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Functional subdivisions of medial parieto-occipital cortex in humans and nonhuman primates using resting-state fMRI

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ABSTRACT

Based on its diverse and wide-spread patterns of connectivity, primate posteromedial cortex (PMC) is well positioned to support roles in several aspects of sensory-, cognitive- and motor-related processing. Previous work in both humans and non-human primates (NHPs) using resting-state functional MRI (rs-fMRI) suggests that a subregion of PMC, the medial parieto-occipital cortex (mPOC), by virtue of its intrinsic functional connectivity (FC) with visual cortex, may only play a role in higher-order visual processing. Recent neuroanatomical tracer studies in NHPs, however, demonstrate that mPOC also has prominent cortico-cortical connections with several frontoparietal structures involved in movement planning and control, a finding consistent with increasing observations of reach- and grasp-related activity in the mPOC of both NHPs and humans. To reconcile these observations, here we used rs-fMRI data collected from both awake humans and anesthetized macaque monkeys to more closely examine and compare parcellations of mPOC across species and explore the FC patterns associated with these subdivisions. Seed-based and voxel-wise hierarchical cluster analyses revealed four broad spatially separated functional boundaries that correspond with graded differences in whole-brain FC patterns in each species. The patterns of FC observed are consistent with mPOC forming a critical hub of networks involved in action planning and control, spatial navigation, and working memory. In addition, our comparison between species indicates that while there are several similarities, there may be some species-specific differences in functional neural organization. These findings and the associated theoretical implications are discussed.

Introduction

The posteromedial cortex (PMC), comprising the precuneus, retrosplenial, and posterior cingulate cortex, is a highly diverse anatomical structure implicated in vast array of higher order cognitive functions and behaviors. In humans, specific sets of cognitive functions have been ascribed to particular subregions of PMC. For example, neural activation responses in dorsal-anterior PMC have been linked to self-referential processes like mental imagery, covert shifts of attention (Cavanna and Trimble, 2006), and the preparation and execution of visually guided behaviors (Wenderoth et al., 2005). Responses associated with dorsal-posterior PMC have been linked to episodic memory retrieval and the processing of emotions (Lundstrom et al., 2003; Lundstrom et al., 2005; Cavanna and Trimble, 2006; Dorfel et al., 2009). In addition, ventral PMC, and the posterior cingulate cortex (PCC) in particular, has been identified as a key hub of the default network (DN), an interconnected set of cortical areas that include the inferior parietal lobule, hippocampal formation, and superior frontal and medial frontal gyri. The DN has been functionally implicated in internal modes of cognition such as autobiographical memory retrieval and envisioning the future (for review, see Buckner et al., 2008), as well as elements of consciousness (Maquet et al., 1997; Fiset et al., 1999; Canavero et al., 2009) and social cognition (Schilbach et al., 2008; Schilbach et al., 2012). Taken together, the available functional evidence implicates the PMC as being heterogeneous and playing an associative and/or integrative role in several aspects of higher-level cognitive processing.

The vast array of cognitive functions ascribed to the PMC matches well with the host of cytoarchitectonic divisions of which it is comprised. Though Brodmann (1909, 2006) originally parcellated the

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PMC into five subregions (areas 23, 29, 30, 31, and 7; see Fig. 1), other anatomists of the 20th century—and even Brodmann himself—have suggested that more cytoarchitectonic subdivisions may exist, particularly within the precuneus (Smith, 1907; Vogt, 1911; Economo and Koskinas, 1925; Von Bonin and Bailey, 1947; Pandya and Seltzer, 1982; Cavada and Goldman-Raiuc, 1989; Scheperjans et al., 2008b; Scheperjans et al., 2008a). Axonal tract tracing studies in monkeys suggest a posterior-to-anterior transitional gradient in the precuneus on the basis of cortico-cortical connectivity patterns, with three broader subdivisions emerging: posterior (area PO), middle (area PGm), and anterior (area PEc). On the basis of its prominent connections to occipital cortex, area PO, which spans the dorsal parieto-occipital sulcus (POS) in mPOC, was thought to primarily play a role in visual processing (Colby et al., 1988). However, more recent evidence from the field of sensorimotor neuroscience has demonstrated functional neuronal properties and patterns of cortico-cortical connectivity in the macaque monkey that are also consistent with the area and its immediate surrounding cortex playing an important role in visuomotor planning and control. In particular, converging work indicates that area PO, and mPOC more generally, rather than being a single homogeneous structure, is actually comprised of three distinct areas, V6, V6Av, and V6Ad (Galletti et al., 2005). These regions differ in their topography, cytoarchitectonics, and structural connections (Galletti et al., 2001; Gamberini et al., 2009; Passarelli et al., 2011), and area V6A has neuronal responses that correspond with visuomotor transformations required for manual behaviors like reaching and grasping (Fattori et al., 2009b; Fattori et al., 2010; Gamberini et al., 2011; Fattori et al., 2012).

In support of functional homologies between the mPOC region of macaques and humans, recent studies using wide-field retinotopic mapping have identified putative human homologues of monkey areas V6 (Pitzalis et al., 2006; Fattori et al., 2009a; Pitzalis et al., 2010) and V6Av (Pitzalis et al., 2013a). Moreover, convergent findings from fMRI (e.g., Prado et al., 2005; Gallivan et al., 2011a; Gallivan et al., 2011b; Tosoni et al., 2014), transcranial magnetic stimulation (e.g., Vesia et al., 2010; Ciavarro et al., 2013), and patient studies (Karnath and Perenin, 2005) all implicate the region surrounding the superior aspect of the POS, the superior parieto-occipital cortex (SPOC), in the preparation and execution of reaching and grasping actions. Despite considerable differences in the methodologies employed in the two species, both macaque and human mPOC appear to have a similar functional neural organization.

Resting-state functional MRI (rs-fMRI) approaches, which typically exploit temporal dependencies of low-frequency blood oxygenation level-dependent (BOLD) oscillations to reveal functional networks in the absence of any explicit task paradigm (Biswal et al., 1995), have emerged as a simple yet powerful tool for comparing the functional neural organization of the human and nonhuman primate (NHP) brains (Vincent et al., 2007; Margulies et al., 2009; Hutchison et al., 2011; Mars

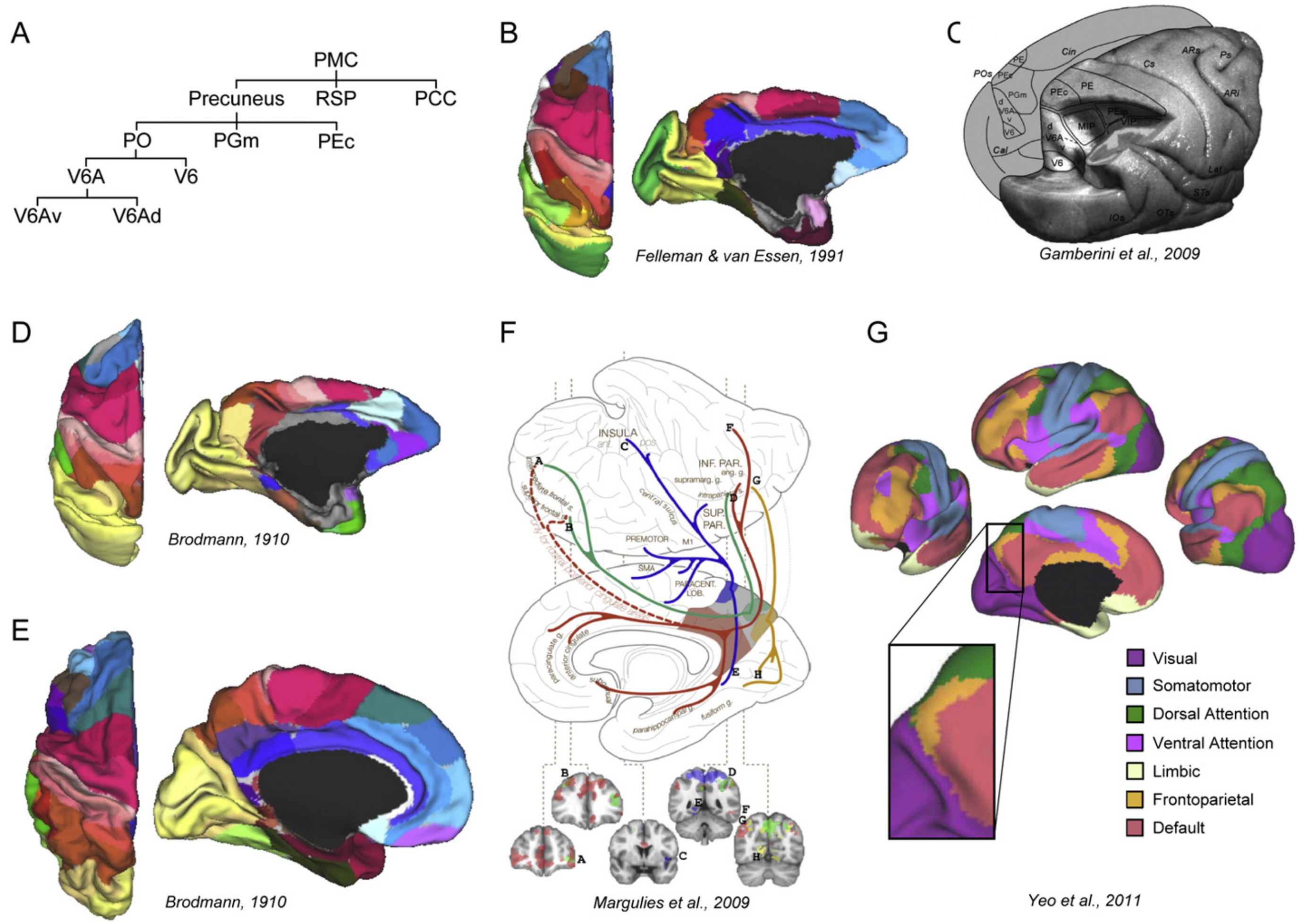

Fig. 1. Previous parcellations of mPOC based on cytoarchitectonics, cortico-cortical connections and functional neural response properties. A) Nomenclature of proposed subdivisions of macaque posteromedial cortex (PMC). RSP = retrosplenial cortex; PCC = posterior cingulate cortex. B–D) Proposed parcellations in the macaque. B) Cytoarchitectonic divisions proposed by Felleman & van Essen. C) Subdivisions, based on cytoarchitectonics, cortico-cortical connections and neurophysiological recordings, proposed by Galletti, Fattori and colleagues. D) Cytoarchitectonic divisions proposed by Brodmann. E–G) Proposed parcellations in the human. E) Cytoarchitectonic divisions proposed by Brodmann. F) Functional subdivisions, based on intrinsic patterns of functional connectivity, proposed by Margulies et al. (2009). G) Whole-brain network parcellations, based on intrinsic patterns of functional connectivity, proposed by Yeo et al. (2011). Inset shows close-up of mPOC parcellation, with colors denoting proposed functional subdivisions for a 7 cluster network.