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Review article

The body and objects represented in the ventral stream of the parieto-premotor network

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ABSTRACT

The network between the parietal cortex and premotor cortex has a pivotal role in sensory-motor control. Grasping-related neurons in the anterior intraparietal area (AIP) and the ventral premotor cortex (F5) showed complementary properties each other. The object information for grasping is sent from the parietal cortex to the premotor cortex for sensory-motor transformation, and the backward signal from the premotor cortex to parietal cortex can be considered an efference copy/corollary discharge that is used to predict sensory outcome during motor behavior. Mirror neurons that represent both own action and other's action are involved in this system. This system also very well fits with body schema that reflects online state of the body during motor execution. We speculate that the parieto-premotor network, which includes the mirror neuron system, is key for mapping one's own body and the bodies of others. This means that the neuronal substrates that control one's own action and the mirror neuron system are shared with the "who" system, which is related to the recognition of action contribution, i.e., sense of agency. Representation of own and other's body in the parieto-premotor network is key to link between sensory-motor control and higher-order cognitive functions.

Contents

1. Introduction

The hands have many functional roles during daily activities. Kamakura (1989) categorized eight functional roles of the hands: (1) exploring (i.e., sensing or exploring the environment), (2) contacts (i.e., holding an object or ones own body), (3) acting as a joint (i.e., working like a joint between the body and an object), (4) tools (i.e., being used as a tools), (5) grasping, (6) manipulating objects or tools, (7) responding (i.e., as an object of action by another hand), and (8) symbolizing (i.e., making a sign). Recently, it has been revealed that the motor control system in the brain not only controls these complex hand actions, but also concerns body representation. The motor control system contributes to perception of the hands as part of the own body. Since the perception of one's own body is the fundamental process of self-recognition (Gallagher, 2005), the hands are not only effectors in movement, but are a link between the mind and motor control.

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As discussed in the next section, connections between the parietal cortex and premotor cortex play a pivotal role in sensory-motor control. The network between the inferior parietal cortex and the ventral premotor cortex (F5), namely the ventro-dorsal stream, plays a role in visually-guided hand actions. The body is represented in the brain according to spatiotemporal dynamic manner (Berlucchi and Aglioti, 1997). The system for body representation is based on visual, somatosensory, and intrinsic motor signals that update the internal representation of one's own body state, and therefore is key for sensory motor control. This is the "who" system described by Jeannerod (2003), which is involved in recognition of action contribution to whether own self or other. In this line of thinking, it is suspected that the ventro-dorsal stream is shared with common neural substrates with the "who" system. Furthermore, in this stream, neurophysiological studies have found mirror neurons that are active during execution of a goal-directed hand action and during observation of the same action performed by another individual (Rizzolatti and Craighero, 2004). Mirror neurons are usually discussed in the principle of shared representation of other's hand action with the own action. We postulate that the mirror neurons contribute to not only shared representation of self and other, but also to the distinction between self and other. As described afterwards, our most recent study supports this hypothesis (Maeda et al., 2015). In this review, we discuss the functional role of the ventro-dorsal stream to the internal representation of the object and the body, and the importance of this link between motor control and cognitive function.

2. Anatomy of the parieto-premotor network

In this section, we would mention about anatomical configuration of parietal-premotor network that is connected with dorsal visual stream. Classically, the parietal association cortex has been thought to be involved in the dorsal visual stream, which contributes to the space perception. However, the parietal cortex is not a terminal station of this stream, and has very strong reciprocal connections with the premotor cortices. This network is key for sensory-motor control. As shown in Fig. 1, there are several parallel pathways between the parietal and premotor cortices that have been revealed in the monkey (Rizzolatti et al., 1998; Galletti et al., 2003), and recent physiological studies have revealed that these parallel pathways have different roles, such as arm reaching and/or hand grasping, along with body mapping (Murata and Ishida, 2007; Rizzolatti et al., 2014).

The dorsal visual pathway is separated into two channels: the dorso-dorsal pathway and the ventro-dorsal pathway (Tanne-Gariepy et al., 2002; Galletti et al., 2003; Rizzolatti and Matelli, 2003). The input to the dorso-dorsal pathway is from area V3/V3A and passes through V6, which is the most caudal dorsal part of the parietal cortex (Galletti et al., 2003). V6 has connections with V6A and the middle intraparietal area (MIP) in the superior parietal lobule. These two areas have strong connections with the dorsal premotor cortex (F2). Neurons in V6A, MIP, and F2 are related to reaching (Battaglia-Mayer et al., 2003) or grasping (Fattori et al., 2004) movements (Fig. 1).

The ventro-dorsal pathway passes through the anterior intraparietal area (AIP), which is located in the anterior part of the lateral bank of the intraparietal sulcus, or the PFG/PF on the lateral convexity of the posterior parietal cortex (Fig. 1). The convexity of the posterior parietal cortex is separated into PF, PFG, and PG (Rizzolatti and Matelli, 2003). According to cytoarchitecture and connections with other areas, classical area 7b involves PF and part of PFG (Pandya and Seltzer, 1982; Gregoriou et al., 2006; Rozzi et al., 2006). AIP and PFG/PF have connections with F5 (Luppino et al., 1999; Lewis and Van Essen, 2000; Rizzolatti and Luppino, 2001; Tanne-Gariepy et al., 2002; Rizzolatti and Matelli, 2003). Many of the neurons in AIP and PFG are related to distal hand movements (Sakata and Taira, 1994; Sakata et al., 1997; Rozzi et al., 2008).

In between these two streams (Rizzolatti and Matelli, 2003), in the fundus of the intraparietal sulcus, lies the ventral intraparietal area (VIP). VIP is on the border of the superior parietal lobule and the inferior parietal lobule (Fig. 1). According to the definition by Rizzolatti's group (Rizzolatti and Matelli, 2003), VIP is involved in the ventro-dorsal stream. The visual afferent input to this area originates from middle temporal area (MT)/medial superior temporal area (MST), and somatosensory afferent input originates from primary somatosensory cortex (SI) and secondary somatosensory cortex (SII) (Lewis and Van Essen, 2000). The VIP has a connection with the caudal part of the ventral premotor cortex (F4), either directly or via PEa (Rozzi et al., 2006) that is in medial bank of intraparietal sulcus and part of area 5 (Luppino et al., 1999; Lewis and Van Essen, 2000; Rizzolatti and Luppino, 2001). Because neurons in V6A, MIP, PEa, PF/PFG, and VIP (shaded area in Fig. 1B) show bimodal sensory properties (i.e., visual and somatosensory properties) (Colby et al., 1993; Iriki et al., 1996; Colby, 1998; Breveglieri et al., 2002), these areas are thought to be involved in the integration of somatosensory and visual information. As described later, the pathway from the VIP to F4, which includes PEa and PF/PFG, is involved in the representation of peripersonal space and body parts (Rizzolatti et al., 1997; di Pellegrino and Ladavas, 2015), and also in hand/arm movement control (Graziano and Cooke, 2006; Rozzi et al., 2008; Rizzolatti et al., 2014).

3. Object affords hand action in the AIP-F5 network

Now, we would like to concentrate on functional properties ventro-dorsal pathway that is related to control object manipulation with the distal hand. Since the end of the last century, several studies have revealed neural mechanisms for distal hand movement control in the monkey parieto-premotor network (Rizzolatti et al., 1988; Sakata et al., 1995; Fogassi et al., 1999; Fattori et al., 2004). Activity of neurons in AIP and ventral premotor area F5 changed when the monkey was manipulating different objects (Rizzolatti et al., 1988; Taira et al., 1990). We will discuss the properties of neurons in the monkey parietal cortex and premotor cortex to reveal functional difference between the two regions.

Sakata's group compared neural activity in AIP during hand manipulation tasks in which a monkey was required to manipulate objects with one hand using full vision and in the dark, and to just fixate on the object for manipulation without grasping it (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000) (Fig. 2). When a red spotlight was presented, the monkey fixated on it, and then press a home key switch. At the same time, the object was illuminated and the monkey could see the object. The monkey fixated on the object until the green light turned on (go signal), then the monkey was required to reach and grasp the object, and hold onto it for a while (movement in the light). The task was the same in the full vision and the dark conditions (movement in the dark), except that in the dark condition the monkey did not have any vision apart from that provided by the spotlight. Sakata and colleagues identified three different types of AIP neurons activated during the task: motor-dominant neurons, visual-dominant neurons, and visual-motor neurons (Fig. 2) (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000). Motor-dominant neurons fired during movement in the light and in the dark condition, but did not show any significant difference in the level of activity between the two conditions. These neurons did not respond to the presentation of objects, nor to any somatosensory stimuli, and were thus considered as being related to the motor component of the task. Visual-dominant neurons fired during movement in the light but not during