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Review article

The macaque lateral grasping network: A neural substrate for generating purposeful hand actions

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ABSTRACT

In primates, neural mechanisms for controlling skilled hand actions primarily rely on sensorimotor transformations. These transformations are mediated by circuits linking specific inferior parietal with ventral premotor areas in which sensory coding of objects' features automatically triggers appropriate hand motor programs. Recently, connectional studies in macaques showed that these parietal and premotor areas are nodes of a large-scale cortical network, designated as "*lateral grasping network*," including specific temporal and prefrontal sectors involved in object recognition and executive functions, respectively. These data extend grasping models so far proposed in providing a possible substrate for interfacing perceptual, cognitive, and hand-related sensorimotor processes for controlling hand actions based on object identity, goals, and memory-based or contextual information and for the contribution of motor signals to cognitive motor functions. Human studies provided evidence for a possible counterpart of the macaque *lateral grasping network*, suggesting that in primate evolution the neural mechanisms for controlling hand actions described in the macaque have been retained and exploited for the emergence of human-specific motor and cognitive motor capacities.

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1. Introduction

In our everyday lives, we routinely interact with different objects in several different ways and for different purposes, thanks to highly evolved neural mechanisms enabling us to generate–in a remarkably fast, effortless, and reliable way–hand actions appropriate to behavioral goals, an object's properties, and external contingencies. A full description of these mechanisms and the underpinning neural substrate is still today a major issue in integrative neuroscience, of utmost relevance also for supporting theoretically sound, research-based clinical practices and the relatively recently developed fields of neuroprosthetics and brain-machine interfaces.

In the last two to three decades, research carried out mostly in non-human primates has clearly pointed out that cortical control of motor behavior primarily relies on integration of sensory with motor information, mediated by strong and reciprocal connections linking agranular frontal (motor and premotor) with posterior parietal areas (see, e.g., Caminiti et al., 2015; Rizzolatti et al., 1998). This integration is the basis of the so-called sensorimotor transformations, in which sensory information processing automatically leads to the activation, in the motor cortex, of representations of "potential actions" (Cisek and Kalaska, 2010; Cisek, 2007; Rizzolatti and Luppino, 2001).

Within this general framework, in the macaque brain there are areas in the inferior parietal lobule (IPL) and in the ventral premotor (PMv) cortex forming parieto-frontal circuits crucially involved in selecting and controlling appropriate object-oriented hand actions. One of these circuits, linking the IPL anterior intraparietal (AIP) area and the PMv area F5, plays a primary role in visuomotor transformations for grasping, in which visual coding of the object's physical properties (e.g., size, shape, orientation) automatically leads to the activation of distal movement representations appropriate for hand-object interactions (Jeannerod et al., 1995). This process has also been referred to as "affordances extraction" (see, e.g., Fagg and Arbib, 1998). According to Gibson (1979), affordances are all the motor possibilities that an object offers an individual, and they depend on the motor capabilities of the observer. Thus, virtually every object typically can offer us several affordances. The selection of one of the several possibilities will then depend upon several different factors, such as object identity, memorized information on object properties, contextual information, or behavioral goals. The neural pathways mediating these aspects of perceptual and cognitive control on the selection and execution of hand actions have been until recently relatively poorly explored and still represent a relatively open issue in even more recent reviews on grasping control (e.g., Castiello, 2005; Grafton, 2010; Janssen and Scherberger, 2014). In recent years, connectional studies in macaques have shown that IPL and PMv areas involved in sensorimotor transformations for grasping are at the core of a large-scale cortical network that includes temporal and prefrontal areas involved in object recognition and executive control of behavior, respectively (Borra et al., 2011, 2008; Gerbella et al., 2013, 2011; Rozzi et al., 2006). This network has been designated as the "*lateral grasping network*" (Borra et al., 2014b).

In this review article, we will first provide a comprehensive description of the anatomical and functional organization of the macaque *lateral grasping network* and suggest that this network is a possible substrate for integration of perceptual and cognitive with hand-related sensorimotor processes for generating purposeful hand actions. We will then review evidence suggesting that, in the evolution of the human lineage, the basic neural mechanisms for controlling hand actions described in the macaque have been retained and involve cortical sectors putatively homologous to the nodes of the macaque *lateral grasping network*. Finally, we will address the issue of the relationship of the *lateral grasping network* with the cortical network involving the caudal superior parietal lobule (SPL) and the dorsal premotor (PMd) cortex, involved in controlling reaching-to-grasp movements.

2. The macaque *lateral grasping network*

2.1. The ventral premotor area F5 and cortical representations of hand motor acts

Area F5, located in the rostral part of the macaque PMv (Fig. 1), is a major hub of the *lateral grasping network*. This area hosts a motor representation of the hand, more dorsally, and the mouth, more ventrally, which overlap to a considerable extent (Gentilucci et al., 1988; Hepp-Reymond et al., 1994; Kurata and Tanji, 1986; Maranesi et al., 2012; Rizzolatti et al., 1988). Neurons in this area typically encode specific hand, mouth, or both hand and mouth motor acts, such as grasping, breaking, and holding, rather than the single movements forming them (Rizzolatti et al., 1988). Furthermore, the activity of many hand-grasping neurons is tuned for the execution of specific hand-grasping configurations (e.g., Bonini et al., 2012; Fluet et al., 2010; Rizzolatti et al., 1988; Schaffelhofer and Scherberger, 2016; Spinks et al., 2008). Finally, while some neurons discharge during the execution of the whole motor act, others fire only during a certain part of it. It is noteworthy that many of these neurons appear to encode the goal of the motor act and not the motor act, per se. Thus, for example, they activate when a given motor goal (e.g., grasping) is achieved either using different effectors (e.g., the right hand, the left hand, or the mouth), or even opposite movements of the same effector (Kakei et al., 2001; Rizzolatti et al., 1988; Umiltà et al., 2008). Based on these findings, it was suggested that F5 contains a storage or "vocabulary" of internal representations of goal-directed hand, mouth, or hand and mouth motor acts. Each "word" of this vocabulary is represented by populations of F5 neurons coding motor acts at different levels of abstraction (see Rizzolatti and Luppino, 2001; Rizzolatti et al., 2014). The presence in the premotor cortex, which is only one step away from the primary motor cortex, of a vocabulary of goal-directed motor acts enormously facilitates the complex neural mechanisms underlying the selection of the effectors and acts most appropriate for achieving a given motor goal. Thus, F5 occupies a key position in the *lateral grasping network*, representing the place where neural processes carried out upstream and related to the selection of appropriate hand and mouth motor acts merge with processes carried out downstream and related to their execution.

2.2. The posterior (F5p) subdivision of F5 and execution of hand motor acts

Though F5 has usually been considered a single cortical entity, architectonic data have suggested that this area is actually a com-