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Research Note

Understanding motor events: a neurophysiological study

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Summary. Neurons of the rostral part of inferior premotor cortex of the monkey discharge during goal-directed hand movements such as grasping, holding, and tearing. We report here that many of these neurons become active also when the monkey observes specific, meaningful hand movements performed by the experimenters. The effective experimenters' movements include among others placing or retrieving a piece of food from a table, grasping food from another experimenter's hand, and manipulating objects. There is always a clear link between the effective observed movement and that executed by the monkey and, often, only movements of the experimenter identical to those controlled by a given neuron are able to activate it. These findings indicate that premotor neurons can retrieve movements not only on the basis of stimulus characteristics, as previously described, but also on the basis of the meaning of the observed actions.

Key words: Hand action encoding – Visual responses – Premotor cortex – Macaque monkey

Introduction

It is well established that in the monkey there is a distal arm movement representation in inferior premotor cortex (Rizzolatti et al. 1981; Kurata and Tanji 1986; Rizzolatti et al. 1988; see also Matsumura and Kubota 1979; Muakkassa and Strick 1979). This representation is located rostrally near the arcuate sulcus, and is largely coextensive with the histochemical area F5 (Matelli et al. 1985). One of the distinguishing characteristics of F5 neurons is that they become active during particular goal-directed hand movements, such as grasping, holding, and tearing. Many of them are specific for different types of hand grip. Some discharge during grip with the index finger and the thumb, some during finger prehension, and others during prehension with the whole hand. Furthermore, a proportion of F5 neurons are activated by visual stimuli which require a particular type of grasping (Rizzolatti et al. 1988).

Our original aim in the present experiments was to study the activity of F5 neurons in a behavioral situation in which we could separate stimulus-associated responses from the activity related to movements. For this purpose a macaque monkey was trained to retrieve objects of different size and shape from a testing box with a variable delay after stimulus presentation. After the initial recording experiments, we incidentally observed that some experimenter's actions, such as picking up the food or placing it inside the testing box, activated a relatively large proportion of F5 neurons in the absence of any overt movement of the monkey. The purpose of this communication is to describe some of the essential features of this surprising new class of premotor neurons.

Methods

The experiments were carried out on a *Macaca nemestrina* monkey. Animal preparation and basic experimental procedures were the same as in our previous experiments (for details see Rizzolatti et al. 1988, 1990). During the recordings the monkey was seated in a primate chair with its head fixed. Single neurons were recorded from inferior area 6 (sector F5) using tungsten microelectrodes (impedance 0.5–2 MΩ measured at 1 kHz frequency). The microelectrode used for recordings was also used for electrical microstimulation. The stimulation was made in each penetration every 500 μm by applying trains of cathodal pulses generated by a constant current stimulator (train duration 50 ms, pulse duration 2 ms, frequency 250 Hz, current intensity 3–40 μA).

The neurons were first tested informally by presenting objects of different size and shape in various spatial positions (for details on testing procedures see Rizzolatti et al. 1988). Once it was clear that a neuron became active during the monkey's hand movements, its dis-

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