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"Motor and Visual-Motor Functions of the Premotor Cortex"

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Motor and Visual-Motor Functions of the Premotor Cortex

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Abstract. The premotor cortex of the macaque monkey consists of at least two major subdivisions: inferior area 6 and superior area 6. These two subdivisions are located respectively lateral and medial to the arcuate spur. In this article new data on the organization of inferior area 6 are reviewed. They can be summarized as follows: a) Distal movements as well as proximal movements are represented in area 6. Distal movements are represented rostrally, mostly in the histochemical area F5; proximal movements caudally in area F4. b) Neurons related to proximal movements respond vigorously to tactile and visual stimuli. Visual fields are located around the body and are in register with tactile fields. The direction of effective active movements is congruent with the location of the visual field. c) Neurons related to distal movements fire during specific motor acts such as grasping, holding, and tearing regardless if the act is made with the right hand, the left hand and, in many cases, the mouth. A large number of these neurons show specificity for different types of object prehension, discharging for example during precision grip but not during whole hand prehension. It is concluded that in area 6 there is a vocabulary of motor acts, coded at a single neuron level. The hypothesis is advanced that vocabularies of motor acts of different complexity are located in various frontal and parietal association areas and that the use of motor acts stored in these areas is at the basis of cortical motor organization.

INTRODUCTION

The rostral part of the agranular frontal cortex (premotor cortex) of the monkey can be subdivided into two large sectors: a superior sector lying medial to the spur of the arcuate sulcus (superior area 6) and an inferior sector lying lateral to it (inferior area 6). Whereas the functional properties of superior area 6 are largely unknown, recent studies carried out in awake monkeys have clarified some aspects of the organization of inferior area 6. Two aspects of this organization will be reviewed. The first is the somatotopy of this area and in particular the controversial issue of distal movements representation. The second is the type of processing that area 6 neurons perform. In this respect a particularly interesting finding was the discovery of neurons whose activity correlates with movements performed by the animal in order to achieve a goal. The discovery that neurons may code an aim and the relevance of this finding for the understanding of motor organization will be discussed.

SOMATOTOPIC REPRESENTATION

Although the problem of movement representation in the motor cortex has been a matter of debate for years, the idea which dominated among the students of motor system in the last three decades was that there is no distal movement representation in area 6 (see Wiesendanger 1981). The strongest evidence in favor of this point of view derived from the stimulation experiments of Woolsey and colleagues (1952). These authors reported that distal movements were exclusively evoked from area 4, whereas proximal and axial movements were mostly elicited from area 6. Their conclusion was that a single motor map exists on the brain convexity and that the cytoarchitectonic differences between area 4 and area 6 are due to different somatotopic representations and not to a difference in function. The data of Woolsey, obtained with surface stimulation of the cortex, were basically confirmed by Kwan et al. (1978) and by Sessle and Wiesendanger (1982) in experiments where intracortical microstimulation was used.

Data reported in the last few years has started to undetermine the belief in a single motor map located on the brain convexity. Injection of HRP in physiologically defined parts of area 4 showed rich connections between the hand representation of area 4 and a zone in inferior area 6 located near the arcuate sulcus (Matsumura and Kubota 1979; Muakkassa and Strick 1979; Godschalk et al. 1984; Strick 1985; Matelli et al. 1986). Obviously this finding did not demonstrate a hand representation in rostral area 6 since cortical areas with a different somatotopic representation may communicate with each other. It suggested however that in area 6 there is a subarea, rostral to that described by Woolsey, which very likely has motor functions. More direct evidence in favor of a distal representation in area 6 was provided by Rizzolatti and his coworkers (1981b). In experiments performed on curarized monkeys they found that near the arcuate sulcus there were a large number of neurons that could be activated with tactile stimuli applied to the hands and the mouth. In a subsequent experiment (Rizzolatti et al. 1981a) carried out on behaving monkeys the same authors described neurons rostrally located in area 6 which fired during active mouth movements.

In the above reviewed physiological experiments either cortical stimulation was employed or single neurons were recorded. In a recent study Gentilucci et al. (1988) reinvestigated the problem of somatotopic representation in area 4 and 6 by combining single neuron recording and intracortical microstimulation in the same experiment. The experiments were carried out on awake semi-restrained monkeys. The neurons were studied during active movements elicited by food and other stimuli and during passive somatosensory and visual stimulation.

The results of one microstimulation experiment are shown in Fig. 1. In this figure the agranular cortex is subdivided into various areas according to the cytochrome oxidase pattern of activity. The three enzymatic areas F1, F4 and F5 approximately correspond to areas FA, FBA and FCBm of Von Bonin and Bailey. The global pattern of the results is very similar to that of the classical cortical motor maps. Distal movements are represented near the central sulcus, proximal movements in F4 and in the rostral part of F1. However, the picture becomes more complicated when the data are examined more closely. First, in F4 movements of the arm were frequently elicited together with those of the face, mouth or neck. These movements were obtained from the same cortical points and using currents of the same intensity. In contrast, in F1 movements evoked with threshold currents involved one joint or, more rarely, adjacent joints. Associations between distant parts of the body were never found. Secondly, electrical stimulation of the rostral end of inferior area 6 occasionally produced distal movements. These responses were weak and inconstant. However, their presence is difficult to reconcile with the idea that area 6 is exclusively devoted to proximal movements. The weakness of the single map idea became more evident when the results of recording experiments were taken into account.

Figure 2 shows a summary map of somatotopic representation in areas 4 and 6 based on neuron responses during active movements and somatosensory stimulation. At variance with Fig. 1, this map shows body parts (not the joints) that were found to be represented in each penetration. This type of data presentation has been chosen because it takes into consideration the neurón responses to tactile stimuli in addition to their discharge during movements. It is clear that two body representations exist in the complex formed by F1, F4 and F5. The distal parts of the body are represented near the central sulcus and again near the arcuate sulcus; the proximal parts are represented on the center of the cortical convexity. The border between the two representations lies at the rostral margin of F1. Proximal neurons related to arm plus mouth or face are located rostral to this border; proximal neurons related to arm movements only are located caudal to it.

Results congruent with those shown in Fig. 2 have been independently found by Kurata and Tanji (1986). These authors used conditioned monkeys whose arm was fixed in a plastic cast, blocking the elbow movements. The

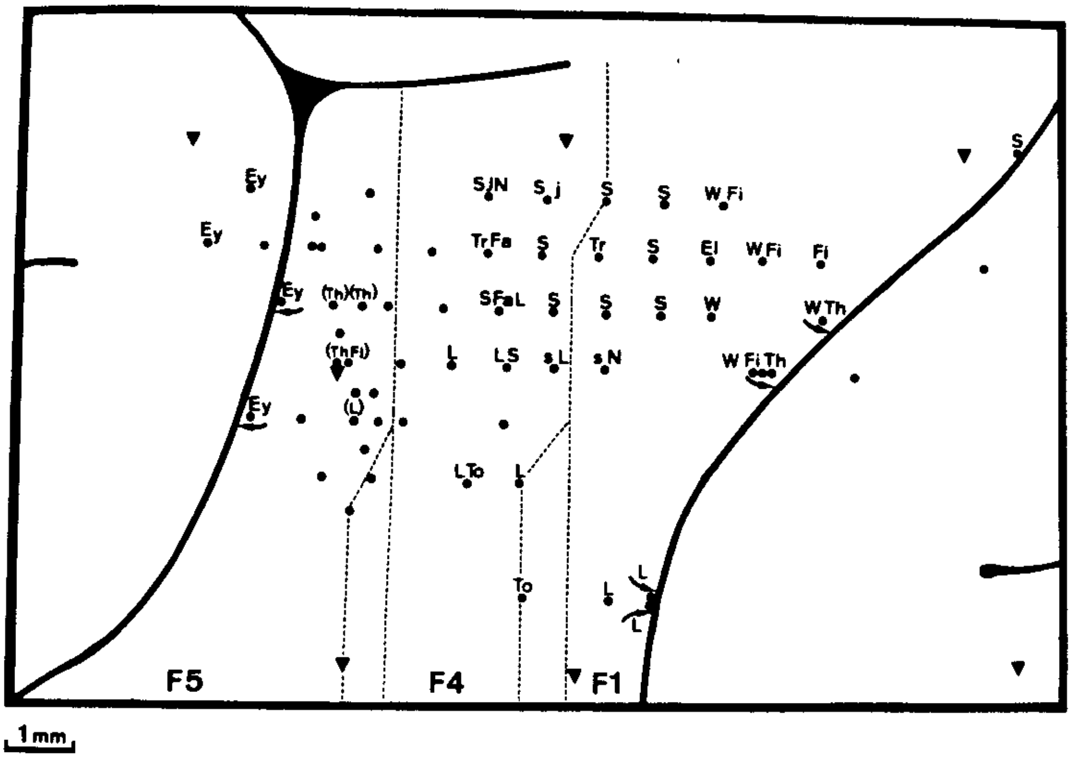

Fig. 1—Distribution of cortical loci responsive to electrical stimulation. Microelectrode penetrations are represented by dots. Letters indicate the joint around which movement was elicited, or the movement of the face and the eyes. Dots without letters mean that no peripheral response was evoked. The dashed lines demarcate the enzymatic areas F1, F4 and F5. El = elbow; Ey = eyes; Fa = face; Fi = fingers; J = jaw; L = lip; N = neck; S = shoulder; Th = thumb; To = tongue; Tr = trunk; W = wrist. Letters in brackets indicate that the movement was erratically elicited with a current of 40 μA.

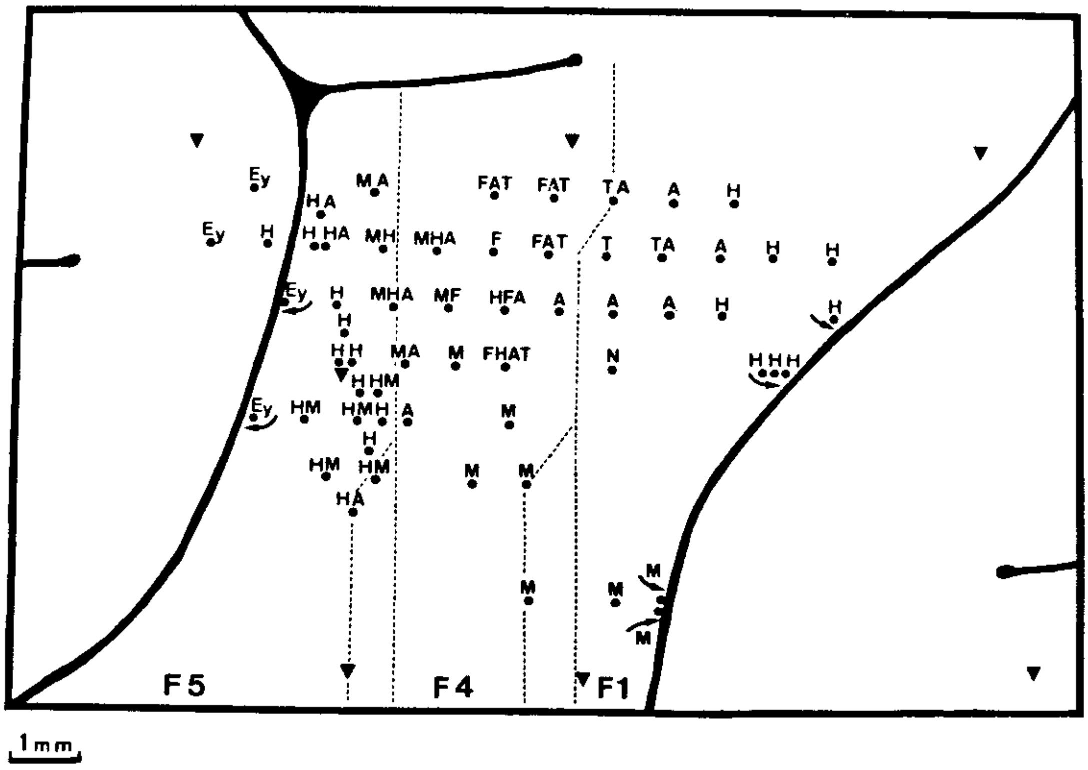

Fig. 2—Somatotopic representation in the inferior part of frontal agranular cortex. A = arm; Ey = eyes; F = face; H = hand; M = mouth; T = upper trunk. Other conventions as in Fig. 1.

animals were trained to move their arm to various preset positions and, when the required position was reached, to press a key attached to the cast. This procedure allowed the experimenters to dissociate proximal and distal movements. Neurons responding to distal as well as to proximal movements were found in inferior area 6. Distal neurons were recorded in rostral penetrations near the arcuate sulcus; proximal neurons were encountered in the caudal part of area 6 and in rostral area 4.

In conclusion, there is no doubt that there are at least two functionally independent representations in the lateral agranular cortex. It may be argued, however, that since this cortex consists of three cytoarchitectonic (and histochemical) areas; namely, FA/F1, FBA/F4, FCBm/F5, a parcellation into three parts is equally tenable. It is apparent, therefore, that the subdivision of the region formed by inferior area 6 and area 4 into two or more subareas depends entirely upon the criteria which one employs. If the basis of the subdivision is the ordered progression from distal to proximal movements and then from proximal to distal, this region should be subdivided into two areas. However, if other parameters are taken into consideration, such as the cytoarchitectonic and histochemical properties, and as will be shown later, the neuron properties, then the subdivision into three parts is the most appropriate. The only way in which this complex cannot be classified is that of a single large motor representation.

INFERIOR AREA 6 AND DISTAL MOVEMENTS

Once it has been demonstrated that area 6 contains a motor representation independent of that of area 4, the function of this motor representation becomes an important issue. Addressing this issue raises some important methodological problems. For example, one might ask how a motor area should be studied when its functional properties are largely unknown. We believe that the best approach to this question is to observe the discharge of single neurons in as wide a range of behavioral activities as possible and then, on the basis of these observations, to make hypotheses which may be later tested with more rigorous methods. Although the weakness of this approach is its subjectivity, its advantage is that the experimental design is not biased by preconceived hypotheses. The alternative approach is to analyze unit activity during highly conditioned movements. We believe that there are two major difficulties with using this approach in examining the properties of neurons in an unexplored area. First, in such studies neurons are examined during fixed and highly stereotyped movements. Thus, correlations are possible with only a limited range of motor activities. If the same neuron controls movements involving several effectors (e.g., mouth and hand), this aspect of neural organization will be missed. Second, correlations may be observed which are not necessarily related to specific functions of the area, but related to attention, set, and other factors linked to the experimental paradigm (Weinrich and Wise 1982; Evarts et al. 1984). In this and in the following section we will review data obtained using the first approach discussed above. The data are from the work of Rizzolatti and colleagues (1987) and have been collected correlating natural movements like reaching, grasping, pushing away, biting, etc. with neuronal activity. The neurons related to distal movements will be discussed first; those related to proximal movements will be dealt with in the next section.

The most striking property of inferior area 6 distal neurons was that they fired in relation to specific, complex movements performed by the animal in order to achieve a particular aim. According to the motor act effective in activating them, they were subdivided into four classes: "grasping-with-the-hand-and-the-mouth neurons," "grasping-with-the-hand neurons," "holding neurons," and "tearing neurons."

Figure 3 illustrates the behavior of a neuron of the first class. This neuron fired when the animal grasped a piece of food with its mouth (A,a), with its contralateral hand (B,a) and, not represented in the figure, with its ipsilateral hand. Opening and closing of the mouth evoked by emotional stimuli, or by food presented too far from the animal to produce the grasping movement (A,b) were ineffective. Similarly, an extension of the arm not followed by the grasping (B,b) did not activate the neuron. No response was observed when the monkey extended its arm and pushed away annoying objects with its hand (B,c). In conclusion, movements of the mouth and the hand having other purposes than grasping did not activate the neuron even when the same muscles were used; conversely, in the effective motor acts, the neuron was activated when completely different set of muscles were contracted to reach an identical goal.

Very interesting was the time relation between the beginning of the neuron discharge and the movements. During standard testing the animal kept its hand near the body. At the food presentation, the arm was projected towards it, then the hand was shaped according to the size of the food and finally the fingers were flexed in order to grasp it. About one third of grasping neurons, regardless of the class to which they belonged, started to fire during this phase of grasping. The remaining neurons fired well in advance of the finger flexion, although their discharge continued during this phase. Half of them started to fire during the shaping of the hand, the other half before any observable distal movement. In the case of these last neurons the discharge was related to the distal movements and not to the proximal ones for the following reasons: a) The discharge increased when the animal started to move the fingers; b) Proximal movements having purposes other than grasping, as for example pushing away an object, were ineffective; and c) A large part of these neurons fired when the proximal movement was followed by a specific distal movement (see below).

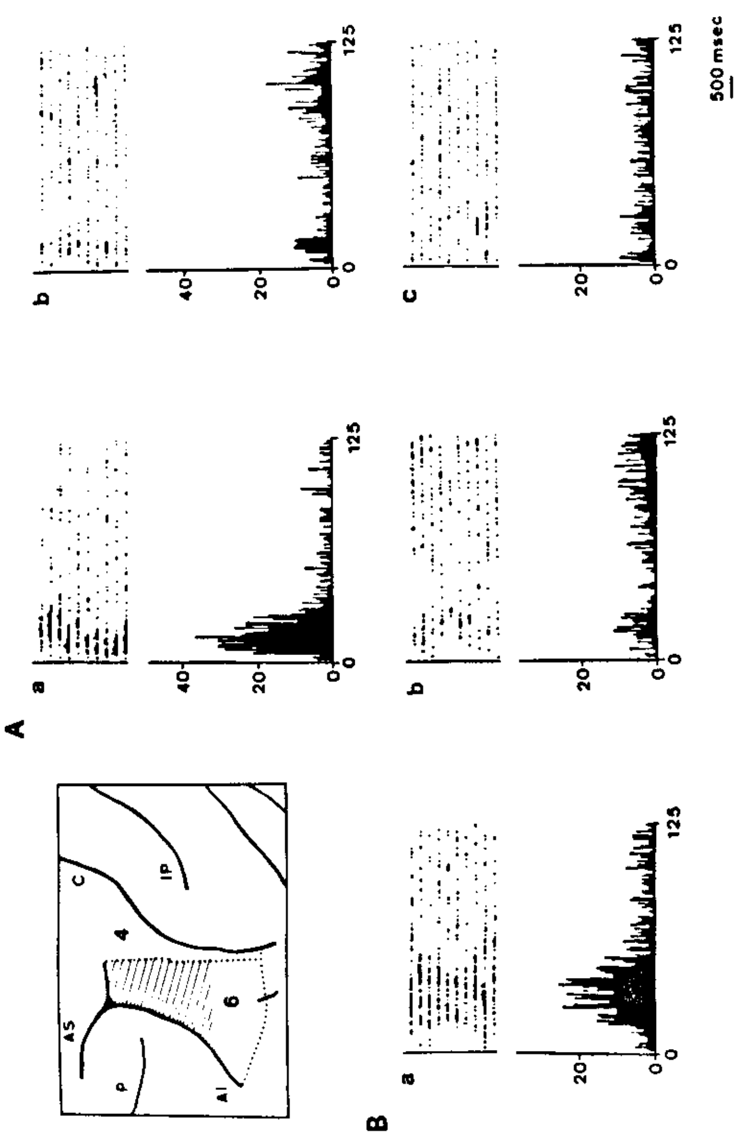

Fig. 3—Study of a "grasping-with-the-hand-and-the-mouth" neuron. On the left a lateral view of monkey inferior area 6 is presented. The dashed area shows the sector of inferior area 6 explored by Rizzolatti et al. (1987); the heavily dashed area indicates where distal neurons were found. C = central sulcus; AS = arcuate superior; AI = arcuate inferior; P = principalis. The rest of the figure illustrates the unit's properties. See text for explanation of the various histograms. Each histogram is the sum of 10 trials. The start of each trial was given by hand synchronously with food or object presentation. Bin with: 40 msec.

It is important to stress that these data concerning the temporal relation between neuron discharge and grasping are clearly in favor of the notion that motor acts rather than simple movements are coded in area 6. Except for those neurons activated during the final phase of grasping, the rest of them (70%) were active *both* during finger extension, typical of the initial phase of grasping (hand shaping), and during finger flexion, typical of the second and final phase of this motor act. Thus an interpretation of the neuron activity as due to a single movement such as flexion or extension appears to be implausible.

Another important characteristic of grasping neurons was that many of them (75%) showed a selectivity for a particular type of prehension. Three types of prehensions were most commonly observed: precision grip, finger prehension, and whole hand prehension. They are illustrated in Fig. 4. Precision grip is used by the monkey to pick up small objects such as sunflower seeds or raisins; finger prehension is used for taking middle-sized objects and to extract objects from a small container; whole hand prehension is used for grasping large objects. Fig. 4 illustrates a precision grip neuron. The response was very strong when the object was taken with a movement of the index finger and the thumb (A), it was dubious during finger prehension (B), and it was absent during the prehension with the whole hand (C). The response was also absent when the monkey used the index finger to take some food from a small hole in a board (D). Precision grip and finger prehension neurons were common among both classes of grasping neurons, while whole hand prehension neurons were rare.

Holding neurons were characterized by the fact that they discharged during the entire time during which the monkey kept an object in its hand. Grasping neurons typically ceased to discharge when the object was grasped. The specificity of different types of prehension was observed both in holding neurons and in grasping cells. Some holding neurons started to fire at the moment in which the monkey touched the object, others during grasping movements.

Tearing neurons formed a tiny class of neurons (5%) which became active when the animal made movements of the fingers, hand and wrist suitable for tearing or breaking the objects. In these neurons the discharge started after the hand touched the stimulus. Tearing neurons were the only F5 neurons which possibly coded force. It must be said, however, that shaping of the hand for motor acts such as tearing or breaking is not the same as for grasping. It may therefore be that the firing of these neurons was not related to the force, but to the distinctive features of the movements which require force in order to be executed.

About 45% of distal neurons could be activated by somatosensory stimuli. The receptive fields were located on the hands, the mouth, or on the hands and mouth. The receptive field location corresponded to the body part

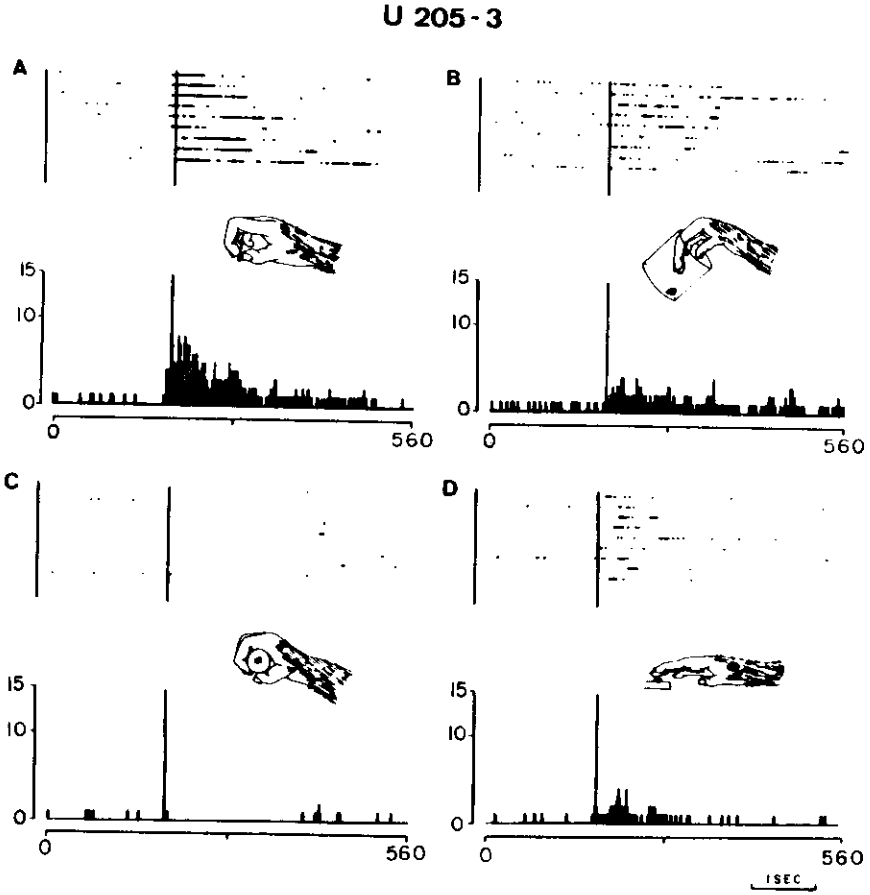

Fig. 4—Study of a "grasping-with-the-hand" neuron. See text for the explanation of the various histograms. The responses are aligned with the moment in which the hand touched the object (vertical bar). Each histogram is the sum of 9 trials. Bin width: 10 msec. Other conventions as in Fig. 3.

whose active movements triggered the neurons. 17% of distal neurons responded to visual stimuli. A neuron was considered visual only if visual responses were obtained in the absence of any movement. Some of the visually responsive neurons were tuned for precision grip movements, others for finger prehension, and still others were unspecific. There was a correlation between type of prehension and preferred visual stimuli. Precision grip neurons responded only to small visual stimuli; those unspecified responded to any type of stimuli. Receptive fields were usually difficult to define.

INFERIOR AREA 6 AND PROXIMAL MOVEMENTS

The great majority of neurons responding to proximal movements were recorded in area F4 and precisely in its electrically excitable part. The properties of these neurons were markedly different from those described in the previous section. Typically, F4 neurons responded strongly to tactile stimuli. Their receptive fields were usually large and could vary from a few cm^2 to vast parts of the body surface. Most receptive fields were located on the face. Neck, chest and arms were also frequently represented. The majority (70%) of the receptive fields were contralateral to the recorded side, 27% were bilateral, and very few (2%) ipsilateral.

The majority of F4 neurons could be activated by visual stimuli (85%). With few exceptions these neurons required, in order to be effectively driven, stimuli moved in the space within the animal's reach (peripersonal space). Stimuli approaching the animal were usually the most effective. The visually responsive area was located around the tactile receptive field. When the tactile field was bilateral the visual field also was bilateral; when the tactile field was unilateral the visual field was unilateral as well. The extension in depth of the visual responsive region varied from one neuron to another. In some neurons constant responses could be obtained only with stimuli very close to the skin (10 cm or less); in others, the responsive region extended for more than 30 cm. F4 neurons did not require particular types of stimuli in order to be driven. A piece of cotton, a black disk, a piece of food, or even the hand of the experimenters moved towards the animal could activate a given neuron.

The visual receptive fields of F4 neurons were coded in terms of body coordinates. This point has been established by Gentilucci et al. (1983), who tested the neurons in the way shown in Fig. 5. A piece of food was moved into the frontal plane around the face of the animal. The food was attached to the free tip of a metal rod supported by a vertical bar. Potentiometers connected with the joints controlling the rod movement gave the position in space of the rod's tip. The stimulus trajectory was recorded on an X–Y oscilloscope and the brightness of the oscilloscope beam was intensified at the occurrence of action potentials. It is clear that the response always remained in the sector of space around the mouth, in register with the tactile receptive field which in this unit extended from the lower lip to the chin. This was also true when the animal followed the stimulus with the eyes (C) and therefore the stimulus location corresponded to the fovea. These results cannot be explained in retinal terms because, in spite of the fact that the stimulus always fell on the fovea, responses were evoked only from a restricted part of the space.

In contrast to F5 neurons, which were all triggered by active movements, only 50% of F4 neurons became active in this condition. The most-represented movements (70%) were those of the arms, followed by face

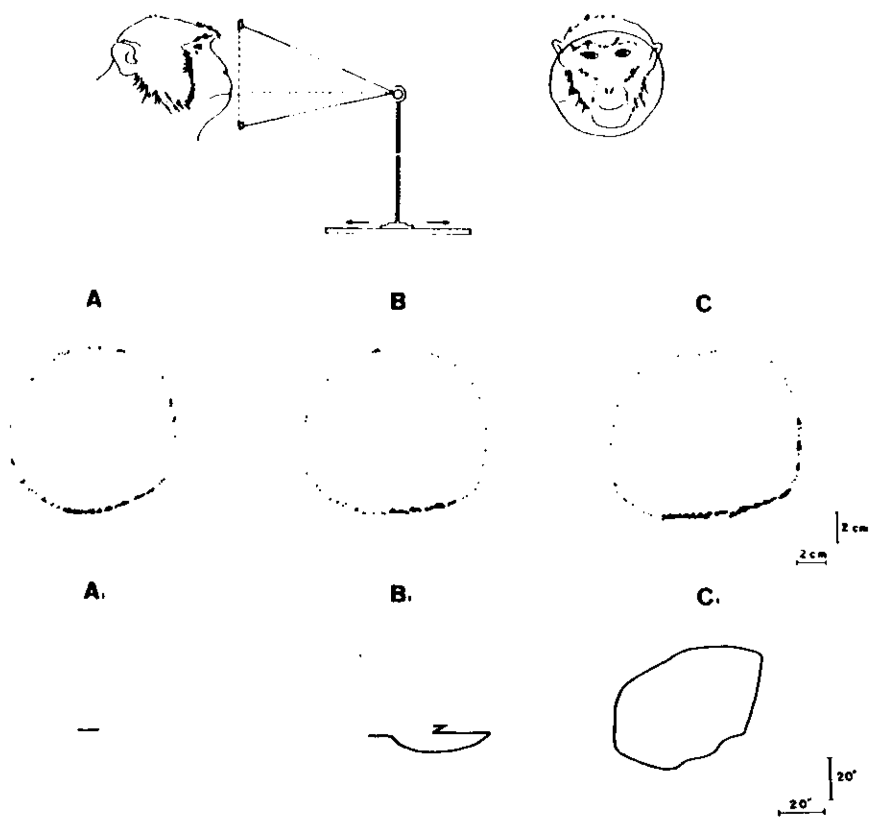

Fig. 5—Study of the visual responses of an F4 neuron. Upper row: (left side) schematic drawing of the device used for visual stimulation; (right side) stimulus trajectory in respect to animal's face. Distance between stimulus and mouth: 5 cm. Trajectory duration: approximately 2 sec. Middle row: neuron's discharge during stimulus trajectory. Each dot indicates one action potential. Lower row: in A1, B1 and C1 are represented the records of the eye movements during the visual stimulation in A, B, and C, respectively. Note the lack of correlation between eye position and neuron's discharge.

movements (24%). Among arm movements two categories were very common: reaching and bringing to the mouth. Reaching neurons responded to arm projection in a certain, usually rather large, space sector; bringing to the mouth neurons responded to movements toward the mouth regardless of the initial starting point.

The receptive field location and the effective movements were organized in F4 in terms of functional relations. Most neurons had tactile receptive fields on the face, visual receptive field in the peripersonal upper space, and were activated by reaching movements toward the upper space. Reaching neurons whose peripheral field was around the body responded to movements to the lower space. Similarly, there was congruence between the side of the peripersonal field and the side toward which reaching was effective. The same functional principle was found in bringing-to-the-mouth neurons. They responded to arm movements directed to the mouth, but not to the body and their tactile and peripersonal fields were around the mouth and the face. In one case in which the effective movement was toward the body the tactile and peripersonal visual fields were also around the body. More simple was the organization of neurons related to facial movements. In this case the receptive field corresponded to the part of the face which was moved.

A VOCABULARY OF MOTOR ACTS

Usually individuals act when they have a goal to reach. In order to attain it, a motor plan is established formed by a sequence of elementary motor acts, each of which has its own limited aim. We propose that in inferior area 6 there is a vocabulary of elementary motor acts coded at the single neuron level. This vocabulary is essentially related to arm-mouth movements. The neurons related to distal movements specify the type of movement necessary to interact with the objects. Similarly, proximal neurons specify the part of space or body toward which the arm should be projected. The motor acts are therefore represented not as abstract commands like "reach," "grasp," or "hold," but in terms of the way in which the motor act can be implemented: "grasp with the index finger and the thumb," "grasp with all fingers," "reach the upper space." This specification of the motor act is congruent with the notion of area 6 as a premotor area and with its rich, direct connections with area 4.

There are two features of the motor acts stored in inferior area 6 which deserve some comments: their complexity and their purposive character. The increase in movement complexity in area 6 with respect to motor cortex is consistent with the trend observed in the nervous system as one goes away from the periphery. In the motor system this trend appears clear if one compares alpha motoneurons with pyramidal tract neurons. The former project to fibers of one, and only one, skeletal muscle; the latter send axons to several motoneurons and interneurons of the spinal cord (Fetz and Cheney 1980; Shinoda 1981). As pointed out by Evarts (1984) the widespread projection of pyramidal tract neurons allows the motor cortex to select populations of motoneurons, whose activation ultimately produces elementary movements. Thus the consequence of this anatomical arrangement is the emergence of a new motor property: muscle contractions are transformed into movements. The same organization principle should be responsible for the emergence of motor acts. If one premotor neuron controls several precentral neurons with different functions (e.g., flexion of the index finger and flexion of the thumb), its firing should activate them simultaneously and produce as a result the complex movements which we have defined as motor acts.

Particularly interesting is the problem of how the purposive character of motor acts may emerge. We must say at the outset that when we speak of neurons that fire in relation to a goal we obviously do not imply any vitalistic principle with which neurons may be endowed. We simply mean that the single neuron behavior correlates more with the aim of the motor act than with any elementary movement forming it. The goal-related neurons have two aspects: first, the same goal is attained with different effectors; second, there is a temporal continuity of their firing during different or even opposite elementary movements. The first aspect is basically spatial. It may therefore be explained with the same principle of widespread connections discussed above. One premotor neuron, which innervates groups of neurons located in parts of the primary motor cortex anatomically connected with the right hand, the left hand, and the mouth, can control movements of different effectors. More difficult to explain is how the same neuron can command opposite movements such as the shaping of the hand before prehension and its flexion during actual grasping. One possibility is to postulate a circuit generating finger extension–flexion movements similar to that described in the spinal cord for walking movements (Grillner 1981). According to this model a premotor neuron simultaneously facilitates groups of cortical motor neurons controlling finger extension and groups of motor neurons controlling finger flexion. Only neurons involved in a particular type of prehension are activated. Simultaneously, the premotor neuron sends command signals to the extension–flexion circuit. If the extension–flexion circuit facilitates the motor cortex also below threshold, the result of the joint effect of the two inputs will be: (a) a specific activation of the neurons selected by the premotor cortex to perform a certain type of prehension; and (b) the specification of the temporal order of muscle contractions. This hypothesis obviously postulates, in analogy with the properties of the walking "central program," that the extension–flexion circuit is modulated by afferent inputs necessary for shifting the program from one phase to another. In conclusion, although a central program for hand movement is at the moment completely hypothetical, the rich connections of area 6 with subcortical centers, and especially via pontine nuclei with the cerebellum, give it a possible anatomical basis.

A final point which deserves some comments concerns the concept of the vocabulary of motor acts. The vocabulary represented in inferior area 6 is certainly rather limited with respect to the animal's motor repertoire. Thus, if the finding that neurons control motor acts is generally valid, other

vocabularies should exist in the cortical areas. For example, movements expressing emotions, which are not represented in inferior area 6, should be located elsewhere, for example in the gyrus cinguli, one of the oldest motor areas. Other premotor areas should control movements of limbs and of the body employed in defense and attack behavior. The fascinating point concerning the vocabulary idea is that, considering the proximity of area 6 to area 4, it predicts the existence of other higher order vocabularies. For example, one may postulate the existence of a vocabulary where eye movements and hand movements are associated, or other vocabularies where segments of a motor plan or even an entire motor plan is represented. Although all of these vocabularies are at the moment purely speculative, some areas such as the parietal lobe where arms, hand and eye movements are represented together suggest that this type of association may not be completely arbitrary.

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