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SMR.853 - 51

ANTONIO BORSELLINO COLLEGE ON NEUROPHYSICS

(15 May - 9 June 1995)

"Understanding motor events: a neurophysiological study"

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These are preliminary lecture notes, intended only for distribution to participants.

Exp Brain Res (1992) 91:176–180

Experimental
Brain Research

Research Note

Understanding motor events: a neurophysiological study

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Received April 15, 1992 / Accepted July 14, 1992

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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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charge was studied in a behaviorally controlled situation. A testing box (45 cm × 30 cm × 35 cm) was placed in front of the monkey at its shoulder level. The box front door was formed by a one-way mirror. Geometric solids of different size and shape were placed inside the box. The room illumination was adjusted to prevent the animal from seeing inside the box. The monkey initiated the trials by pressing a switch, formed by two thin plates, with the thumb and index finger. Pressing the switch lit the box and made the object visible. After a delay of 1.2–1.5 s, the door opened and the monkey was allowed to reach for the object. The animal was rewarded with a piece of food located under the object. If the monkey released the switch before the door opened the trial was aborted. Arm and hand movements were recorded using a computerized movement recording system (ELITE system, Ferrigno and Pedotti 1985). This system, as used in the present experiment, consists of two infrared TV cameras and a processor which elaborates the video images in real time and reconstructs the positions of infrared reflecting markers in three dimensions. The markers used for reconstructing hand and arm movement were placed on the first phalanges of the index finger and thumb and on the radial apophysis. Neural activity, kinematic recordings and event time markers (light on, door opening) were acquired by the ELITE system and recorded on a magnetic medium for off-line analysis.

Following the discovery that some experimenter's actions could activate F5 neurons, all recorded neurons were examined by performing a series of motor actions in front of the animal. These actions were related to grasping food (e.g., presenting the food to the monkey, putting it on a surface, retrieving it, giving it to a second experimenter, taking it away from him), to manipulation of food and other objects (breaking, tearing, folding), or were gestures with or without emotional content (threatening, lifting the arms, waving the hands). In addition, the following actions were also performed in order to control whether the recorded neurons coded specifically hand-object relationships: movements of the hand without food, prehension of the food with a tool (e.g., forceps, pincers), simultaneous combined movements of the food and hand spatially separated one from the other. All experimenter's actions were repeated on the right and on the left of the monkey at various distances (50 cm, 1 and 2 m). The animal's behavior and experimenters' actions during testing were recorded on one track of a video tape; the neural activity was simultaneously recorded on a second track in order to correlate the monkey's behavior or the experimenters' actions to the unit firing.

Arm and forearm muscles, including flexors and extensors of the fingers, were recorded unipolarly with stainless steel electrodes. The electromyographic recordings were made in special sessions in which testing procedures were identical to those in which neurons were recorded.

Results

The activity of two neurons during the monkey's grasping of small and large objects is illustrated in Fig. 1. Unit 483 discharged vigorously during precision grip (upper panel), whereas it was only weakly activated during whole hand prehension (lower panel). Unit 481 did not show any specificity for grip type. Its discharge, which was spontaneously high, was strongly inhibited during all types of grasping. The spontaneous activity of the two neurons was influenced neither by the object presentation nor by movement preparation during the waiting period.

Figures 2 and 3 show the responses of units 483 and 481 while the monkey observed grasping movements performed by the experimenters. The correlation between movements and neural activity was made in this case using video recordings. Modifications in neuronal

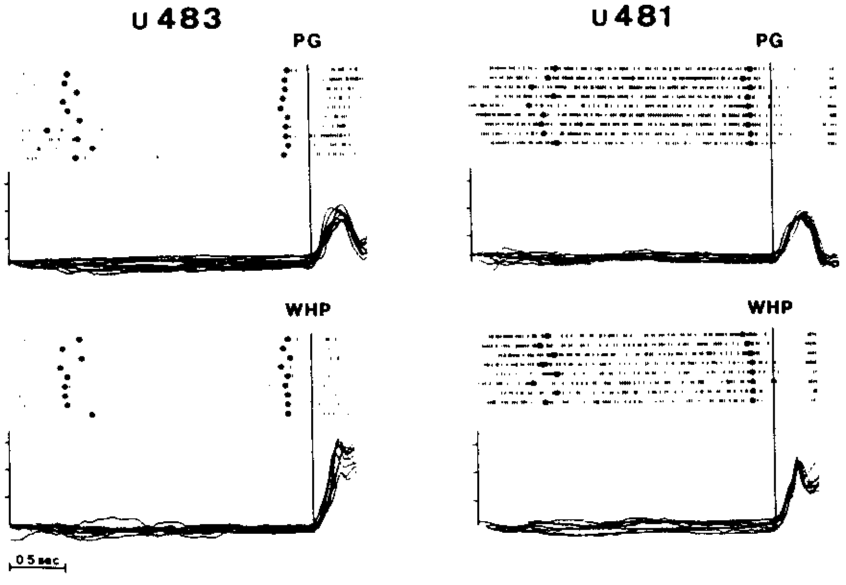

Fig. 1. Discharge of two premotor neurons during hand prehension. Neuronal activity (raster display) and kinematic recordings of the grip size (modulus of the vector distance between the thumb and index finger) are shown. *Upper panels:* neuronal response during precision grip (*PG*); *lower panels:* neuronal response during whole hand prehension (*WHP*). The objects were a small sphere (diameter 0.4 cm) in the case of PG and a large sphere (diameter 4 cm) for unit 483 and a large cylinder (diameter 2 cm) for unit 481 in the case of WHP. Neuronal discharge and kinematic recordings are aligned with the onset of hand opening (*continuous vertical lines*). The *first filled dot* of each raster marks the object presentation; the *second filled dot* marks when the object was allowed to be grasped. Each bin represents 20 ms. *Ordinate:* each subdivision represents 0.7 cm

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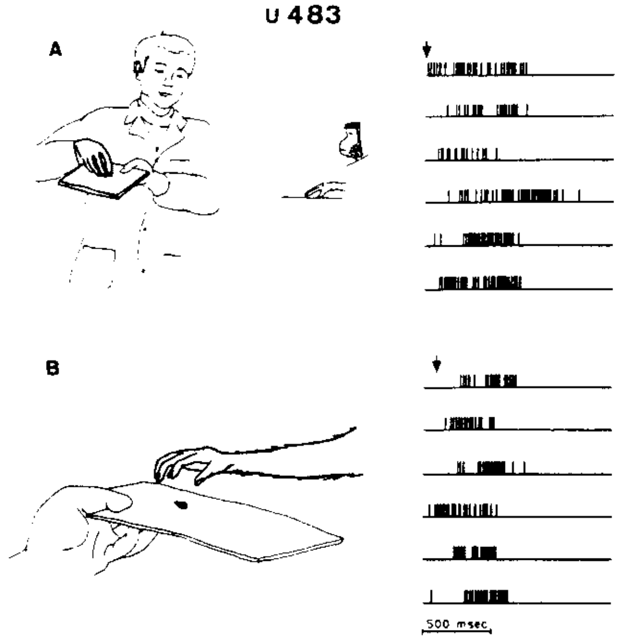

Fig. 2A, B. Example of a unit selectively discharging during monkey grasping movements and during monkey observation of grasping movements made by the experimenter. **A** The experimenter grasps the food; **B** the monkey grasps the food. *Arrows* indicate the (approximate) onset of grasping. Formal testing of this unit (483) is shown in Fig. 1, left side

discharge were as sharply defined during grasping observation (Figs. 2A, 3A, B) as during grasping execution (Figs. 2B, 3C). Of particular interest is Fig. 3B. Here the records show the neuronal activity with no interruption from the moment in which the experimenter picked up the food (first arrow) to when the monkey grasped it (second arrow). Both the observed grasping and the executed grasping inhibited the neuron discharge. In contrast, neither the movement of the experimenter's hand towards the food (records before the first arrow) nor the presentation of food to the monkey (records before the second arrow) influenced the neuronal firing. Note that after the experimenter's act of grasping the discharge was back to its high rate in spite of the fact that after the grasp the food was moved towards the animal and, as a consequence, the monkey's interest and preparation to perform arm and hand movements increased.

A total of 184 F5 neurons were studied. In agreement with previous findings, almost all neurons became active during different types of distal movements (grasping, holding, tearing). Microstimulation performed in correspondence to the sites from which the neurons were recorded elicited hand and finger movements. Eighty-seven neurons responded to visual stimuli. Forty-eight of them responded to simple meaningful stimuli (e.g., food) as previously described (Rizzolatti et al. 1988), while 39 had complex visual properties similar to those of units 481 and 483. Neurons with complex visual properties fell into four broad categories. The first category ($n=12$) consisted of units in which the effective observed action and the effective executed action corresponded. The coded action could be grasping with the mouth, grasping with the hands (the most frequently represented), object rotation, or object manipulation. The second category ($n=6$) was formed by neurons in which the effective observed action was the one effective when executed by the monkey (e.g., grasping) plus other actions *visually* similar to the executed one (e.g., hand placing an object on a table). The third category ($n=11$) consisted of neu-

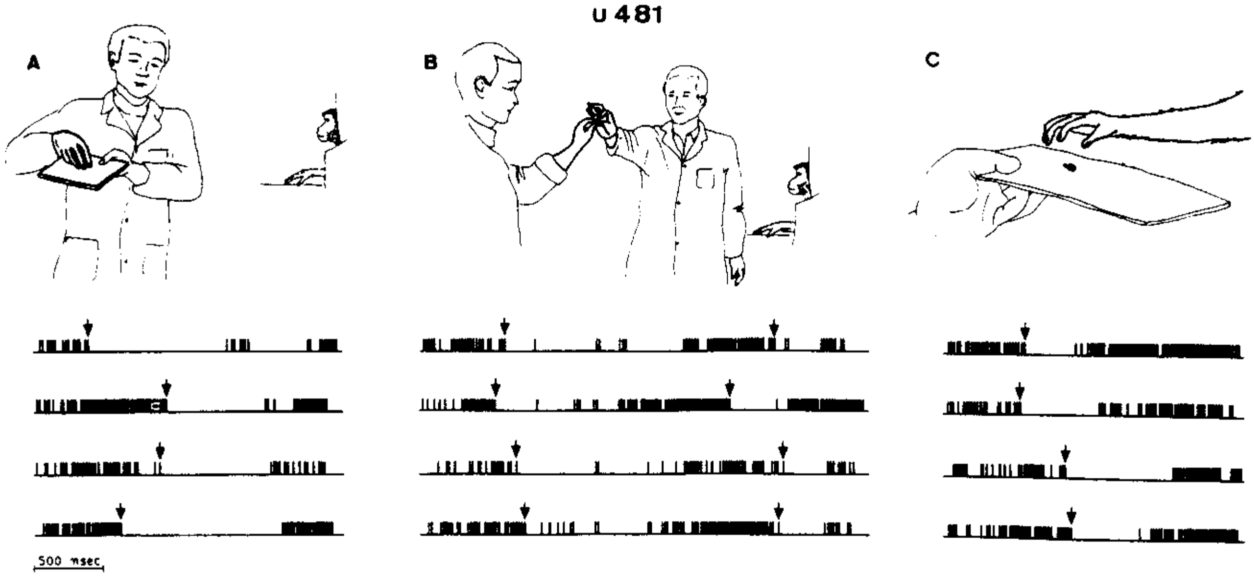

Fig. 3A–C. Example of a unit selectively discharging during monkey grasping movements and during monkey observation of grasping movements made by the experimenter. The situations in **A** and **C** are the same as in Fig. 2A and B respectively. In **B** The experimenter took a piece of food from another experimenter (*first arrow*) and brought it towards the monkey. The *second arrow* indicates the moment when the monkey grasped the food from the experimenter's hand. Formal testing of this unit (481) is shown in Fig. 1, right side rons in which the effective observed actions were *logically* related to the effective executed actions and could be seen as preparatory to them. For example, the effective observed action was placing an object on the table, whereas the effective executed action was bringing food to the mouth or grasping the object. The last class ($n = 10$) was formed by neurons which responded to observed actions similar to those described above, but had no activity correlated with the animal's movement. Active movements of the animal without visual control were effective in triggering the neurons of the first three classes. Not all neurons, however, were tested in the absence of visual control.

Control testing for the specificity of the hand-object interrelations (see Methods) showed that movements of the experimenter's hand alone or the combined movements of hand and object spatially separated one from the other were not effective in triggering neurons of all classes. Similarly, grasping the food with forceps, pincers, or other tools did not affect the neuron discharge. Threatening movements were also not effective.

Appropriate movements of the experimenter triggered the neurons whether performed within the monkey's peripersonal space or outside it. The responses, however, were usually stronger when the observed stimuli were close to the animal. For some units the stimulation side influenced the response intensity.

In order to verify whether the neuron activation during the observed actions could be related to movements of the animal that went unnoticed by observers, the monkey's arm and hand extrinsic movements were recorded electromyographically during the experimenters' actions. Distal movements were monitored because these movements are represented in F5, and because the quantitative analysis of the neurons discharging in relation to the experimenters' actions showed a clear correlation, in most cases, between firing and distal movements. Changes of electromyographic activity related to observed action were never found.

Discussion

One of the fundamental functions of the premotor cortex is that of retrieving appropriate motor acts in response to sensory stimuli. Evidence has been provided that action retrieval can occur in response to two-dimensional patterns (Mitz et al. 1991), color (Halsband and Passingham 1985; Passingham 1988), and size and shape of three-dimensional objects (Petrides 1982; Rizzolatti et al. 1988; Gentilucci and Rizzolatti 1990). The present data indicate that in addition to these physical factors, retrieval can also occur in response to the meaning of the gestures made by other individuals. If one considers the rich social interactions within a monkey group, the understanding by a monkey of actions performed by other monkeys must be a very important factor in determining action selection. Thus, the capacity of inferior premotor neurons to select actions according to gesture meanings fits well in the conceptual framework of current theory on the functions of premotor cortex and expands it to include movement selection related to interpersonal relations.

The discovery in the premotor cortex of neurons sensitive to the meaning of actions was unexpected. However, the presence of these neurons is consistent with previous findings. Perrett and coworkers (1989, 1990) described neurons in the temporal lobe whose responses depended upon the interrelation of hand and object movements. The characteristics of these neurons are very similar to those of our last, purely visual category. It appears, therefore, that hand-object interactions belong to those categories of complex stimuli which, like faces (Gross et al. 1972; Rolls 1984; Perrett et al. 1984, 1987; Desimone 1991), are explicitly coded by individual neurons. The behavioral importance of a fast selection of the appropriate movements according to the movements of other individuals has probably favored this type of coding which allows a rapid recognition of the stimuli.

Another, very interesting finding in our experiments was the observation that some neurons were activated *only* by movements of the experimenters that closely coincided with those that activate the neuron when performed by the monkey. There are reports in the literature that patients with ideomotor apraxia may have difficulty (Heilman et al. 1982) in recognizing the meaning of gestures performed by other persons. These findings have been interpreted as evidence that gesture perception and limb praxis share the same cortical circuits (Rothi et al. 1991). Similarly, the finding that the acoustic patterns of synthetic speech had to be modified if an invariant phonetic percept was to be produced across different contexts led several authors to propose that the objects of speech perception were to be found not in the sounds, but in the phonetic gestures of the speaker, represented in the brain as invariant motor commands (see Liberman and Mattingly 1985). Although our observations by no means prove motor theories of perception, nevertheless they indicate that in the premotor cortical areas there are neurons which are endowed with the properties that such theories require. It is interesting to note that the anatomical location of inferior area 6, and in particular of F5, corresponds in large part to that of Broca's area in the human brain (Freund 1991).

Acknowledgements. We thank M. Gentilucci, G. Luppino, and M. Matelli for their help in part of the experiments. We thank also A. Allport for his comments on the manuscript. This research was supported by the Human Frontier Science Programme and by grants from CNR and MURST to GR.

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