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The mirror system and its role in social cognition

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Experiments in monkeys have shown that coding the goal of the motor acts is a fundamental property of the cortical motor system. In area F5, goal-coding motor neurons are also activated by observing motor acts done by others (the 'classical' mirror mechanism); in area F2 and area F1, some motor neurons are activated by the mere observation of goal-directed movements of a cursor displayed on a computer screen (a 'mirror-like' mechanism). Experiments in humans and monkeys have shown that the mirror mechanism enables the observer to understand the intention behind an observed motor act, in addition to the goal of it. Growing evidence shows that a deficit in the mirror mechanism underlies some aspects of autism.

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Introduction

Social cognition is the study of how people interact with other individuals in social situations. A fundamental aspect of social interaction is the capacity to understand what others are doing, their intention and their feelings. A series of experiments carried out in the last decade showed that this capacity is mediated, in part, by a specific mechanism called the mirror mechanism [1,2]. This mechanism transforms sensory information describing actions of others into a motor format similar to that the observers internally generate when they imagine themselves doing that action or when they actually perform it. The similarity between the motor format generated by observing others and that internally generated during motor and emotional behavior allows the observer to understand others' behavior, without any complex cognitive elaboration [3].

The mirror mechanism is present in various cortical areas and according to its location mediates different functions. The mirror mechanism is located in the parieto-frontal network and underlies the understanding of the goal of the observed motor acts and the intention behind them. The mirror mechanism is also located in human Broca's area and transforms heard phonemes into the motor format necessary to produce them. Finally, the mirror mechanism is present in the insula and anterior cingulate cortex. It mediates the understanding of emotions of others. In the present article we will deal only with the parieto-frontal mirror network (for recent reviews on other systems endowed with the mirror mechanism see [4,5]). Our review will be not exhaustive. Only those studies that are relevant with the main theme of this article will be reviewed.

The mirror mechanism in monkeys

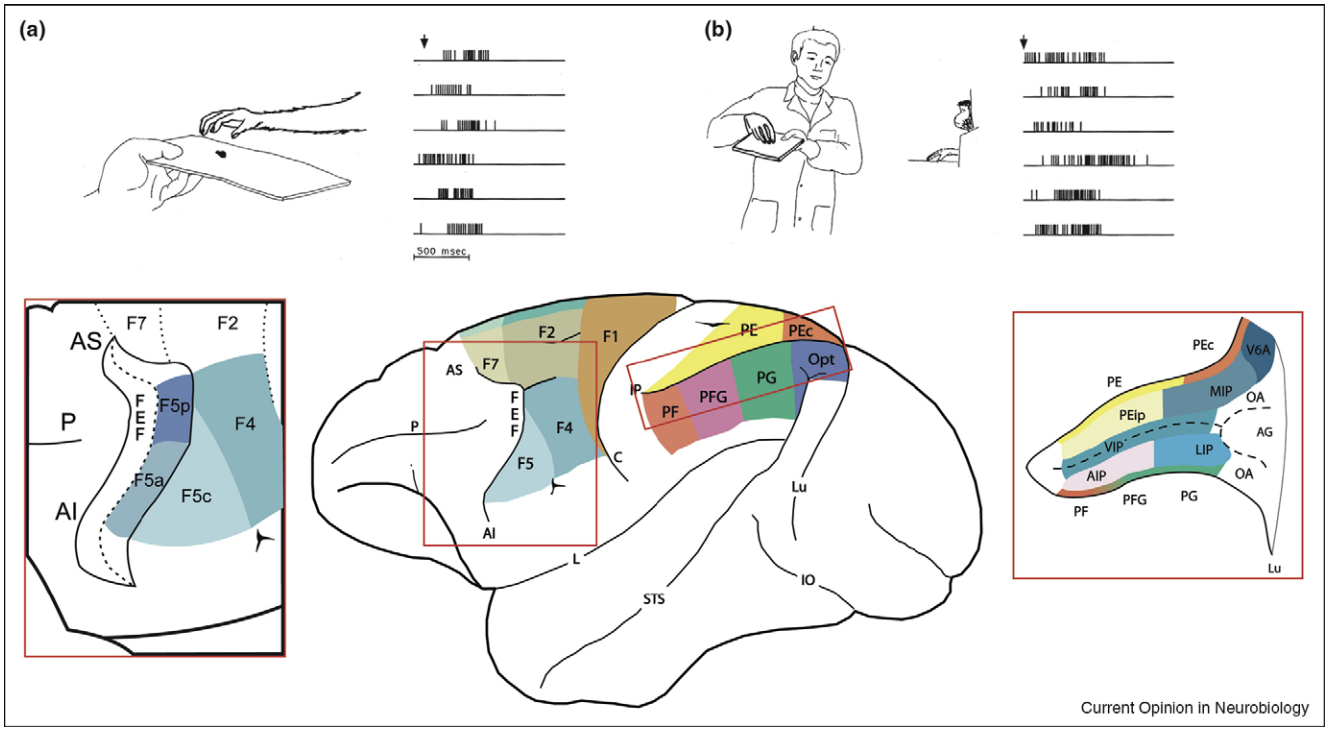
Goal coding in the monkey motor areas

The mirror mechanism is embedded in the motor system (Figure 1). Crucial, therefore, for understanding its function is to understand which are the motor properties of the areas where the mirror neurons are located. As far the parieto-frontal circuit is concerned early experiments showed that, in F5, many neurons fire regardless of whether the motor act is done using the right hand, the left hand or the mouth [6]. This was interpreted as evidence that area F5 codes the goal of the motor act rather than the single movements forming it [7].

The problem of goal coding in area F5 has been recently re-examined in a more stringent way. Macaque monkeys were trained to use two tools: normal pliers and 'reverse' pliers (an implement that requires finger opening, instead of closing, to grasp an object). Single neurons were recorded from F5 and the primary motor cortex (F1). The result showed that all the recorded neurons from F5 and about 40% of neurons recorded from F1 discharged in relation to the goal of the motor act independent of whether it was achieved by closing the hand (normal pliers) or opening it (reverse pliers) [8••].

The goal representation in the cortical motor system is not a peculiarity of F5, but has been also described in other sectors of the premotor cortex and in F1 [9–12]. However, because, alternative explanations could not be ruled out, the claim of goal coding in the cortical motor system was advanced with caution. The new data just reviewed show beyond any doubt that the cortical motor system has the goal of a motor act (grasping, holding, reaching) inbuilt in its organization. This organization has fundamental conceptual consequences because it indicates that the firing

Figure 1



Example of a mirror neuron and anatomy of agranular frontal and posterior parietal cortex of the macaque monkey. (Upper part) F5 mirror neuron. The neuron discharges when the monkey grasps an object (**a**) and when it observes the experimenter grasping it (**b**). (Lower part) the central part of the figure shows the cytoarchitectonic parcellation of the agranular frontal cortex (areas indicated with F and arabic numbers) and of the parietal lobe (areas indicated with P and progressive letters). The enlargement of the frontal region (rectangle on the left) shows the parcellation of area F5. The rectangle on the right shows the areas buried within the intraparietal sulcus. AIP, anterior intraparietal area; IP, intraparietal sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; POs, parieto-occipital sulcus; As, superior arcuate sulcus; Ai inferior arcuate sulcus; C, central sulcus; Ca, calcarine fissure; CG, cingulate cortex; FEF, frontal eye field; L, lateral sulcus; Lu, lunate sulcus; P, principal sulcus; STS, superior temporal sulcus. (Modified from [5]).

elicited in F5 mirror neurons by the observation of a motor act describes the goal of the observed motor act. This enables the observer to understand it, without the need to postulate a dichotomy between putative posterior goal-understanding areas (e.g. STS) and motor areas.

Mirror-like mirror neurons

Typically, the mirror mechanism in the monkey has been studied in ethological situations. A few years ago evidence was provided that, in the dorsal premotor cortex (PMd or F2) there are neurons that discharge both when a monkey executes a conditioned task (moving a cursor on a computer screen) and when the animal observes the same task done by the experimenter. Unlike 'classical' mirror neurons these neurons did not require, to be triggered, the observation of an effector (e.g. a hand) that acts on the object. The mere observation of goal achievement was sufficient [13].

A recent study extended this observation. Monkeys were trained to move repetitively a cursor to targets that appeared at random locations. The experiment consisted of two phases: An active movement phase in which the monkey moved the cursor, and an observation phase in which the monkey observed the replayed movements generated in the active phase. The observation phase has three conditions. In the first, both the cursor and the targets were visible; in the second, the monkey saw only the replayed targets; in the third, the monkey saw only the moving cursor, but not the targets. The results showed that, in both PMd and F1 passive observation of the task elicited a neural discharge similar to that found during task execution. The observation of the cursor without targets and of the targets without cursor gave either no responses or responses weaker than those found during the observation of both cursor and targets [14•].

The most likely explanation of these findings is that these mirror-like neurons are sensitive to the goal of the motor act. In fact, the moment in which the cursor reaches the target corresponds to the goal achievement, normally obtained using natural effectors. The study does not report whether these neurons discharge during the observation of motor act done with natural effectors, yet the