

Object Representation in the Ventral Premotor Cortex (Area F5) of the Monkey

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Murata, Akira, Luciano Fadiga, Leonardo Fogassi, Vittorio Gallese, Vassilis Raos, and Giacomo Rizzolatti. Object representation in the ventral premotor cortex (area F5) of the monkey. *J. Neurophysiol.* 78: 2226–2230, 1997. Visual and motor properties of single neurons of monkey ventral premotor cortex (area F5) were studied in a behavioral paradigm consisting of four conditions: object grasping in light, object grasping in dark, object fixation, and fixation of a spot of light. The employed objects were six different three-dimensional (3-D) geometric solids. Two main types of neurons were distinguished: motor neurons ($n = 25$) and visuomotor neurons ($n = 24$). Motor neurons discharged in association with grasping movements. Most of them ($n = 17$) discharged selectively during a particular type of grip. Different objects, if grasped in similar way, determined similar neuronal motor responses. Visuomotor neurons also discharged during active movements, but, in addition, they fired also in response to the presentation of 3-D objects. The majority of visuomotor neurons ($n = 16$) showed selectivity for one or few objects. The response was present both in object grasping in light and in object fixation conditions. Visuomotor neurons that selectively discharged to the presentation of a given object discharged also selectively during grasping of that object. In conclusion, object shape is coded in F5 even when a response to that object is not required. The possible visual or motor nature of this object coding is discussed.

INTRODUCTION

Area F5 (Matelli et al. 1985) is a premotor area located in the posterior bank of the inferior arcuate sulcus and the cortical convexity immediately caudal to it. Microstimulation and recording studies showed that F5 is involved mostly in the control of hand movements (Hepp-Reymond et al. 1994; Kurata and Tanji 1986; Rizzolatti et al. 1981, 1988). F5 neurons discharge during specific goal-directed actions such as grasping, tearing, holding, and manipulating. Many of them fire selectively during particular types of grip. Some become active at the visual presentation of food or other interesting objects (Rizzolatti et al. 1988).

In the present experiment, we investigated the visuomotor properties of F5 neurons using a behavioral paradigm in which object-related visual responses could be dissociated from motor responses directed to the same object (see Murata et al. 1996). Our aim was to assess, in a controlled condition, whether individual F5 neurons respond selectively to different object presentation, even in the absence of a subsequent grasping, and to compare these responses to the grasping properties of the same neuron.

The results showed that a high percentage of F5 task-related neurons responded to the presentation of 3-D objects, most of them showing a remarkable object specificity. The response to objects was present also in the absence of a subsequent movement directed toward them. Finally, a congruence usually was observed between the type of grip coded by a given neuron and its object-determined visual responses.

METHODS

Behavioral procedures

The experiments were carried out on one monkey (*Macaca nemestrina*), using the same apparatus, procedures and stimuli previously used by Murata et al. (1996). The experimental situation (here only briefly summarized) was the following. The monkey was seated in front of a box that housed a PC-controlled rotating turntable subdivided into six sectors, each containing an object of different shape: plate, ring, cube, cylinder, cone, and sphere. The objects were presented one at the time, always in the same central position. A spot of light from a red/green light-emitting diode (LED) was projected onto the object. Neurons were tested in four experimental conditions run separately one after the other. 1) grasping in light. When the LED was turned on (red color), the monkey had to fixate it and to press a key for a period of 1.0–1.2 s. When the key was pressed, the box was illuminated and the object became visible. Subsequently, when the LED changed color (from red to green), the monkey was required to release the key, reach for and grasp the object, pull, and hold it until the LED changed color again. The different objects were presented in random order. 2) Grasping in dark. After a first trial in which the object was grasped in light, the light inside the box was turned off and all the following trials were executed in complete darkness. The objects were presented in blocks. 3) Object fixation. When the LED was turned on (green color), the monkey had to fixate the spot of light projected onto the object and press the key. The monkey had to maintain fixation for 1.0–1.2 s and to release the key when the LED changed color. The objects were presented in random order. The initial different LED color (green or red) used in different conditions allowed the monkey to discriminate immediately one condition from another. 4) LED fixation. The task was the same as in 3) but carried out in the dark. The monkey simply was required to fixate the spot of light.

Three turntables, each carrying a set of six objects having the same shape but different size (small, medium, and large) were employed. For most neurons, one set of objects only was used. The types of grip evoked by the various objects varied according to their shape and size. The grips were as follows. Small objects:

plate, hand half pronated, precision grip performed using the thumb and the radial surface of the second and third phalanges of the index finger; ring, hand pronated, index finger inserted into the ring; cube, cone, and sphere, hand half pronated, precision grip performed using the thumb and the radial surface of the last phalanx of the index finger; distance between the two fingers greater than for plate; cylinder, hand half pronated, finger prehension using the first three fingers. Medium and large objects were grasped essentially in the same way as small objects but using more fingers. Grasping movements were monitored using an infrared TV camera.

Neuronal recording and data analysis

Activity from single neurons was recorded using tungsten microelectrodes. Neuron activity plus the event markers were fed to a computer and subsequently used for constructing response histograms. Surgical and recording procedures were described in detail in our previous articles on premotor cortex (Fogassi et al. 1996; Gentilucci et al. 1988; Rizzolatti et al. 1990).

The analysis of the neuron activity during the grasping conditions was made subdividing the neural discharge during each trial in the following task epochs: 1) rest: time before the onset of the trial (red LED turned on), duration 500 ms; 2) object presentation: from 100 to 400 ms after key press/object illumination (this epoch was analyzed also in dark as a control); 3) set: from 400 ms before the LED change of color (go signal) to 100 ms before key release/grasping movement onset; 4) movement: from 100 ms before key release to the moment in which the monkey grasped the object; and 5) grip keeping: a period of 500 ms calculated from the moment in which the monkey began to pull the object. In fixation conditions, there were only three epochs: rest, from 500 ms to the onset of trial (green LED on); object presentation, period from 100 to 400 ms after key press/object illumination; and set, from 400 ms before the LED change of color (signal for key release) to 100 ms before key release.

The neurons described in the present study were all tested in all the experimental conditions. All stimuli were presented eight times in each experimental condition. In each trial, the mean discharge frequency was calculated for each epoch and compared with the rest using a two-tailed *t*-test (significance level, $P < 0.001$). Visual and motor selectivity of neurons to different objects was statistically assessed as described in RESULTS (significance level $P < 0.001$).

RESULTS

Neurons were recorded from the posterior bank of the arcuate sulcus (inferior limb) and the cortical convexity immediately adjacent to it. Both right and left hemispheres were studied. The anatomic location of the studied region was identified using magnetic resonance imaging (MRI). Out of 165 recorded neurons, all showing functional properties typical of F5, 49 were task-related and were studied for the long time required for a complete testing.

All recorded neurons were subdivided into two main types: motor neurons ($n = 25$) and visuomotor neurons ($n = 24$). Neurons of both types discharged during grasping movements. Visuomotor neurons, in addition, showed responses linked to the object presentation. The object-related response (activity during object presentation epoch significantly higher than during rest) was present when the object presentation was followed subsequently by the grasping movement (grasping in light condition) and when no such a movement was present (object fixation condition).

TABLE 1. *Selectivity of motor and visuomotor F5 neurons*

	Motor Neurons	Visuomotor Neurons
Selective	17	16
Nonselective	8	8
Total	25	24

The number of the motor neurons and visuomotor neurons are shown in Table 1. For both neuron types, the number of neurons classed as motor selective is indicated, i.e., of neurons whose activity during the grasping of one or a small set of objects (movement-related epoch) was significantly higher than during the grasping of others and the discharge value of which in response to the former exceeded that in response to the latter of $\geq 20\%$.

Selectivity for a single object (ring, plate, cylinder) was found in 10 motor neurons. Six neurons responded equally well to cube, cone, and sphere. One neuron responded equally well to plate and cylinder and was inhibited by ring. It is interesting to note that cube, cone, and sphere on one side and (at a lesser degree) plate and cylinder on the other elicit a similar grip (see METHODS). It is likely therefore that, although geometrically different, these two clusters of stimuli formed two sets of motorically similar stimuli. Visuomotor neurons were also selective for single objects ($n = 12$) or the two object clusters ($n = 4$).

Figures 1–3 illustrate the behavior of a visuomotor selective neuron. Figure 1 shows its activity during grasping in light. Observation and grasping of the ring determined strong responses. Responses to the other five objects were modest (sphere) or practically absent (other objects).

Figure 2 shows the neuron's activity during grasping in dark. Motor selectivity was the same as in light. The discharge began well before movement onset, immediately after key press, and continued during the whole period preceding movement onset. A tonic activity similar to that exhibited by this neuron was found in most visuomotor neurons.

Figure 3A illustrates the activity of the previous neuron during object fixation. Note the strong response to the ring. The response consisted of a phasic component starting ~ 100 ms after the object visual presentation, followed by a tonic discharge lasting the whole fixation period. Figure 3B demonstrates that the visual response in Fig. 3A was not due to ocular fixation.

All visuomotor neurons that showed motor selectivity were also visually selective, i.e., their discharge during fixation of some objects was significantly higher than during fixation of others and the discharge value in response to the former exceeded that in response to the latter of $\geq 20\%$. The visual selectivity established in object fixation condition coincided with that found in grasping in light condition during the object presentation epoch.

A comparison between visual and motor selectivity showed that nine neurons behaved as the neuron illustrated in the figures, i.e., they exhibited the same visual and motor selectivity. Out of the remaining seven visuomotor selective neurons, four showed a motor selectivity higher than visual selectivity, two showed the reverse. One neuron did not show any correlation between visual and motor selectivity.

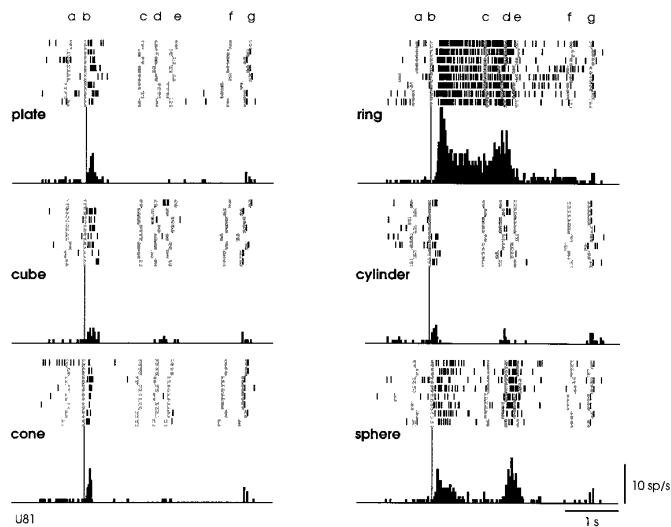


FIG. 1. Example of a selective F5 visuomotor neuron. Panels show neural activity recorded during the grasping in light task with 6 objects of large size. Rasters and histograms are aligned (vertical bar) with key press (onset of object presentation). Small gray bars in each raster indicate onset of red LED (*a*), key press (*b*), onset of first green LED (*c*), key release (*d*), onset of object pulling (*e*), onset of second green LED (*f*), and object release (*g*), respectively. Horizontal scale: 1 s. Vertical scale: 10 spikes/bin. Bin width: 20 ms.

DISCUSSION

The present study shows that a high percentage of F5 grasping neurons is activated by presentation of visual objects. This activation is observed also within a behavioral context that explicitly excludes any grasping movement (object fixation condition). Many neurons show visual selectivity for one object or a small-objects set, thus suggesting that F5 neuron response represents an object description either in visual or motor terms.

Classically, object description was considered an exclusive attribute of inferotemporal cortex (Ungerleider and Mishkin 1982). More recently, neurophysiological experi-

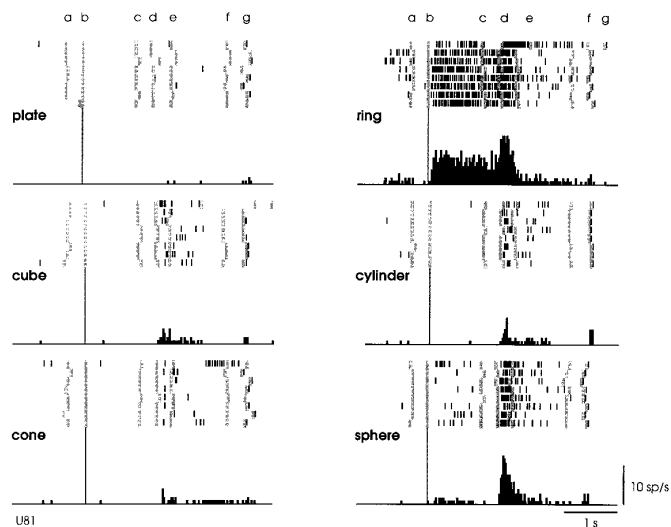


FIG. 2. Neural activity of the same neuron shown in Fig. 1 recorded during the grasping in dark task. Conventions as in Fig. 1.

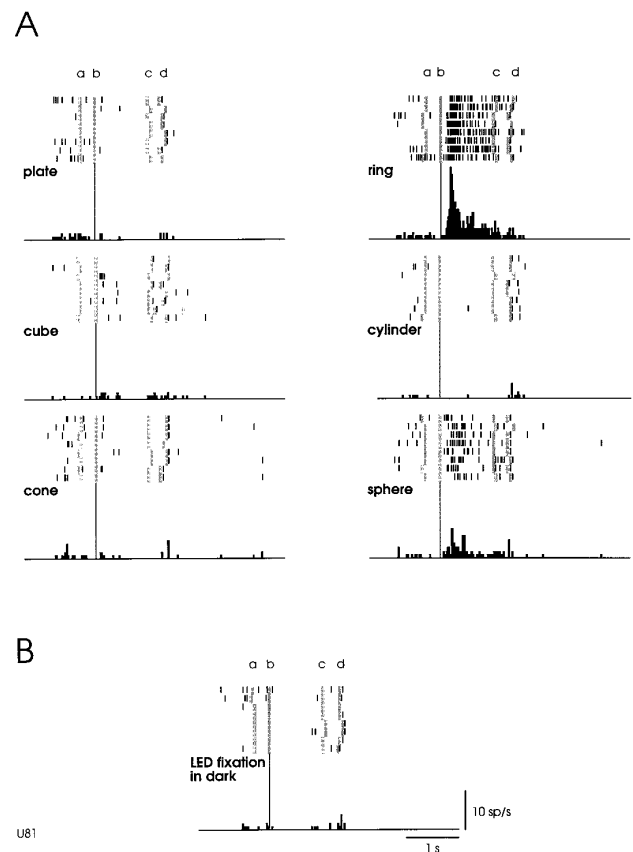


FIG. 3. *A*: neural activity of the same neuron shown in Fig. 1 recorded during the object fixation task. Rasters and histogram are aligned with key press. Small gray bars in each raster indicate onset of green LED (*a*), key press (*b*), onset of red LED (*c*), and key release (*d*), respectively. Other conventions as in Fig. 1. *B*: neural activity of the same neuron shown in *A* recorded during the LED fixation in dark task. Conventions as in *A*.

ments showed that object size and shape also are coded in the inferior parietal lobe and specifically in the caudal part of the lateral bank of the intraparietal sulcus (Shikata et al. 1996) and in anterior intraparietal area (AIP) (Sakata et al. 1995; Taira et al. 1990).

AIP has rich anatomic connections with F5 (Matelli et al. 1994), and the two areas share many functional similarities (Gallese et al. 1997; Jeannerod et al. 1995). In spite of this, the observation that F5 neurons respond to visual objects is rather intriguing, especially so if one considers that F5 is a premotor area belonging to that group of premotor areas that send fibers to the spinal cord (He et al. 1993) and that are connected directly with the precentral motor cortex (Kurata 1991; Matelli et al. 1986; Matsumura and Kubota 1979; Muakkassa and Strick 1979). Is this motor characterization of F5 reconcilable with its responsiveness to object presentation?

To answer this question, let us examine more closely the functional properties of F5 visuomotor neurons. The responses of F5 neurons to objects are highly reliable, they are locked temporally to the stimulus presentation and do not depend on subsequent grasping movements, being still present in the object fixation condition. These characteristics usually are considered as a good evidence in favor of a true

sensorial nature of a response. Is this interpretation necessarily correct? Or is there any other possible interpretation of F5 visual responses?

A similar issue was addressed previously in experiments on the dorsal premotor cortex where neurons that have both motor and visual properties also are found. Experiments aiming to solve this issue (Boussaoud and Wise 1993; see also Boussaoud et al. 1996; Crammond and Kalaska 1994) showed that in most dorsal premotor neurons the visual responses disappeared when the stimulus presentation was not followed by a movement. These visual responses therefore were interpreted as a reflection of an intention to move. For the remaining neurons, the conclusion was that, given their rather unspecific character, the stimulus-related discharges were signals for summoning attention rather than responses describing the stimulus visual characteristics.

Both these interpretations are not adequate to explain the responses of F5 neurons. First, the object-related discharges of F5 neurons do not depend on a subsequent object grasping behavior, which excludes the intentional interpretation. Second, their responses are frequently object-selective, which excludes also, at least for the selective neurons, the attentional interpretation. These facts do not imply, however, that the responses of F5 visuomotor neurons are necessarily visual (although for some of them, this may be the case). The interpretation we favor is that the responses of F5 neurons to object presentation are neither visual nor intentional but represent the description of the presented object in motor terms. That is, every time an object is presented, its visual features are automatically (regardless of any intention to move) "translated" into a potential motor action. This potential action describes the pragmatic physical properties of the objects.

An interpretation in terms of a potential motor action directed toward a stimulus has been proposed also by Kalaska and Crammond (1995). They reported that in a go/no go reach task, area 5 neurons discharge almost equally to the presentation of a visual stimulus when the monkey has to reach it or to refrain from moving. A similar but not identical interpretation recently was advanced by Snyder et al. (1997) to explain the discharge of arm-related movement neurons in the posterior parietal cortex. These parietal neurons discharged during a delay period preceding both arm and eye movements directed toward a certain stimulus location. The discharge, however, disappeared when the saccade was made to the preferred location, but the arm was moved to an opposite one. On the contrary the neuron fired when the arm was moved toward the preferred direction and the eye to the opposite one. The authors concluded that the occurrence of neuron's discharge during the condition in which only the saccade was made toward the target, but the arm remained still, was due to an arm movement "planning". Their interpretation of this planning, however, was not, as ours, in terms of an automatic retrieval of an action, but in terms of a "desire" (intention) to move.

It is important to note that the "pragmatic" interpretation of object-related responses fits well with that advanced for explaining the functional properties of another class of F5 neurons, the "mirror" neurons, i.e., those neurons that show similar responses when the animal both observes and per-

forms similar actions (Gallese et al. 1996; Rizzolatti et al. 1996). In this latter case is the observation of an action, rather than the observation of an object as in the neurons of the present study, that evokes an internal motor representation congruent to the observed visual stimulus.

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