

# Large-Scale Brain Networks in Cognition: Emerging Principles

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## A Network Perspective on Cognition

Functional brain imaging has focused primarily on localization of function, revealing activation in specific brain regions during the performance of particular cognitive tasks. It is becoming increasingly apparent that cognitive neuroscience needs to go beyond this mapping of complex cognitive and psychological constructs onto individual brain areas (Fuster, 2006). As a result, a network paradigm is becoming increasingly useful for understanding the neural underpinnings of cognition (Bressler and Menon, 2010). Furthermore, a consensus is emerging that the key to understanding the functions of any specific brain region lies in understanding how its connectivity differs from the pattern of connections in other functionally related brain areas (Passingham et al., 2002). In recent years, neuroscientists' interests have shifted towards developing a deeper understanding of how intrinsic brain architecture influences cognitive and affective information processing (Greicius et al., 2003; Fox and Raichle, 2007; Dosenbach et al., 2008).

In the sections that follow, we briefly review emerging methods for characterizing and identifying major neurocognitive networks in the human brain. We then provide two specific examples of how such networks can provide fundamental new insights into the brain bases of fundamental cognitive processes. The first example focuses on the surprisingly crucial role of the insular cortex in salience, attention, and cognitive control. The second example demonstrates how intrinsic functional and structural connectivity of the parietal cortex can inform and constrain information processing models across multiple cognitive domains.

## Identifying Major Cognitive Networks

A formal characterization of core brain networks—anatomically distinct, large-scale brain systems having distinct cognitive functions—was first enunciated by Mesulam (1990). In this view, the human brain contains at least five major core functional networks:

1. A spatial attention network anchored in posterior parietal cortex (PPC) and frontal eye fields;
2. A language network anchored in Wernicke's and Broca's areas;
3. An explicit memory network anchored in the hippocampal–entorhinal complex and inferior parietal cortex;
4. A face-object recognition network anchored in midtemporal and temporopolar cortices; and

5. A working memory–executive function network anchored in prefrontal and inferior parietal cortices.

The nodes of these core networks have been inferred from the results of fMRI studies, during tasks that manipulate one or more of these cognitive functions. A full characterization of core functional brain networks, however, will require additional studies to validate the nodes of these networks using other criteria, to measure their edges, and to determine whether other core networks exist.

In recent years, diffusion tensor imaging (DTI) and resting state fMRI have emerged as novel tools for characterizing structural and functional brain networks. They are able to do so independently of cognitive domains, experimental manipulations, and behavior. Recent work in systems neuroscience has characterized several major brain networks that are identifiable in both the resting brain (Damoiseaux et al., 2006; Seeley et al., 2007b) and the active brain (Toro et al., 2008). Importantly, major functional brain networks (and their composite subnetworks) show close correspondence in independent analyses of resting and task-related connectivity patterns (Smith et al., 2009), suggesting that functional networks coupled at rest are also systematically engaged during cognition. The analysis of resting state functional connectivity, using both model-based and model-free approaches, has proved to be a useful technique for investigating functionally coupled networks in the human brain. Although the method relies on analysis of low-frequency signals in fMRI data, electrophysiological studies point to a reliable neurophysiological basis for these signals (He et al., 2008; Nir et al., 2008).

The analysis of resting state fMRI allows us to discover the organization and connectivity of several major brain networks that cannot be easily captured with the help of other techniques. Conceptualizing the brain as comprising multiple distinct, interacting networks provides a systematic framework for understanding fundamental aspects of human brain function.

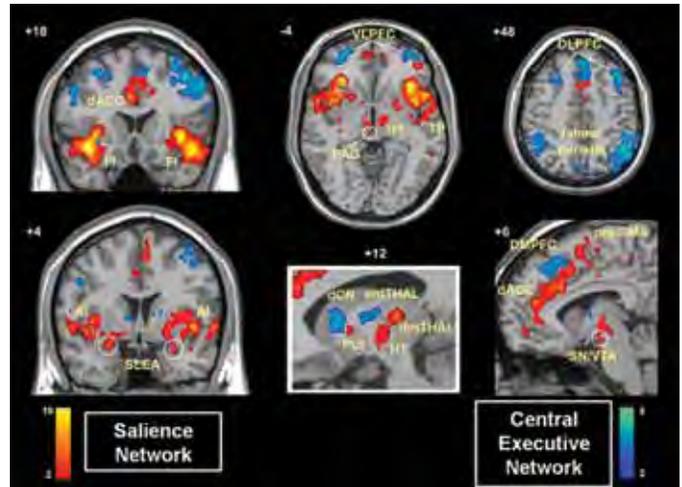
Independent component analysis (ICA) has turned out to be an important method for identifying intrinsic connectivity networks (ICNs) from resting state fMRI data (Damoiseaux et al., 2006; Seeley et al., 2007a). ICA has been used to identify ICNs involved in executive control, episodic memory, autobiographical memory, self-related processing, and detection of salient events. ICA has also revealed a sensorimotor ICN anchored in bilateral somatosensory and motor cortices; a

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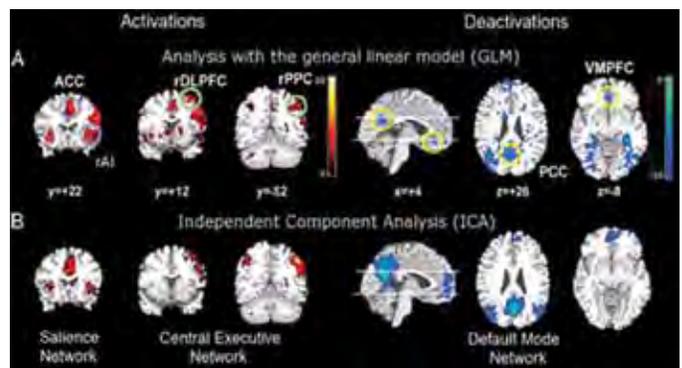
visuospatial attention network anchored in intraparietal sulci and frontal eye fields; a higher-order visual network anchored in lateral occipital and inferior temporal cortices; and a lower-order visual network anchored in the striate and extrastriate cortex (Damoiseaux et al., 2006). This technique has also allowed intrinsic (Fig. 1) as well as task-related (Fig. 2) fMRI activation patterns to be used for the identification of distinct functionally coupled systems. These systems include a central-executive network (CEN) anchored in dorsolateral prefrontal cortex (DLPFC) and PPC, and a salience network (SN) anchored in anterior insula (AI) and anterior cingulate cortex (ACC) (Seeley et al., 2007a; Sridharan et al., 2008).

These prominent networks can be readily identified across a wide range of cognitive tasks, and their responses increase and decrease proportionately with task demands. The CEN and SN typically show increases in activation, whereas the default-mode network (DMN) shows decreases in activation (Raichle et al., 2001; Greicius et al., 2003; Greicius and Menon, 2004). CEN nodes that show strong intrinsic functional coupling also show strong coactivation during cognitively challenging tasks. In particular, the CEN is critical for actively maintaining and manipulating information in working memory, and for judgment and decision-making in the context of goal-directed behavior (Miller and Cohen, 2001; Petrides, 2005; Muller and Knight, 2006; Koehlin and Summerfield, 2007).

The DMN includes the medial temporal lobes and the angular gyrus (AG), in addition to the posterior cingulate cortex (PCC) and the ventromedial prefrontal cortex (VMPFC). These areas perform a variety of functions: The PCC is activated during tasks that involve autobiographical memory and self-referential processes (Buckner and Carroll, 2007); the VMPFC is associated with social cognitive processes related to self and others (Amodio and Frith, 2006); the medial temporal lobe is engaged in episodic and autobiographical memory (Cabeza et al., 2004); and the



**Figure 1.** Two core neurocognitive networks identified using intrinsic physiological coupling in resting state fMRI data. The SN (shown in red) is important for monitoring the saliency of external inputs and internal brain events, and the CEN (shown in blue) is engaged in higher-order cognitive and attentional control. The SN is anchored in AI and ACC and features extensive connectivity with subcortical and limbic structures involved in reward and motivation. The CEN links the dorsolateral prefrontal and posterior parietal cortices, and has subcortical coupling that is distinct from that of the SN. Seeley et al. (2007), their Fig. 2, reprinted with permission. antTHAL, anterior thalamus; dACC, dorsal anterior cingulate cortex; dCN, dorsal caudate nucleus; dmTHAL, dorsomedial thalamus; FI, fronto-insular cortex; HT, hypothalamus; PAG, periaqueductal gray; Put, putamen; SLEA, sublenticular extended amygdala; SN/VTA, substantia nigra/ventral tegmental area; TP, temporal pole.



**Figure 2.** Three major functional networks in the human brain. Task-related activation patterns in the CEN and SN, and deactivation patterns in the DMN, during an auditory event segmentation task. Activation and deactivation patterns can be decomposed into distinct subpatterns. **A**, Analysis with the general linear model (GLM) revealed regional activations (Left) in the right anterior insula (rAI) and ACC (blue circles); DLPFC and PPC (green circles) and deactivations (Right) in the VMPFC and PCC. **B**, ICA provided converging evidence for spatially distinct networks. From left to right: SN (rAI and ACC), CEN (rDLPFC and rPPC), and DMN (VMPFC and PCC). Sridharan et al. (2008), their Fig. 1, reprinted with permission.

AG is implicated in semantic processing (Binder et al., 2009). The DMN thus collectively comprises an integrated system for autobiographical, self-monitoring, and social cognitive functions, even though a unique task-based function cannot be assigned to each of its nodes (Spreng et al., 2009). Furthermore, the identification and characterization of these distinct networks provide a framework for systematically examining attentional and control processes in the brain.

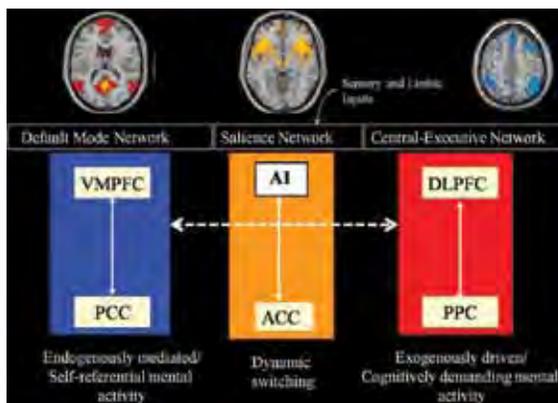
### An Example: Insula — a Network Model of Saliency, Attention, and Control

The insula is a brain structure implicated in disparate cognitive, affective, and regulatory functions, including interoceptive awareness, emotional responses, and empathic processes. Although classically considered a limbic region, recent evidence from network analysis suggests a critical role for the insula, particularly the anterior division, in high-level cognitive control and attentional processes. The insula's complex and as yet only partially characterized pattern of structural connectivity highlights the need for a more principled understanding of its functional links. In task-based functional imaging, it has been difficult to isolate insula responses because it is often coactivated with the ACC, the DLPFC and ventrolateral prefrontal cortex (VLPFC), and the PPC. To circumvent this problem, Dosenbach and colleagues used resting state functional connectivity to show that these regions can be grouped into distinct frontoparietal and cingulo-opercular components (Dosenbach et al., 2007). Similarly, Seeley and colleagues used region-of-interest (ROI) and ICA of resting state fMRI data to demonstrate the existence of an ICN comprising the AI, dorsal ACC, and subcortical structures, including the amygdala, substantia nigra/ventral tegmental area, and thalamus (Seeley et al., 2007a).

The crucial insight that network analysis affords is of the AI as an integral hub in mediating dynamic interactions between other large-scale brain networks involved in externally oriented attention and internally oriented, or self-related, cognition (Sridharan et al., 2008), as Figure 3 illustrates. This model postulates that the insula is sensitive to salient events, and that its core functions are to mark such events for additional processing and to initiate appropriate control signals. The AI and the ACC form a “saliency network” that functions to segregate the most relevant internal and extrapersonal stimuli in order to guide behavior.

Within the framework of a network model, the disparate functions ascribed to the insula can be conceptualized by a few basic mechanisms:

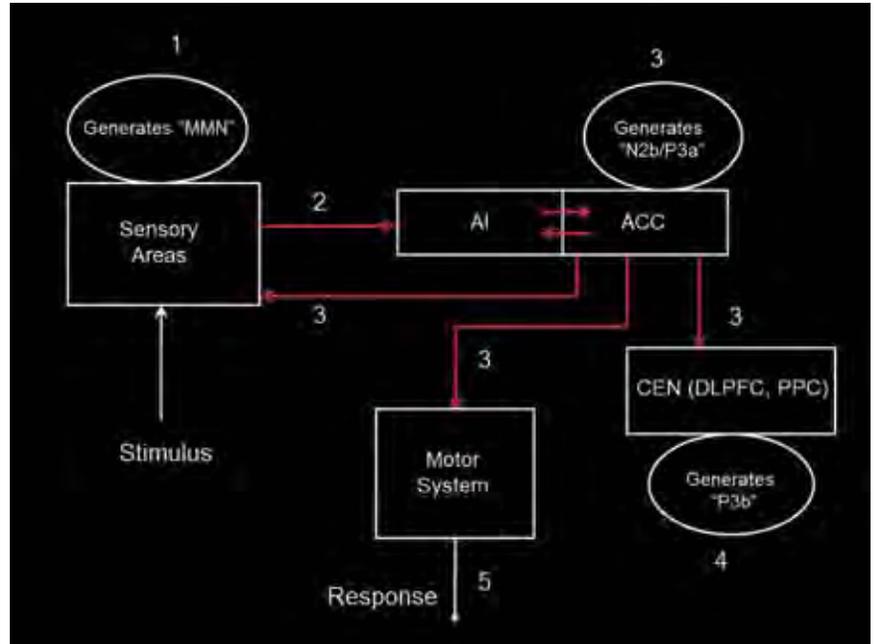
1. Bottom-up detection of salient events;
2. Switching between other large-scale networks to facilitate access to attention and working memory resources when a salient event occurs;
3. Interaction of the anterior and posterior insula to modulate autonomic reactivity to salient stimuli; and
4. Strong functional coupling with the ACC that facilitates rapid access to the motor system.



**Figure 3.** Multinetwork switching initiated by the SN (saliency network). The SN is hypothesized to initiate dynamic switching between the CEN (central-executive network) and DMN (default-mode network), and to mediate between attention to endogenous and exogenous events. In this model, sensory and limbic inputs are processed by the AI, which detects salient events and initiates appropriate control signals to regulate behavior via the ACC and homeostatic state via the mid and posterior insular cortex. Key nodes of the SN include the AI and ACC; the DMN includes the VMPFC and PCC; the CEN includes the DLPFC and the PPC. Bressler and Menon (2010), their Fig. 1, reprinted with permission.

With the AI as its integral hub, the SN assists target brain regions in the generation of appropriate behavioral responses to salient stimuli. We have proposed that this framework provides a parsimonious account of insula function in neurotypical adults and may provide novel insights into the neural basis of disorders of affective and social cognition (Menon and Uddin, 2010).

Previous studies have suggested that the inferior frontal gyrus and ACC are involved in a variety of monitoring, decision-making, and cognitive control processes (Crottaz-Herbette and Menon, 2006; Cole and Schneider, 2007; Johnston et al., 2007; Posner and Rothbart, 2007; Dosenbach et al., 2008; Eichele et al., 2008). However, the AI has not been a particular focus of most of these studies. Our model posits that the core function of the proposed SN, and



**Figure 4.** Schematic model of dynamic bottom-up and top-down interactions underlying attentional control. See text for description of stages. Crottaz-Herbette and Menon (2006), their Fig. 6, adapted with permission.

the AI in particular, is to first identify stimuli from the vast and continuous stream that impacts the senses. Once such a stimulus is detected, the AI facilitates task-related information processing by initiating appropriate transient control signals. These signals engage brain areas that mediate attentional, working memory, and higher order cognitive processes while disengaging the DMN via mechanisms that have been described in the previous section.

These crucial switching mechanisms help focus attention on external stimuli; as a result, they take on added significance or saliency. The large-scale network switching mechanisms we have described here can be thought of as the culmination of a hierarchy of saliency filters. In these filters, each successive stage helps to differentially amplify a stimulus sufficiently to engage the AI. The precise pathways and filters underlying the transformation of external stimuli, and the manner in which the AI is activated, remain to be investigated. Of critical importance, our model suggests that, once a stimulus activates the AI, it will have preferential access to the brain's attentional and working memory resources.

Although dynamical systems analysis of fMRI data can help capture aspects of causal interactions between distributed brain areas, a more complete characterization of bottom-up and top-down attentional control requires access to temporal dynamics on the 30-70 ms time scale. Analysis of

combined EEG and fMRI data provides additional insights into how the SN plays an important role in attentional control (Crottaz-Herbette and Menon, 2006). Figure 4 is a schematic model of bottom-up and top-down interactions that underlie attentional control. This model was suggested by the relative timing of responses in the AI and ACC, versus other cortical regions, based on our dynamic source-imaging study and by lesion studies of the P3a complex (Soltani and Knight, 2000). The spatiotemporal dynamics underlying this process have five distinct stages:

- *Stage 1:* ~150 ms poststimulus, primary sensory areas detect a deviant stimulus, as indexed by the mismatch negativity (MMN) component of the evoked potential;
- *Stage 2:* This bottom-up MMN signal is transmitted to other brain regions, notably the AI and the ACC;
- *Stage 3:* ~200-300 ms poststimulus, the AI and ACC generate a top-down control signal, as indexed by the N2b/P3a component of the evoked potential. This signal is simultaneously transmitted to primary sensory areas, as well as other neocortical regions;
- *Stage 4:* ~300-400 ms poststimulus, neocortical regions, notably the premotor cortex and temporoparietal areas, respond to the attentional shift with a signal that is indexed by the time-averaged P3b evoked potential; and

- *Stage 5:* The ACC facilitates response selection and motor response via its links to the midcingulate cortex, supplementary motor cortex, and other motor areas (Rudebeck et al., 2008; Vogt, 2009).

Within the framework of the network model described above, we suggest that the AI plays a more prominent role in detecting salient stimuli, whereas the ACC plays a more prominent role in modulating responses in the sensory, motor, and association cortices. A wide range of functional imaging studies and theoretical models has suggested that the ACC plays a prominent role in action selection (Rushworth, 2008). Together, as part of a functionally coupled network, the AI and ACC help to integrate bottom-up attention switching with top-down control and biasing of sensory input. This dynamic process enables an organism to sift through many different incoming sensory stimuli and to adjust gain for task-relevant stimuli—processes central to attention (Yantis, 2008).

An examination of the differential pattern of input–output connectivity of the AI and the ACC yields further insights into the functions of the AI and SN. While the AI receives multimodal sensory input, the ACC and associated dorsomedial prefrontal cortex (DMPFC) receive very little sensory input (Averbeck and Seo, 2008). Conversely, while the ACC and associated DMPFC send strong motor output, there is very little direct motor input to, or output from, the AI. Furthermore, the ACC and DMPFC have direct connections to the spinal cord and subcortical oculomotor areas (Fries, 1984), giving them direct control over action. With these differential anatomical pathways and von Economo neurons, which facilitate rapid signaling between the AI and the ACC, the SN is well positioned to influence not only attention but also motor responses to salient sensory stimuli. In this manner, the AI plays both a direct and an indirect role in attention, cognition, and behavioral control. In the context of our model, this critical input–output pattern suggests that the AI may generate the signals to trigger hierarchical control. Consistent with this view, among patients with frontal lobe damage, those with lesions in the AI were the most impaired in altering their behavior in accordance with the changing rules of an oculomotor-switching task (Hodgson et al., 2007). Our model further suggests that when the ACC is dysfunctional (Fellows and Farah, 2005; Baird et al., 2006), the AI is well positioned to trigger alternative cognitive control signals via other lateral cortical regions such as the VLPFC and the DLPFC (Johnston et al., 2007). Thus, our network model helps to clarify an important controversy regarding

the primacy and uniqueness of control signals in the prefrontal cortex (Fellows and Farah, 2005).

## A Second Example: Dissecting Parietal Circuits

The PPC, and in particular the inferior parietal lobule (IPL), is a brain region that is engaged in a wide variety of cognitive domains ranging from visuospatial attention (Corbetta and Shulman, 2002) to episodic memory (Cabeza et al., 2008) and numerical cognition (Menon et al., 2000). The human IPL consists of three prominent functional and anatomical subdivisions: the AG, the supramarginal gyrus, and the banks of the intraparietal sulcus (IPS). Situated at the junction of the temporal, parietal, and occipital lobes, the AG is a heteromodal region. Previous functional neuroimaging studies have focused mainly on its role in language and semantic processing (Binder et al., 2009; Brownsett and Wise, 2009) and spatial attention and orienting (Chambers et al., 2004), but it has also been implicated in verbally mediated fact retrieval during mathematical cognition tasks (Dehaene et al., 2004). However, resting state fMRI and positron emission tomography (PET) studies have consistently identified the AG as a key parietal node of the DMN (Raichle et al., 2001; Greicius et al., 2003; Uddin et al., 2009). Also, task-related deactivations have been widely reported in the AG (Shulman et al., 1997; Wu et al., 2009).

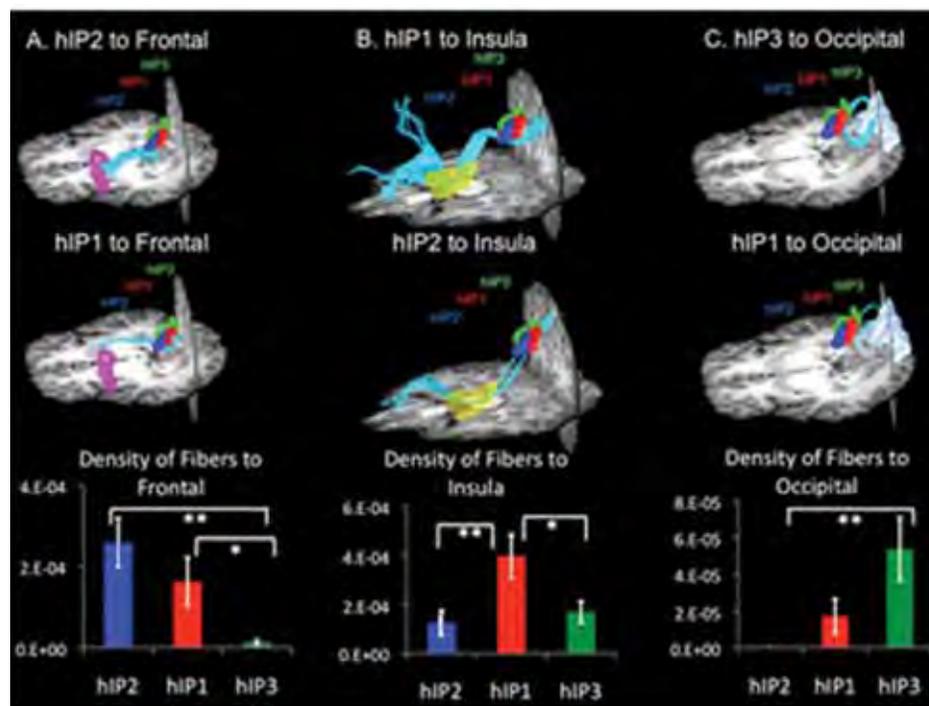
The IPL's involvement in multiple cognitive operations suggests that it is highly functionally heterogeneous. Until recently, the subdivisions of the human IPL were not well understood, and their relation to functional and structural connectivity was completely unknown. Autoradiographic tracer studies in the macaque brain had demonstrated a rostrocaudal gradient of connectivity within the IPL, with rostral IPL connected to ventral premotor areas, and caudal IPL connected to Brodmann areas 44 and 45 (Petrides and Pandya, 2009). However, the extent to which the human IPL can be considered strictly homologous to its monkey counterpart is a matter of debate. While Brodmann's initial characterization of the region led him to conclude that the human IPL consists of novel cortical areas not present in the monkey, others have argued that the IPL is similar across both species (Husain and Nachev, 2007). Thus, it is unclear to what degree monkey anatomical tracer studies can be extrapolated to understanding these pathways in the human brain.

By capitalizing on methodological advances for examining the connectivity of putative distinct cortical regions, we can gain new insights into the functional roles of specific regions within the PPC.

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Furthermore, recent cytoarchitectonic analyses of the human IPL have suggested that the AG and IPS can be parcellated into distinct subregions (Choi et al., 2006; Caspers et al., 2008). Using observer-independent definitions of cytoarchitectonic borders, Caspers and colleagues have defined two subdivisions within the AG: one anterior (PGa), and one posterior (PGp) (Caspers et al., 2006). Within the IPS, this research group has demonstrated at least three cytoarchitectonically distinct human intraparietal (hIP) areas, labeled hIP2, hIP1, and hIP3 (Caspers et al., 2008). Resting state functional connectivity analyses showed that PGa was more strongly linked to basal ganglia, ventral premotor areas, and VLPFC, whereas PGp was more strongly connected with VMPFC, PCC, and hippocampus: regions comprising the default mode network. The anterior-most IPS ROIs (hIP2 and hIP1) have been linked with ventral premotor and middle frontal gyrus, whereas the posterior-most IPS ROI (hIP3) showed connectivity with extrastriate visual areas. Tractography using DTI revealed structural connectivity between most of these functionally connected regions (Fig. 5).

These findings provide evidence for functional heterogeneity of cytoarchitectonically defined subdivisions within the IPL. They also offer a novel framework for synthesizing and interpreting the task-related activations and deactivations that involve the IPL during cognition. Our connectivity analyses of networks associated with the IPS suggest a general principle of organization; by means of it, posterior IPS regions that are closely linked to the visual system transform stimuli into motor action via anterior IPS connections to the prefrontal cortex. Specifically, functional and structural connectivity results point to strong connections between hIP1 and insula. Along with the findings noted in the previous section, this observation suggests that such an interconnected system may help to mediate the detection of visually salient stimuli. More broadly, such investigations provide new information about the functional and structural organization of the human parietal cortex. This understanding, in turn, places constraints on information processing models of parietal cortex function, with broad implications across multiple cognitive domains (Uddin et al., 2010).



**Figure 5.** Differential structural connectivity within the PPC. Structural connectivity of hIP subdivisions. **A**, DTI tractography and density of fibers between hIP2, hIP1, and hIP3 and target inferior frontal opercular ROIs. Both hIP2 and hIP1 showed greater structural connectivity with inferior frontal opercular than did hIP3 ( $*p < 0.05$ ,  $**p < 0.01$ ). **B**, DTI tractography and density of fibers between hIP2, hIP1, and hIP3 and target insula ROIs. hIP1 showed greater structural connectivity than hIP2 and hIP3 with insula ( $*p < 0.05$ ,  $**p < 0.01$ ). **C**, DTI tractography and density of fibers between hIP2, hIP1, and hIP3 and target superior occipital cortex ROIs. hIP3 showed greater structural connectivity with superior occipital cortex than did hIP2 ( $**p < 0.01$ ). Uddin et al. (2010), their Fig. 5, reprinted with permission.

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