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Organization and evolution of parieto-frontal processing streams in macaque monkeys and humans



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ABSTRACT

The functional organization of the parieto-frontal system is crucial for understanding cognitive-motor behavior and provides the basis for interpreting the consequences of parietal lesions in humans from a neurobiological perspective. The parieto-frontal connectivity defines some main information streams that, rather than being devoted to restricted functions, underlie a rich behavioral repertoire. Surprisingly, from macaque to humans, evolution has added only a few, new functional streams, increasing however their complexity and encoding power. In fact, the characterization of the conduction times of parietal and frontal areas to different target structures has recently opened a new window on cortical dynamics, suggesting that evolution has amplified the probability of dynamic interactions between the nodes of the network, thanks to communication patterns based on temporally-dispersed conduction delays. This might allow the representation of sensory–motor signals within multiple neural assemblies and reference frames, as to optimize sensory–motor remapping within an action space characterized by different and more complex demands across evolution.

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Review

1. Introduction

It is widely assumed that in the cerebral cortex operations such as encoding sensory information, or using one's own intention to plan and control movement are performed by distributed systems (Mountcastle, 1978), i.e. by assemblies of neurons which cooperate in the task. A crucial question today is the nature of the network that binds neurons in the cooperative assemblies underlying directed visual attention, cognitive motor functions, movement planning and control. In most of these processes cortico-cortical connections presumably play a key role in coordinate transformation of different nature. Therefore the definition of the cortical areas involved and of their connectivity is a necessary prerequisite to the study of the operations underlying such complex functions. This information is also crucial for interpreting the visuo-motor disorders of parietal patients from a neurobiological perspective.

2. Identification of posterior parietal areas and connections in monkeys

In this section we will illustrate the anatomical organization and the connections with the frontal lobe of the areas of the posterior parietal cortex in macaque monkeys (see Table 1).

The identification of areas within the homotypical cortex of the parietal lobe in macaque monkeys is based on multiple criteria (Fellemann and Van Essen, 1991; Pandya and Seltzer, 1982. The Brodmann (1909) cytoarchitectonic subdivision into area 5 in the superior parietal lobule (SPL), and area 7 in the inferior parietal lobule (IPL) and mesial wall of SPL (now area 7m, or PGm), has evolved into more complex schemes (Fig. 1A), based on the cortico-cortical connectivity and on the activation properties of parietal neurons. Today, the SPL is subdivided into areas PEa and MIP in the dorsal bank of the IPS, PE and PEc in the exposed aspect, the latter area also extending in the medial wall of the hemisphere, where it is located dorsally to area 7m (PGm). PEc and 7m form the anterior and central regions of the precuneus (Margulies et al., 2009), respectively. Caudally, areas V6 and V6A occupy the rostral wall of the parieto-occipital sulcus (POS) and border medially with area 7m. The lateral bank of the IPS consists of the anterior (AIP), lateral (LIP) and caudal (CIP) intraparietal areas, while the ventral intraparietal area (VIP) lies in the depth of the IPS. The lateral exposed surface of IPL, from anterior to posterior, includes areas PF, PFG, PG, Opt. Parietal areas PFop and PGop (not shown in Fig. 1A) are located in the dorsal bank of the Sylvian fissure, at similar rostrocaudal locations of PF and PFG, respectively. It is worth stressing that this subdivision of parietal areas cannot be considered as conclusive, since they could be further subdivided as new methods or functional studies of their properties will became available. This is a critical issue when considering the macaque to human differences in cortical organization. In fact, the non-uniform expansion of human cerebral cortex often involved duplication or parcellation of areas (see Chaplin et al., 2013).

Thanks to hierarchical cluster analysis, parietal and frontal areas with similar connectivity can be grouped in clusters (Averbeck et al., 2009), which lay at the core of parieto-frontal interactions (Fig. 1B). In SPL, areas MIP, PEc and PEa define a *dorsal parietal cluster* (*PAR-d*), while areas SI, SII and PE form a *somatosensory cluster* (*SS*). A cluster spanning medio-laterally (*PAR-ml*) from the parieto-occipital junction through the IPL includes areas PGm (7m), V6A, Opt, LIP, and VIP, and probably area CIP as well, for which, however, scant information is available in terms of cortico-cortical connectivity (Borra et al., 2008). In IPL, areas PF, PFG, PG and AIP belong to a *ventral parietal cluster* (*PAR-v*). Cortico-cortical connectivity tends to be stronger locally, thus defining small world networks including nearby areas. These clusters are reciprocally connected

with complementary clusters in frontal cortex (Fig. 1B). Finally, a *parieto-cingulate stream* can be identified from the combined input to cingulate cortex stemming from selected areas of the *SS–M1 cluster* and *PAR m–l cluster*.

2.1. Different macaque parieto-frontal streams encode different functions

This section will be devoted to analysis of the functional organization of the different parieto-frontal streams identified by neuroanatomical tracing studies in macaques. In fact, parietal and frontal clusters linked by cortico-cortical connections define different processing streams, endowed with multiple functional roles.

2.1.1. The parieto-prefrontal stream (PAR-ml/PFC clusters)

Within this stream, the areas of the PAR-ml cluster contains at least four different representations of the visual field, which are located in areas LIP (Arcaro et al., 2011; Ben Hamed et al., 2001; Blatt et al., 1990; Patel et al., 2010), V6A (Galletti et al., 1999) and in the posterior part of IPS, and a spatial map of saccade trajectories in LIP (Savaki et al., 2010). Physiological studies indicate that the areas of this cluster are involved in directed visual attention (Bushnell et al., 1981; Lynch et al., 1977, area 7), saliency, including salient distractors (LIP; Bisley and Goldberg, 2010; Colby and Goldberg, 1999; Gottlieb et al., 1998; Qi et al., 2015; Suzuki and Gottlieb, 2013), novelty (LIP; Foley et al., 2014), and reorienting of attention (LIP; Steinmetz and Constantidinis, 1995). In LIP neurons with mirror properties (Shepherd et al., 2009) discharge when a monkey moves the focus of attention toward the cell's receptive field and when observing another monkey attending in the same direction. The locus of attention in area 7a is represented by patches of activation about 800 µm wide, which are embedded within a matrix of eye position signals (Raffi and Siegel, 2005), which together with eye movement (LIP/7a; Barash et al., 1991) influence neural activity across different IPL areas. An influential line of investigation, stemming from the original Mountcastle's concept of command functions of PPC (Mountcastle et al., 1975), has stressed the role of LIP in motor intention for eye movement control (Gnadt and Andersen, 1988; Snyder et al., 1997, 1998; see Andersen and Cui, 2009 for a review). Dorsal LIP (LIPd) is mostly involved in oculomotor planning, ventral LIP (LIPv) contributes to both attentional and oculomotor mechanisms (Liu et al., 2010). LIP also combines visual and motor variables concerning goal directed or symbolically cued hand movement (Oristaglio et al., 2006). While some studies (Dean et al., 2012) have proposed a role of LIP in eye-hand coordination, Yttri et al. (2013) have opposed this conclusion, by stressing its involvement in saccade planning and related attention.

Concerning visual analysis, LIP neurons encode the 3D structure and properties of visual objects (Gnadt and Mays, 1995; Sereno et al., 2002; Shikata et al., 1996; Vanduffel et al., 2002; for a review, see Orban, 2011). Area LIP is a central node of the decision-making network of PPC (for reviews, see Gold and Shadlen, 2007; Gottlieb et al., 2014; Kable and Glimcher, 2009). Its neurons vary their firing frequency as a function of the accumulation of evidence in favor or against each of the possible choices (Churchland et al., 2008; Roitman and Shadlen, 2002; Shadlen and Newsome, 2001) available before making a decision, and with the probability of reward during response selection (Kiani and Shadlen, 2009). During perceptual decisions, LIP neurons use available perceptual information for shaping the decision on which direction to move the eyes (Shadlen and Newsome, 1996). LIP decision-related activity reflects a sensorimotor integration process that encodes action value (Louie and Glimcher, 2010) relative to alternative options (Louie et al., 2011; Louie et al., 2014).

Within the domain of goal and action selection, flexibility plays a crucial role and is encoded within a parieto-prefrontal network, Download English Version:

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