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TWO DIFFERENT MIRROR NEURON NETWORKS: THE SENSORIMOTOR (HAND) AND LIMBIC (FACE) PATHWAYS

P. F. FERRARI, [a,b*] **M. GERBELLA,** [b,c] **G. COUDÉ** [a] **AND S. ROZZI** [b]

[a] *Institut des Sciences Cognitives – Marc Jeannerod, CNRS/Université Claude Bernard Lyon, 67 Pinel, 69675 Bron Cedex, France*

[b] *Dipartimento di Medicina e Chirurgia, Unità di Neuroscienze, 39 Volturno, 43125 Parma, Italy*

[c] *Istituto Italiano di Tecnologia (IIT), Center for Biomolecular Nanotechnologies, Lecce, Italy*

Abstract—The vast majority of functional studies investigating mirror neurons (MNs) explored their properties in relation to hand actions, and very few investigated how MNs respond to mouth actions or communicative gestures. Since hand and mouth MNs were recorded in two partially overlapping sectors of the ventral precentral cortex of the macaque monkey, there is a general assumption that they share a same neuroanatomical network, with the parietal cortex as a main source of visual information. In the current review, we challenge this perspective and describe the connectivity pattern of mouth MN sector. The mouth MNs F5/opercular region is connected with premotor, parietal areas mostly related to the somatosensory and motor representation of the face/mouth, and with area PrCO, involved in processing gustatory and somatosensory intraoral input. Unlike hand MNs, mouth MNs do not receive their visual input from parietal regions. Such information related to face/communicative behaviors could come from the ventrolateral prefrontal cortex. Further strong connections derive from limbic structures involved in encoding emotional facial expressions and motivational/reward processing. These brain structures include the anterior cingulate cortex, the anterior and mid-dorsal insula, orbitofrontal cortex and the basolateral amygdala. The mirror mechanism is therefore composed and supported by at least two different anatomical pathways: one is concerned with sensorimotor transformation in relation to reaching and hand grasping within the traditional parietal-premotor circuits; the second one is linked to the mouth/-face motor control and is connected with limbic structures, involved in communication/emotions and reward processing.

Key words: mirror neurons, premotor cortex, limbic, communicative, neuroanatomy.

Contents

INTRODUCTION

The anterior part of the ventral premotor cortex of the monkey has been investigated from anatomical and functional points of view by several researchers. The anatomical work by Matelli and colleagues (1985) showed that the most ventral portion of the agranular frontal cortex, extending from the central sulcus to the inferior limb of the arcuate sulcus, is formed by three different architectonic areas: the primary motor area F1, located in the depth of the anterior bank of the central sulcus and in the convexity immediately rostral to it, and the ventral premotor areas F4 (caudal) and F5 (rostral). In recent years, the combination of the cytoarchitectonic techniques with the neurochemical ones has proven to be useful for providing a more detailed definition of areal borders (see Belmalih et al., 2007). This multi-architectonic approach led to the parcellation of F5 into three sectors: F5c (convexity), F5p (posterior) and F5a (anterior). F5c extends on the convexity of the postarcuate cortex adjacent to the inferior arcuate sulcus, F5p and F5a lie within the postarcuate bank, at different antero-posterior levels (Fig. 1A).

*Correspondence to: P. F. Ferrari, Institut des Sciences Cognitives – Marc Jeannerod, CNRS/Université Claude Bernard Lyon, 67 Pinel, 69675 Bron Cedex, France.
E-mail address: pff@isc.cnrs.fr (P. F. Ferrari).

Abbreviations: AC, anterior commissure; ACC, anterior cingulate cortex; AIP, anterior intra-parietal area; DO, dorsal opercular area; GrFO, granular frontal opercular area; IPL, inferior parietal lobule; MD, mediodorsal nucleus; MNs, mirror neurons; PFop, parietal operculum; PMv, premotor cortex; PrCO, precentral opercular area; SII, secondary somatosensory cortex; STS, superior temporal sulcus; VA, ventral anterior nucleus; VLPC, ventrolateral prefrontal cortex.

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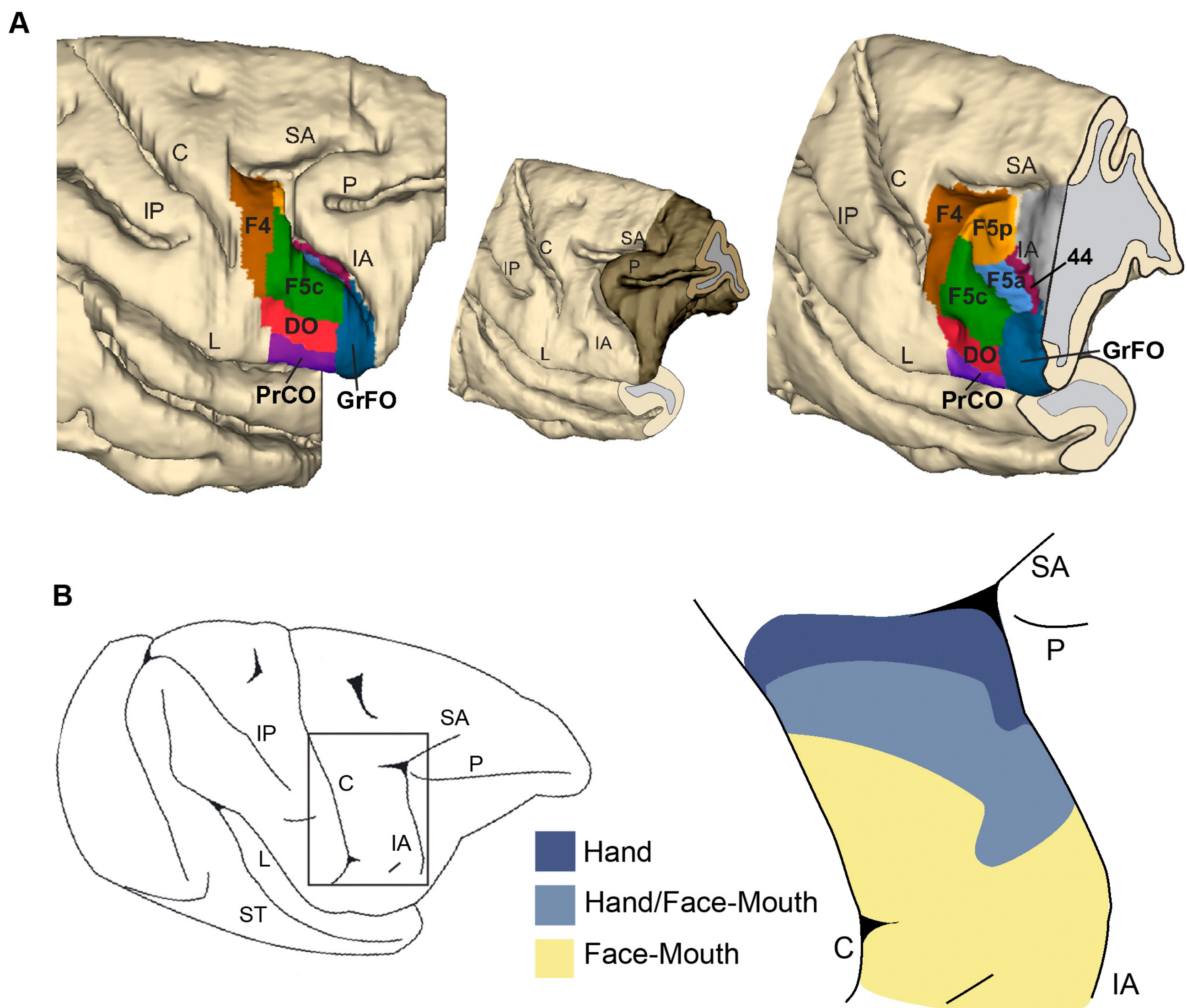

Fig. 1. (A) Three-dimensional reconstruction of the frontal lobe of a macaque brain showing the location of the various ventral premotor and opercular areas. The reconstruction is shown from a dorsolateral view (left) and from a rostrolateral (right) view in which the posterior bank of the arcuate sulcus was exposed with dissection of the 3D reconstruction along its fundus. The brain sector removed to expose the postarcuate bank is shown in a darker color in the smaller 3D reconstruction shown in the middle. The map is based on the architectonic features described in Belmalih and colleagues (2009) and in Gerbella and colleagues (2016). (B) Lateral view of the brain of a monkey employed in an experiment aimed to map the functional properties of ventral premotor cortex (left). The rectangle indicates the location of the region enlarged on the right). Cortical fields (right) in which extracellular multi-unit activity is related to brachio-manual (dark blue), mouth (yellow) or brachio-manual and mouth (light blue) effectors. C: central sulcus; DO (dorsal opercular area); GrFO (Granular frontal opercular area) IA: inferior arcuate sulcus; IP: intraparietal sulcus; L: lateral fissure; P: principal sulcus; PrCO (precentral opercular area); SA: superior arcuate sulcus; ST: Superior temporal sulcus. Modified from Belmalih and colleagues (2009), Gerbella and colleagues (2016) and Maranesi and colleagues (2012).

Several neurophysiological investigations (Kurata and Tanji, 1986; Gentilucci et al., 1988; Rizzolatti et al., 1988; di Pellegrino et al., 1992; Hepp-Reymond et al., 1994; Gallese et al., 1996; Ferrari et al., 2003; Maranesi et al., 2012) showed that area F5 hosts a motor representation of the hand (medially) and of the mouth (laterally) and plays a role in the generation and control of goal-directed motor acts such as grasping or biting (Fig. 1B). In addition, other neurons have been described which have visuomotor properties in F5. These neurons fall into two classes: "canonical" neurons and "mirror" neurons. Canonical neurons discharge to the observation of graspable objects and during the execution of a grasping movements (Murata et al., 1997; Raos et al., 2006); mirror neurons (MNs) fire both when the monkey is performing a motor act and also when the same, or a similar act is performed by another individual (di Pellegrino et al., 1992; Gallese et al., 1996; Ferrari et al., 2003; Caggiano et al., 2009; Kraskov et al., 2009; Maranesi et al., 2012, 2015; Bonini et al., 2014; Coudé et al., 2016). Other studies found MNs also in regions anatomically connected with the premotor cortex (PMv) such as the parietal cortex (Fogassi et al., 2005; Pani et al., 2014; Maeda et al., 2015), the dorsal premotor cortex (Tkach et al., 2007), and the primary motor cortex (Vigneswaran et al., 2013). The properties of MNs in these areas were investigated in relation to hand/arm movement directed toward a target. Despite some differences in neuronal specificity