The inferior parietal lobule and temporoparietal junction: A network perspective

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ABSTRACT

Information processing in specialized, spatially distributed brain networks underlies the diversity and complexity of our cognitive and behavioral repertoire. Networks converge at a small number of hubs – highly connected regions that are central for multimodal integration and higher-order cognition. We review one major network hub of the human brain: the inferior parietal lobule and the overlapping temporoparietal junction (IPL/TPJ). The IPL is greatly expanded in humans compared to other primates and matures late in human development, consistent with its importance in higher-order functions. Evidence from neuroimaging studies suggests that the IPL/TPJ participates in a broad range of behaviors and functions, from bottom-up perception to cognitive capacities that are uniquely human. The organization of the IPL/TPJ is challenging to study due to the complex anatomy and high inter-individual variability of this cortical region. In this review we aimed to synthesize findings from anatomical and functional studies of the IPL/TPJ that used neuroimaging at rest and during a wide range of tasks. The first half of the review describes subdivisions of the IPL/TPJ identified using cytoarchitectonics, resting-state functional connectivity analysis and structural connectivity methods. The second half of the article reviews IPL/TPJ activations and network participation in bottom-up attention, lower-order self-perception, undirected thinking, episodic memory and social cognition. The central theme of this review is to discuss how network nodes within the IPL/TPJ are organized and how they participate in human perception and cognition.

1. Introduction

The many specialized areas of the human cerebral cortex form nodes in a densely interconnected complex network. When the network organization of the brain is resolved by functional or structural neuroimaging studies, nodes generally cluster into sparsely interconnected, functionally relevant sub-systems (van den Heuvel and Sporns, 2013). For example, in an influential study, Yeo et al. (2011) used cluster analysis of functional connectivity patterns in 1000 subjects to produce maps of cortical networks at resolutions of 7 and 17 networks (Fig. 1A, B). Particularly well-connected nodes are called hubs, and are thought to be critically important for information integration associated with higher-order cognition (van den Heuvel and Sporns, 2013). One brain region identified as a major hub in functional magnetic resonance imaging (fMRI) studies is the inferior parietal lobule (IPL) – a region implicated in a diverse range of higher cognitive functions (Buckner et al., 2009; Cabeza et al., 2012a; Tomasi and Volkow, 2011) (Fig. 1C). The IPL (blue in Fig. 1D), including the overlapping temporoparietal junction (TPJ) (red in Fig. 1D), is one of the least

understood regions of the human brain. The IPL is massively expanded compared to non-human primates and matures late in human development, consistent with higher order functions (Fjell et al., 2015; Hill et al., 2010). Hundreds of neuroimaging studies, involving many domains of behavior, have reported activations in the IPL/TPJ, often involving seemingly overlapping cortical regions. Therefore, a commonly discussed question is whether this region performs some domain-general computation or contains multiple domain-specific processes (e.g. Cabeza et al., 2012a; Corbetta et al., 2008; Seghier, 2013).

One way of addressing this question is to look for evidence of functional subdivisions within the region and examine their properties and connectivity patterns (Bzdok et al., 2016, 2013; Caspers et al., 2006, 2013; Igelström et al., 2015, 2016b; Mars et al., 2011, 2012b). If there are multiple discrete subdivisions with different connectivity patterns, it may reflect the presence of multiple network nodes. It has been suggested that it may not be possible to understand this brain region without considering it as part of an integrative multi-network system (Seghier, 2013). In this paper, we review neuroimaging studies

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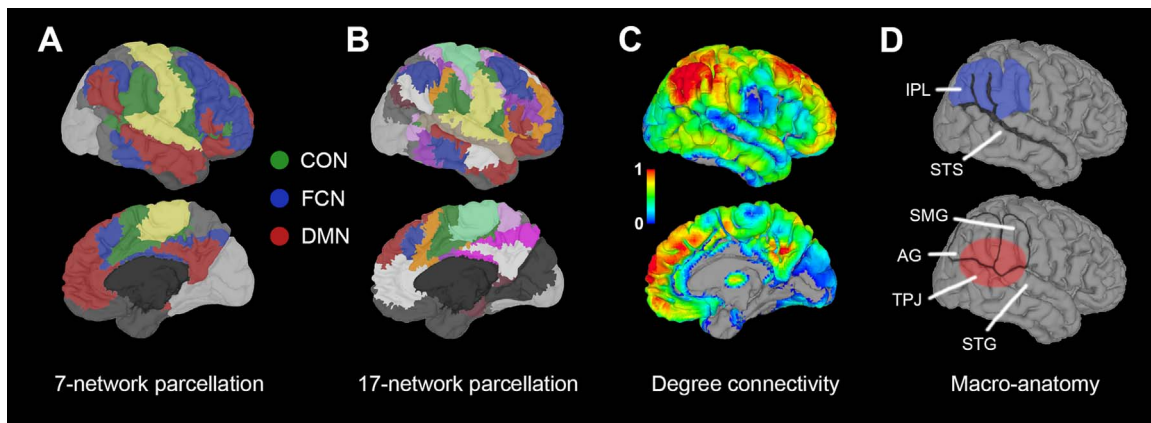
Fig. 1. The network structure of the brain and the anatomy of the inferior parietal lobule/temporoparietal junction (IPL/TPJ). (A) Brain networks at a resolution of 7 networks based on functional connectivity (Yeo et al., 2011). Three cognitive networks overlap the IPL/TPJ: the frontoparietal control network (FCN; blue), the default mode network (DMN; red) and the cingulo-opercular network (CON; green). (B) Functional connectivity networks at a resolution of 17 networks (Yeo et al., 2011). Compared to the 7-network parcellation shown in (A), further subdivisions of the networks are visible. (C) The IPL/TPJ as a network hub. Shown is a consensus estimate of cortical hubs in resting state data from 127 participants (data from Figure 7 in Buckner et al., 2009). The color scale reflects the z-scored degree centrality, which is an estimate of the number of connections of each voxel to other voxels. See Buckner et al. (2009) for details on analysis. The image volume was kindly shared by Buckner et al. (2009) and projected on the right hemisphere of the cvs_avg35_inMNI152 brain using AFNI/ SUMA software (Cox, 1996; Saad and Reynolds, 2012). (D) Macro-anatomy of the IPL/TPJ. The IPL (blue overlay, top panel) consists of the angular gyrus (AG) and the supramarginal gyrus (SMG) (black outlines, bottom panel), separated by the intermediate sulcus of Jensen. The posterior branches of the superior temporal sulcus (STS) reach into the IPL (black, top panel). The TPJ (red overlay, bottom panel) is usually defined as the cortical regions around the posterior STS and superior temporal gyrus (STG) and ventral AG and SMG (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

on the organization of the IPL/TPJ in human participants. Our focus lies on the localization of brain processes and their roles in brain-wide networks. We will start by describing the macro-anatomy of the region and outlining the nomenclature used across different branches of the literature. The first half of the article will describe resting state fMRI and structural connectivity studies aimed at identifying subdivisions or network nodes in the IPL/TPJ. The second half of the article will discuss task-based studies and the possible localization of function.

2. Macro-anatomy and nomenclature

The diverse conditions under which the IPL/TPJ is activated, including language processing, social cognition, bottom-up attention, response inhibition and memory retrieval, have led to partial isolation of subspecialties in the literature and variable naming of brain regions. The macro-anatomy of the IPL/TPJ is illustrated in Fig. 1D. The IPL (blue overlay) consists of two major gyri: the supramarginal gyrus (SMG; Brodmann area 40) and the angular gyrus (AG; Brodmann area 39) (black outlines in bottom panel). The sulcal patterns in the IPL are very variable between people, but the superior temporal sulcus (STS) extends its caudal branches into the IPL (black lines in top panel), and the SMG and AG are usually separated by the intermediate parietal sulcus of Jensen (Segal and Petrides, 2012; Zlatkina and Petrides, 2014). The TPJ is a variably defined region located roughly where the IPL meets the superior temporal lobe, and is not associated with any objective landmarks (red overlay in bottom panel). The term TPJ has been used for activations observed in most of the IPL as well as in dorsal parts of the posterior superior temporal lobe. Occasionally, activations extending as far as the middle temporal gyrus and lateral occipital lobe have also been labeled TPJ. Most investigators would probably define the TPJ as a small region that overlaps only the most ventral part of the IPL at the true intersection of the AG, SMG and posterior superior temporal lobe (Fig. 1D). Because of the ubiquitous use of the term TPJ, and its inclusion of the often co-activated posterior superior temporal regions, we use the compound term "IPL/TPJ" in this review. However, it is important to remember that there is no consensus on the anatomical definition of the extent and precise location of the TPJ, and that many other labels are used to describe activations around this region (e.g. IPL, ventral parietal cortex, lateral parietal cortex, AG, SMG, and posterior STS). It is also important to

remember that, even though the IPL and TPJ overlap, even with the most conservative definition of the TPJ, they are not synonymous with each other.

3. Organization of the IPL/TPJ in the task-free state

In this section we review findings from resting state fMRI and diffusion MRI studies that aimed to isolate subdivisions and network nodes in the IPL/TPJ, and we discuss the network organization of this region.

3.1. IPL/TPJ parcellation based on the local fMRI signal

Resting state fMRI has proven useful for defining the functional macro-architecture of the human brain (e.g. Yeo et al., 2011). Voxels that are part of the same functional brain network show temporal synchrony of the low-frequency (< 0.1 Hz) blood-oxygen-level dependent (BOLD) signal (Biswal, 2012; Biswal et al., 1995; Lowe, 2012). The relevance of resting state functional connectivity is supported by relatively good test-retest reliability (Shehzad et al., 2009), high similarity of resting state networks with task-related activations (Hoffstaedter et al., 2014; Smith et al., 2009), and correspondence with structural pathways (Greicius et al., 2009; Hagmann et al., 2008; Honey et al., 2009). One method for identifying resting state networks is to quantify temporal correlations between a chosen region-of-interest (ROI) and all brain voxels. Such seed-based functional connectivity analysis is highly influenced by the position of the seed region. For example, if the seed is located in a transition zone between two specialized areas, the connectivity pattern may reflect a mixture of two brain-wide networks (Daselaar et al., 2013). Another method for isolating resting state networks is independent component analysis (ICA), which does not require a seed region and is less influenced by noise sources (Beckmann et al., 2005; McKeown et al., 2003). ICA algorithms operate on all voxels simultaneously to unmix the BOLD signal into maximally independent spatiotemporal sources (independent components, ICs). ICA isolates several well-known resting state networks with nodes that overlap with the IPL/TPJ region, including the default mode network (DMN), the frontoparietal control network (FCN) and the cingulo-opercular network (CON) (red, blue and green in Fig. 1A, respectively) (Smith et al., 2009). When resolved by whole-

brain ICA, the IPL/TPJ clusters associated with these networks usually appear large and mutually overlapping.

It is possible to enhance the spatial specificity of IPL/TPJ clusters if ICA is applied on a smaller number of voxels around the IPL/TPJ region, rather than to the whole brain. This use of local ICA has been effective in other regions, including the motor cortex, brainstem and cerebellum (Beissner et al., 2014; Moher Alsady et al., 2016; Sohn et al., 2012). In a recent study (Igelström et al., 2015), we used this method, applying the analysis to voxels within an ROI that included the bilateral IPL/TPJ. The ICA output may vary slightly depending on the investigator's choice of a suitable model order for an initial dimensionality reduction of the fMRI data. This choice, however, introduces an unwanted variable as different model orders may yield different results (Abou-Elseoud et al., 2010; Beckmann and Smith, 2004). To overcome this source of variability, we applied ICA at model orders ranging from 2 to 50 (49 ICAs per subject cohort). We also analyzed data from three independent subject samples (resting state data acquired at three different institutions), and examined the stability of the findings across the three datasets and across the 49 model orders using spatial correlation methods of the voxels in the IC statistical maps (Igelström et al., 2015). Using this method, we found five reproducible subdivisions of the IPL/TPJ in the right hemisphere and four in the left (Igelström et al., 2015). In a second study, we identified one more caudal subdivision in each hemisphere, by extending the ROI into the most posterior parts of the IPL (Igelström et al., 2016a). This ICA-based parcellation is shown in Fig. 2A, and the properties of each IC will be summarized in the following paragraphs.

The most robust IC in the IPL/TPJ was located in the dorsal AG (dorsal TPJ, TPJd; blue in Fig. 2A). The activity in this part of the temporoparietal cortex was highly lateralized; the BOLD signal on the right and left were sufficiently dissimilar to cause a split into separate lateralized clusters (TPJd-R and TPJd-L), even at low ICA model orders. The data-driven identification of subdivisions allowed us to use the IC coordinates for a seed-based functional connectivity analysis without the potential bias of subjective seed placement. This showed connectivity of the TPJd-R and TPJd-L with lateralized networks resembling the FCN, including the lateral prefrontal cortex (PFC), inferior temporal cortex, precuneus and posterior cingulate cortex. Mars et al. (2012b) found a dorsal subdivision (called "IPL" in their study) with similar functional connectivity patterns in a connectivity-based parcellation of a smaller ROI around the right TPJ.

We obtained a second IC, ventral to the TPJd, at the intersection between the posterior IPL and temporal lobe (red in Fig. 2A). We termed this IC the TPJp. It was divisible at low model orders into a right and left hemisphere component, the TPJp-R and the TPJp-L. Seed-based functional connectivity analysis showed that the TPJp was connected to a network that included the STS, precuneus and medial PFC (mPFC), resembling the DMN (red in Fig. 1A). A posterior TPJ subdivision with similar connectivity was described previously both in the right hemisphere (Bzdok et al., 2013; Mars et al., 2011, 2012b) (Fig. 1B and C) and in the left hemisphere (Wang et al., 2015). In a second study, we identified another subdivision, posterior to the TPJp, in the posterior AG, which we named the AGp (Igelström et al., 2016a) (white in Fig. 2A). This region is also known to have connectivity to the DMN (Fig. 1A).

We obtained a third IC in an anterior part of the IPL/TPJ, that we termed the TPJa (green in Fig. 2A). This IC split into right and left components at much higher model orders than the TPJd and TPJp, indicating a greater degree of interhemispheric symmetry. Seed-based functional connectivity analysis showed it to be connected with CON regions (anterior insula/operculum, anterior cingulate and thalamus) (green in Fig. 1A). It was similar in location and connectivity to a previously described subdivision in the right TPJ (Bzdok et al., 2013).

We found a fourth IC in a central region of the IPL/TPJ, that we termed the TPJc. This IC was right-lateralized. It was located between and partially overlapping with the TPJd-R and TPJa-R in the posterior
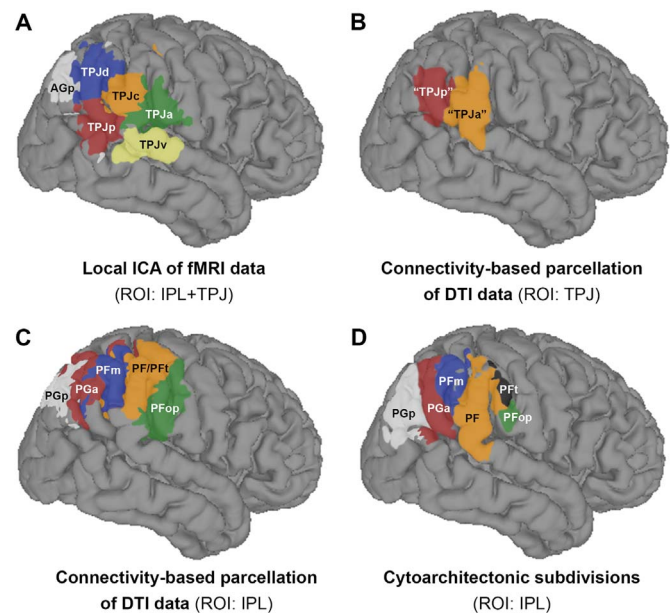
Fig. 2. Parcellations of the IPL/TPJ derived from different methods within different regions-of-interest (ROIs). (A) Subdivisions identified with independent component analysis applied within an ROI comprising the AG, SMG, posterior STS and posterior superior temporal gyrus (Igelström et al., 2016a). (B) TPJ subdivisions identified with structural connectivity-based parcellation, applied within an ROI bounded by the intraparietal sulcus dorsally, and the dorsal bank of the STS ventrally. Shown is a winner-take-all map constructed from the TPJ parcellation atlas available in FSL (Mars et al., 2012b), thresholded at 25% for illustration. (C) Subdivisions identified with structural connectivity-based parcellation of the IPL within a ROI in the IPL, reaching ventrally to the level of the ventral tip of the postcentral sulcus and the horizontal segment of the STS. Shown is a winner-take-all map constructed from the Parietal Cortex atlas available in FSL (Mars, et al., 2011), thresholded at 25% for illustration. The labels reflect a comparison with the cytoarchitectonic atlas (Caspers et al., 2008; Mars, et al., 2011). (D) Cytoarchitectonic subdivisions of the IPL (Caspers et al., 2008). Shown are the subdivisions reported in Caspers et al. (2008), as represented in the Juelich histological (cyto- and myelo-architectonic) atlas available in FSL. All data are shown as colored overlays on a standard cortical surface in MNI space (cvs_avg35_inMNI152 brain). Colors are matched to improve clarity, and are based on similarities in locations, connectivity patterns or task-related activations (see main text for discussion). Note that some differences in the spatial extent of the subdivisions (e.g. PGa versus TPJp, PF versus TPJc) are the result of major differences in the dorsoventral coverage of the ROIs chosen for the studies (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

SMG (orange in Fig. 2A). The TPJc was connected with a right-lateralized network, resembling the ventral attention network (VAN), including the inferior/middle frontal gyrus, anterior insula and precuneus. Its location and connectivity patterns were similar to a subdivision described by Mars et al. (2012b) (named "TPJa" in their study; Fig. 2B). The TPJc was the least stable IC in our study, showing significant variability in its precise location across model orders and between datasets (Igelström et al., 2015, 2016a).

Finally, we found an IC in a ventral region of the ROI, the TPJv, located in the superior temporal gyrus (light yellow in Fig. 2A). This IC was bilateral and was connected with a network consisting of the auditory cortex, sensorimotor cortex and the insula, similar to the sensorimotor network in Fig. 1A (light yellow). The TPJv was similar to a subdivision reported in the left hemisphere in a study that focused on language functions (Wang et al., 2015). Its anterior position in the superior temporal gyrus and its connectivity patterns to sensorimotor regions suggested that the TPJv is not involved in computations generally associated with the IPL/TPJ, so it will not be discussed extensively in this review.

In summary, resting state fMRI studies by us and others support the existence of 4–6 subdivisions in each hemisphere in the IPL/TPJ, each with a specialized pattern of brain-wide connectivity. Connectivity analyses indicated that the subdivisions are network nodes in separate

Table 1
Networks involving the IPL/TPJ and their putative network nodes.

Label	Network	Major nodes
FCN	Frontoparietal control network	IPL/TPJ Dorsolateral and anterior PFC Anterior and mid-cingulate cortex Precuneus Anterior insula Middle/inferior temporal cortex Intraparietal sulcus Caudate nucleus Cerebellum
DMN	Default mode network	IPL/TPJ mPFC Posterior cingulate/retrosplenial cortex Lateral temporal cortex Anterior temporal lobe MTL Cerebellum
CON	Cingulo-opercular network	IPL/TPJ Anterior cingulate cortex/medial superior frontal cortex Anterior insula/frontal operculum Anterior PFC Anterior thalamus Cerebellum
VAN	Ventral attention network	Right IPL/TPJ Right IFG Right anterior insula Right middle frontal gyrus

Data combined from Andrews-Hanna et al. (2010), Buckner et al. (2008, 2011), Corbetta et al. (2008), Dosenbach et al. (2007) and Vincent et al. (2008). The list of nodes may not be exhaustive.

brain-wide networks. In the following sections, we will put the findings into the context of resting state networks and compare them to anatomical data. An overview of the relevant networks is presented in Table 1.

3.2. The TPJd as a node in the frontoparietal control network

As described above, the TPJd had a specific pattern of connectivity with the FCN (blue in Fig. 1A). This network was first characterized in resting state fMRI data by Vincent et al. (2008) and named based on its overlap with regions implicated in cognitive control, such as the lateral PFC and anterior cingulate cortex (Table 1). Several other names have also been used for this network, including the multiple demand system and working memory network (Duncan, 2010; Koshino et al., 2014). The FCN is highly lateralized: In whole-brain ICA decompositions, the FCN appears as one right-lateralized and one left-lateralized component (Allen et al., 2011; Damoiseaux et al., 2006; Smith et al., 2009), and there is stronger connectivity between ipsilateral than between contralateral nodes in seed-based analysis (Vincent et al., 2008). The FCN has extensive and flexible connectivity with other networks and has been suggested to regulate the balance between the externally directed dorsal attention network (DAN) and the internally focused DMN (Gao and Lin, 2012; Gerlach et al., 2011; Power et al., 2011; Spreng et al., 2013). Activation of the FCN with transcranial magnetic stimulation (TMS) inhibited the DMN at rest (Chen et al., 2013), but the FCN and DMN can also co-activate during performance of goal-directed, internally oriented tasks (Ellamil et al., 2012; Gerlach et al., 2011; Spreng et al., 2010). Conversely, the FCN can couple with the DAN in tasks requiring externally directed attention (Gao and Lin, 2012). Thus, the network nodes in the FCN appear to flexibly adapt

their brain-wide interactions according to task demands (Cole et al., 2014; Spreng et al., 2010). How the FCN achieves this flexibility and whether there are subsystems within the network, is not well understood.

Initial studies using a seed placed in the dorsolateral PFC suggested that the FCN intersects the parietal lobe in the anterior dorsal part of the IPL (Vincent et al., 2008). However, parcellations and ICA-based studies that did not depend on the placement of a seed have suggested substantial involvement of more posterior regions in the AG, consistent with the TPJd (e.g. Smith et al., 2009; Yeo et al., 2011). These regions show substantial inter-individual variability (Caspers et al., 2008, 2006; Hasson et al., 2004; Mueller et al., 2013; Segal and Petrides, 2012; Zlatkina and Petrides, 2014), suggesting that single-subject studies will be necessary to understand the architecture of the FCN node in the IPL/TPJ.

Much of the literature on the executive functions associated with the FCN has focused on the pivotal role of the PFC. However, the IPL/TPJ nodes of the FCN are also commonly activated in tasks involving executive functions, including working memory, response inhibition and interference control, with clusters extending across the dorsal AG and SMG (Cieslik et al., 2015; Rottschy et al., 2012). Activation of an area consistent with the TPJd was also seen in a meta-analysis of fMRI studies on sustained attention (Langner and Eickhoff, 2013). In summary, though all brain areas can be said to have a complex and dynamic role in brain function, the TPJd seems to be involved in an especially large and constantly shifting range of computations.

3.3. IPL/TPJ nodes associated with default mode and social networks

The TPJp and AGp were part of the DMN (Igelström et al., 2015; Mars et al., 2012b), which strongly overlaps with the network activated by theory-of-mind tasks (Buckner et al., 2008; Mars et al., 2012a) (red in Fig. 1A; Table 1). In addition to the IPL/TPJ, DMN network nodes include the mPFC, the medial posterior parietal lobe (posterior cingulate and retrosplenial cortex), anterior temporal regions and the medial temporal lobe. The DMN was originally identified based on its consistent deactivation during tasks requiring focused attention, but it is now known to also be activated during broadly tuned attention to the environment as well as active internal cognition, such as mentalizing, autobiographical memory retrieval, or envisioning the future (Buckner et al., 2008). As mentioned above, the DMN is often inhibited by the FCN, but the two networks appear to co-activate in tasks that demand internally directed attention (Ellamil et al., 2012; Gerlach et al., 2011; Spreng et al., 2010).

Based on fMRI data, the DMN was suggested to consist of two core hubs, the anterior mPFC and posterior cingulate cortex, connected with two subsystems (Andrews-Hanna et al., 2010). One subsystem included an area consistent with our TPJp, together with the dorsal mPFC, lateral temporal cortex and temporal poles ("dMPFC subsystem"). The other subsystem included an area consistent with our AGp, the ventral mPFC, posterior midline and medial temporal lobe ("MTL subsystem"). Thus, it appears that the DMN has two distinct network nodes in the IPL/TPJ, one located at the intersection between the AG, SMG and superior temporal gyrus (TPJp), and one located posterior to the TPJp in the AG (AGp). The MTL subsystem was engaged when subjects were asked about hypothetical autobiographical events (thinking about their personal future), whereas the dMPFC subsystem was more strongly activated when subjects made judgments concerning their present situation (Andrews-Hanna et al., 2010). Although not discussed in depth in Yeo's original paper (Yeo et al., 2011), their 17-network parcellation (Fig. 1B) contains two networks that appear to reflect a split of the DMN resolved in their 7-network parcellation (Fig. 1A). The white network in Fig. 1B probably corresponds to the MTL subsystem, with large clusters in the ventral mPFC and posterior AG. The red network may correspond to the dMPFC subsystem, with clusters in the dorsal mPFC and temporal poles (a small IPL/TPJ node

inside the STS is not visible on the pial surface in Fig. 1B). In summary, the AGp and the TPJp may be network nodes of two subsystems of the DMN, possibly playing distinct roles in internally directed processing and broadly tuned attention to the environment.

3.4. Participation of IPL/TPJ nodes in cingulo-opercular and ventral attention networks

The TPJa, located in the anterior SMG, was part of the CON, also sometimes called the salience network (Dosenbach et al., 2006; Seeley et al., 2007) (Table 1). Some have suggested that the CON and the salience system may be two separate networks (Power and Petersen, 2013), but this has not yet been fully resolved and the terminology varies in the literature. In some contexts, this network has also been interpreted as the VAN (e.g. Yeo et al., 2011) (Table 1), even though the VAN is generally considered to have a more posterior IPL/TPJ node lateralized to the right hemisphere (Corbetta et al., 2008; Geng and Vossel, 2013; Mantini et al., 2013), which corresponds better to the TPJc subdivision described above (Igelström et al., 2015, 2016a, 2016b). Because the VAN was originally defined based on a small number of tasks that do not necessarily generalize to other paradigms (see Section 4.1 for details), comparisons between the VAN and networks defined in resting-state data should be made with some caution.

The core of the CON consists of the dorsal anterior cingulate cortex, mPFC and the anterior insula/frontal operculum (Dosenbach et al., 2007, 2006). The network does not seem to contain a major hub in the IPL/TPJ. For example, in a graph analysis of nodes across the CON and FCN, the TPJ formed an isolated cluster (Dosenbach et al., 2007), and IPL/TPJ clusters that are derived from functional connectivity analyses of the CON can be small or non-existent (Mantini et al., 2013; Sadaghiani and D'Esposito, 2014; Seeley et al., 2007). However, the 7-network parcellation shown in Fig. 1A indicates that a region consistent with the TPJa, as well as a more posterior region consistent with the TPJc, are part of the CON (green network in Fig. 1A; Yeo et al., 2011). Similarly, the CON isolated with whole-brain ICA shows large IPL/TPJ clusters (Weissman-Fogel et al., 2010).

The medial and insular regions of the CON are thought to play a critical role in cognitive control, supporting the instantiation, maintenance and error-based adjustments of task sets independent of task domain (Dosenbach et al., 2006; Sestieri et al., 2014). In contrast, the IPL/TPJ node may have a different role in the network, because its activity was specifically associated with cues that signaled the beginning of a task set. This pattern of activity may also be consistent with a role for the TPJa in bottom-up attentional reorienting, a function associated with the VAN (Corbetta and Shulman, 2002; Mitchell, 2008). The TPJa in association with the CON has also been suggested to be involved in tonic alertness (vigilant/sustained attention) (Langner and Eickhoff, 2013; Sadaghiani and D'Esposito, 2014) and salience detection (Seeley et al., 2007).

Critically, the location of the IPL/TPJ node in studies of the CON has seemed to vary substantially. Loci have included areas consistent with the TPJa in the anterior SMG, and areas consistent with the TPJc in the posterior SMG and STS (Cole et al., 2013; Dosenbach et al., 2006; Kucyi et al., 2012; Tu et al., 2012; Wu et al., 2016). This variation is compatible with several possibilities. The variable locations in the IPL/TPJ might reflect two distinct loci with different functions, a large IPL/TPJ area with a gradient of functions, or a region of connectional flexibility, much like the proposed role of FCN nodes as flexible hubs. The two network parcellations in Fig. 1A and B support the first possibility of distinct loci. The large IPL/TPJ cluster of the CON seen in the 7-network parcellation (green cluster) appears to split into anterior and posterior clusters in the more fine-grained 17-network parcellation (green and orange, respectively). The anterior cluster is connected with the CON whereas the posterior cluster is connected to a network consistent with the VAN. However, the great degree of overlap between

the CON and the VAN suggests that they are highly interrelated. The cortical region around the TPJc and TPJa was identified as a zone of particularly high variability in a resting-state study incorporating temporal dynamics of connectivity patterns (Allen et al., 2012). We observed that the TPJc was less spatially stable than any of the other components (Igelström et al., 2015, 2016a, 2016b), again emphasizing that this part of the IPL/TPJ may be particularly challenging to characterize.

3.5. Anatomy-based parcellation of the IPL/TPJ

Another approach to identifying subdivision of the IPL/TPJ is to identify zones with distinct structural features. An influential series of postmortem studies generated a parcellation of the IPL based on cytoarchitectonic features such as laminar cell density (Caspers et al., 2008, 2011, 2006, 2013). Seven zones were reported, two in the AG (PGa and PGp) and five in the SMG (PFm, PF, PFt, PFcm and PFop). Fig. 2D shows a surface projection of a probabilistic atlas of the subdivisions based on 10 subjects (Caspers et al., 2008). There was considerable variability in the size and location of the cytoarchitectonic zones between different brains and between hemispheres of the same brain, but the topographical pattern was consistent across subjects. Notably, there were no macroanatomical landmarks that reliably predicted the borders between any of the zones (Caspers et al., 2006). Thus it is not possible to use the pattern of sulci and gyri to reliably locate any of these functional subdivisions.

Similar subdivisions have been found in studies using connectivity-based parcellation of diffusion MRI data in living subjects (Mars et al., 2011; Wang et al., 2012). The IPL parcellation by Mars et al. (2011) has been made available as an atlas and is shown on a lateral cortical surface in Fig. 2C. A parcellation of the right TPJ using the same method (Mars et al., 2012b) is shown in Fig. 2B. Interestingly, the agreement between the above mentioned anatomical parcellation studies was lower in the region of the posterior SMG (Caspers et al., 2008, 2006; Mars et al., 2011; Wang et al., 2012), which corresponds to the region of the TPJa and TPJc that showed higher inconsistency in fMRI studies, as discussed in the previous section (Allen et al., 2012; Igelström et al., 2015).

In the cytoarchitectonic parcellation of Caspers and colleagues, the two posterior subdivisions PGp and PGa (white and red in Fig. 2D) appeared similar to the AGp and TPJp of the DMN subsystems identified in fMRI data (white and red in Fig. 2A), although their dorsal aspect also overlapped with the TPJd region (Andrews-Hanna et al., 2010; Caspers et al., 2008, 2006; Igelström et al., 2015, 2016a). PGp was located in the most posterior part of the AG, whereas PGa was located in the anterior part of the AG (Caspers et al., 2006). The anterior border of PGa did not correlate with any macroanatomical features, but the border between PGa and PGp was located in the middle branch of the posterior STS (also known as the angular sulcus) (Caspers et al., 2006). Like the TPJp (red in Fig. 2A), PGa was found to have functional connectivity to the DMN (Gillebert et al., 2013). Consistent with a correspondence between PGp and the MTL-DMN subsystem, functional connectivity fMRI analysis showed strong connectivity of PGp with the parahippocampal gyrus (Mars et al., 2011; Uddin et al., 2010). In a cluster analysis of the neurotransmitter receptor profiles of the seven cytoarchitectonic zones, PGa and PGp were suggested to be functionally related (Caspers et al., 2013), in line with the possibility that both are nodes in the DMN. In diffusion MRI studies, the PG areas both showed structural connectivity to the temporal lobe, inferior frontal cortex, insula and middle/superior frontal cortex, and PGp showed greater connectivity with temporo-occipital regions (Caspers et al., 2011; Wang et al., 2012).

Of the five cytoarchitectonic subdivisions in the SMG in the parcellation of Caspers et al. (2006), PF was the largest, often reaching into the superior temporal gyrus (orange in Fig. 2D). Its location appears most similar to the TPJc in Igelström et al. (2015, 2016a)

(Fig. 2A), and it was functionally connected to the VAN in task-based fMRI (Gillebert et al., 2013). However, the degree of correspondence is uncertain, especially given the high inter-individual variability of this region. PFm (blue in Fig. 2D), the subdivision located between PF and PGa, was suggested to be a transition zone between the AG and SMG subdivisions (Caspers et al., 2006). Spatially, PFm overlapped mainly with the TPJd component in Igelström et al. (2015) and it had lateralized functional connectivity with the posterior cingulate and dorsolateral frontal cortex, similar to the TPJd (blue network in Fig. 1A) (Gillebert et al., 2013; Wang et al., 2012). The remaining rostral regions, PFt, PFop and PFcm, were located in the anterior SMG (Fig. 2D). The regions PFt and PFop were located anterior to PF (black and green in Fig. 2D), and PFcm was largely buried in the Sylvian fissure (Caspers et al., 2008, 2006). PFop most closely matched the TPJa, based on its location and its functional and anatomical connectivity in human MRI with regions of the CON (green network in Fig. 1A) (Caspers et al., 2008; Wang et al., 2012). In human MRI studies, most PF areas showed structural connectivity to the inferior frontal cortex, ventral premotor cortex, superior parietal cortex, opercular regions, and insula (Caspers et al., 2011; Rushworth et al., 2006; Tomassini et al., 2007; Wang et al., 2012).

3.6. Parcellation of the IPL/TPJ based on multimodal data

A recent parcellation by Glasser et al. (2016a) divided the cerebral cortex into 180 regions, based on a combination of resting-state fMRI connectivity, task-based activations, cortical thickness and estimated myelin content, using high-quality MRI data from 210 subjects from the Human Connectome Project. This parcellation replicated the IPL subdivisions reported by Caspers et al. (2008, 2006) with some refinements. The major difference was a further subdivision of PGa into one dorsal and one ventral area (called PGs and PGi in their study). Area PGp was suggested to be a transitional area with unique connectivity to the higher visual cortex (Glasser et al., 2016a), a finding supported by its neurotransmitter receptor fingerprint, which was similar to that of the ventral extrastriate visual cortex (Caspers et al., 2013). Consistent with cytoarchitectonic findings (Caspers et al., 2006), area PFm was a transition zone between the PF and PG areas.

In addition to the IPL subdivisions, five relevant small areas were reported in the TPJ region, ventral to the IPL. The Peri-Sylvian Language (PSL) area and the Superior Temporal Visual (STV) area, located ventral to the PF areas, showed greater interhemispheric asymmetry than most other subdivisions. Areas TPOJ1–3 were located inferior to PGi, between higher visual and higher auditory areas. None of these five areas corresponded to previously defined subdivisions, but seemed to partially overlap with our TPJc and with cytoarchitectonic area PF. The existence of small lateralized subdivisions, potentially with specialized functions, might explain the particularly high variability observed in this region.

3.7. Summary

The correspondence of subdivisions across studies must be interpreted with caution, especially given the high inter-subject variability of the IPL/TPJ and the small number of subjects used in most MRI and postmortem studies. However, when considering the existing functional and structural data, some consistent patterns emerge. First, the two most posterior zones in the AG (Caspers et al., 2008) appeared to be part of two related subsystems of the DMN. Second, the cytoarchitectonic subdivision PFop, corresponding to the functionally defined TPJa, was part of the CON. Third, the TPJd appeared to span the dorsal portion of several cytoarchitectonic subdivisions in the IPL, although this could be an artifact of inter-subject variability. One speculation is that this reflects the flexible and widespread connectivity of the FCN. Fourth, the middle zones PF, PFt, PFm and PFcm, overlapping the functional zone TPJc, were more variable than other zones.

Taken together, the data indicate that it is possible to distinguish IPL/TPJ network nodes from each other using a variety of methods on structural and functional MRI data. But how do the subdivisions identified at rest correspond to the activity of the IPL/TPJ during human behavior? In the next section, we examine how functional activations in different domains relate to the zones and networks identified above.

4. Functional activations of the IPL/TPJ in task-based studies

Activation foci in the IPL/TPJ have been reported in fMRI studies across a large number of functional domains. Reviewing them all in detail is beyond the scope of this review, and we refer the reader to previous reviews that have focused on specific domains or subregions in more depth (e.g. Binder et al., 2009; Cabeza et al., 2012a; Cole et al., 2014; Corbetta et al., 2008; Seghier, 2013). In this section we aim to give a broad overview of IPL/TPJ activations in a selection of domains. We will start by discussing IPL/TPJ participation in bottom-up attention, followed by lower-level processing of one's own body and sense of agency. Then we will move on to higher-order processing, describing studies of internal cognition, such as mind-wandering and memory retrieval, and, finally, social cognition. In our last section, we describe a study focusing on the participation of specific network nodes in social, attentional and memory tasks.

4.1. IPL/TPJ nodes in bottom-up attention

The IPL/TPJ has been implicated in stimulus-driven reorienting of attention, in particular when the stimulus is unexpected and relevant for the current behavior (Corbetta et al., 2000, 2008). Early event-related fMRI studies found an IPL/TPJ region that was activated by reorienting to targets at unattended locations and by unexpected changes in sensory inputs (Corbetta et al., 2000; Downar et al., 2000). These findings, combined with the observation of convergent IPL/TPJ activity across vision, touch and audition, quickly led to the concept of the IPL/TPJ as a supramodal network node in a "ventral attention network", which also contained the inferior frontal gyrus (IFG) and anterior insula (Corbetta et al., 2000, 2002, 2008; Downar et al., 2000). In this section, we review IPL/TPJ activations seen in studies of attentional reorienting and target detection.

Posner spatial-cueing tasks (Posner, 1980) have been instrumental in establishing the concept of a VAN. In a typical Posner task, each trial begins with a central cue that predicts the spatial location of a subsequent task-relevant target. In a minority of trials, the target appears in an unexpected location (invalidly cued target). In order to correctly process the target, attention must be redirected to the unexpected location. The behavioral cost of this reorienting process is evident as a slowing of response times in invalid compared to valid trials, and target-related brain activations in invalid trials compared to valid trials are interpreted as reorienting-specific.

The IPL/TPJ is activated during reorienting to invalidly cued targets, especially when the valid cue is highly predictive of the target location (Corbetta et al., 2000, 2002; Vossel et al., 2006). It was not activated by the cue itself or in catch trials when the target was absent (Corbetta et al., 2002; Thiel et al., 2004), and the activation was not solely explained by the unexpectedness or salience of the invalidly cued targets (Indovina and Macaluso, 2007; Kincade et al., 2005). Activations have often been bilateral, but generally stronger or more extensive in the right hemisphere (Corbetta et al., 2000, 2002; Kincade et al., 2005). A common locus of IPL/TPJ activation in these tasks is a region consistent with the TPJc, located in the posterior SMG, often overlapping with the posterior STS and extending into the superior temporal gyrus (Corbetta et al., 2002; Gillebert et al., 2013; Igelström et al., 2016b; Kincade et al., 2005; Mitchell, 2008; Natale et al., 2009). However, others have also reported more dorsal and posterior AG

locations (Gillebert et al., 2013; Indovina and Macaluso, 2007). Continuous theta-burst stimulation with TMS to a region most consistent with the TPJp, but perhaps overlapping TPJc, appeared to slow the reorienting reaction to invalidly cued stimuli (Krall et al., 2015, 2016). Gillebert et al. (2013) quantified the overlap of attentional activity with the IPL subdivisions in the cytoarchitectonic atlas (Fig. 2D). They found the most specific reorienting-related activity in cytoarchitectonic area PF (TPJc), but there was also significant, less specific, activity in area PFm (TPJd) and PGa (TPJp). IPL/TPJ activity was also seen when the usual button press requirement was replaced by foot movements, saccadic eye movements or covert attention shifts (Astafiev et al., 2006), and when auditory cues were used to predict the target location (Macaluso et al., 2002). Commonly co-activated with the IPL/TPJ in Posner tasks, apart from the IFG and insula, are the middle frontal gyrus, precuneus, intraparietal sulcus, and premotor/precentral cortex (Corbetta et al., 2002; Indovina and Macaluso, 2007; Kincade et al., 2005; Natale et al., 2009; Thiel et al., 2004, 2005; Vossel et al., 2006, 2012, 2009). The IPL/TPJ has also been found to be active in relation to some non-Posner visual reorienting paradigms (Asplund et al., 2010; DiQuattro et al., 2014; Serences et al., 2005). IPL/TPJ appears to be particularly sensitive to stimuli that have potential behavioral relevance, need evaluation by higher-order systems, and that can potentially become the focus of attention of the top-down attention system (DAN) (Asplund et al., 2010; DiQuattro et al., 2014; Kincade et al., 2005; Serences et al., 2005).

Chen et al. (2012) introduced depth cues in the classical Posner task, making it possible to establish reorienting between different locations in the third dimensions. A cluster in the right IPL/TPJ, extending into the superior and middle temporal gyrus, was activated during reorienting to invalidly cued locations, both within and between depths. However, the co-activated network did not resemble the VAN, instead comprising the middle occipital and temporal gyri, dorsal AG, superior parietal cortex, precuneus and precentral gyrus. In addition, other networks were involved in more specific aspects of three-dimensional reorienting. The bilateral precentral gyrus was activated during reorienting between different depths, and a DMN-like network was involved in reorienting to invalidly cued objects that appeared closer to the observer (Chen et al., 2012). The right-lateralized TPJ-IFG network also did not seem to be activated during reorienting to auditory spatial targets after invalid auditory cues (Mayer et al., 2009, 2006). These experiments confirm that bottom-up reorienting of attention is frequently associated with IPL/TPJ activity, but they also suggest that this activity is not always associated with VAN involvement.

The IPL/TPJ is also often activated by infrequent target stimuli in oddball paradigms, which initiate brief stimulus-driven shifts in attention. Oddball tasks most commonly employ repeated presentation of auditory tones or visual stimuli (standard stimuli), which are infrequently and unpredictably replaced by deviant oddball stimuli (targets). The target stimuli are made task-relevant by asking the subject to mark them with a button press, or silently count them. In contrast to Posner tasks, oddball tasks are often non-spatial. Oddballs engage extensive brain networks, including regions from the VAN, DAN, sensorimotor regions and subcortical structures (Kiehl et al., 2005; Kim, 2014). Regions activated by task-relevant oddballs in both the auditory and visual domains include the IPL/TPJ, IFG, insula, middle frontal cortex, and anterior cingulate cortex, in a network that resembles the CON (Downar et al., 2001; Kim, 2014; Stevens et al., 2000). The location of the IPL/TPJ activation is often more anterior than the region recruited by invalidly cued targets in Posner tasks, and is more consistent with the TPJa as defined in our studies (Igelström et al., 2015, 2016a; Kim, 2014; Kubit and Jack, 2013).

General oddball effects are present in any behavioral paradigm that uses infrequent unpredictable targets, including Posner paradigms. Vossel et al. (2009) isolated the oddball phenomenon from attentional reorienting by including task-irrelevant oddballs in a Posner paradigm.

Activations specific for Posner reorienting were seen in regions consistent with the TPJc, the right posterior middle temporal gyrus and the right superior parietal lobe. The oddball trials specifically activated the inferior occipito-temporal cortex, the right IFG, the left IPL, the right anterior insula and the left cerebellum. Common activations were seen in the right IFG and in the dorsal right AG, in a location consistent with the TPJd-R. These results suggest that oddball effects are not responsible for TPJc activations in Posner tasks, but that more dorsal regions around the TPJd-R may play a more general role in the detection of unexpected stimuli. In addition, the findings indicate that activation of the VAN regions IFG and insula may be related to the oddball properties of the invalidly cued target.

Taken together, data on bottom-up attention suggest that Posner and oddball tasks engage slightly different IPL/TPJ regions with similar participation in the VAN and CON networks. Further, a more dorsal IPL/TPJ area, connected with the FCN and possibly corresponding to the TPJd as defined in our studies (Igelström et al., 2015, 2016a, 2016b), is involved in both tasks, suggesting an overarching role of this region in attentional function.

4.2. IPL/TPJ nodes in self-perception

The IPL/TPJ has been associated with integration of internal and external inputs into a coherent perception of oneself. For example, the IPL/TPJ has been implicated in the feeling of residing in one's own body and the experience of being the cause of one's actions (agency) (Blanke et al., 2002; Decety and Lamm, 2007). Our understanding of the neural correlates of these phenomena is very limited, but some studies have indicated that the IPL/TPJ might be necessary for normal bodily self-consciousness, self-location and agency. This section therefore reviews data on IPL/TPJ activation in these domains.

Electrical stimulation, lesions or seizures in the IPL/TPJ can cause out-of-body experiences, a perceived mismatch between one's "self" and the physical location of one's body (Blanke et al., 2005, 2002; De Ridder et al., 2007; Heydrich et al., 2011; Ionta et al., 2011). Intracranial recordings, neuroimaging and lesion mapping in patients have indicated the involvement of a zone around the intersection of the AG, SMG and superior temporal gyrus/sulcus, lateralized to the right hemisphere (Blanke et al., 2005, 2002; De Ridder et al., 2007). Perturbation of this region with TMS in healthy volunteers impaired performance in a discrimination task requiring mental simulation of an out-of-body experience (Blanke et al., 2005). A slightly more anterior region of the IPL/TPJ, between the SMG and superior temporal gyrus, was activated in fMRI experiments that simulated an out-of-body experience by inducing an illusion in which subjects misattributed a virtual body as their own (Ehrsson, 2007; Ionta et al., 2011; Lenggenhager et al., 2009, 2007). This anterior IPL/TPJ region was functionally connected with a network that partially overlapped the network activated by attentional reorienting, and also included the supplementary motor area (SMA), ventral premotor cortex, intraparietal sulcus and occipitotemporal cortex (Ionta et al., 2014). Thus, several parts of the IPL/TPJ may be implicated – and even causally involved – in the experience of residing in one's own body.

Agency, the experience of being the cause of one's actions, additionally requires processing of one's own motor output. If an action and the sensory perception of that action are mismatched, the sense of agency is disrupted and a subject reports the feeling that someone or something else is causing the action (reviewed in Sperduti et al. (2011)). This illusion has been harnessed in neuroimaging studies, to isolate the neural correlates of (perturbed) agency. The IPL/TPJ has consistently been found to activate in response to incongruent visual inputs during actions, with peaks in either the AG or the SMG depending on paradigm (see meta-analyses in Decety and Lamm (2007), Miele et al. (2011), Sperduti et al. (2011)). The right posterior STS and the SMG were activated when participants performed a hand movement while watching delayed or incongruent

recordings of the hand (Kontaris et al., 2009; Leube et al., 2003; Tsakiris et al., 2010). The AG and STS were activated by incongruent visual feedback when subjects controlled a virtual hand with a joystick (Farrer et al., 2003), or when inconsistencies were introduced into a newly learned action-response association (Spengler et al., 2009). The SMG was activated when subjective control was manipulated in a computer game (Miele et al., 2011; Schnell et al., 2007). Activations have consistently been greater in the right hemisphere, even though smaller left-sided activations have also been seen. Subjects were more likely to experience compromised agency during TMS to the right IPL, although the stimulation site appeared more dorsal than most activations described above (Ritterband-Rosenbaum et al., 2014). The IPL/ TPJ does not seem to be involved in higher cognitive processes related to agency, such as conscious reflection on whether or not an action was caused by someone else (Miele et al., 2011). Instead, it activates when discrepancies occur between visual, proprioceptive and motor inputs, indicating a role in lower-order, automatic processing.

A meta-study of agency attribution indicated that the brain regions most frequently co-activated with the IPL/TPJ during perturbed agency were the precuneus, pre-SMA and dorsomedial PFC (Sperduti et al., 2011). The participation of the pre-SMA may be associated with its involvement in intention and motor preparation. TMS to the pre-SMA interfered with "intentional binding", a marker of agency characterized by a perceived shortening of the interval between an action and a sensory effect (Moore et al., 2010). In a finger tapping task with visual feedback, Nahab et al. (2011) found two right-dominant networks that both responded proportionally to the loss of agency. Both networks involved several clusters in the IPL/TPJ, with uncertain correspondence to known subregions. One network included the right anterior insula, right superior frontal gyrus and right precuneus, and was suggested to be involved in mismatch detection due to the short latency of its BOLD response. The second network included the middle frontal gyrus, and its BOLD response showed a longer latency to peak and was more sustained.

In summary, the IPL/TPJ has frequently been identified as a core region in bodily self-consciousness and agency, in both correlational studies in which task-related activity was measured and causal studies in which activity in the cortex was directly manipulated.

4.3. IPL/TPJ nodes in introspection and memory

The IPL/TPJ is strongly associated with internally directed processes such as mind wandering and thinking about one's past or future (Buckner et al., 2008). Imaging studies on mind wandering have consistently shown activation in bilateral IPL/TPJ nodes associated with the DMN. Activity was also found in other nodes of the DMN (e.g. mPFC, precuneus, MTL) and the FCN (e.g. dorsolateral PFC, anterior cingulate cortex) (see Fox et al. (2015), for a recent meta-analysis). One interpretation is that mind wandering may involve coupling of the FCN with the DMN (see Section 3.2 for discussion of the flexible coupling of the FCN with other networks).

Undirected thinking arises in large part from the episodic memory system. The IPL/TPJ has often been shown to activate during retrieval of autobiographical or other episodic memories (Cabeza et al., 2012a; Svoboda et al., 2006). Retrieval of autobiographical memories engages a system consisting of the IPL/TPJ, medial and ventrolateral PFC, temporal lobe and posterior cingulate/retrosplenial cortex (Svoboda et al., 2006). This network is similar to the MTL subsystem of the DMN (Andrews-Hanna et al., 2010). Lesions in the IPL/TPJ and other DMN regions can cause impairments in autobiographical memory (Philippi et al., 2015). Neuroimaging activation patterns have been variable, in part due to variations in control conditions, which have included rest, semantic memory tasks and fictitious memories (Martinelli et al., 2013; Svoboda et al., 2006). The specific role of the IPL/TPJ in autobiographical memory is not understood, but might be related to more general aspects of memory retrieval (Cabeza et al., 2004). Activations

have largely been localized to the posterior AG, and have often, but not always, been left-lateralized (e.g. Levine et al., 2004; Summerfield et al., 2009; Svoboda et al., 2006). The localization of IPL/TPJ activity is consistent with AGp in our studies (Fig. 2A; cytoarchitectonic area PGp in Fig. 2D), which is structurally connected to the MTL memory system (Addis et al., 2004; Caspers et al., 2008; Denkova et al., 2006; Greenberg et al., 2005; Igelström et al., 2016a; Maguire and Frith, 2003; Rushworth et al., 2006; Vandekerckhove et al., 2005).

The current understanding of autobiographical memory is limited in part due to methodological challenges, such as the subjective nature of memories, the inability to control and verify memory retrieval, and challenges in the design of appropriate control tasks (Svoboda et al., 2006). In contrast, both encoding and retrieval can be tightly controlled if learning is limited to items presented in the laboratory. Such shorter-term episodic memory has been studied extensively, and the IPL/TPJ has been a primary focus of many of these studies. Episodic memory paradigms generally consist of an encoding phase during which participants learn a number of stimuli, and a retrieval phase that involves discrimination between studied (Old) and novel (New) items. A distinction is made between recollection and familiarity, where recollection is a vivid memory of contextual details surrounding the learning, and familiarity is a more intuitive feeling of having seen the item before. In neuroimaging experiments, the contrast between correctly recognized Old and correctly rejected New stimuli reveals activation of the IPL/TPJ, together with the precuneus, posterior cingulate cortex, left dorsolateral and dorsomedial PFC, bilateral superior parietal lobe and the caudate nucleus (meta-analysis in Kim (2013)). The magnitude of IPL/TPJ activation was greater for recollection than for familiarity, and was correlated with the degree of confidence reported by subjects (Daselaar et al., 2006; Frithsen and Miller, 2014; Kim, 2013; Kim and Cabeza, 2009; Vilberg and Rugg, 2008; Yonelinas et al., 2005). These observations indicate a role of the IPL/TPJ, as a node of the DMN, in the subjective experience of recalled memories. However, several of the commonly activated regions were also part of the FCN.

The location of IPL/TPJ activity in these Old/New tasks was similar to the location of activity in autobiographical memory retrieval, but posterior (and largely contralateral) to attention-related foci (Hutchinson et al., 2009). Thus, bottom-up attention and episodic memory retrieval seem to at least in part engage different IPL/TPJ regions and divergent brain-wide networks. The relationship between attentional and memory functions in the IPL/TPJ is still debated. One hypothesis is that memory retrieval involves attentional reorienting to spontaneously evoked memories, in a manner analogous to visuospatial reorienting (Cabeza et al., 2012a, 2008, 2011; Ciaramelli et al., 2008). Another hypothesis is that the IPL/TPJ may act as an "episodic buffer" to hold and manipulate retrieved information (Baddeley, 2000; Vilberg and Rugg, 2008). Yet another hypothesis is that the IPL/TPJ may act as a "mnemonic accumulator" that contributes to decision making (such as Old/New judgments) by temporally integrating recognition memory signals (Wagner et al., 2005).

4.4. IPL/TPJ nodes in social cognition

Social cognition is a major domain of IPL/TPJ function (Molenberghs et al., 2016; Schurz et al., 2014; Van Overwalle, 2009). In particular, the IPL/TPJ is activated during social attribution of temporary beliefs to other people (reviewed in Schurz et al. (2014)). The fMRI literature on social cognition is large and diverse, utilizing tasks ranging from gaze processing to strategic game playing. We limit our discussion here to false belief attribution, which has been solidly linked to IPL/TPJ activation (Schurz et al., 2014).

One of the most common fMRI paradigms for studying belief attribution is a story-based false belief task first used by Saxe and Kanwisher (2003). Stories describe a scene that changes in some respect between Time 1 and Time 2. In False Belief stories, a

protagonist is only aware of the scene at Time 1. The fMRI participant must answer a question about the protagonist's (false) belief about the scene at Time 2. The control condition consists of False Photograph stories, which also describe a scene that changes between Time 1 and Time 2. In these stories, a photograph or other depiction is created at Time 1. The participant must answer a question about the content of the photograph at Time 2, which now misrepresents reality (Saxe and Kanwisher, 2003). The BOLD contrast between the False Belief and False Photograph conditions has consistently revealed activation of the bilateral IPL/TPJ, around the location of the TPJp, together with precuneus/posterior cingulate, anterior STS, and mPFC (Dodell-Feder et al., 2011; Perner et al., 2006; Saxe and Kanwisher, 2003; Schurz et al., 2014). This IPL/TPJ activation could not be explained by task difficulty or the presence of a person (Saxe and Kanwisher, 2003), and the right and left IPL/TPJ were not activated by control stories requiring attribution of internal physical sensations or personal appearance (Saxe and Powell, 2006). Activation of the right IPL/TPJ was much more specific for theory-of-mind than the left IPL/TPJ, which also activated in response to some non-social stories as well as socially relevant background information that did not involve mental state attribution (Perner et al., 2006; Saxe and Wexler, 2005). However, the left IPL/TPJ may still play a critical role in belief reasoning, because lesions of the left IPL/TPJ caused specific deficits in theory-of-mind (Samson et al., 2004).

The location of IPL/TPJ activity at the border between the AG and superior temporal gyrus has been consistent across studies using the Belief/Photograph paradigm. The involvement of network nodes in the mPFC and precuneus in belief attribution has also been reproducible (Schurz et al., 2014). The mPFC is not specific or necessary for theory-of-mind and has been suggested to process more general socially relevant information (Bird et al., 2004; Saxe and Powell, 2006). The precuneus has been hypothesized to be involved in perspective taking through a role in mental imagery (Aichhorn et al., 2008; Cavanna and Trimble, 2006; Perner et al., 2006; Saxe and Powell, 2006).

Some studies have used cartoon representations of a classical false belief task that involves the transfer of an object from one location to another, unbeknownst to the protagonist ("Sally-Anne test"; Baron-Cohen et al., 1985). Subjects are asked to specify at which location the protagonist will search for the object when she returns to the scene, or indicate whether or not her search location is unexpected (Döhnel et al., 2012; Sommer et al., 2007, 2010). Control conditions have included questions about where the object is in reality (Döhnel et al., 2012) and true-belief trials in which the protagonist observes the transfer of the object (Sommer et al., 2010). When compared to reasoning about reality, false and true belief reasoning activated a common zone in the right IPL/TPJ (Döhnel et al., 2012), that corresponded well to the TPJp-R (red in Fig. 2A). Activation of the right IPL/TPJ by attribution of true beliefs was some cases weaker than that evoked by attribution of false beliefs (Aichhorn et al., 2008; Döhnel et al., 2012; Rothmayr et al., 2011; Sommer et al., 2007, 2010).

Many other laboratories have used other false belief paradigms, often to investigate functions that interact with cognitive theory of mind, such as deception, empathy, intention, emotion or humor. IPL/TPJ activations across these studies are more difficult to compare due to the great variability of stimuli and control conditions, and are thus beyond the scope of this review. Meta-analyses taking a more inclusive approach have consistently found activations of the bilateral IPL/TPJ, mPFC and precuneus, supporting this network as a general theory-of-mind network (Mar, 2010; Molenberghs et al., 2016). The IFG was also identified as part of the theory-of-mind network (Mar, 2010; Molenberghs et al., 2016), although it may be more robustly activated for lower-order (Schurz et al., 2014) and affective theory-of-mind processing (Molenberghs et al., 2016) compared to cognitive theory-of-mind. Other regions identified in comprehensive meta-studies included the anterior cingulate cortex, middle temporal gyrus, STS and anterior temporal lobe (Mar, 2010; Molenberghs et al., 2016).

Apparent overlap between social and attentional processes in the IPL/TPJ has triggered discussions about a potential common neural substrate. The findings reviewed above suggest that attentional reorienting and theory-of-mind engage different brain networks and IPL/TPJ nodes. However, voxels identified in general linear model (GLM) analyses appear to overlap at least in part. It has been suggested that attentional functions may underlie, or at least contribute to, social cognition in the IPL/TPJ. Decety and Lamm (2007) suggested that lower-order IPL/TPJ processes, such as attention and agency, may reflect a domain-general computation that is required for social cognition. Cabeza et al. (2012a) argued that bottom-up attention may account for activations in many tasks, including Belief/Photograph tasks. Graziano and Kastner (2011) argued that controlling one's own attention involves monitoring one's own attention, and that the mechanisms for monitoring one's own attention may overlap within the IPL/TPJ with the mechanisms that we use socially to monitor the attentional states of other people. Some overlap of social and attentional processes have been found in within-subject studies and meta-analyses, but separation has also been reported, with a more posterior location for theory-of-mind activity (Bzdok et al., 2013; Carter and Huettel, 2013; Decety and Lamm, 2007; Krall et al., 2015; Kubit and Jack, 2013; Lee and McCarthy, 2016; Mitchell, 2008). The data reviewed in this article are consistent with a separation of functional subdivisions within the IPL/TPJ, but in no way exclude that there are zones with converging functions. In particular, the TPJd in the dorsal IPL appears to show particularly extensive functional overlap. This question will become easier to resolve with the advent of improved neuroimaging methods and high-resolution parcellations (Glasser et al., 2016a, 2016b).

In addition to the TPJp clusters seen across story-based false belief studies, a meta-analysis of Belief/Photograph studies also found significant activation in a more dorsal region, in the AG near the TPJd, in both hemispheres (Schurz et al., 2014). Does this indicate that the FCN is involved in theory-of-mind? Executive control does play a role in successful theory-of-mind reasoning (Bull et al., 2008; Kloo and Perner, 2003; McKinnon and Moscovitch, 2007), in particular inhibitory control (Perner and Lang, 1999). Rothmayr et al. (2011) combined a cartoon-based false belief task and a Go/No-Go task, constructed using identical visual stimuli, and found overlapping activations in the dorsolateral PFC and a region consistent with the TPJd-R. Comparisons between false belief and true belief reasoning, which differ in their demands on executive resources, have also revealed activation of FCN nodes, in particular the lateral PFC and anterior cingulate cortex (Döhnel et al., 2012; Hartwright et al., 2012; Sommer et al., 2007). The possible role of the FCN in belief attribution remains to be characterized, but it could be speculated that theory-of-mind involves coupling of the FCN with DMN regions to achieve goal-directed social cognition.

4.5. Global activation of the dorsal IPL/TPJ across task domains

A recent study of ours suggested that the TPJd may play a general role across a broad range of task domains. We used our local ICA method (Section 3.1) to isolate network nodes within the IPL/TPJ and test their participation in a battery of five tasks involving attentional, social and memory functions (Igelström et al., 2016b). We collected functional MRI data during task performance (19–20 subjects/task), and parcellated the IPL/TPJ into ICs, as an unbiased way to identify network nodes (Igelström et al., 2015, 2016a, 2016b). Subject-specific IC time courses (Beckmann and Smith, 2004) were first used in a GLM analysis to identify task-related ICs, and then in a whole-brain connectivity analysis to verify their network involvement (Igelström et al., 2016b). We identified ICs that showed 1) a positive response for the condition of interest (e.g. the Belief story in a Belief/Photograph task), and 2) a significant contrast between the condition of interest and the control condition (e.g. Belief versus Photograph in a Belief/

Social attribution of beliefs
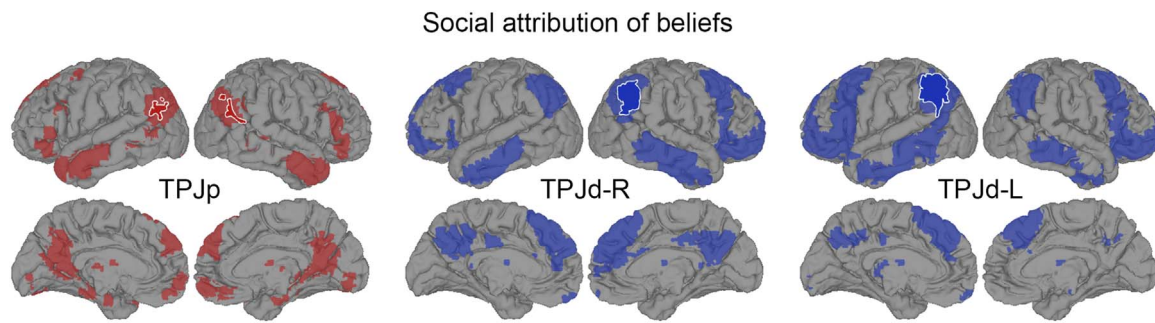
Fig. 3. Independent components (ICs) involved in a false belief task, and their connectivity patterns. The ICs are displayed in solid colors with white outlines, and their connectivity networks are in solid semi-transparent colors. Three ICs showed significant activation in the Belief/Photo contrast: the TPJp, connected to the default mode network (left), the TPJd-R, connected to the FCN (middle), and the TPJd-L, also connected to the FCN (right). Data from Igelström et al. (2016b) were plotted on pial surfaces. See Section 4.5 for details.

Photograph task).

We used two tasks probing social cognition: a story-based Belief/ Photograph task (Dodell-Feder et al., 2011) and a task involving social attribution of attention (Kelly et al., 2014). In the latter task, subjects were required to integrate emotional and gaze cues to rate the perceived awareness of a cartoon face of an object next to it. The social processing load was manipulated by presenting different combinations of matching and mismatching cues, and the BOLD activations during integration of mismatching social cues were compared with processing of matching cues.

In the Belief/Photograph task, we found three ICs with a significant response during Belief trials and a significant Belief/Photograph contrast (Fig. 3). The first IC was bilateral and located in the posterior ventral AG, in a region consistent with the AGp and/or TPJp (red clusters with white outlines in the left panel). It was connected to a network resembling the DMN, including the precuneus, dorsomedial PFC and anterior temporal lobe (red semi-transparent overlay in Fig. 3). The other two ICs were right- and left-lateralized, located in regions consistent with the TPJd-R (middle panel) and TPJd-L (right panel), and were connected to the FCN (blue semi-transparent overlays in Fig. 3). In the attribution of attention task, we found significant activity in a region consistent with the TPJd-R, which again was connected to the FCN (Igelström et al., 2016b).

We used two tasks in the domain of bottom-up attention: a Posner reorienting task (Mitchell, 2008) and a visual oddball task (Stevens, et al., 2000). In both tasks, we found two right-lateralized IPL/TPJ components (Fig. 4). As expected (see Section 4.1), the Invalid/Valid contrast returned a right-lateralized IC in a region consistent with the TPJc (orange with white outlines in the left panel of Fig. 4A), whereas the Target/Standard contrast in the oddball task returned a right-lateralized IC in a region consistent with the TPJa (green with white outlines in the left panel of Fig. 4B). Their connectivity patterns were consistent with the VAN/CON (orange and green semi-transparent overlays in Fig. 4A and B). However, in addition to these activations, both tasks engaged a right-lateralized IC in the dorsal IPL/TPJ, in a region consistent with the TPJd-R, with connectivity to FCN regions (blue semi-transparent overlays in Fig. 4A and B).

Finally, we used an Old/New task to test episodic memory retrieval (Stevens et al., 2000). This task showed significant activity only in the TPJd-R, with connectivity to the right FCN. This right-lateralization seems unexpected given the many reports of left-bias in memory function. However, BOLD time course analyses have suggested that the positive Old/New contrast in the left IPL/TPJ reflects a deactivation in the control condition rather than a positive BOLD response during recollection (Nelson et al., 2010). This activation pattern would not have met our criterion of a positive BOLD response in Old trials.

These experiments provided direct evidence of the involvement of the TPJd-R and the FCN in a range of tasks involving social cognition, bottom-up attention and episodic memory retrieval. In addition, task-specific IPL/TPJ node activations were seen in the TPJp in the Belief/

Photograph task, the TPJc in the Posner task, and the TPJa in the oddball task. The activation locations and connectivity patterns of these domain-specific nodes were consistent with previous studies (Sections 4.1, 4.3 and 4.4).

Taken together, studies by us and others indicate that the TPJd node of the FCN is indeed a flexible hub, which can couple functionally with all the networks that intersect the IPL/TPJ region. This executive control network may thus regulate and monitor a variety of functions, ranging from bottom-up perception to higher-order cognition. This global function may be critical for normal regulation of cognition and behavior, as FCN dysfunctions are particularly common in many psychiatric disorders (Cole et al., 2014).

5. Summary and future directions

This review examined data from a broad selection of neuroimaging studies of the IPL/TPJ, including resting-state and diffusion tensor MRI, as well as task-based fMRI involving attentional reorienting, self-perception, undirected thinking, memory and social cognition. Taken together, the data show unequivocally that the IPL/TPJ contains subregions that form network nodes in several brain-wide networks. The extensive connectivity of the IPL/TPJ – in particular of the dorsal regions – supports its role as a major network hub, and is likely to underlie its activation in a large number of task-based studies across multiple functional domains. While some functional domains (e.g. memory, social cognition and bottom-up attention) are strongly associated with certain IPL/TPJ nodes and brain networks, others show less consistency. For example, it is not yet clear how the potentially causal role of the IPL/TPJ in agency and self-location relates to the functional or anatomical organization of the region. Given its central placement in important brain networks, the IPL/TPJ is also likely to be involved in many functions not reviewed here (see for example a detailed review of additional functions of the AG in Seghier (2013)).

Many important questions remain to be addressed. One is the lateralization of function in the IPL/TPJ, which was addressed only briefly in this review. The right-dominance of attentional functions, and left-dominance of memory and language processing, are reflected in the localization of activations in task-based studies. Symmetrically located network nodes in the left and right IPL/TPJ may thus play distinct functional roles. This possibility is still far from understood and is an important topic for future studies (Seghier, 2013). Another topic that we did not discuss at length was the prominent debate between the "fractionation view" (the theory that the IPL/TPJ is modular in function) and the "overarching view" (the theory that the IPL/TPJ contains one larger area with an overarching function) (e.g. Cabeza et al., 2012a, 2012b; Nelson et al., 2012). The data reviewed here support zones of overlap where overarching computations may occur (such as border areas and perhaps the TPJd region). At the same time, the literature unequivocally shows the existence of multiple
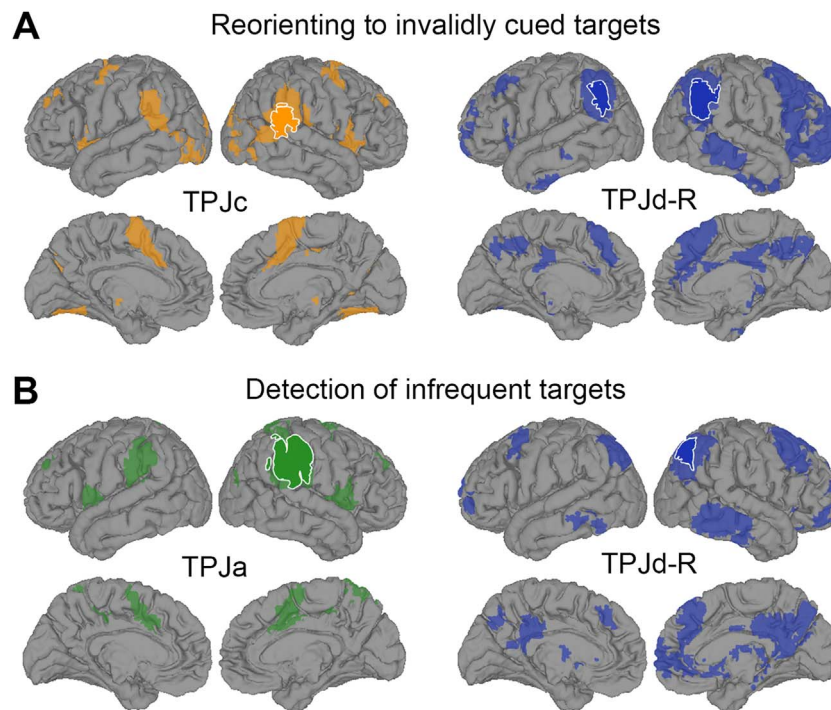
Fig. 4. Attention-related independent components (ICs) and their connectivity patterns. The ICs are displayed in solid colors with white outlines, and their connectivity networks in solid semi-transparent colors. (A) Two ICs were identified during reorienting to invalidly cued targets in a Posner spatial-cueing task: the TPJc, connected to the CON (or VAN) (left), and the TPJd-R, connected to the FCN (right). (B) Two ICs were activated by infrequent visual oddball targets: the TPJa, connected to the CON or VAN (left), and the TPJd-R, connected to the FCN. The data in Igelström et al. (2016b) were plotted on pial surfaces. See Section 4.5 for details.

subdivisions that are nodes in widely separate brain networks. We believe that the IPL/TPJ region should be viewed as relatively unchartered territory and that its functions are probably not yet ready for dichotomous views. This perspective is similar to that of Seghier's view of the AG (2013). This recent paper summarized current conceptual and methodological issues, outlined known subdivisions and AG activations across many domains, and proposed an integrative account comprising both specialization and convergence (Seghier, 2013). Further research is also needed to begin to elucidate exactly how the IPL/TPJ nodes contribute to cognition and behavior. Most task-based studies to date have been correlational, and the diversity of task designs often prevents generalization and comparison across studies (Seghier, 2013). Emerging technologies that greatly improve data quality and analysis methods are likely to lead to rapid progress in the coming years (Glasser et al., 2016a, 2016b). It will be important to focus not only on within-network interactions, but also on how different networks are interconnected. The IPL/TPJ might be a site for communication between neighboring, perhaps partially overlapping, network nodes, and thereby form a cognitive hub where multiple networks converge and interact.

Acknowledgments

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