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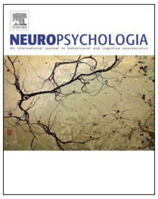

The inferior parietal lobule and temporoparietal junction: A network perspective

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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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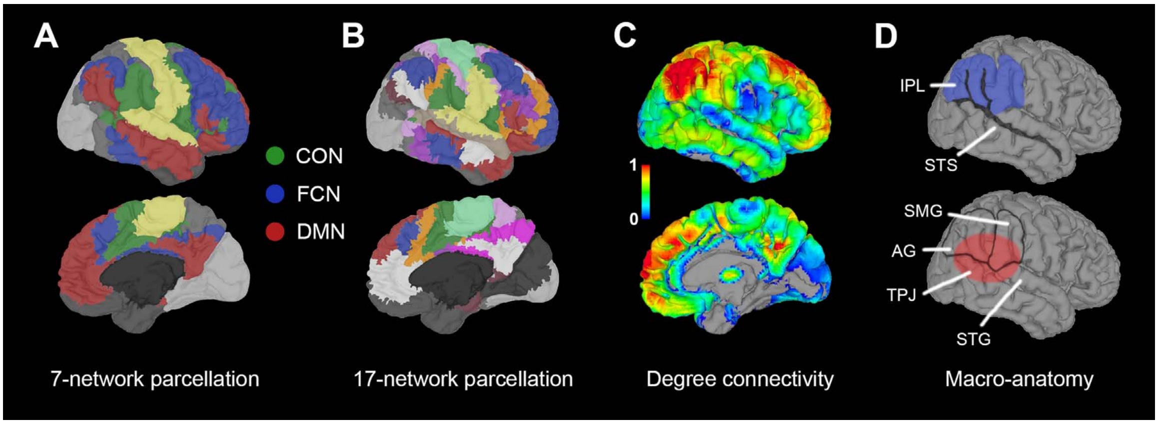

Fig. 1. The network structure of the brain and the anatomy of the inferior parietal lobule/temporoparietal junction (IPL/TPJ). (A) Brain networks at a resolution of 7 networks based on functional connectivity (Yeo et al., 2011). Three cognitive networks overlap the IPL/TPJ: the frontoparietal control 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-