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A brief comparative review of primate posterior parietal cortex: A novel hypothesis on the human toolmaker

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ABSTRACT

The primate visual system contains two major cortical pathways: a ventral-temporal pathway that has been associated with object processing and recognition, and a dorsal-parietal pathway that has been associated with spatial processing and action guidance. Our understanding of the role of the dorsal pathway, in particular, has greatly evolved within the framework of the two-pathway hypothesis since its original conception. Here, we present a comparative review of the primate dorsal pathway in humans and monkeys based on electrophysiological, neuroimaging, neuropsychological, and neuroanatomical studies. We consider similarities and differences across species in terms of the topographic representation of visual space; specificity for eye, reaching, or grasping movements; multi-modal response properties; and the representation of objects and tools. We also review the relative anatomical location of functionally- and topographically-defined regions of the posterior parietal cortex. An emerging theme from this comparative analysis is that non-spatial information is represented to a greater degree, and with increased complexity, in the human dorsal visual system. We propose that non-spatial information in the primate parietal cortex contributes to the perception-to-action system aimed at manipulating objects in peripersonal space. In humans, this network has expanded in multiple ways, including the development of a dorsal object vision system mirroring the complexity of the ventral stream, the integration of object information with parietal working memory systems, and the emergence of tool-specific object representations in the anterior intraparietal sulcus and regions of the inferior parietal lobe. We propose that these evolutionary changes have enabled the emergence of human-specific behaviors, such as the sophisticated use of tools.

1. Introduction

The notion of two functionally segregated visual pathways has significantly shaped our conception of primate vision over the last few decades. The initial conception of the two pathway hypothesis, based largely on empirical studies of the macaque monkey, stated that the ventral-temporal pathway serves object vision, whereas the dorsal-parietal pathway serves spatial vision (Mishkin and Ungerleider, 1982). In accordance with this hypothesis, early monkey physiology studies showed shape- and object-selective responses in neurons of inferior temporal (IT) cortex (Desimone et al., 1984; Gross et al., 1972; Logothetis and Sheinberg, 1996). In contrast, neurons in the posterior parietal cortex (PPC) transform visual information into different spatial reference frames with respect to the eyes, body, or world (Andersen et al., 1997), and this information is further integrated with spatial information from the auditory and somatosensory systems.

Observations of the human visual system are also consistent with the two-pathway hypothesis. For example, a large swath of ventral temporal and lateral occipital cortex, referred to as the lateral occipital complex (LOC), responds more strongly to pictures of objects than to their scrambled counterparts (Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2001; Malach et al., 1995). Both IT and LOC represent objects independent of the precise physical cues that define them (Grill-Spector et al., 1998) and regardless of changes in external viewing conditions that affect an object's appearance, but not its identity (Grill-Spector et al., 1999; James et al., 2002; Sawamura

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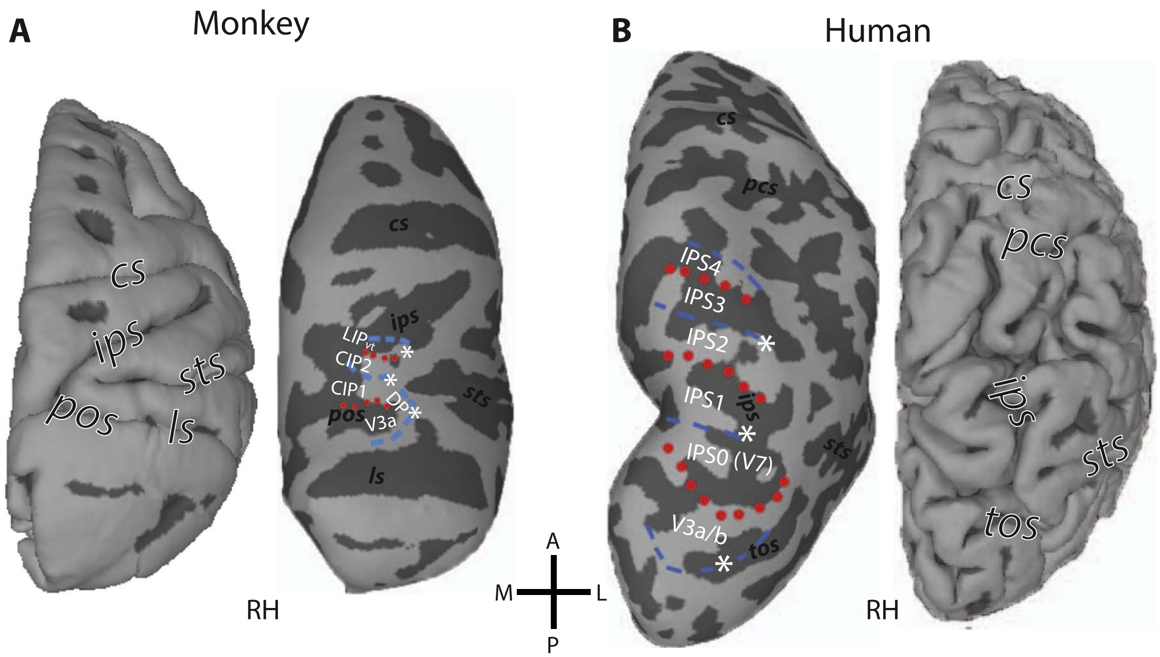

Fig. 1. : *Topographic organization of primate PPC.* Comparison of the fMRI-defined retinotopic organization of dorsal occipital and parietal cortex in both monkeys (A) and humans (B). Lines denote areal boundaries formed by phase angles at or close to the upper (red, dotted) or lower (blue, dashed) vertical meridian. Surfaces are rendered with anterior (A) up, posterior (P) down, medial (M) left, and lateral (L) right. Major sulci are labeled in each view: *cs*, central sulcus; *pcs*, postcentral sulcus; *ips*, intraparietal sulcus; *ls*, lunate sulcus; *pos*, parieto-occipital sulcus; *tos*, transverse occipital sulcus. (After: Arcaro et al., 2011).

et al., 2005; Vuilleumier et al., 2002). Hence, IT and LOC display response properties that characterize an effective object recognition system subserving perceptual object constancy. With respect to spatial cognition, lesions of human PPC can lead to the neglect of contralateral space with respect to different spatial reference frames (e.g., spatial neglect, Corbetta and Shulman, 2011) or visuomotor deficits (e.g., optic ataxia, Perenin and Vighetto, 1988). PPC is also an important node in the spatial attention network, which underlines its more general role in spatial cognition (Szczepanski et al., 2010).

However, other observations from human subjects suggested that this original framework was incomplete. For example, some patients (most notably patient D.F.) with ventral stream lesions show severe forms of visual agnosia, yet can perform visually-guided reaching and grasping movements towards those same objects (Goodale et al., 1991; James et al., 2002). Such observations led to a reformulation of the two-pathway hypothesis, with an emphasis on vision for perception for the ventral pathway versus vision for action for the dorsal pathway (Goodale and Milner, 1992). In this influential framework, spatial cognition is one among other aspects of the dorsal visual representation. Notably, there is an assumption that there is also a representation of object information in the dorsal stream, which is specifically utilized for visually-guided movement.

In the past few decades, continued study of the human and macaque visual systems (reviewed below) has provided support for the broad framework of the action-perception two-pathway hypothesis. However, recent studies have revealed important differences across the two species, in particular with respect to dorsal object representations. As we review in detail below, the object vision system of the human dorsal pathway is much more developed and refined that in the macaque. Indeed, the complexity of the human dorsal object representations appears to mirror the complexity of those found in ventral representations (Konen and Kastner, 2008a).

Here, we review and compare some of the literature on the dorsal pathway in humans and monkeys with particular emphasis on PPC. We show that many of the disparate findings are due to species differences in the functional organization of the dorsal pathway. Finally, we propose a novel hypothesis as to why the human dorsal pathway may have undergone significant functional transformations relative to other species in the primate lineage.

2. Topographic organization

Phase-encoded retinotopic mapping along the polar angle and eccentricity dimensions using functional magnetic resonance imaging (fMRI) has been widely used to reveal topographic organization within the human (Arcaro et al., 2009; Brewer et al., 2005; Engel et al., 1997; Hagler and Sereno, 2006; Kastner et al., 2007; Konen and Kastner, 2008a; Larsson and Heeger, 2006; Schneider et al., 2004; Sereno et al., 1995; Swisher et al., 2007) and also the macaque monkey visual system (Brewer et al., 2002; Kolster et al., 2009). Specifically, such topographic mapping enables the simultaneous investigation of visuotopic organization across a large region of cortex, thereby allowing the visuospatial map of an individual area to be anchored in the framework of the topographic organization across multiple surrounding areas. Thus, comparing the topographic large-scale organization of primate PPC at the level of maps serves as a first useful approach in our comparative review.

In macaque monkeys, multiple visual areas within and adjacent to the intraparietal sulcus (IPS) have been identified in PPC (Andersen et al., 1990; Pandya and Seltzer, 1982; Van Essen, 2004). Visual areas within PPC have been distinguished based on their cyto- and myeloarchitecture, as well as their connectivity patterns, including the ventral and dorsal lateral intraparietal areas (LIPv/d), and two cortical zones, dorsal prelunate (DP) and lateral occipital parietal (LOP), also referred to as caudal intraparietal (CIP). Arcaro et al. (2011) studied the visuotopic organization of these regions. They identified two visual field maps anterior to area V3A within caudal PPC (named CIP1 and CIP2). In the polar angle dimension, the representation in CIP1 extended from regions near the upper vertical meridian (that is the shared border with V3A) to those within the lower visual field (that is the shared border with CIP2), thus spanning a contralateral hemifield. The polar angle representation in CIP2 was found to be a mirror reversal of the CIP1 representation. Anterior to CIP2, a third polar angle representation was found within LIP (visuotopic LIP, LIP_{vt}),