J. Physiol. (1981), **311**, *pp.* 521–540
With 8 text-figures
Printed in Great Britain

VARIETY OF FUNCTIONAL ORGANIZATION WITHIN THE MONKEY MOTOR CORTEX

BY R. N. LEMON

From the Erasmus University, Rotterdam, Department of Anatomy, P.O. Box 1738, Rotterdam, The Netherlands

(*Received 21 April 1980*)

SUMMARY

1. Single-unit recordings have been made from 606 neurones in the arm region of area 4 in five conscious monkeys. Their activity during a stereotyped motor task and their responses to passive natural stimulation of the limb have been investigated.

2. 88% of area 4 neurones responsive to natural stimulation received their afferent input from a restricted region of the contralateral arm.

3. The activity and afferent input to cell groups have been determined by comparing the properties of neurones located within 500 μm of each other and recorded in one and the same micro-electrode penetration. 115 such cell groups containing 344 neurones were investigated.

4. 75/115 cell groups (65%) contained neurones with input from the same arm zone (shoulder, elbow, wrist or hand) and with a similar pattern of task-related activity. Cell groups containing neurones with identical afferent inputs never showed contrasting behaviour during movement.

5. 40/115 cell groups (35%) contained neurones receiving inputs from more than one arm zone. Twenty-five cell groups (22%) had two contiguous zones (e.g. wrist and hand) represented and ten groups had input from two discontinuous zones (e.g. elbow and hand). These differences in input within a cell group were usually reflected in contrasting behaviour of its constituent neurones during movement.

6. Pyramidal tract neurones (PTNs) lying immediately adjacent to one another usually received similar inputs and exhibited matching behaviour. PTNs lying further apart in the same penetration often showed different activity and responded to different stimuli.

7. The topographic distribution of afferent input to area 4 revealed multiple representation of input from a single zone combined with considerable intermingling of input from all four zones. Neurones with shoulder and elbow inputs surrounded those with wrist inputs which in turn lay scattered around a central zone. This central zone only contained neurones with hand inputs, although neurones with hand inputs were found outside this central zone.

8. The significance of this complex organization is discussed in terms of motor cortex input and output.

0022-3751/81/3690-0936 $07.50

INTRODUCTION

The classical concept of a 'motor map' in the primate precentral gyrus reflects the functional proximity of the motor cortex to motoneurones and muscles. The concept of different muscle-groups being represented in different areas of the cortex, originated from experiments using stimulation of the cortical surface (Phillips & Porter, 1977). Introduction of the intracortical microstimulation (ICMS) technique initially re-emphasized the discrete, mosaic output organization of the motor cortex (Asanuma & Rosén, 1972; Asanuma, 1975). More recently, however, it has been demonstrated that the 'colonies' of cortical neurones projecting to a single motoneurone or muscle may be large and discontinuous and may overlap with cortical colonies of other muscles (Phillips & Porter, 1964; Andersen, Hagan, Phillips & Powell, 1975; Jankowska, Padel & Tanaka, 1975; Kwan, MacKay, Murphy & Wong, 1978; Armand & Aurenty, 1977). There is also evidence that the afferent input from periphery to motor cortex does not fit a simple somatotopic pattern, but that multiple representation of one part of the limb may occur with some degree of overlap between separate zones of the limb (Lemon & Porter, 1976; Wong, Kwan, MacKay & Murphy, 1978; Strick & Preston, 1978*a*).

These departures from the traditional somatotopic map of the motor cortex have been paralleled by studies showing that one output neurone from the cortex may influence a number of different muscles (Fetz & Finnochio, 1975; Fetz, Cheney & German, 1976), possibly by branching within the spinal cord (Shinoda, Zarzecki & Asanuma, 1979).

The present study attempts to illustrate fine organization within the motor cortex by analysis of afferent input to small groups of neurones within it together with a description of their 'motor field' assessed by recording activity during a variety of voluntary movements (Lemon, Hanby & Porter, 1976; Lemon, 1981).

METHODS

The methods have been fully described elsewhere (Lemon *et al.* 1976; Lemon, 1981). The object of the present experiment was to study as many neurones as possible within a single micro-electrode penetration, so that a direct comparison could be made of the properties of neurones located within the same group or cluster of cells. In order to make a further comparison between neurones recorded in different penetrations, these penetrations had to be identified histologically and reconstructed. To facilitate this reconstruction the stereotaxic co-ordinates of the recording cylinder were accurately measured during implant. The cylinder was positioned to allow electrode penetrations normal to the cortical surface. The depth of the dura mater below the top of the cylinder was then measured and a chart was drawn up relating the cylinder co-ordinates to the position of the central sulcus. The co-ordinates of each penetration were plotted on this chart. The depth of each neurone, and the cortical grey matter was estimated (Lemon, 1981). In each monkey, thirty to fifty penetrations were made over a period of 6–20 weeks. At the end of this period marking lesions were made at key points. A few days later, the monkey was killed with an overdose of anaesthetic and perfused with 0·9% saline followed by formal saline. The stereotaxic position of the cylinder was re-measured, and the sulcus co-ordinates checked against those found during implant. Frozen sections (40 μm) were cut in the stereotaxic plane, and carefully examined for gliosis around electrode tracks. In the brain of two monkeys, all of the penetrations were identified. Each track was reconstructed throughout the cortical grey matter and the position at which it penetrated the cortical surface determined. The latter was compared with the chart made during the experiment. In the rostral bank of the central sulcus, penetrations were reconstructed with particular attention

to the orientation of the track to large pyramidal neurones in layer V. Most sulcus penetrations were parallel, although some showed deviations within the tissue which could not be explained by tissue shrinkage (Lemon & Porter, 1976). The position of each neurone within the cortex was estimated by combining data concerning (*a*) the point at which the penetration containing that neurone passed through the pial surface of the cortex, (*b*) the orientation of the penetration and (*c*) the depth of the neurone read from the microdrive and corrected for dimpling.

RESULTS

Spatial organization of forelimb afferent input to area 4

The results are drawn from five conscious monkeys in which recordings were made of 749 neurones in 241 electrode penetrations in area 4. Of these 749 neurones, 130 were unresponsive to natural stimulation and thirty had input zones on face, lips or jaw. The remaining 606 neurones had inputs from the contralateral forelimb. The nature of these inputs was in good agreement with previous studies on afferent projections to area 4 (Lemon & Porter, 1976; Fetz & Baker, 1972; Rosén & Asanuma, 1972; Wong *et al.* 1978).

The organization of this afferent input was analysed at three different levels. First, the modality and size of input zones of individual neurones was assessed. Secondly, the afferent input to groups or clusters of neurones within one and the same penetration was determined by comparing the input properties of each neurone within the group. From five to twenty-four neurones were studied in each penetration. This cell group analysis provided detailed information on afferent organization without the necessity of comparing neurones recorded in different penetrations. This latter method, which constituted the third level of analysis, required detailed reconstruction of the large number of electrode tracks made in each monkey, combined with accurate measurement of the cortical depth of each neurone. This was particularly difficult for penetrations deep in the rostral bank of the central sulcus. However, this approach was used in two monkeys, in which depth measurement was considered reliable (due to lack of appreciable dimpling by the electrode (see Lemon, 1981)) and in which all the electrode tracks were successfully recovered in the histological material. In these two monkeys, a topographic reconstruction of the afferent input was assayed by plotting the estimated position of each responsive neurone onto an unfolded map of the precentral gyrus, as described by Wong *et al.* (1978).

Restricted nature of afferent input to individual area 4 neurones

In agreement with previous studies, most area 4 neurones had small, restricted input zones. This characteristic feature of the input to *individual* neurones was quantified because of the contrast to findings for *groups* of neurones within area 4.

Table 1 lists the adequate stimuli for the 606 neurones with input from four different regions of the monkey's arm: shoulder, elbow, wrist and hand. The criteria of Lemon & Porter (1976) were used for detecting and classifying responses to different types of stimuli. Most neurones received afferent input from a single forelimb zone or region (536 neurones, 88 %) and only seventy (12 %) from more than one region. Thus, 334 neurones were influenced by movement of a single joint (e.g. wrist flexion) or of multiple joints within the same zone (e.g. phalangeal joints of all four fingers). By comparison, only forty responded to movement of joints spanning two arm zones (e.g. elbow flexion and wrist flexion). Twenty-nine neurones responded to

palpation of a single muscle belly or group of synergistic muscles, and those influenced by cutaneous stimuli had input zones restricted to the hand and fingers, or to a small region of the arm or forearm (109 neurones). Only twenty neurones had large 'stocking' zones spanning more than one arm region.

TABLE 1. Afferent input from the forelimb to individual area 4 neurones ($n = 606$)

	Adequate stimulus and size of input zone	
Stimulus	Neurones with afferent input from a single forelimb zone	Neurones with afferent input from more than one forelimb zone
Joint movement	334	40
Muscle palpation	29	0
Joint movement + muscle palpation	41	7
Cutaneous	109	20
Cutaneous + joint movement	23	3
Totals	536	70

The 536 neurones with input from a single arm zone had input from the hand and fingers (216 neurones), wrist (128), elbow (141) and shoulder (51). The bias towards hand-input neurones probably resulted from the greater number of penetrations made in the hand region close to the central sulcus.

Afferent input to cell groups in area 4

A cell group was defined as containing neurones all lying within 500 μm of each other and recorded during the downward course of one and the same electrode penetration. This criterion was used to prevent the inclusion within one cell group of neurones recorded in separate regions of the motor cortex due to the electrode traversing the radial architecture of the cortex, which is inevitable within the bank of the central sulcus (Fig. 4*A*) but which also may occur in the convexity of the gyrus due to deviation of electrodes (Fig. 4*B*).

Table 2 lists the 115 cell groups analysed. They were recorded in ninety-eight different penetrations, some deep sulcus penetrations contributing several different groups. The total number of responsive neurones was 344, and the number of neurones per group is plotted in Fig. 1*A*. Most of the cell groups studied contained two to four responsive neurones within the 500 μm limit; eight groups contained five neurones or more.

Fig. 1*B* shows the number of forelimb zones represented within a particular group. In most cases (75/115 groups; 65%), the input to each neurone within a group came from the same forelimb region or zone. The proportion of these single input cell groups was similar in each monkey studied, ranging from 55 to 73% (Table 2). Thirty-two groups received their input exclusively from the hand, nineteen from the wrist, seventeen from the elbow and seven from the shoulder (Fig. 1*C*).

Results from a single representative penetration made in the convexity of the precentral gyrus 3·5 mm rostral to the central sulcus are shown in Fig. 2. The orientation of the track normal to the cortical surface is based on the histological findings. Input from the wrist clearly dominated the tissue explored by this

penetration. A group of four neurones were found between 1·1 and 1·4 mm deep: two responded to wrist flexion and two to light touch over areas including the wrist. This group was therefore classified as having a single input. However a second, deeper

TABLE 2. Distribution of inputs to cell groups in area 4

Monkey	Penetrations	Cell groups	Single input groups	Two input groups	Three input groups
7	22	22	11	10	1
8	14	14	10	4	0
9	13	13	10	2	1
13	29	45	28	15	2
15	20	21	16	4	1
Totals	98	115	75	35	5

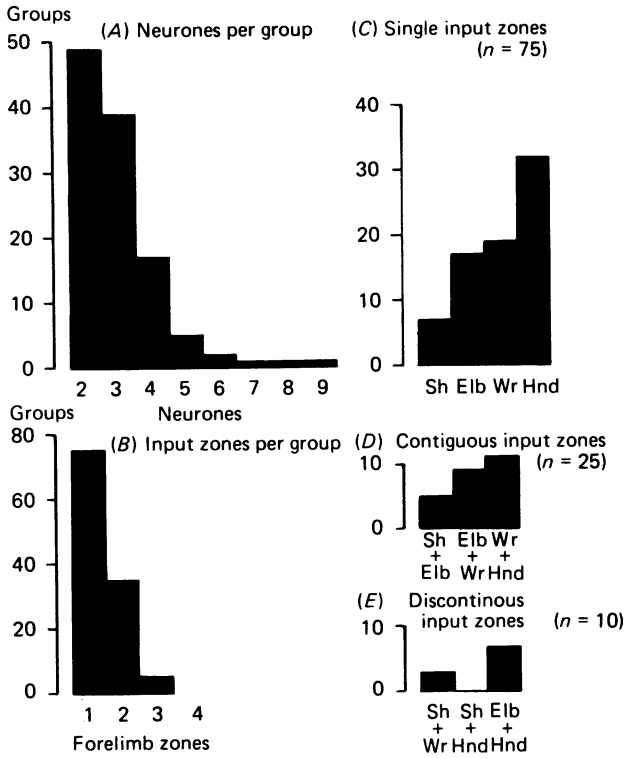

Fig. 1. *A*, number of neurones within each cell group (i.e. within 500 μm limits) for the 115 cell groups studied. *B–E*, number of forelimb zones represented in the 115 cell groups. The forelimb was divided into shoulder (Sh), elbow (Elb), wrist (Wr) and hand (Hnd) zones, each counting as one input zone. The distribution of the input to seventy-five cell groups with single input zones is shown in *C*, and that of the twenty-five groups with two contiguous inputs and of the ten groups with two discontinuous inputs in *D* and *E* respectively.

group had both wrist and hand inputs. The first neurone in this group (unit 17.12) was not influenced by any natural stimulus applied to the wrist area, including wrist pronation (Fig. 2, upper right). However, further investigation revealed a powerful,

reproducible response to finger flexion. (Fig. 2, lower right). A second neurone, 100 μm deeper, had a similar input. The next responsive neurone (unit 17.13) was driven by wrist movement (pronation: Fig. 2, upper left) but had no hand input and showed no responses to digit flexion (Fig. 2, lower left). The cell group including 17.12 and 17.13 was classified as receiving input from two contiguous arm zones.

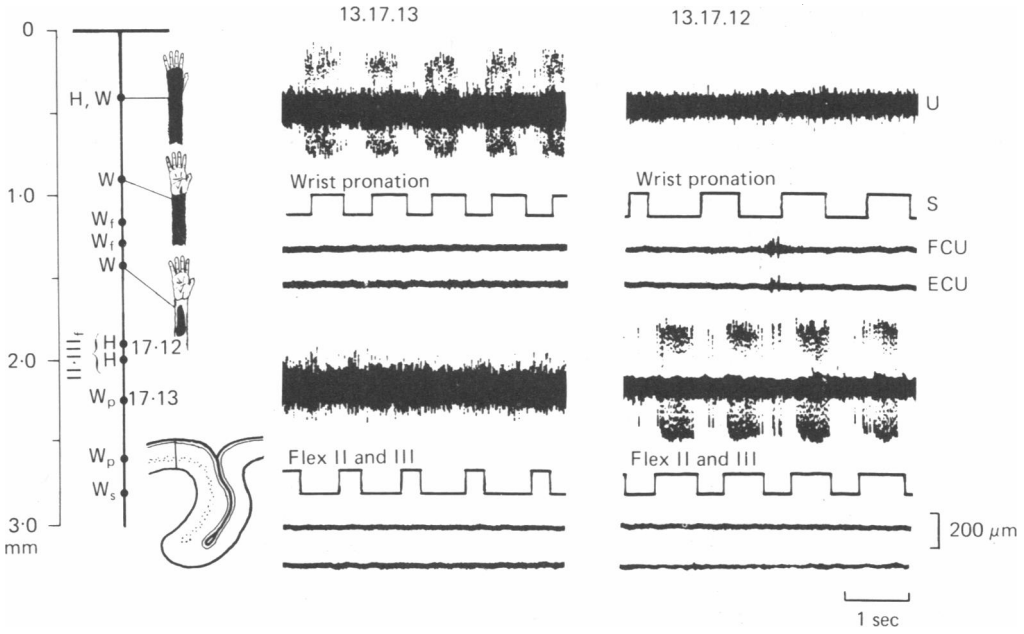

Fig. 2. Results from a penetration made through the convexity of the precentral gyrus. The inset, sagittal section is cut in a plane orthogonal to the central sulcus and shows the estimated position of the electrode track; layer V giant pyramidal neurones in area 4 are marked by dots. Location of neurones in the penetration are marked at the depth at which they were recorded together with forelimb zone providing their input (H, hand; W, wrist). Suffixes (f, flexion; p, pronation; s, supination) denote neurones responsive to joint motion. Neurones influenced by cutaneous stimuli carry no suffix; their input zone is marked on the arm and hand figurines. On the right are shown unit records (U) from two neurones in the track (17.12 and 17.13) during the application of passive wrist pronation (upper records) and flexion of the index (II) and middle (III) fingers. The approximate onset and duration of the stimulus is marked by the signal, S. Note absence of activity in e.m.g. records made during the joint motion from flexor and extensor carpi radialis (FCU and ECU respectively).

In all, 40/115 cell groups (35%) received inputs from more than one input zone (Fig. 1*B*). Groups with two inputs were subdivided into those resembling the group in Fig. 2 with two contiguous zones (e.g. wrist and hand or elbow and shoulder) and those with discontinuous input zones (e.g. wrist and shoulder). The former division contained 25/115 groups (22%) and latter, 10/115 groups (9%) and their distribution is shown in Fig. 1 *D* and *E*. Finally, 5/115 groups (4%) had inputs from three separate arm zones.

Cell groups with single input zones. Typical cell groups with *single input* are shown in Fig. 3*A*. Penetration 1 encountered seven neurones, all with hand inputs. Six lay

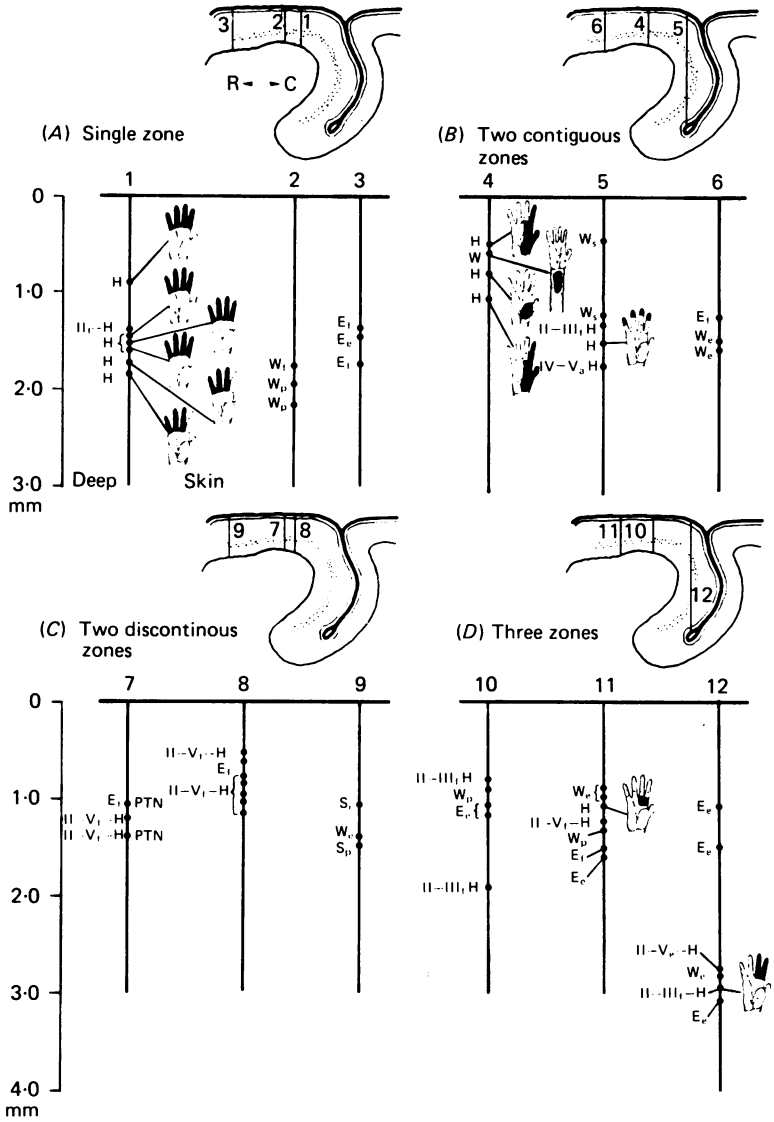

Fig. 3. Afferent input to cell groups in area 4. *A–D* each show three sample penetrations containing cell groups with inputs from one (*A*), two (*B* and *C*) or three (*D*) zones of the contralateral forelimb. The estimated position and trajectory of these penetrations is shown on the inset diagrams. R, rostral; C, caudal. Notation of neurone position and input as for Fig. 2. Abbreviations: H, hand; W, wrist; E, elbow; S, shoulder; a, ab, abduction; e, extension; f, flexion; r, retraction; s, supination; p, pronation (W neurones) or protraction (S neurones); II, index; III, middle; IV, ring and V, little fingers.

within 500 μm of each other and five of these had cutaneous input zones on the glabrous skin of the fingers. Penetration 2 contained a three-neurone group; each neurone responded to passive wrist movement. Penetration 3 yielded three neighbouring neurones, all with elbow inputs. The inset diagram in this and succeeding figures again indicates the approximate location of the respective penetrations.

Cell groups with two input zones. Examples of cell groups with *two contiguous inputs* are shown in Fig. 3*B*. Penetration 4 yielded three neurones with cutaneous inputs from the radial side of the hand. These neurones bounded a fourth with input from an adjacent area of the wrist. Penetration 5 contained three hand-input neurones which lay close ($< 100\ \mu$m) to a neurone responding to supination of the wrist. A neurone with a similar wrist input was found superficial to this cell group. Penetration 6 encountered two neurones driven by wrist extension which were located less than 200 μm away from one responsive to elbow flexion.

Groups with two *discontinuous input zones* are shown in Fig. 3*C*. Penetration 7 yielded two pyramidal tract neurones (PTNs), the first responsive to elbow movement, but the second, only 200 μm away, had input from the digits. Both inputs were thoroughly checked, but neither neurone had input from the zone affecting its neighbouring PTN. A non-PTN, also with a hand input, lay in between the two PTNs. The elbow input neurone of track 8 was clearly located within a hand-input cell group, while the wrist input neurone in penetration 9 was found between two neurones responding to shoulder movement.

Cell groups with three input zones are shown in Fig. 3*D*. Only one of them was found deep in the bank of the sulcus (penetration 12) and all five groups included neurones with hand inputs.

Modality of inputs to cell groups

Some individual neurones in area 4 showed responses to both 'deep' stimulus modalities (joint movement or muscle palpation) and 'cutaneous' modalities (hair movement, light touch, maintained indentation of the skin) (see Table 1). This convergence of modalities was also seen in cell groups. A total of 30/115 groups contained separate neurones with different input modalities. The remaining eighty groups contained neurones responding exclusively to deep stimuli (sixty groups) or to cutaneous stimuli (twenty groups). Convergence of modality was observed with equal frequency in cell groups with input from a single forelimb zone as in groups with more than one input zone. During the course of some penetrations there were clear changes in modality, with cutaneous responsive neurones lying superficially and neurones responding to joint motion lying deeper.

Location of cell groups

Single input groups were found both in the convexity of the gyrus and in the bank of the sulcus. Penetrations made through the rostral bank of the sulcus yielded neurones to depths of 6 mm (Fig. 4*A*). Surprisingly, in view of the manner in which such penetrations repeatedly cut across the radial architecture of the cortex, cell groups with two or three different input zones were not commonly found in the bank of the sulcus. In one monkey, 6/7 tracks made in the depth of sulcus encountered cell groups which all received inputs exclusively from the hand. However, the hand inputs to these separate groups did vary in terms of location, size and modality. Cell groups with two or more input zones were mostly found in penetrations made through the convexity of the gyrus, and particularly in the region 2–4 mm rostral to the central sulcus (e.g. penetrations 4, 7, 8 and 10, Fig. 3).

Topographic distribution of afferent input to area 4

Only two monkeys were used in this part of the experiment for the reasons given above. In monkey 13 (*Macaca fascicularis*), forty-five penetrations yielded 205 responsive neurones. No pyramidal tract electrodes were implanted in this monkey, so no identification of PTNs or non-PTNs was possible. In monkey 15 (*Macaca nemestrina*), thirty-one penetrations yielded sixty-five responsive neurones, thirty-four of which were identified PTNs. In monkey 13 a cortical surface area of about 45 mm^2 was investigated, and in monkey 15, about 32 mm^2 (see Lemon, 1981, Fig. 1).

Graphical representation of area 4

The position of each responsive neurone was plotted on an unfolded map of area 4 (cf. Wong *et al.* 1978). Fig. 4*C* represents the precentral gyrus, as seen from above, unfolded so as to reveal the cortex buried in the rostral bank of the central sulcus. Lines *aa*, *bb* and *cc* represent, respectively, the rostral extent of area 4, the top and the bottom of the bank of the sulcus. All these lines run medio-laterally, and are roughly parallel to the sulcus. Fig. 4*A* shows these boundaries (*a*, *b* and *c*) as seen on a sagittal section cut in a plane orthogonal to the sulcus.

Thus, in Fig. 4*C*, tissue lying between lines *aa* and *bb* represents the convexity of the gyrus, and that lying between *bb* and the line *cc* represents the rostral bank of the sulcus. Most convexity penetrations travelled normal to the cortical surface and cut through the cortical laminae at right angles (Fig. 4*B* and penetration 1, Fig. 4*A*). The location of neurones recorded in such penetrations was therefore plotted directly onto the unfolded map at the point between lines *aa* and *bb* at which the respective penetration was made.

For neurones in penetrations in the bank of the sulcus (e.g. penetration 2, Fig. 4*A*), the position of the neurone along the appropriate penetration (*x*, Fig. 4*A*) was marked according to its microdrive depth reading. A line (*xy*, Fig. 4*A*) drawn orthogonally to the plane of layer V passed through *x*. The curvilinear distance *y–b* measured along layer V gave the distance from the line *bb* at which the neurone lay on the unfolded map. Thus neurones recorded at progressively greater depths in the sulcus come to lie closer to line *cc* (Fig. 4*C*).

Location of responsive neurones in area 4

The plots obtained in this way for the two monkeys are shown in Fig. 4*C* and *D*. In monkey 13 (Fig. 4*C*), a distinct central zone was present in which only neurones with inputs from the hand and digits were found. This zone extended deep into the bank of the central sulcus and had its rostral border on the convexity of the gyrus immediately rostral to the sulcus. It was bounded rostrally and medially by neurones with inputs from wrist, elbow and shoulder regions and laterally by neurones with inputs from face, lip and jaw. On the edge of this central hand or digit zone there was extensive intermingling of hand-input neurones with neurones with more proximal inputs, particularly from the wrist. Hand-input neurones were also found scattered at a distance from the central hand or digit zone; the observed hand or digit projection comprised a total area of about 25 mm^2 compared to only 13 m^2 for the central zone devoted exclusively to neurones with hand or digit inputs.

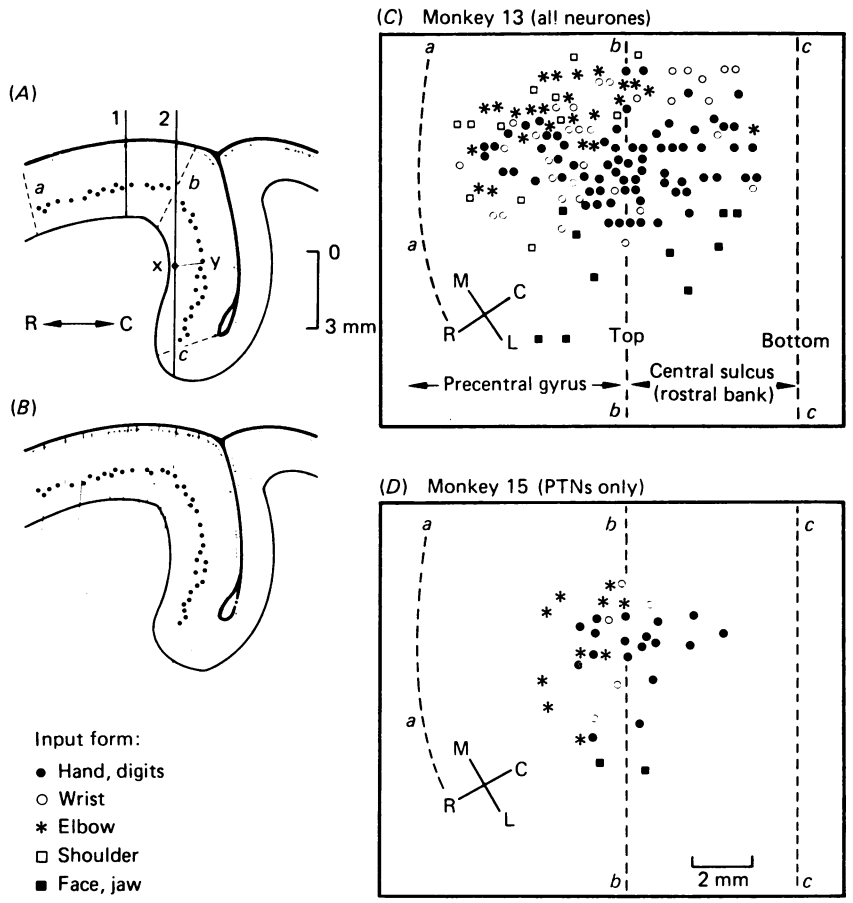

Fig. 4. Topographic distribution of afferent input in area 4. *A*, sagittal section of central sulcus and precentral gyrus made in a plane orthogonal to central sulcus. Location of giant pyramidal cells marked by dots. Dashed lines *a* and *c* represent the most rostral and most caudal extent of these cells, respectively. Line *b* is drawn through layer V as it bends downwards into the buried sulcus. Penetration marked 1 is a sample penetration made in the convexity of the gyrus, normal to both cortical surface and layer V. Penetration 2 passes through the rostral bank of the sulcus and *x* represents a neurone recorded in this penetration. Its location in the unfolded cortex was determined by its relationship to layer V in the buried sulcus (for details, see text). Scale adjusted for tissue shrinkage. *B* shows reconstructed penetrations from monkey 13. Penetrations have been superimposed from twenty-five successive 40 μm sections (= 1 mm) taken from the centre of the recording area. Note variations in the trajectories of different tracks. *C*, unfolded area 4 seen from above (monkey 13). Dotted lines *aa*, *bb* and *cc* run approx. mediolateral and parallel to the central sulcus along the boundaries indicated in *A*. Location of neurones marked by symbols indicating arm zone from which they received afferent input. To preserve clarity a group of neurones recorded within 500 μm of each other in the same penetration and with the same input are represented by a single symbol. M, medial; L, lateral; R, rostral; C, caudal. *D*, unfolded map of area 4 (monkey 15), showing location of responsive PTNs.

In the convexity of the gyrus there was no clear segregation of neurones with wrist inputs from those with elbow or shoulder inputs. These two latter projections were also closely intermingled. There was also no segregation of neurones responding to, for example, wrist flexion–extension from those responding to wrist abduction–adduction. Rather, a pattern of multiple representation in area 4 of responses to one particular movement was observed. The plot shown in Fig. 4*C* re-emphasizes the findings of the cell group analysis in that adjacent neurones with different input zones were most frequently found in penetrations close to the central sulcus, just to the left of *bb*. In contrast, many penetrations made deep in the sulcus only encountered neurones with hand inputs.

Fig. 4*D* shows the distribution of thirty-four responsive PTNs in monkey 15. A central zone near the top of the sulcus contained most of the hand-input PTNs. There was intermingling of elbow and wrist with hand-input PTNs just outside this central zone.

Detailed topography of hand and finger inputs

The spatial distribution found in monkey 13 is shown in Fig. 5*A*. It reveals a mixed distribution with a clear multiple representation of inputs from the digits. Neurones responding to natural stimulation of the thumb alone occupied a lateral area within the hand zone and were often found in close proximity to neurones with inputs from the index finger (digit II). Neurones with input from the ring and little fingers (digits IV and V) were found medially while those with zones comprising the palm of the hand were found in the centre of the hand zone. Fig. 5*A* emphasizes the predominance of glabrous skin input from the hand.

The distribution of modality among hand-input neurones (Fig. 5*B*) shows some segregation in that neurones responsive to light touch of the glabrous skin (but not to joint motion) were concentrated in the centre of the zone and in the depth of the sulcus. Only a few neurones with strictly cutaneous input of this type were found further forward in the convexity of the gyrus, where most of the neurones were only activated by joint movement. Several neurones with responses to both types of stimulus were found between the more rostral joint zone and caudal cutaneous zone. Segregation of these zones was not absolute since some exclusively joint-sensitive neurones were found deep in the sulcus.

Activity in cell groups during voluntary movement

The activity of neighbouring neurones during voluntary movement was compared. For this purpose, most of the 344 neurones located in the cell groups described above were examined during the performance of a task, fully described in the preceding paper (Lemon, 1981). Cine-film evidence, e.m.g. and lever movement signals all indicated that the monkey performed this simple lever-pull task in a highly stereotyped manner. Although there were slight variations from day to day, performance was consistent in any one monkey during any one recording session (normally 2–3 h). The activity of neurones recorded within 500 μm of each other in the same penetration was analysed off-line.

Area 4 neurones showed a great variety of differences in activity patterns during the task; some were reflected in their afferent input, as described previously (Lemon,

1981). No quantitative comparison of activity histograms was attempted. However, a qualitative examination of these histograms allowed division of the cell groups according to the activity of their constituent neurones showing (*a*) similar, (*b*) reciprocal, or (*c*) contrasting patterns of activity.

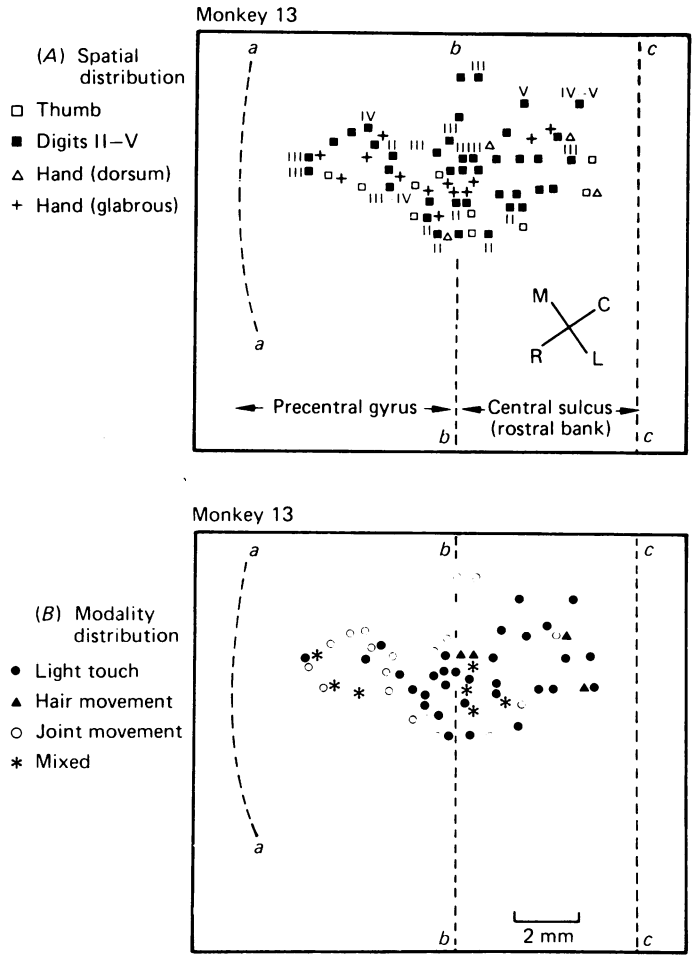

Fig. 5. *A*, distribution of inputs from the hand to neurones in monkey 13, plotted in the same way as Fig. 4. Roman numerals next to squares, e.g. (II), indicate input zone confined to that finger or fingers. Black squares with no numerals indicates input from all four fingers. Note proximity of some neurones with index finger zones to those with thumb zones, the latter lying mainly lateral. Ring and little finger inputs were found mainly in the medial part of the hand zone. *B*, distribution of hand-input neurones according to modality of the effective natural stimulus for each neurone. Note that neurones influenced by joint motion lay mainly in the rostral part of the hand zone, while cutaneous inputs predominated in the bank of the sulcus.

Cell groups with similar activity patterns. The most common finding was that different neurones within the same cell group showed a similar pattern of behaviour during the task. Three examples are shown in Fig. 6. All of the neurones in penetration 1 showed two clear bursts of activity, one associated with knob grip before lever pull

(time zero) and a later, larger burst associated with food pick-up ('pick-up' unit, Lemon, 1981). There was little modulation of activity during other parts of the task. Thus, this group of neurones showed similar activity during performance of different

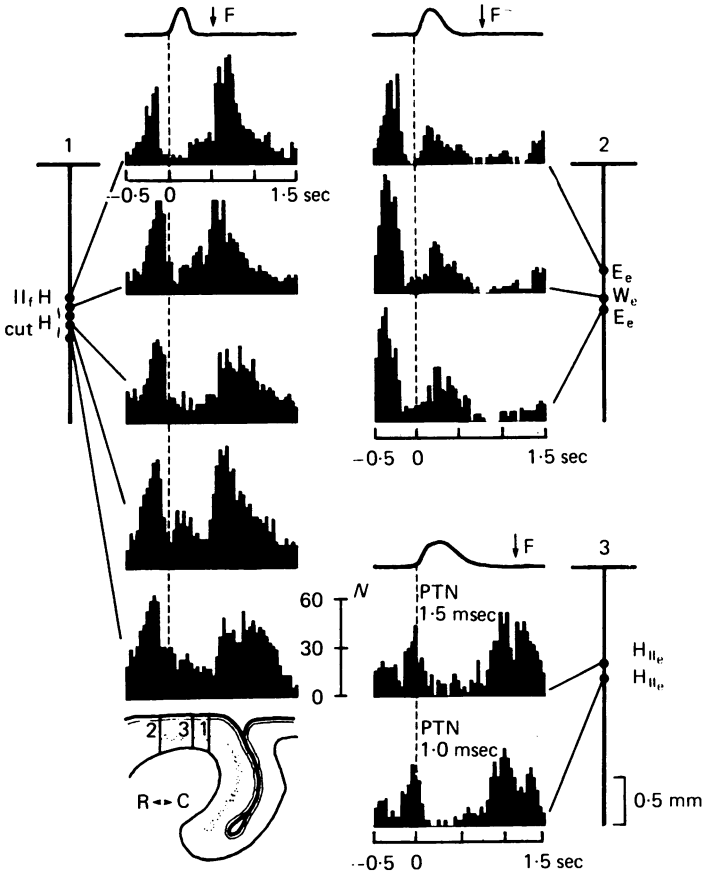

Fig. 6. Histograms of activity during the trained task for three cell groups, each of which contained neurones showing similar activity patterns. Description of afferent input and track location as for Figs. 2 and 3. Histograms represent cumulative activity of each neurone for sixteen successive lever pulls for a period 0·5 sec before and 1·5 sec after beginning of lever movement (time zero and vertical dotted line). Histogram binwidth 40 msec. Scale shows number (N) of spikes/bin and applies to all histograms except uppermost in penetration 1 and both histograms in penetration 3. These neurones had lower discharge frequencies and histograms have been plotted at half the scale of the other neurones. Averaged excursion of lever during the recording period for each cell group is shown above histograms. Arrow (F) indicates average time of contact of the monkey's hand with food reward. In penetration 3, antidromic latencies of the PTNs are shown. The three groups shown were recorded in three different monkeys.

parts of the task. There were small variations from neurone to neurone, no two of them showing identical patterns. The five neurones in penetration 1 all had hand inputs; the same group appears in Fig. 3, penetration 1 which shows that four of them had cutaneous inputs from the digits. Cell groups with similar, single input zones and

similar activity patterns were repeatedly observed, and cell groups with identical input zones never showed strongly contrasting behaviour during the trained task. This also applied to neighbouring PTNs (Fig. 6, penetration 3).

In some cell groups, constituent neurones with two different peripheral input zones still showed rather similar patterns of activity during the task. The cells recorded in Fig. 6, penetration 2, showed remarkably similar activity patterns, despite their dissimilar inputs (two elbow and one wrist). None of the neurones was active during retrieval and manipulation of the food reward ('lever-type' units, Lemon, 1981).

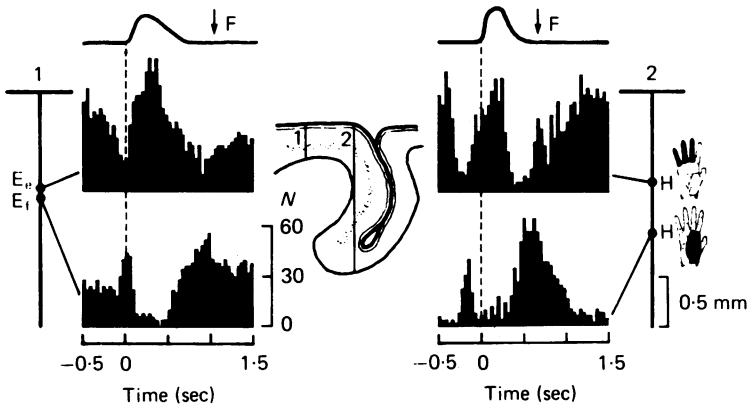

Fig. 7. Reciprocal behaviour in adjacent neurones. For details of histograms, etc., see Figs. 2, 3 and 6.

Cell groups with reciprocal activity patterns. Some closely adjacent neurones showed exactly reciprocal patterns of activity. Examples are shown in Fig. 7. On the left, the upper neurone showed a clear excitation during the lever pull, while the lower one was inhibited. The lower neurone also showed a brief excitation just before the pull; this was associated with inhibition in the upper unit. These neurones responded to reciprocal movements of the elbow joint (one extension, one flexion). Some cell pairs with reciprocal patterns had different input zones (Fig. 7, penetration 2).

Cell groups with contrasting activity patterns. Although similarities in behaviour were consistently sought, a minority of cell groups displayed strongly contrasting patterns of activity. An example is shown in Fig. 8, penetration 1, which contained a group of six neurones, five of which lay within 500 μm. Only the most superficial neurone in this group responded to natural stimulation.

In most cases, however, differences in activity were reflected in differences in peripheral input. In Fig. 8, penetration 2, two neurones with wrist inputs showed a similar pattern of behaviour, the neurone located between them responded to elbow flexion and showed a different pattern, discharging strongly during the lever pull, unlike the other two which clearly paused during this period. The pair of PTNs recorded in penetration 3 also had different inputs and activity.

Afferent input and natural activity of neighbouring PTNs. Nine pairs of PTNs were recorded, each pair being less than 500 μm apart. One group of four adjacent PTNs was studied. All four had elbow input, three responding to elbow extension

and one to flexion. In six PTN pairs, each pair of neurones received similar inputs (e.g. Fig. 6, penetration 3); in the three other pairs, different inputs were represented (e.g. Fig. 8, penetration 3). In two pairs, both PTNs were recorded simultaneously at the same electrode placement; these two pairs had similar afferent input and natural activity. This was also observed in a third pair (Fig. 6, penetration 3) which were

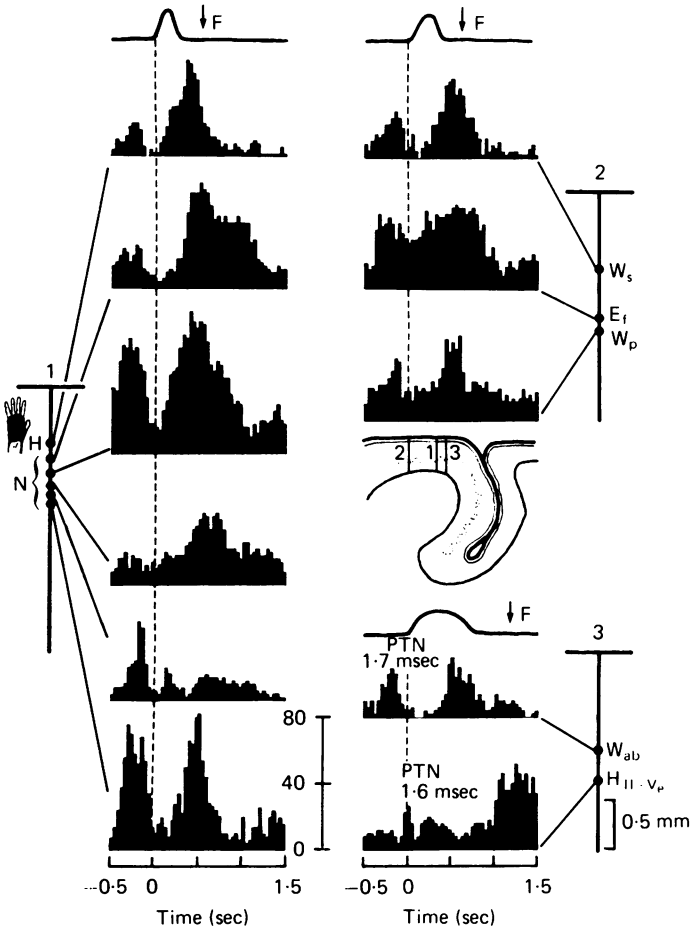

Fig. 8. Contrasting patterns of behaviour in neurones of the same cell group. For details of histograms, etc., see Fig. 2, 3 and 6. N, no apparent response to natural stimulation.

100 μm apart. All the other pairs studied were at least 300 μm apart and all showed contrasting behaviour during at least one phase of the trained task. Further observations were made on other PTNs that were recorded in the same convexity penetration but located more than 500 μm apart; these PTNs rarely showed similar activity patterns.

DISCUSSION

Analysis of cell groups. Two characteristic features of motor cortex neurones are their distinctive behaviour during voluntary movement and their responses to passive stimulation of the limb. Many neurones show optimal activity associated with one particular active movement (Evarts, 1967; Fetz & Finnochio, 1975; Lemon *et al.* 1976) and receive a specific afferent input from the limb (Rosén & Asanuma, 1972; Lemon & Porter, 1976; Wong *et al.* 1978).

Although these features are now well established, little is known about their topographic organization within the motor cortex. A strictly somatotopic representation would predict that neighbouring neurones would show a similar relationship to movement and receive input from similar peripheral zones. This question is answerable by comparison of the features described above in groups of adjacent neurones. This approach is further justified by the following considerations. First, detailed comparison of responses obtained in a systematic micro-electrode exploration of the entire motor cortex is made difficult by the need to reconstruct the very large number of penetrations made in such a long-term experiment. Second, exact depth measurement within the cortex is frequently complicated by dimpling and by deviation of micro-electrodes. Third, conscious, behaving monkeys may alter their attitude towards natural stimulation and task performance from day to day, introducing a further variable into comparison of responses obtained from different penetrations on different days. In the present study, neurones less that 500 μm apart were analysed in order to prevent comparison of neurones lying in remote cortical zones or columns, as described anatomically (Colonnier, 1966; Asanuma, 1975).

Most area 4 neurones receive their input from a restricted peripheral zone. This property is shared by 65% of the cell groups studied, and by a similar proportion (6/9 pairs) of neighbouring PTNs. All these cell groups receive input from the same arm zone. Many of them contain neurones showing similar activity patterns during movement and adjacent neurones with similar input never showed marked differences in behaviour during movement. Finally, cell groups with similar afferent inputs and activity profiles can be detected in widely separated locations within the motor cortex (Lemon *et al.* 1976).

It is clear, however, that a significant proportion (35%) of cell groups include cells which receive their afferent input from different peripheral zones (Fig. 1*B*). For this experiment, the arm was divided into four simple separate zones. As pointed out above, some single input groups received projections from different parts of any one single zone (e.g. from the index finger and from the thumb). Therefore it can be argued that groups with input from both wrist and hand zones, for instance, only represent a difference in scale of the spatial projection of afferent input onto the motor cortex. The important conclusion which transcends any arbitrary division of the arm is that adjacent neurones may receive a restricted afferent input from separate regions of the arm; in addition they may show contrasting patterns of activity during movement. These conclusions also apply to some adjacent pairs of PTNs.

Topographic organization within area 4

The cell group analysis would predict that a topographic map of the arm region of area 4 would show multiple representation of input from a single arm zone. In addition, one might expect to see considerable intermingling of inputs from different arm zones. In confirmation of this, the most striking result obtained from plotting responsive neurones onto an unfolded map of the cortex is the heterogenous nature of the afferent input to any one cortical area. Two other features are discernible. First, there is a central zone which, unlike the rest of the arm area, is devoted to input from one zone, the hand. The exclusive nature of its input explains the disproportionately large number of single input cell groups with projection from the hand (Fig. 1*C*). Secondly, neurones with shoulder and elbow inputs lie on the perimeter of area 4, encircling the wrist inputs which, in turn, lie scattered on the edge of the central hand zone. The lateral border of this zone gives a direct transition to neurones with inputs from the face and lips. The representation of shoulder, elbow and wrist projections is supported by the findings that cell groups with different, but contiguous arm zones outnumbered those with discontinuous zones.

Wong *et al.* (1978), in a similar study in two macaque monkeys, claimed that 'vertical aggregates' of motor cortex neurones encountered in the same penetration received identical afferent inputs. Clusters with inputs from different limb zones were explained by oblique penetrations traversing the radial architecture of the cortex; 'unfolding' of the cortex was claimed to reveal that these apparently adjacent neurones lay in different cortical regions. However, in the present experiment, cell groups with multiple inputs were repeatedly detected in penetrations made orthogonal to the cortical surface and confined to the convexity of the gyrus. Wong *et al.* (1978) emphasized the nested organization of successive wrist, elbow and shoulder 'rings' which encircle the hand zone. But superimposition of all their data clearly shows some cortical regions with intermingling of inputs from different arm zones, similar to that reported here. This intermingling makes it unlikely that penetrations in these regions would always yield neurones with the same input zone. In conclusion, unfolding area 4 does reveal additional features of organization but does not remove or explain the complex intermingling of afferent inputs.

Termination of afferent projections to area 4

The varied organization of the motor cortex contrasts with the ordered topography found in the primary visual (Hubel & Wiesel, 1962) and sensory cortices (Mountcastle, 1957; Werner & Whitsel, 1973). It also implies that the afferent projection to area 4 should provide a restricted input to most individual neurones, while neighbouring neurones may receive different inputs. Neurones in the cat ventrolateral thalamus have been shown to branch within the motor cortex (Asanuma, Fernandez, Schiebel & Schiebel, 1974; Rispal-Padel, Massion & Grangietto, 1973), but little is known of the intracortical distribution of those afferents which convey peripheral inputs to area 4 from the oral part of the ventro-posterior nucleus (VPLo) (Lemon & van der Burg, 1979; Horne & Tracey, 1979; Asanuma, Larsen & Yumiya, 1979).

Cortico-cortical inputs from somatosensory cortex also relay peripheral input to the motor cortex (Thompson, Stoney & Asanuma, 1970; Pandya & Kuypers, 1969;

Jones, Coulter & Hendry, 1978). Jones *et al.* (1978) made a single injection of isotope in the somatosensory cortex and saw patchy labelling of several independent columns within the motor cortex, and suggested that this represents a multiple distribution of cortico-cortical input to area 4. This finding may explain the multiple representation reported here and elsewhere (Wong *et al.* 1978, Strick & Preston, 1978*a*).

Organization of outputs from area 4

There is already plentiful evidence that the motor functions of area 4 cannot be organized in a simple columnar arrangement. It is now known that a single PTN can branch to innervate different motor nuclei (Shinoda *et al.* 1979). Fetz *et al.* (1976) have used cross-correlation analysis between single area 4 units and e.m.g. activity in various forelimb muscles, and have shown direct correlations between one neurone and several muscles. One interpretation of this result is that the neurone distributed collaterals which synapsed onto several different species of motorneurone. Other studies have examined the cortical input to a single motorneurone and demonstrated widespread and discontinuous cortical territories for single cervical and lumbar motorneurones (Andersen *et al.* 1975; Jankowska *et al.* 1975). These experiments also demonstrated overlap of cortical areas projecting to different motoneurones (cf. Phillips & Porter, 1964). Recent studies show that adjacent PTNs in monkey area 4 sometimes distribute their axons to separate motor nuclei (Asanuma, Zarzecki, Jankowska, Hongo & Marcus, 1979).

The present results agree with these observations in regard to multiple representation and overlapping projections. Groups of neurones with inputs from different parts of the limb may, nevertheless, show similar patterns of activity related to movement about one and the same joint. This type of organization within area 4 may be important for movements which occur at one joint but which may depend on muscles acting at other joints. Such as organization might explain why some motor cortex neurones which discharge during a precision grip between thumb and index finger only do so when the wrist is in one particular orientation (R. N. Lemon, in preparation). The organization of the motor cortex would seem ideally suited for such synergistic activities.

However, the majority of cell groups do appear to be related to a single arm zone. These groups might be expected to show a relationship with one particular movement and to be uninfluenced by movement at distant joints. Many hand and finger-related neurones are organized within this type of group, and show activity during finger movements that is quite independent of proximal arm movement or posture (Lemon *et al.* 1976; Lemon, 1981).

Hand neurones in the bank of the central sulcus seem to be mostly influenced by cutaneous stimulation, while those lying further rostral are dominated by proprioceptive input. A similar type of organization has been observed in a New World monkey (Strick & Preston, 1978*b*) who suggested that it might reflect separate functional zones for hand movements. Further studies are now needed to examine more closely different types of hand movement to see if this is the case. It is also important to examine area 4 neurones during movements which call up different strategies of muscular co-ordination to determine whether the fine organization of the motor cortex is designed to make such strategies possible.

J. Cookson, J. van der Burg, E. Dalm, W. van den Oudenalder and P. van Alphen are thanked for their excellent technical assistance and E. Jongbloed-Klink for typing the manuscript. Professor R. Porter and A. Hanby provided help with computer analysis. Professor C. G. Phillips, Professor H. G. J. M. Kuypers and Dr R. B. Muir are thanked for their useful comments. The financial support of the U.K. National Fund for Research into Crippling Diseases is gratefully acknowledged. Part of this work was also funded by grant 13-46-15 of the FUNGO/ZWO (Dutch Organization for Fundamental Research in Medicine).

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