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Distinct connectivity patterns in clusters of inferior parietal cortex: from a cognitive control hub to modulating cortical areas

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ABSTRACT

The inferior parietal cortex (IPC) is a complex brain region, composed of the rostral, the middle and the caudal clusters, and functionally connected to several other parts of the brain. Various executive functions are suggested to be governed by the IPC, however, by ignoring the tripartite structure of this region, contradictory research reports abound in the literature. Here, we elaborated on the functional connectivity patterns of the clusters of the IPC, highlighting evidence that only the rostral cluster of this part of the brain is involved in cognitive control, not the entire IPC. We also underscored the unique connectivity profile of the middle and the caudal clusters which are not accommodated by the traditional classification of brain areas as either being task-based or being related to the resting-state functionality of the brain. The middle and the caudal IPC demonstrate negative functional associations with cortical areas involved in general cognitive functions, executive functions, in addition to the precuneus cortex, proportional to cognitive demand, in a modulating manner, while remaining distinct from resting-state related parts of the cortex.

Introduction

The inferior parietal cortex (IPC) is usually known as being involved in executive functions, such as auditory selective attention, memory, and processing language (Bareham et al., 2018; Buchsbaum et al., 2011; Bzdok et al., 2016). However, such roles are contrasted with some other research findings that consider this region part of the default mode network (see Doose et al., 2020; Mars et al., 2012; Raichle, 2015) which decreases its activity when brain is focused on explicit tasks (Smallwood et al., 2021); such contradictory findings about the functions of the IPC have remained in the literature for years.

With reference to the correlated transmitter receptor-based organizations of the IPC, this brain region consists of three clusters, namely, the rostral (areas PFop, PFt, PFcm), the middle (areas PF and PFm) and the caudal (areas PGa and PGp) (Caspers et al., 2006, 2008). The white matter connectivity of the IPC also suggests differentiations within this parietal area. According to Caspers et al. (2011), regarding the fiber tracts between the clusters of the IPC and other parts of the brain, the rostral IPC is predominantly connected to the superior parietal cortex and the somatosensory cortex, while the caudal IPC is strongly connected to the lateral occipital cortex and the anterior temporal cortex, in addition to the superior parietal cortex. The white matter connectivity of the caudal IPC with the occipital gyrus is also reported by Petit et al. (2023). The middle IPC, however, is suggested to have associations with cortical areas that the rostral and the caudal clusters are structurally connected to. It is noteworthy that both the rostral and caudal parts of this brain region are also connected to the inferior frontal cortex, and the posterior temporal cortex (Caspers et al., 2011) with the fiber tracts between the caudal IPC and the frontal and the temporal lobes being also corroborated by Burks et al. (2017).

The structural parcellation of the IPC logically suggests functional differentiation within this parietal region, however, in investigating the contributions of this part of the brain to different cognitive functions, numerous studies considered the IPC as a whole, regardless of the fact that each cluster of this brain region might demonstrate a distinctive behavior. Until recently, the functional connectivity of the clusters of the IPC related to cognitive control had not been mapped (Tabassi Mofrad and Schiller, 2020; 2022; 2023). As a result, the contribution of the rostral, the middle and the caudal IPC to such functions had not been clarified in a comparative manner, and the inconsistent research findings on how the IPC functions remained unaddressed. It is worth mentioning that brain areas associated with cognitive control of

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language are similar to cortical/subcortical areas involved in other executive functioning (Abutalebi and Green, 2008; Branzi et al., 2016).

In this perspective, we elaborate on the discrepancies that arise from overlooking the cluster-specific organization of the IPC, starting with the contribution of the (rostral) IPC to cognitive control and clarifying that the involvement of the IPC in executive functions is limited to this cluster.

We also refer to the opposing research findings that strongly consider the IPC related to the resting-state functionality of the brain, while the negative functional associations of the middle and the caudal IPC, being generalized to the whole IPC, have made this cortical region seem resting-state related. Thus, the objectives of this perspective are to elucidate on the underlying reasons for the contradictory research reports in the literature regarding how the IPC functions and elucidating the distinctive connectivity patterns of the caudal and the middle IPC, which are unaccommodated by traditional categorization of brain areas as being either involved in task performance or being resting-state related.

Contradictory research reports about IPC

IPC as a cognitive control region

For over twenty years, the IPC has been considered a cognitive control-related brain region and associated with different executive functions; in early studies, the involvement of this part of the cortex in visual, auditory, haptic attention (for a review see Culham and Kanwisher, 2001), and in shift of attention – with damage to this region resulting in spatial neglect in patients (for a review see Behrmann et al., 2004) – was predominately emphasized in the literature. Examples of other executive functions reported to be controlled by the IPC include working memory (Baldo and Dronkers, 2006), action plans (Jubault et al., 2007), sequence processing (Bahlmann et al., 2012), cognitive flexibility and inhibition (Niendam et al., 2012).

According to Wisniewski et al. (2015), the IPC has an important role in associating behavior to its outcomes by flexibly reconfiguring its functions. The correlation of performance in executive functions with the IPC, using multiple executive tasks, were also reported by Breukelaar et al. (2017). Besides, controlling auditory selective attention (Bareham et al., 2018), and conflict modulation, in particular, during Flanker and Stroop tasks (Xiao et al., 2023) are some of other functions attributed to the IPC.

The rostral, the middle and the caudal IPC each has a different transmitter receptor-based organization and although the structural differentiations in the clusters of the IPC have already been pointed out (Caspers et al., 2006, 2008, 2013; Ruschel et al., 2014), by considering this brain region as a whole, associating various cognitive control functions to the entire IPC has continued to this date.

Considering Brodmann areas, the IPC is divided into the supramarginal gyrus (area 40), which predominately includes the rostral IPC, and the angular gyrus (area 39) which covers the caudal IPC; this is in fact the supramarginal gyrus which is associated with cognitive control related functions. Contradictory research reports could have also been prevented by considering the IPC as areas 39 and 40, although the middle IPC is not addressed by that division. In some research reports the supramarginal gyrus was even considered separate from the IPC, adding to the inconsistent research findings on how the IPC is understood. For example, by investigating the activations of brain areas related to information uncertainty (Wu et al., 2021) and in reporting the functional anatomy of the cognitive control network (Wu et al., 2020), the activations of the IPC and the supramarginal gyrus were reported unconnectedly, while part of the activations of the IPC is due to the behavior of the supramarginal gyrus.

IPC as part of the default mode network

In defining the resting-state functionality of the brain and the concept of the default mode, the IPC has also been numerously considered a task-negative part of the cortex. Among early studies, Gusnard et al. (2001), considered the lateral parietal lobule, of which the IPC is a part, task-independent. Besides, they specifically refereed to Brodmann areas 39 and 40, as part of the brain with a baseline or resting-state function; Raichle et al. (2001) also attributed the parietal areas with the default mode of the brain. By this time, the structural differentiations of the clusters of the IPC were not yet clarified, however, in later studies the IPC was yet considered as a unified whole, resulting in the contradictory research findings in the literature.

In some research reports, the IPC was believed to be one of the four core brain regions that decreased activation during attention demanding tasks (see Whitfield-Gabrieli and Ford, 2012), and in various studies this part of the cortex has been strongly reiterated as being part of the default mode network (d'Acremont et al., 2013; Davey et al., 2016; Domakonda et al., 2019; Doose et al., 2020; Lu et al., 2012; Raichle et al., 2015).

Undoubtedly, the IPC cannot be a cognitive control area and at the same time being related to the default mode of the brain. This is in fact the rostral IPC that contributes to executive functions; however, the functional associations of the caudal and the middle clusters of the IPC have made this part of the brain seem resting-state related; yet, these two parietal areas have very distinctive functional connectivity profile that characterizes them even unassociated with the brain baseline function.

Contributions of the rostral IPC to cognitive control

The rostral IPC is the only cluster of this brain region that is involved in cognitive control. By addressing the functional connectivity profile of the clusters of the IPC related to cognitive control, Tabassi Mofrad and Schiller (2020) reported that under more demanding contexts the rostral IPC has negative functional coupling with the superior frontal gyrus, the postcentral gyrus, and positive association with the cerebellum (the posterior lobe, the declive). Regarding the postcentral gyrus, as the location of the primary somatosensory cortex, previous studies reported positive functional connectivity between this brain area and the FPN in individuals with better performance in executive functions during resting-state fMRI (Reineberg et al., 2015). However, since Tabassi Mofrad and Schiller (2020) used task-based fMRI, the decreased functional connectivity between the rostral IPC and the superior frontal gyrus contributes to cognitive control. Besides, the cerebellum is known to contribute to higher order cognitive functions (Bellebaum and Daum, 2007), in addition to being part of the language control network (Green and Abutalebi, 2013; Krienen and Buckner, 2009). Thus, the positive functional connectivity of the rostral IPC and the cerebellum corroborates previous findings of the involvement of these two brain areas in cognitive control (see Fig. 1).

Under the same experimental conditions, both the right and the left rostral IPC have negative functional connectivity with the precuneus cortex. When brain processes external stimuli, the precuneus cortex reduces its activity 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 et al., 2013); hence, the reason the rostral IPC, as a task-related cortical area, demonstrate negative functional connectivity with this part of the brain.

When thers is less cognitive demand, the right rostral IPC has positive functional connectivity with the anterior cingulate cortex (ACC) and the precentral gyrus. The ACC, as part of the control network (Abutalebi and Green, 2008, 2016) is involved in e.g. speech monitoring (Christoffels et al., 2007), monitoring the conflict between languages (Abutalebi et al., 2012), affective evaluation of conflict (Braem et al., 2017), adaptation of action plans (Brockett et al., 2020) and perdition of error (Alexander and Brown, 2019). The positive coupling of the rostral

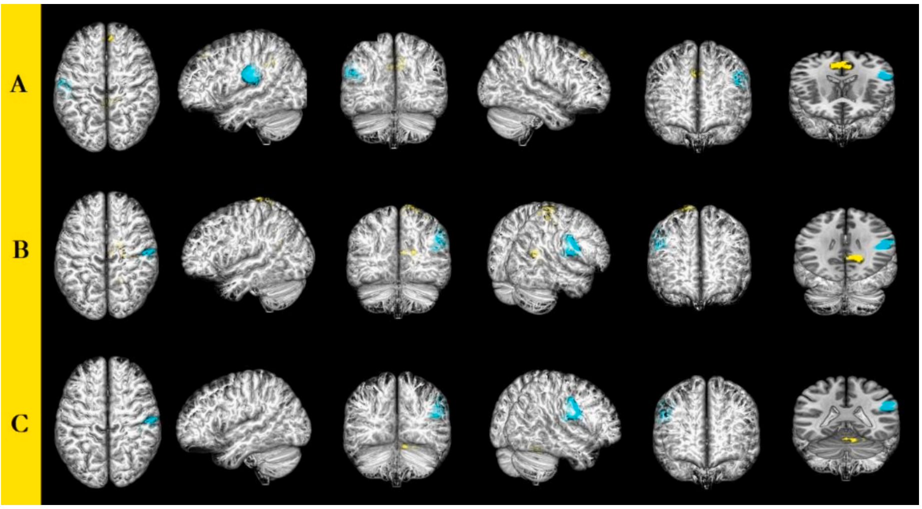

Fig. 1. The yellow color shows brain areas that the rostral IPC (shown in cyan) is functionally connected to, in the more demanding contexts of cognitive control. The descriptions of each row are as follows: A) negative functional connectivity of the left rostral IPC with the superior frontal gyrus and the precuneus cortex, B) negative functional connectivity of the right rostral IPC with the postcentral gyrus and the precuneus cortex, C) positive functional connectivity of the right rostral IPC with the posterior lobe of the cerebellum (Tabassi Mofrad and Schiller, 2020). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

IPC with the ACC, by forming a strong circuit and resulting in better task performance, in addition to the coupling of this parietal area with the precentral gyrus, brings about a facilitatory function in cognitive control (see Fig. 2).

Regarding the white matter connectivity of the rostral IPC with other parts of the brain, it is reported that this parietal area is connected to the superior parietal cortex, the inferior frontal cortex, the posterior temporal cortex and the somatosensory cortex (Caspers et al., 2011). Given brain functional connectivity is controlled by the underlying structural connectivity (Honey et al., 2009), the functional associations of the rostral IPC elucidated by Tabassi Mofrad and Schiller (2020) accord with the white matter structural connectivity of this brain area.

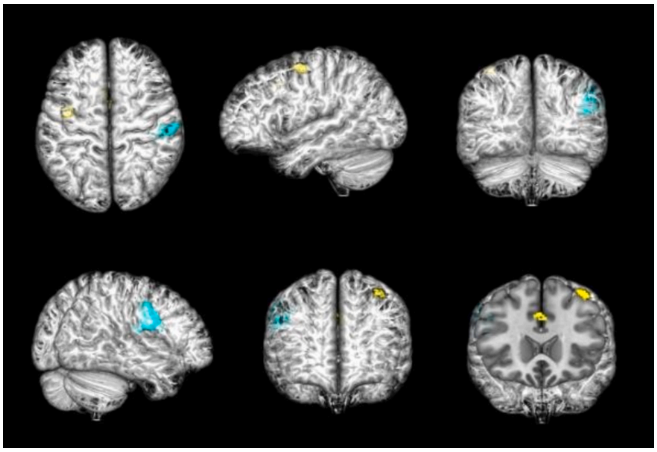

Fig. 2. The yellow color shows brain areas (the precentral gyrus and the anterior division of the cingulate gyrus) that the right rostral IPC (shown in cyan) has positive functional connectivity with, in the less demanding contexts of cognitive control (Tabassi Mofrad and Schiller, 2020). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Unique connectivity profile of the caudal and middle IPC

Connectivity patterns of caudal IPC

The caudal IPC, however, is characterized by entirely different connectivity patterns from those of the rostral IPC. In fact, this part of the cortex has no similarity to a cognitive control area, in particular, by having negative functional connectivity with the ACC (Tabassi Mofrad and Schiller, 2020) which is heavily involved in processing cognitive control (Braem et al., 2017; Brockett et al., 2020). Besides, regardless of the degree of the cognitive demand, the left caudal IPC has negative coupling with the frontal pole, the anterior part of the prefrontal cortex, which contributes to cognitive control (Hartogsveld et al., 2018; Menon and D'Esposito, 2022; Zanto and Gazzaley, 2013); such negative functional associations of the caudal IPC with cognitive control-related parts of the cortex present evidence that the caudal IPC is not involved in processing cognitive control in the FPN (see Figs. 3 and 4).

According to Tabassi Mofrad and Schiller (2022), the caudal IPC also has negative functional connectivity with different parts of the visual cortex when the task requires cognitive control. In comparison, under more demanding contexts, the caudal IPC demonstrates negative functional connectivity with the fusiform gyrus, posterior division, the cuneal cortex, the lateral occipital cortex, the inferior division, and the lingual gyrus; under the less demanding contexts, the caudal IPC has negative functional connectivity with the lateral occipital cortex, the superior division (Tabassi Mofrad and Schiller, 2022). Thus, more cognitive demand results in more negative functional connectivity of the caudal IPC with different parts of the visual cortex.

While positive coupling of brain areas in the FPN with the visual cortex would bring about better cognitive abilities such as word recognition (Twait and Horowitz-Kraus, 2019) and reading (Horowitz-Kraus and Holland, 2015), the lack of a positive fluctuation between the caudal IPC and different parts of the visual cortex – the type of functional connectivity which is dissimilar to those of cognitive control-related parts of the brain – demonstrates that this parietal area is not involved in other cognitive functions either.

Regarding the precuneus cortex, this part of the brain is active in the absence of external stimuli. Taking into account that cortical areas that are involved in task performance decrease activity during the resting-state, and those parts of the cortex that are active when brain is not busy with processing explicit tasks decrease activity when performing a

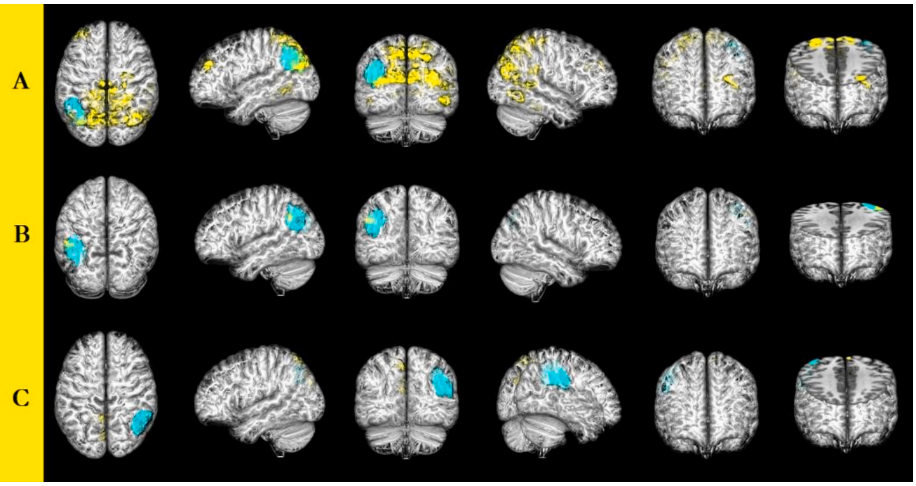

Fig. 3. The yellow color shows brain areas that the caudal IPC (shown in cyan) is functionally connected to, in the more demanding contexts of cognitive control. The descriptions of each row are as follows: A) negative functional connectivity of the left caudal IPC with the precuneus cortex, the inferior 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 caudal IPC with the cuneal cortex (Tabassi Mofrad and Schiller, 2022). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

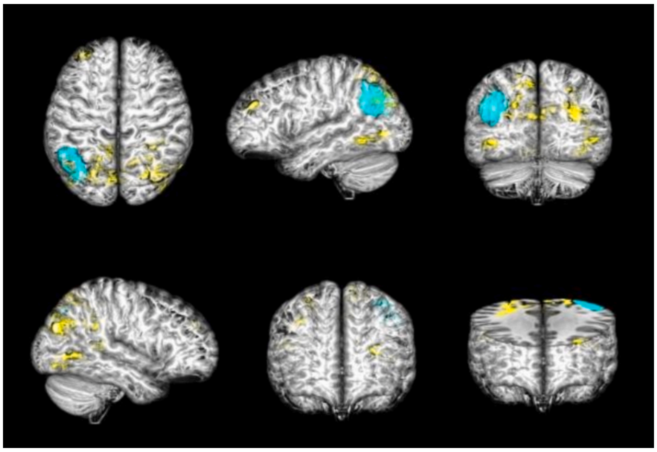

Fig. 4. The yellow color shows brain areas (the inferior and posterior divisions of the lateral occipital cortex and the frontal pole) that the left caudal IPC (shown in cyan) has negative functional connectivity with, in the less demanding contexts of cognitive control (Tabassi Mofrad and Schiller, 2022). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

task, the negative functional connectivity of the caudal IPC with the precuneus cortex indicates that this parietal area is not resting-state related. As mentioned earlier, the negative coupling of the caudal IPC with cognitive control-related brain areas provides evidence that this part of the cortex does not contribute to cognitive control in the FPN. Furthermore, the negative functional connectivity of the caudal IPC with different parts of the visual cortex demonstrates that this brain area is not involved in general cognitive functions. Thus, the caudal IPC is not a task-related part of the brain either.

As for the fiber tracts between the caudal IPC and other cortical areas, the structural connectivity of this parietal area with the occipital cortex, the temporal cortex, the frontal cortex, and the superior parietal cortex are emphasized in the literature (Burks et al., 2017; Caspers et al., 2011; Petit et al., 2023). Such structural connectivity also explains the functional associations of the caudal IPC e.g. with different parts of the visual cortex, the precuneus cortex, and the frontal pole.

Connectivity patterns of middle IPC

Regarding the middle IPC, Tabassi Mofrad and Schiller (2023) reported that the connectivity patterns of this brain area are very similar to those of the caudal IPC, by having negative coupling with different parts of the visual cortex, the precuneus cortex, the anterior division of the cingulate gyrus, and the paracingulate gyrus, which are cognitive control-related parts of the brain (Jobson et al., 2021; Kragel et al., 2018).

In previous studies, the functions of the cingulate gyrus anterior division in different executive functions such as decision making, task monitoring, error prediction (Khamassi et al., 2015; Shenhav et al., 2016; Silvetti et al., 2013) and the involvement of the paracingulate gyrus in cognitive control (Kragel et al., 2018) have been elaborated on. The negative functional connectivity of the middle IPC with such brain areas underline that the middle IPC does not contribute to cognitive control.

The negative functional associations of the middle IPC are influenced by cognitive demand, with the more cognitively demanding conditions, resulting in more negative functional coupling with other parts of the brain involved in task performance (see Figs. 5 and 6). However, such negative functional associations of the middle IPC do not indicate that this part of the brain is resting-state related because of its negative coupling with the precuneus cortex – a brain area with reduced activity when performing a task. Furthermore, the middle IPC has negative connectivity with different parts of the visual cortex; improving cognitive performance, by better visualizing the stimuli, is the result of positive functional coupling of brain areas involved in cognitive control with the visual cortex. The absence of such positive functional associations of the middle IPC with e.g. the lateral occipital cortex, the occipital fusiform gyrus, and the lingual gyrus emphasize that this parietal area does not contribute to general cognitive functions and is not a task-related part of the cortex.

Modulating cortical areas

Having negative connectivity patterns with both task-related parts of the brain and cortical areas related to the resting-state functionality of the brain characterize the caudal and the middle IPC by distinctive functions, highlighting that the traditional categorization of cortical areas as either resting-state related or task-related does not

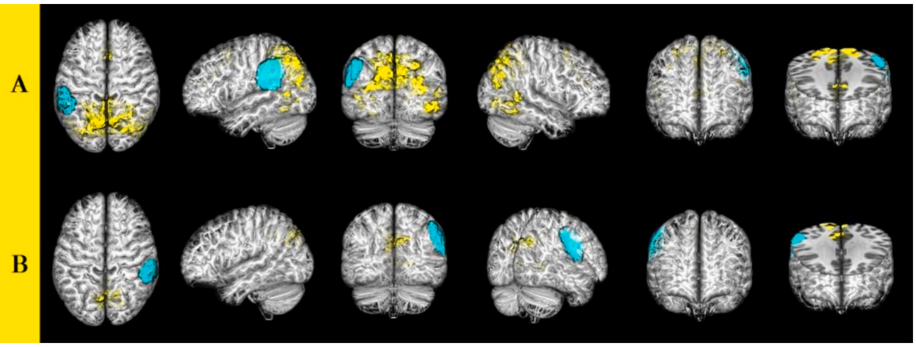

Fig. 5. The yellow color shows brain areas that the middle IPC (shown in cyan) is functionally connected with, in the more demanding contexts of cognitive control. The descriptions of each row are as follows: A) negative functional connectivity of the left middle IPC with the precuneus cortex, the inferior division of the lateral occipital cortex, the anterior division of the cingulate gyrus, the occipital fusiform gyrus, and the lingual gyrus, B) negative functional connectivity of the right middle IPC with the precuneus cortex and the intracalcarine cortex (Tabassi Mofrad and Schiller, 2023). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

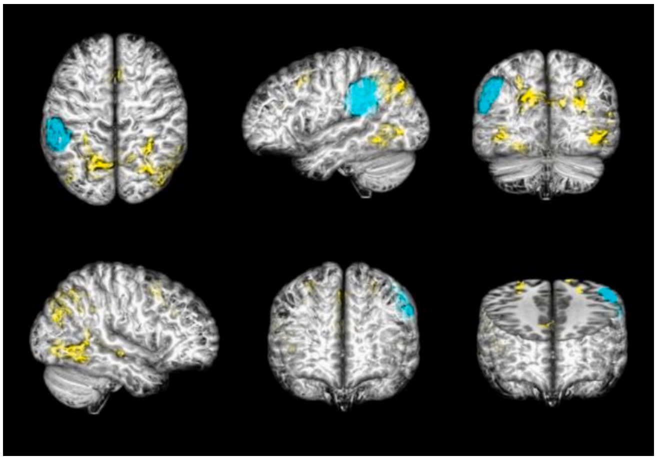

Fig. 6. The yellow color shows brain areas (the inferior and posterior divisions of the lateral occipital cortex, the paracingulate gyrus and the anterior division of the cingulate gyrus) that the left middle IPC (shown in cyan) has negative functional connectivity with, in the less demanding contexts of cognitive control (Tabassi Mofrad and Schiller, 2023). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

accommodate the behavior of these parietal areas. To clarify, the negative functional associations of the caudal and the middle IPC with the precuneus cortex, which is resting-state related, demonstrate that they are not fluctuating together. Since the caudal and the middle IPC have negative functional coupling with parts of the FPN, thus such parietal areas are not part of the control network. Besides, the negative functional connectivity of these clusters of the IPC with different parts of the visual cortex provide evidence that the caudal and the middle IPC are not involved in general cognitive functions.

The functional associations of the caudal and the middle IPC have demonstrated the distinctive functions of these parts of the cortex, characterized by deactivations in coupling with other brain areas, proportional to the level of cognitive demand. These parts of the brain function in a modulating manner, in the sense that the deactivations of the caudal and the middle IPC, relative to cognitive demand, contribute to task performance. The more difficult the task is, the more the number of negative functional connectivity of the middle and the caudal IPC as modulating cortical areas, with both task-related and resting- state related parts of the cortex would be.

Conclusion

The connectivity profile of the clusters of the IPC elucidate that it is not the whole IPC that is involved in cognitive control but only the rostral cluster of this brain region (Tabassi Mofrad and Schiller, 2020) with the middle and the caudal IPC demonstrating negative associations with parts of the brain that are engaged in executive functions (Tabassi Mofrad and Schiller, 2022; 2023). In previous studies, by ignoring the tripartite structure of the IPC, if the experimental conditions necessitated cognitive control, the functions of the rostral IPC were generalized to the whole IPC; however, if the experiment was conducted during the resting-state or in the absence of an explicit task, the negative functional associations of the middle and the caudal IPC were considered as representative of the whole IPC; hence, the contradictory research results on how this part of the brain functions. Given the unique connectivity profile of the middle and the caudal IPC, we considered modulating roles for these parietal areas, which demonstrate negative functional coupling with different parts of the visual cortex, cognitive control-related parts of the brain and with the precuneus cortex (Tabassi Mofrad and Schiller, 2022; 2023); the more difficult the task is, the more negative functional associations of these clusters of the IPC with other parts of the brain would be observed, while their connectivity profile make these cortical areas dissimilar to task-related and resting state-related brain areas. The functional connectivity patterns of the middle and the caudal IPC provide evidence that the traditional categorization of cortical areas does not accommodate the functions of these parietal areas; the functional associations of the middle and the caudal IPC have highlighted another brain functional category as modulating cortical areas, beyond the classical definitions, the functional connectivity of which are disparate from parts of the cortex that are involved in task performance and brain areas related to the resting-state functionality of the brain.

CRediT authorship contribution statement

Fatemeh Tabassi Mofrad: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Niels O. Schiller:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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