# 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 7

# General discussion

## 7.1 Summary of the findings

This dissertation addressed whether individual differences in cognitive control of language are reflected by resting state networks involved in cognitive control, namely, the frontoparietal network (FPT), the default mode network (DMN), and the salience network (SN). By focusing on the inferior parietal cortex (IPC), and the connectivity profiles of the clusters of this part of the cortex, this dissertation elucidated that it is not the whole IPC that contributes to language control and it elaborated on modulating cortical areas.

### 7.1.1 Individual differences in cognitive control

As reported in Chapter 2, by doing the independent component analysis, ten independent components related to three intrinsic networks of interest involved in cognitive control of language, that is, the FPT, the DMN, and the SN, were detected in the participants of my study. Conducting dual regression on the identified independent components between groups of participants with better and poorer performance in cognitive control of language revealed that two subcomponents of the FPN, that is, the dorsolateral prefrontal cortex (DLPFC) and the inferior parietal cortex (IPC) were involved in individual differences in this executive function - in the sense that there was increased functional connectivity between the left primary somatosensory cortex and the DLPFC in participants with better performance in language control. However, in participants with poorer performance in the same cognitive control function, there was increased coupling between the right primary somatosensory cortex and the inferior parietal cortex.

The fact that the DLPFC and the IPC are involved in cognitive control, in particular, in tasks requiring switching between stimuli, has already been mentioned in previous studies (Collette et al., 2005; Derrfuss et al., 2005). However, what the present research added to the literature concerns the contribution of these two cortical areas to cognitive control, due to the functional connectivity of the primary somatosensory cortex with these brain areas, how such connectivity profiles characterize individual differences in cognitive control of language.

#### 7.1.1.1 Primary somatosensory cortex and cognitive control

Generally, the left motor cortex is involved in mental rotation and motor control (Tomasino et al., 2005; Cona et al., 2017) if participants are right-handed. Since the somatosensory cortex converges to the motor cortex circuitry (for a review see Hooks, 2017), the functional connectivity between the DLPFC and the left primary somatosensory cortex in participants with better performance in cognitive control of language is indicative of using the left motor cortex circuitry to switch between languages. However, as the right primary somatosensory cortex apparently does not have the same efficient connections with the motor cortex circuitry, the functional connectivity between the IPC and the right primary somatosensory cortex marks poorer performance in switching between languages (see Chapter 2).

Reineberg et al. (2015) also reported the involvement of the primary somatosensory cortex in some executive functions such as working memory updating, task set shifting, and response inhibition, as reflected by the functional connectivity of this part of the cortex during resting state. They also emphasized the involvement of the somatosensory region in stimulus-response mapping when performing a task, as one of the reasons this part of the cortex is contributing to cognitive control. Since the DLPFC is also a cognitive control area, it seems that the functional coupling of the DLPFC and the left primary somatosensory creates a strong circuitry in cognitive control behavior. Besides, better performance in cognitive control of language - as indicated by the functional connectivity between the DLPFC and the left primary somatosensory in the present research (see Chapter 2) - has demonstrated that it is not the whole primary somatosensory cortex that contributes to cognitive control, but only the left part of this cortical area. This also highlights a dual function for the primary somatosensory cortex, depending on whether it is the left or the right side of this cortical area that couples with the sub-components of the FPN.

### 7.1.2 Contributions of rostral IPC to cognitive control

In Chapter 3, it is delineated how the rostral IPC contributes to cognitive control of language. As revealed by the psychophysiological interaction analyses, in language control, this part of the brain has asymmetrical and lateral functional connectivity with other cortical areas, modulated by cognitive demand.

#### 7.1.2.1 Connectivity profile of rostral IPC in switching to L1

In the context of the language switching experiment, when switching to the L1, both the right and the left rostral IPC had negative functional connectivity with the precuneus cortex. Besides, there were negative functional coupling between the left rostral IPC and the superior frontal gyrus, and between the right IPC rostral cluster and the postcentral gyrus. However, there was positive coupling of the right IPC rostral cluster with the cerebellum (the posterior lobe, the declive). Switching to L1 is cognitively more demanding than switching to L2 (Meuter & Allport, 1999), and the way the precuneus cortex contributes to cognitive control is by reducing its activity and connectivity relative to the degree of the difficulty of the task. That is, the more difficult the task is, the more negative activity of the precuneus cortex would be observed (Dang, O'Neil & Jagust, 2013; Gilbert et al., 2012). Hence, the reason the rostral IPC demonstrated negative functional connectivity with this part of the cortex when switching to the L1.

The superior frontal gyrus as part of the prefrontal cortex, is involved in selecting a response among competing candidates and activating possible responses (Bunge et al., 2002). The present research corroborated the interconnection between this part of the cortex and the parietal area reported in previous studies. Regarding the postcentral gyrus, as the location of the primary somatosensory cortex, previous studies reported positive functional connectivity between this brain area and the fronto-parietal network in individuals with better performance in executive functions during resting state fMRI (Reineberg et al., 2015). Since in that study I used task-based fMRI, decreased functional connectivity between the rostral IPC and the superior frontal gyrus was observed when switching to the L1.

Though the involvement of the cerebellum in cognitive control is not fully understood, it is known that this subcortical area contributes to the higher order cognitive functions (Bellebaum & Daum, 2007), in addition to the language control network (Green & Abutalebi, 2013; Krienen & Buckner, 2009). That supports my finding of the interconnection between the rostral IPC and the cerebellum, in particular in the more cognitively demanding context.

#### 7.1.2.2 Connectivity profile of rostral IPC in switching to L2

The psychophysiological interaction analyses also revealed that in switching to the L2, the right rostral IPC had positive functional connectivity with the anterior cingulate cortex (ACC) and the precentral gyrus. The ACC is involved in general speech monitoring (Christoffels, Formisano, & Schiller, 2007) and in monitoring conflict between languages and selecting the response language (Abutalebi et al., 2012). The ACC is also part of the language control network (Abutalebi & Green, 2008, 2016). Since the parietal areas also control response selection (Abutalebi et al., 2008), the positive coupling of the rostral IPC and the ACC, by forming a circuit for response selection, resulted in shorter reaction times in switching to the L2. On the other hand, the precentral gyrus affects the speed of responding (McGuire & Botvinick, 2010) and is involved in language switching (Hernandez et al., 2009; Luk et al., 2012). Previous studies also reported the interconnection between the fronto-parietal network and the precentral gyrus (Ma et al., 2014); the present research not only demonstrated the functional association of the rostral IPC and the precentral gyrus, but also specified that the precentral gyrus is involved in forward switching (switching to the L2) but not in backward switching. Moreover, the connectivity of the rostral IPC and the precentral gyrus highlights the facilitatory function in faster L2 production in the language switching context.

#### 7.1.2.3 Connectivity profile of rostral IPC modulated by cognitive demand

As explained in Chapter 3, cognitive demand modulated the connectivity patterns of the rostral IPC with other parts of the cortex. That resulted in differences in the type of functional connectivity and in laterality, when switching to the L1 (associated with higher cognitive demand) and switching to the L2 (associated with lower cognitive demand). While in switching to the L1, both negative and positive functional connectivity of the rostral IPC with other brain areas was observed, switching to the L2 was only associated with positive functional coupling of this part of the cortex. Furthermore, while both the right and the left rostral IPC had connectivity with other brain areas in switching to the L1, it is only the right rostral IPC that had functional associations when switching to the L2. Thus, the more cognitively demanding context of my experiments resulted in recruiting more underlying neural resources in a bilateral manner.

### 7.1.3 Unique connectivity profile of caudal IPC

As elaborated in Chapter 4, the functional connectivity analyses of the caudal IPC demonstrated that this part of the cortex had no similarity to a cognitive control area. More importantly, the caudal IPC showed negative functional connectivity with both the precuneus cortex, which is resting state-related, and other brain areas involved in processing general cognitive functions, in addition to cognitive control-related parts of the cortex. The connectivity profile of the caudal IPC provided enough evidence for the idea that the traditional categorization of different cortical areas into resting state and task related could not accommodate the functions of this part of the brain. Hence, the hypothesis for a new brain functional category as a modulating cortical area.

#### 7.1.3.1 Lateral connectivity patterns of caudal IPC

Both in switching to the L1 and to the L2, the caudal IPC demonstrated heavily left lateralized functional connectivity with other parts of the brain. However, the way the rostral and the caudal IPC showed lateral coupling is different from each other. Firstly, the laterality in functional associations of the rostral IPC - with this cortical area being involved in cognitive control - is determined by the cognitive demand, but the caudal IPC is not involved in cognitive control. In addition, the lateral functioning of this cortical area does not appear to be language related. The reason is that the left lateralized functional connectivity of the caudal IPC comes from the negative coupling of this brain area with other parts of the cortex, e.g., parts of the brain involved in general cognitive functions such as visual cortex, cognitive control related brain areas, and even part of the brain related to resting state, i.e., the precuneus cortex. However, the left lateralized function of the brain that previous studies reported in processing language is the result of positive activations and functional connectivity of language related left cortical areas. Besides, the general connectivity patterns of the caudal IPC make this part of the cortex different from resting state and task related parts of the brain.

#### 7.1.3.2 Similar connectivity profiles of caudal IPC in switching to L1 and L2

The left caudal IPC demonstrated negative coupling with the frontal pole, the anterior part of the prefrontal cortex, in both L1 and L2 switching contexts. This cortical area contributes to cognitive control and in general it is involved in higher-order cognitive functions (Hartogsveld et al., 2018; Zanto & Gazzaley, 2013). However, the negative functional connectivity of the caudal IPC with the frontal pole shows that the caudal IPC does not function like a cognitive control area.

The caudal IPC also demonstrated negative functional connectivity with the lateral occipital cortex, the inferior division, in switching to L1 and to L2. While positive coupling between the FPN and the visual cortex would result in better cognitive abilities such as word recognition (Twait & Horowitz-Kraus, 2019) and reading (Horowitz-Kraus & Holland, 2015), the lack of a positive fluctuation between the caudal IPC and the lateral occipital cortex shows that this parietal area is not involved in other cognitive functions.

#### 7.1.3.3 Different connectivity profiles of caudal IPC in switching to L1 and L2 switching

In comparison, in switching to the L1, which is cognitively more demanding than switching to the L2, the caudal IPC demonstrated more negative functional connectivity with other brain areas in different parts of the visual cortex, resting state-related cortical areas, and other part of the cortex related to cognitive control. Those brain areas include the fusiform gyrys, posterior division, the cuneal cortex and the lingual gyrus in the visual cortex, the precuneus cortex, and the cingulate gyrus, anterior division. When switching to L2, the caudal IPC did not have functional connectivity with such brain areas. Instead, the caudal IPC had negative functional connectivity with other parts of the visual cortex, that is, the lateral occipital cortex, superior division, which was not observed when switching to the L1. Having said that, the posterior fusiform gyrus, the cuneal cortex, the lingual gyrus (relating to switching to the L1), and the lateral occipital cortex, superior division (relating to switching to the L2) are all part of the visual cortex. The negative functional association of the caudal IPC with the visual cortex, as mentioned before, evidences that this cortical area is not involved in general cognitive functions. Besides, the negative functional connectivity of the caudal IPC with the precuneus cortex was observed when switching to the L1 which is cognitively more demanding. Regarding cognitive control areas, while in both L1 and L2 switching conditions, the caudal IPC had negative functional connectivity with the frontal pole, in switching to the L1, the seed region also had negative connectivity with the anterior cingulate gyrus. The negative coupling of the caudal IPC with more cognitive control areas when the task is cognitively more demanding also points to the modulating function of the caudal IPC.

#### 7.1.3.4 Modulating function of caudal IPC

Since in performing the language switching experiment, the caudal IPC showed negative coupling with the precuneus cortex, this parietal area cannot be associated with the resting state brain areas. Likewise, the negative coupling of the caudal IPC with cognitive control areas evidences that this part of the brain does not contribute to cognitive control in the FPN. Furthermore, the negative connectivity of the caudal IPC with different parts of the visual cortex shows that this brain area is not involved in general cognitive functions. Thus, the caudal IPC is not a task-related part of the brain.

The present research revealed that the traditional categorization of brain areas does not explain the connectivity profile of the caudal IPC. This cortical area functions in a modulating manner, in the sense that the deactivations of the caudal IPC, relative to task difficulty, contributes to task performance. The more difficult the task is or rather the higher the cognitive demand is, the more the number of negative functional connectivity of the caudal IPC with both task and resting state-related parts of the brain would be observed. Hence, the modulating role of this part of the cortex.

### 7.1.4 Connectivity profile of middle IPC

In Chapter 5, the connectivity profile of the middle IPC in the context of the language switching experiment was investigated, by which the hypothesis about the modulating cortical areas was advanced.

The connectivity patterns of the middle IPC, similar to those of the caudal IPC, were highly lateralized - independent of the cognitive demand - while being negatively connected with different parts of the visual cortex, the precuneus cortex and the anterior division of the cingulate gyrus, in addition to the paracingulate gyrus which is also involved in cognitive control functions (Jobson et al., 2021; Kragel et al., 2018). At the same time, the negative functional associations of the middle IPC was influenced by cognitive demand, with the more cognitively demanding experimental condition, resulting in more negative functional connectivity with other parts of the brain.

The connectivity profile of the middle IPC demonstrates that this part of the cortex, like the caudal IPC, is not a cognitive control area due to its negative functional connectivity with the anterior division of the cingulate gyrus and the paracingulate gyrus. Moreover, the negative functional associations of the middle IPC do not mean that this part of the brain is resting state-related because of its negative coupling with the precuneus cortex. Moreover, the negative connectivity of this parietal area with different parts of the visual cortex suggests that the middle IPC does not contribute to general cognitive functions and is not a task-related part of the cortex.

Similar to the caudal IPC, the connectivity profile of the middle IPC is not explained by the classic categorization of brain areas as resting state and task-related, further supporting the hypothesis about modulating cortical areas.

## 7.2 Integration of findings

According to the structural properties of the IPC, this part of the brain consists of three clusters, namely, the rostral, the middle and the caudal (Caspers et al., 2006; 2013). Based on the idea that the functional characteristics of the sub-regions of the IPC are underlined by their structural organization and given the inconsistent nature of research findings on how the IPC functions, under the same experimental conditions I investigated the functional connectivity profiles of the clusters of the IPC in a task which required cognitive control of language, with two different levels of cognitive demand.

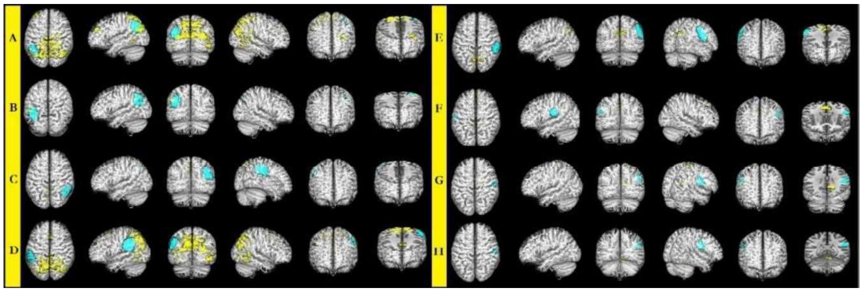
Research findings (Figures 7.1 & 7.2) revealed that it is not the whole IPC that is involved in cognitive control but only the rostral cluster of this brain area (Tabassi Mofrad & Schiller, 2020). The rostral IPC via positive functional connectivity with the anterior division of the cingulate gyrus, the precentral gyrus and the posterior lobe of the cerebellum, forms a strong response selection circuit in the frontoparietal network, facilitates cognitive control of language and further evidences its involvement in the language control network, respectively.

The caudal IPC, however, is not only characterized with entirely different connectivity patterns as those of the rostral IPC but proves lack of involvement in cognitive control (Tabassi Mofrad & Schiller, 2022). Firstly, this brain area has negative functional connectivity with different parts of the visual cortex. Given this is the positive functional association between brain areas involved in cognitive control and the visual cortex that improves cognitive performance, the negative coupling of the caudal IPC with e.g., the inferior and posterior divisions of the lateral occipital cortex, the cuneal cortex, the temporal occipital fusiform, and the lingual gyrus highlight the type of functional connectivity which is dissimilar to those of cognitive control-related parts of the cortex. In addition, the caudal IPC has negative functional associations with the frontal pole as well as the anterior division of the cingulate gyrus. While these brain areas are heavily involved in processing executive functions, such negative functional associations show that the caudal IPC is not involved in processing cognitive control in the frontoparietal network. Furthermore, it is revealed that this cluster of the IPC also has negative functional connectivity with the precuneus cortex which is a resting state-related part of the brain.

Taking into account that brain areas that are involved in task performance decrease activity during the resting-state, and those parts of the cortex that are active in the absence of external stimuli decrease activity when involved in a task, the negative functional connectivity of the caudal IPC with the precuneus cortex indicates that the caudal IPC is not resting state-related part of the brain. Having negative connectivity patterns with both the resting-state and the task based-related cortical areas characterize the caudal IPC with a distinctive function, highlighting that the traditional classification of brain areas as being active either when involved in a task or when not focusing on external stimuli cannot explain the behavior of the caudal IPC.

**Figure 7.1**

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

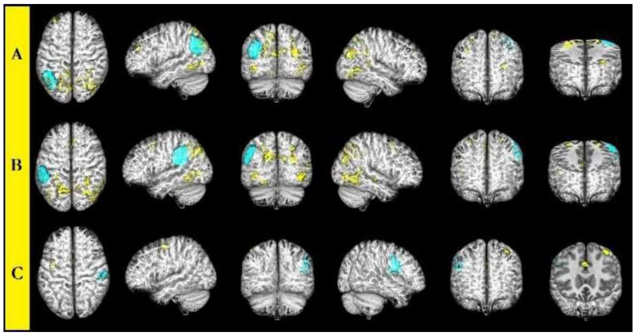


*Note*. The yellow color demonstrates brain areas that the clusters of the IPC (shown in cyan) are functionally connected with, under the more demanding context of cognitive control of language. The descriptions of each row are as follows: A) negative functional connectivity of the left caudal IPC with the precuneus cortex, the inferior and posterior divisions of the lateral occipital cortex, the frontal pole, the anterior division of the cingulate gyrus, the posterior division of the temporal occipital fusiform and the lingual gyrus, B) positive functional connectivity of the left caudal IPC with the IPC caudal cluster left (PGa), C) negative functional connectivity of the right IPC with the cuneal cortex, D) negative functional connectivity of the left middle IPC with the precuneus cortex, the inferior division of the lateral occipital cortex, the anterior division of the cingulate gyrus, the occipital fusiform gyrus, and the lingual gyrus, E) negative functional connectivity of the right middle IPC with the precuneus cortex and the intracalcarine cortex, F) negative functional connectivity of the left rostral IPC with the superior frontal gyrus and the precuneus cortex, G) negative functional connectivity of the right rostral IPC with the postcentral gyrus and the precuneus cortex, H) positive functional connectivity of the right rostral IPC with the posterior lobe of the cerebellum.

The negative functional connectivity of the caudal IPC with other parts of the brain is influenced by cognitive demand - the more demanding the task is, the more negative functional connectivity of this subdivision of the IPC with both the resting state-related and the cognitive control-related brain areas would be observed. Therefore, it is the decreased activation in the functional connectivity of the caudal IPC with other parts of the brain, relative to the level of cognitive demand, that contributes to task performance.

**Figure 7.2**

*Demonstration of the clusters of the IPC and brain areas that the seed regions had functional connectivity with, when switching to L2.*



*Note*. The yellow color demonstrates brain areas that the clusters of the IPC (shown in cyan) are functionally connected with, under the less demanding context of cognitive control of language. The descriptions of each row are as follows: A) negative functional connectivity of the left caudal IPC with the inferior and posterior divisions of the lateral occipital cortex and the frontal pole, B) negative functional connectivity of the left middle IPC with the inferior and posterior divisions of the lateral occipital cortex, the paracingulate gyrus and the anterior division of the cingulate gyrus, C) positive functional connectivity of the right rostral IPC with the precentral gyrus and the anterior division of the cingulate gyrus.

Given such unique connectivity profile of the caudal IPC, I considered a modulating role for this brain area. My assumption on such a concept was further confirmed having observed the functional connectivity patterns of the middle IPC which are comparable to those of the caudal IPC, by demonstrating negative functional connectivity with similar parts of the visual cortex, with cognitive control-related parts of the brain and with the precuneus cortex, which is resting state-related (Tabassi Mofrad & Schiller, 2023). The middle inferior parietal cortex is likewise characterized with more negative functional associations with other parts of the brain when the task is more demanding, while its connectivity profile makes this cortical area dissimilar to task-related and resting state-related parts of the cortex.

The connectivity profiles of the clusters of the IPC that I have discussed elucidate that only the rostral IPC is involved in processing cognitive control - with the middle and the caudal IPC demonstrating negative connectivity with parts of the brain that are engaged in executive functions, such as the frontal pole, the paracingulate gyrus and the cingulate gyrus anterior division. Moreover, the functional connectivity patterns of the middle and the caudal IPC have highlighted another brain functional category beyond the classic definitions, as modulating cortical areas, the functional associations of which are disparate from parts of the cortex that are involved in task performance and brain areas which are active during the resting-state.

## 7.3 Limitations and future research

For the studies reported in this dissertation, participants' behavioral data from a language switching experiment were collected four weeks after their neuroimaging data were acquired in the MRI lab. This procedure is in line with previous studies (e.g., Anderson et al., 2018; Grady et al., 2015). However, it is also possible to collect the behavioral data at the same time when participants do the experiment inside the MRI scanner by using an MRI compatible microphone. Using such a microphone - although being very expensive - obviates the need for the researcher to repeat the experiment, and that would save time both for the researcher and for the participants. Unfortunately, however, I did not have access to such a microphone at the time.

In this dissertation, I presented the research results from resting-state fMRI and task-based fMRI, by which it became clear that it is only the rostral part of this cortical area that contributes to cognitive control in the FPN - among other findings. In contrast, the middle and the caudal IPC have distinctively modulating functions marked by their deactivation in task performance relative to the degree of the cognitive demand of the task while such functions are not similar to parts of the cortex involved in resting-state. Future research may investigate the white matter connectivity of the rostral, the middle, and the caudal IPC to examine whether different functional profiles of the clusters of the IPC are also reflected by white connectivity with other parts of the brain.

In this study, I recruited healthy individuals without any report and history of neurological or psychiatric problems. Future research may address the functional connectivity profiles of the clusters of the IPC in individuals with dysfunction in cognitive control to examine how the cognitive control functions of the rostral IPC and the modulating roles of the middle and the caudal IPC would demonstrate different patterns of activity, to contribute to the literature of clinical neuroscience.

## 7.4 Conclusion

Resting state functional connectivity of brain areas in the FPN reflected individuals' performance related to cognitive control. The present research demonstrated that the connectivity of DLPFC with the left primary somatosensory cortex (BA1) and the association of the inferior parietal cortex with the right primary somatosensory cortex (BA2) indicate better and poorer performance in cognitive control of language, respectively. Moreover, during task-based fMRI the connectivity profile of the rostral IPC was not only modulated by the cognitive demand both asymmetrically and laterally, but this part of the brain also proved to contribute to cognitive control in the FPN - while that is not the case with the middle and the caudal IPC. The functional connectivity of these two cortical areas revealed that they have negative functional associations in a modulating manner not only with some cortical areas in the FPN – suggesting that they are not part of the control network – but also with brain areas involved in general cognitive functions such as the visual cortex. At the same time the connectivity profile of the middle and the caudal IPC have no similarity to those of the resting state-related cortical areas. In fact, in task performance, the middle and the caudal IPC demonstrated deactivations in the patterns of their functional connectivity, influenced by cognitive demand. In the more demanding context, the number of the negative functional couplings of these parts of the cortex with other brain areas increased. However, that does not associate the middle and the caudal IPC with the resting-state parts of the brain as these parietal areas also demonstrated negative connectivity with the precuneus cortex. The present research revealed that the traditional categorization of cortical areas as task-related and resting state-related cannot accommodate the functions of the middle and the caudal IPC, by which I hypothesized a functional brain category, beyond classic definitions, namely modulating cortical areas.

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