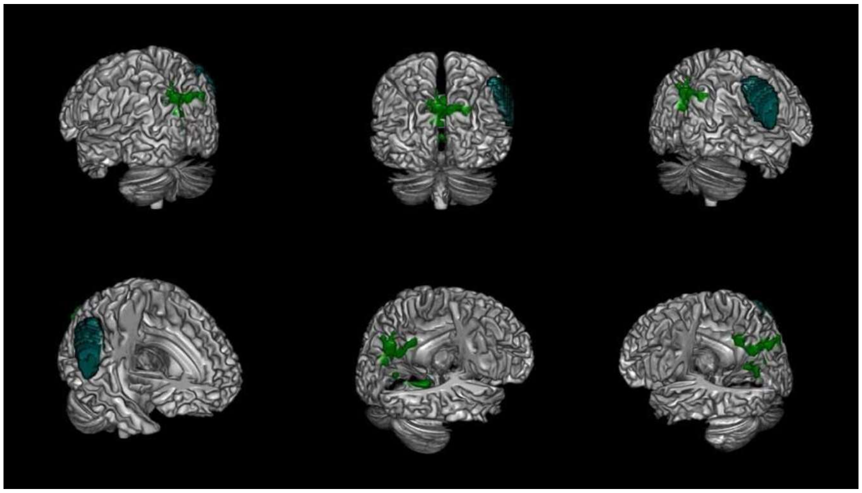
Figure 5.2

Demonstration of the seed regions, the left and the right IPC middle clusters, and brain areas that the seed regions had functional connectivity with, when switching to L1.

Panel A



Panel B



Note. The seed region is marked by the cyan color and the green color demonstrates clusters that the seed regions had negative functional connectivity with. Panel A regards the left middle IPC and its coupling when switching to L1 and Panel B relates to the right IPC middle cluster and its functional associations under the same experimental conditions.

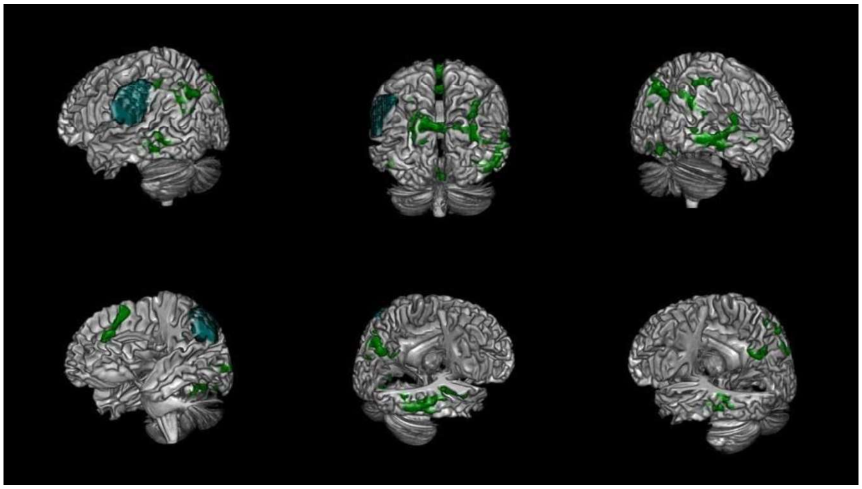
Besides, the right middle IPC demonstrated negative functional connectivity with two clusters, one in the precuneus cortex and the other in the intracalcarine cortex (see Figure 5.2 Panel B). In switching to the L1, left and right middle IPC did not show any positive functional connectivity with other cortical areas.

5.4.2.2 PPI results from switching to L2

When switching to the L2, the left middle IPC had negative functional coupling with multiple clusters in the lateral occipital cortex, inferior and superior divisions, the cingulate gyrus, anterior division and the paracingulate gyrus. The left middle IPC did not show any positive functional connectivity with other cortical areas. In addition, the right middle IPC did not demonstrate any positive or negative associations with other cortical areas either, when participants switched to the L2 (see Figure 5.3).

Figure 5.3

Demonstration of the seed region, the left IPC middle cluster, and brain areas that the seed region had functional connectivity with, when switching to L2.



Note. The cyan color demonstrates the seed region, and the green color shows clusters that the seed region had negative functional connectivity with, when participants switched to the L2.

Table 5.1

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

Clusters	Switch L1/L2	Voxels	Coupling	Z-Max	R/L Seed	Location (Z-COG) X Y Z
Precuneus cortex	L1	5949	Negative	5.67	L	1.93, -68.9, 42.4
Lateral occipital cortex inferior division	L1	924	Negative	4.96	L	50.4, -62.5, -2.51
Lateral occipital cortex inferior division	L1	207	Negative	4.17	L	-45.9, -69, 4.92
Cingulate gyrus anterior division	L1	318	Negative	4.24	L	-1.83, 31.9, 23.1
Occipital fusiform gyrus	L1	226	Negative	4.34	L	-26.5, -66, -11.6
Lingual gyrus	L1	104	Negative	4	L	19.5, -57.4, 3.66
Precuneus cortex	L1	797	Negative	4.43	R	3.81, -71.6, 38.4
Intracalcarine cortex	L1	181	Negative	4.42	R	15.7, -62.7, 7.35
Lateral occipital cortex inferior division	L2	717	Negative	4.66	L	49, -64.2, -2.42
Lateral occipital cortex superior division	L2	549	Negative	4.75	L	31.8, -67.7, 38.9
Paracingulate gyrus	L2	268	Negative	4.58	L	2.35, 13.5, 50.5
Cingulate gyrus anterior division	L2	150	Negative	4.26	L	3.6, 29.3, 27.3

5.5 Discussion

Despite the cytoarchitectonically tripartite structure of the IPC into the caudal, the middle and the rostral clusters (Caspers et al., 2013), by considering general characteristics for this part of the brain, for years the IPC was believed to be a cognitive control area while the functions of the subsections of this cortical area are not representative of the whole IPC. In this study we addressed the connectivity profile of the middle IPC in the context of a task requiring cognitive control, characterized by two different levels of cognitive demand – with switching to the L1 being cognitively more demanding compared with switching to the L2. The results (see Table 5.1 for a summary) advanced our hypothesis about the modulating cortical areas (Tabassi Mofrad & Schiller, 2022); such brain areas are characterized by negative functional connectivity with cortical areas that are involved in task performance proportional to task difficulty. Yet, their patterns of functional associations in some other respects are not similar to the resting state-related parts of the brain. Thus, considering brain areas as either task-related or resting-state related cannot explain the functions of the modulating cortical areas.

Like the connectivity profile of the caudal IPC (Tabassi Mofrad & Schiller, 2022), the middle IPC demonstrated highly lateralized negative functional couplings with the cingulate gyrus anterior division in the cognitive control network, multiple parts of the visual cortex as well as the precuneus cortex, when participants performed the experiment. A negative functional connectivity refers to a negative Pearson cross-correlation coefficient between two brain areas (see Chen et al., 2011). According to our research findings, the number of the functional connectivity of the middle IPC with other cortical areas is affected by the level of cognitive demand since under the condition requiring a higher level of cognitive control (switching to the L1) the middle IPC had more functional connectivity with other cortical areas. However, the lateral functional association of this brain area remains independent of the cognitive demand as switching to the L1 is heavily (left) lateralized and switching to the L2 is entirely (left) lateralized.

As mentioned above, the cingulate gyrus anterior division is one of brain areas that regardless of the level of cognitive demand, the middle IPC has negative functional coupling with. In general, the cingulate gyrus anterior division is implicated in attention (Aarts & Roelofs, 2010), error prediction (Silvetti et al., 2013), task monitoring (Khamassi et al., 2015), anticipation of effort and reward in cognitive tasks (Vassena et al., 2014) and decision-making (Klein-Flügge et al., 2016; Shenhav et al., 2016). Besides, for long, the interplay of the IPC in its traditional definition and the ACC as part of the frontoparietal network has been reported in the literature, for example in flexibility, inhibition, working memory (Yarkoni et al., 2005), and during action observation (Apps et al., 2016). However, in investigating the involvement of the IPC in different executive functions and even the interaction of this cortical area with the ACC, previous studies considered the IPC as a whole while the tripartite structure of the IPC based on the correlated transmitter-receptor based organization of this brain area, into the caudal, the middle and the rostral clusters have clarified specific functional characteristics for the sub-divisions of the IPC (Corbetta et al., 2008; Caspers et al., 2013; Keysers & Gazzola, 2009). In fact, this is not the whole part of the IPC, but only the rostral IPC, that via positive functional coupling with the ACC and forming a strong circuit in the frontoparietal network, is involved in cognitive control (Tabassi Mofrad & Schiller, 2020). Nevertheless, the negative functional association of both the caudal IPC (Tabassi Mofrad & Schiller, 2022) and the middle IPC with the ACC, according to the current research results, prove lack of involvement for these two clusters of the IPC in the cognitive control network; both the middle and the caudal IPC have entirely dissimilar functions compared with those of the rostral IPC.

The middle IPC also showed negative functional association with the paracingulate gyrus which is in the medial prefrontal cortex. This cortical area is generally involved in attention, working, spatial or long-term memory (see Jobson et al., 2021), decision making (Euston et al., 2012) and cognitive control (Kragel et al., 2018). The negative functional coupling of the middle IPC with the paracingulate gyrus forms additional evidence for the fact that the middle IPC has no contribution to cognitive control.

In our study, the negative functional connectivity of the middle IPC with multiple parts of the visual cortex i.e. the lateral occipital cortex, the inferior and the posterior divisions, the occipital fusiform gyrus, the lingual gyrus, and the intracalcarine cortex – also demonstrated that this cortical area is not involved in general cognitive functions. Based on previous studies, positive functional association between the visual cortex and cortical areas in the frontoparietal network contributes to improved performance in tasks requiring cognitive abilities, for instance reading words (Horowitz-Kraus & Holland, 2015), in addition to word recognition and generating verbs (Twait & Horowitz-Kraus, 2019). Enhanced performance in the aforementioned cognitive functions, because of the positive functional association between parts of the cortex involved in cognitive control and visual regions, is believed to be the result of better visualization of the stimuli and hence the enhanced cognitive performance. However, the negative functional association of the middle IPC with different parts of the visual cortex, when participants did the experiment suggests deactivation of this part of cortex when cognitive control was required.

The deactivation in the functional connectivity of the middle IPC with brain areas involved in both cognitive control and general cognitive functions can feed the idea that this part of the cortex is resting state-related, however, our research results demonstrated that the functions of the middle IPC do not fit into that category either. As mentioned earlier, the middle IPC has negative functional association with the precuneus cortex. As reported by Fair et al. (2007), there is a high correlation between cortical areas which are involved in brain resting-state functional connectivity in the sense that they fluctuate together. In general, cortical areas which are active during the resting-state demonstrate negative activation when conducting a task, and those brain areas that are active when doing a task show negative activation during the resting-state condition, of which the functional connectivity of the somatosensory cortex with some brain areas involved in the frontoparietal network is an example (see Tabassi Mofrad & Schiller, 2019; Tabassi Mofrad et al., 2020). Since the middle IPC showed negative functional connectivity with the precuneus cortex, which is active during the resting-state, the middle IPC cannot be considered a resting state-related part of the cortex.

In detecting the connectivity profile of the caudal IPC, we reported that this cortical area does not fit into the classic categorization of brain areas as task-related, i.e., parts of the cortex that show activities related to task performance, and resting state-related, i.e. brain areas that are active in the absence of processing any external stimuli - according to which we proposed the hypothesis about modulating cortical areas (Tabassi Mofrad & Schiller, 2022). While the connectivity patterns of the rostral IPC demonstrated that this brain area in the frontoparietal network is involved in cognitive control functions (Tabassi Mofrad & Schiller, 2020), the middle IPC showed similar connectivity patterns to those of the caudal IPC.

Investigating the connectivity profile of the middle IPC has demonstrated that this part of the cortex also has distinctive connectivity patterns with other cortical areas in a modulating manner, characterized by deactivations in its functional associations, proportional to the difficulty of the task. This is in fact the negative functional connectivity of the modulating cortical areas with other parts of the cortex that contributes to task performance. The more demanding the task is, the more negative functional associations of the modulating cortical areas, in particular, with parts of the cortex in the visual region and in the cognitive control network/frontoparietal network would be observed. However, the functional connectivity patterns of the middle IPC, by having negative functional associations also with the precuneus cortex, revealed that this part of the brain is not resting state-related. This advanced our hypothesis about modulating cortical areas (Tabassi Mofrad & Schiller, 2022), the characteristics of which are not accommodated by the classic categorization of brain areas.

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