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Using action understanding to understand the left inferior parietal cortex in the human brain



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ABSTRACT

Humans have a sophisticated knowledge of the actions that can be performed with objects. In an fMRI study we tried to establish whether this depends on areas that are homologous with the inferior parietal cortex (area PFG) in macaque monkeys. Cells have been described in area PFG that discharge differentially depending upon whether the observer sees an object being brought to the mouth or put in a container. In our study the observers saw videos in which the use of different objects was demonstrated in pantomime; and after viewing the videos, the subject had to pick the object that was appropriate to the pantomime. We found a cluster of activated voxels in parietal areas PFop and PFt and this cluster was greater in the left hemisphere than in the right. We suggest a mechanism that could account for this asymmetry, relate our results to handedness and suggest that they shed light on the human syndrome of apraxia. Finally, we suggest that during the evolution of the hominids, this same pantomime mechanism could have been used to 'name' or request objects.

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1. Introduction

Anatomical and physiological studies of macaque monkeys provide two keys to understanding the inferior parietal cortex.

The first is that the area provides the sensory information that is necessary for using objects. The second is that it provides the sensory information that is necessary for one animal to benefit from seeing another animal doing so.

Abbreviations: AIP, Anterior intraparietal area; F5a, Region of ventral premotor cortex; HAIP, Human anterior intraparietal area; IPS, Intraparietal sulcus; LIP, Lateral intraparietal area; MIP, Medial intraparietal area; MST, Multisensory temporal area; MT+, Motion complex; PF, Cytoarchitectonic division of the macaque inferior parietal cortex; PFG, Cytoarchitectonic division of the macaque inferior parietal cortex; PFop, Cyotarchitectonic division of the human inferior parietal cortex; PFt, Cyotarchitectonic division of the human inferior parietal cortex; PG, Cytoarchitectonic division of inferior parietal cortex; PMv, Ventral premotor cortex; V6, Visual area 6

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Fig. 1 – Location of areas mentioned in text on macaque monkey brain.

Fig. 1 illustrates the anatomical organization of the inferior parietal cortex in macaque monkeys.

There are three cytoarchitectonic divisions of the inferior parietal cortex, PF, PFG and PG (Pandya and Seltzer, 1982). Area PG is interconnected with the medial intraparietal area MIP (Rozzi et al., 2006); this lies in the upper bank of the intraparietal sulcus (IPS) (Fig. 1). Area PFG is interconnected with the anterior intraparietal area AIP (Rozzi et al., 2006); this lies anteriorly in the IPS (Fig. 1).

The function of these areas can be illustrated by describing three phases in feeding. The first involves reaching towards the food, before contact has been made. Lesions of that include PG and the lateral intraparietal area LIP in the intraparietal sulcus (Fig. 1) lead to severe misreaching for pieces of food as visual targets (Rushworth et al., 1997a). However, the guidance of the limb also requires proprioceptive signals, and area MIP receives a proprioceptive input to the shoulder (Prevosto et al., 2009). Superior parietal lesions that include MIP impair the proprioceptive guidance of the hand; this can be tested by requiring that the movements be made in the dark (Rushworth et al., 1997c).

The second phase involves the period just before contact is made with the food. Visual information about the size and shape of the object is needed to shape the hand before contact. This 3-D information is transmitted from the caudal part of the IPS to AIP (Sakata et al., 1997). Inactivation of AIP impairs the pre-shaping of the fingers before the food is felt (Fogassi et al., 2001).

The final phase involves moving the hand with the food in it. The natural course of action involves bringing the food to the mouth. Many cells in the inferior parietal area PF respond to stimulation of the mouth (Rozzi et al., 2008); and there are cells in the area PFG that respond to the combined stimulation of the hand and mouth (Yokochi et al., 2003). It is a critical finding that many cells in PFG are sensitive to the specific action. Bonini et al. (2011) trained monkeys to put an object in their mouth or in a container. These cells respond differentially depending on what is done with the object.

This inferior parietal system for using objects also provides a means for monkeys to understand the actions with objects that they observe. Since monkeys live in groups, one animal can observe another animal as it feeds. It pays to do so because information can be transmitted about the locations of the most valuable food items. Visual information about the movements of another animal reaches areas PFG and PG via an input from the middle superior temporal motion area (MST) (Rozzi et al., 2006) (Fig. 1). There is also a projection to PFG from the upper bank of the superior temporal sulcus (STS) (Nelissen et al., 2011) (Fig. 1), and there are cells in the sulcus that respond differentially depending on the direction in which an individual is seen to walk (Jellema and Perrett, 2003). As expected from these inputs, cells can be found in area PFG and PG that respond to biological motion (Rozzi et al., 2008). By contrast, area AIP does not receive a motion input from MST (Rozzi et al., 2006).

Around 50% of the cells in area PFG respond to visual stimulation (Rozzi et al., 2008). But, surprisingly, as many as 80% of the cells in area PFG are active during the movements of the animal itself. There could be two reasons for the latter finding. The first is that the cells could be responding to somatosensory signals arising from movement. The second is that they could be responding because they are reciprocally connected with the premotor areas, and thus reflect activity in those areas through back projections.

Roughly 10–15% of the cells in PFG are active both during movement and also during observation of similar movements (Rozzi et al., 2008). It has been suggested that these 'mirror neurons' may be crucial in understanding an action (Rizzolatti et al., 2001). They could acquire their property in the following way.

The sight of action, such as feeding, could 'afford' or lead to activity in the premotor areas with which PFG is interconnected. These include areas 44 and 45 (Fig. 1), termed Broca's area in the human brain (Frey et al., 2013). Cells in PFG can then receive feedback via back projections from areas 44 and 45 to PFG. This feedback could, in principle, be used to represent the action as observed and the action as experienced by the animal when it makes a similar movement itself. If so, one might expect cells with conjunctive properties; and some of these could code for a 'match' in the same way as prefrontal cells can code for a visual match (Wallis et al., 2001).

One could argue that the ability to understand actions need not depend on such a mechanism, and that vision provides sufficient evidence. But there is evidence from experiments on human subjects that motor feedback might indeed be essential. In imaging experiments on action observation, the activation is greater if the observer is an expert in the action observed (Calvo-Merino et al., 2005). And it is familiarity with performing the movements, not simply with seeing them, that turns out to be the critical factor for the effect of expertise (Calvo-Merino et al., 2006).

One advantage of studying human rather than monkey observers is that it is easier to devise formal tests of action understanding for people. Whereas such tests would require many months of training for monkeys, human subjects can simply be instructed to do what is required. But if human subjects are to be studied, the question arises whether the areas that are involved in action knowledge are the same as in monkeys.

That they might not be is suggested by the syndrome of apraxia in stroke patients. This results from lesions that are Download English Version:

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