J. Physiol. (1984), **350**, *pp.* 33–54
With 9 text-figures
Printed in Great Britain

TOPOGRAPHICAL LOCALIZATION IN THE MOTOR CORTEX OF THE CAT FOR SOMATIC AFFERENT RESPONSES AND EVOKED MOVEMENTS

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(*Received 4 October 1983*)

SUMMARY

1. Microwires chronically implanted in the pericruciate cortex of free-to-move cats were used to record extracellularly from cortical neurones and to deliver intracortical stimulation.

2. Natural stimulation of cutaneous and/or deep mechanoreceptors in limbs and trunk evoked discharges in 89 % of 165 neurones, 57 % of which were pyramidal tract neurones.

3. Out of 112 cells with receptive fields on the contralateral forelimb, 41 % had cutaneous fields, 29 % had fields involving deep tissues and 30 % were driven from both sources.

4. Cutaneous receptive fields were much commoner than deep ones among cells with fields including the forefoot; this relationship was reversed for cells with more proximal fields. Many more cells had distal than proximal fields.

5. The 'zones' of the forelimb (i.e. foot, wrist, elbow, shoulder) provided input to widespread and overlapping cell populations within the coronal gyrus and the lateral parts of the anterior and posterior sigmoid gyri.

6. Despite the overlap a somatotopy existed with successively more distal limb zones represented successively further laterally in the pericruciate area.

7. Intracortical stimulation (eleven cathodal pulses, duration 0·2 ms, frequency 330 Hz, intensity 35 μA or less) evoked flick movements of the contralateral limbs which were abolished by pyramidectomy.

8. In the forelimb, shoulder movements were commonest and elbow, wrist and digits were represented with decreasing frequency.

9. Both for 35 μA and for threshold stimulation the distributions of the effective electrodes revealed an overlapping somatotopy such that the wrist movements were almost restricted to the coronal gyrus and shoulder movements were most often evoked from the lateral part of the anterior sigmoid gyrus.

10. The movement and receptive field somatotopies overlapped heavily but the former showed a distinct lateral shift relative to the latter. As a result shoulder movements were not uncommonly evoked from the coronal gyrus although the shoulder provided almost no input to cells in that area.

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INTRODUCTION

Many studies have shown that motor cortical neurones in the cat (including pyramidal tract neurones; p.t.n.s) are readily discharged by natural stimulation of cutaneous and deep mechanoreceptors of the limbs and trunk (e.g. Brooks, Rudomin & Slayman, 1961*a*, *b*; Welt, Aschoff, Kameda & Brooks, 1967; Baker, Tyner & Towe, 1971). Receptive fields have been defined in detail and it has been demonstrated that cells encountered in the course of a micro-electrode track perpendicular to the cortical surface have receptive fields which are usually similar in location, though not necessarily in modality. Receptive field locations can differ markedly from track to track but little attention has yet been paid to systematic mapping of these changes: there have been no studies comparable to those in awake monkeys (e.g. Wong, Kwan, Mackay & Murphy, 1978; Lemon, 1981*a*, *b*) which have shown the details of an overlapping somatotopical arrangement of receptive fields across the surface of the pre-central gyrus.

For this reason we have used arrays of chronically implanted micro-electrodes to study the somatosensory-evoked discharges of individual pericruciate neurones in unrestrained cats and compared the spatial distributions of cells with receptive fields in different parts of the contralateral forelimb in order to determine an 'afferent' topography for the forelimb portion of the motor cortex.

Previous investigations (e.g. Asanuma & Sakata, 1967; Asanuma, Stoney & Abzug, 1968; Sakata & Miyamoto, 1968) have also shown that, when intracortical electrodes are used to deliver brief trains of weak electrical stimuli to the pericruciate area, motor responses (i.e. movements, electromyographic responses, facilitations or depressions of the responses of spinal motoneurone pools to test peripheral afferent volleys) are readily produced. Stimulation at different loci evokes responses in different parts of the musculature so that the motor cortex clearly exhibits an efferent or motor topography. In the awake cat, where the complications of anaesthesia are absent this pattern has been most fully studied for movements by Nieoullon & Rispal-Padel (1976). In some studies (e.g. Asanuma *et al.* 1968; Sakata & Miyamoto, 1968) the somatosensory responses of single neurones have been compared with motor responses evoked by stimulating via the micro-electrode in an attempt to infer the input–output characteristics of small portions of the cortex. However, there has again been no systematic attempt to make such comparisons over a wide area. We have therefore compared the somatosensory topography determined as above with a motor topography determined for flick movements of the forelimb evoked by weak electrical stimulation via the micro-electrodes.

The experiments were performed using the same animals as in two previous reports (see Armstrong & Drew, 1984*a*, *b*).

METHODS

Microwires chronically implanted into the pericruciate cortex were used to record extracellularly from individual motor cortical neurones. The recording techniques, numbers of animals, cell identification criteria and histological procedures are fully described in Armstrong & Drew (1984*a*, *b*). Pyramidal tract neurones (p.t.n.s) with axonal conduction velocities in excess of or less than 21 m/s were classed as fast-axon and slow-axon p.t.n.s respectively (cf. Takahashi, 1965; Armstrong & Drew, 1984*a*).

Receptive field determinations

Peripheral receptive fields were determined in the resting animal by manual application of stimuli such as brushing of hairs, light tapping of hairy and glabrous skin, firm tapping and palpation of muscle bellies, tendons etc. and passive movement of joints. The animals accepted these manoeuvres contentedly and care was taken to avoid producing small 'startle' movements. However, receptive fields could not be defined with the precision achievable in anaesthetized or paralysed animals (cf. Baker *et al.* 1971; Armstrong & Drew, 1984*b*).

Cortical stimulation

The micro-electrodes were used to evoke flick movements of the (contralateral) limbs. Trains of eleven cathodal pulses duration 0·2 ms, frequency 330 Hz were used, the anode being a diffuse electrode outside the skull. Intensity was normally limited to 35 μA or less and the stimuli never caused the slightest sign of discomfort or distress. Movements were initially noted to be somewhat variable depending on posture and were therefore routinely observed whilst the animals were supported under the belly and by the loose skin over neck and shoulders. Under these conditions the animals were relaxed and movements were readily detected in all limbs.

In some cases stimulation was carried out both before and after ipsilateral pyramidectomy. The animal was anaesthetized (see Armstrong & Drew, 1984*a*) and with full aseptic precautions the ventral surface of the medulla was exposed via a parapharyngeal approach. The pyramid was divided at mid-olivary level using watchmaker's forceps under stereomicroscopic control and each lesion was verified histologically using the method of Swank & Davenport (Carleton, 1967). Post-operatively the animals were not distressed and recovery was rapid. Cortical stimulation was carried out after 4–7 days by which time the animals walked well. In one case a control operation was carried out in which the pyramid was exposed but not divided: no motor deficits were observed and the movements and thresholds for cortical stimulation were unchanged.

Cortical mapping

A photograph of the pericruciate area was used to record the location of the entry point of each electrode in each animal (see Armstrong & Drew, 1984*a*). The locations of electrodes yielding a particular movement or cells with a particular type of receptive field were subsequently pooled onto a single cortical diagram according to their mediolateral and rostrocaudal distances from the lateral tip of the cruciate sulcus and the resulting electrode distributions were compared. As found by Pappas & Strick (1981) there is significant individual variation in the morphology of the pericruciate area so that distributions derived by pooling results from several animals cannot be regarded as giving more than an approximate indication of the distribution relative to sulcal landmarks to be expected in any one brain. However, any 'blurring' effect of pooling operates similarly on each distribution so that comparisons between different distributions remain allowable and we have concentrated on this aspect of our findings (see also Results and Discussion). We have followed Livingston & Phillips (1957) in dividing the pericruciate area into coronal gyrus plus anterior and posterior sigmoid gyri.

RESULTS

Extracellular recordings were made from 165 neurones in the right pericruciate cortex in fifteen cats. Of 115 cells tested 65 (57%) responded antidromically to stimulation of the ipsilateral medullary pyramid and were classed as p.t.n.s (cf. Armstrong & Drew, 1984*a*).

In all 165 cells peripheral receptive fields were sought as described in the Methods. In two cases the only detectable response was a decrease in discharge rate and these cells are not considered further. The locations of the remaining 163 neurones are shown by filled and open circles in Fig. 1*A*. There were eighteen cells (11%) in which no change in discharge could be evoked from any part of the body surface but for all other cells some peripheral stimulus could be found which evoked a discharge. Among cells with little background activity the response to brief stimuli was one

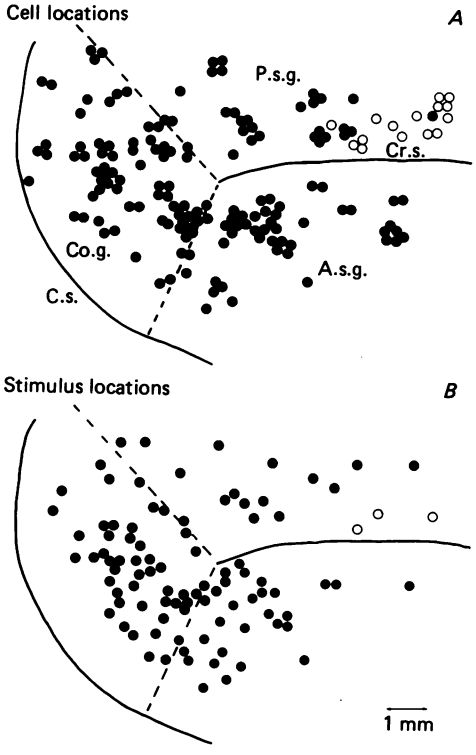

Fig. 1. Over-all distribution of neurones and of electrodes which evoked movements. *A*, circles indicate locations in the pericruciate area of the neurones studied. The clusters mostly reflect the fact that some electrodes recorded more than one cell (up to six). Note that the cells were scattered throughout cytoarchitectonic area IV of Hassler & Muhs-Clement (1964). *B*, locations of the entry points of electrodes from which movements were evoked by intracortical stimulation (see text). The dashed lines indicate the junctions between coronal gyrus (co.g.), anterior sigmoid gyrus (a.s.g.) and posterior sigmoid gyrus (p.s.g.) as defined here. C.s., coronal sulcus; cr.s., cruciate sulcus. In both *A* and *B* filled circles represent electrodes inserted to a depth of 1·5–2·0 mm. Open circles represent electrodes inserted more deeply in posterior wall of cruciate sulcus (cf. Armstrong & Drew, 1984*a*).

impulse or (more usually) a brief burst. Among cells with higher background activity the response was a brief acceleration of the discharge. Maintained stimuli (e.g. pressure on skin or maintained joint position) usually evoked 'on' and 'off' responses but convincing demonstrations of maintained responses were unusual.

Fig. 2*A* and *B* show records from one typical neurone. Fig. 2*A* shows the irregular but maintained discharge in the absence of stimulation while Fig. 2*B* shows responses to three brief taps to the glabrous skin of the main pad of the contralateral forepaw.

For 115 cells (71 %) of the receptive field was confined to the contralateral forelimb (including shoulder) whilst for twenty-two other cells (13 %) it was confined to the contralateral hind limb. In the remaining eight cells (5 %) the receptive field was wide (i.e. included the trunk as well as one or both contralateral limbs) but in only two of these did the field extend onto the ipsilateral half of the body. Cell locations are given below.

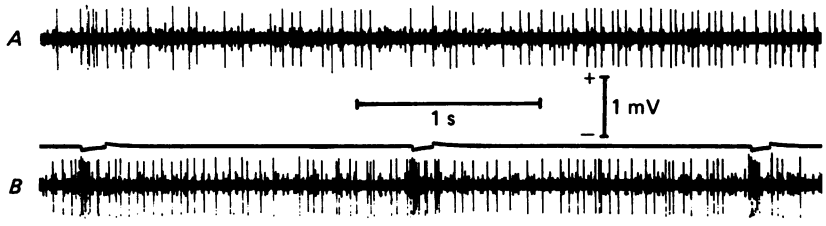

Fig. 2. Responses to peripheral input. *A* shows background activity of one neurone located in coronal gyrus. *B* shows three successive responses of the same neurone to a firm tap to the glabrous skin of the main pad on the contralateral forefoot. Top trace in *B* is a marker produced by a microswitch on the stimulus probe. Note response onset precedes marker owing to inherent delay in the switch.

Receptive fields: stimulus type

For cells with receptive field on the contralateral forelimb both the type of effective stimulus and the location of the field were studied. Stimulus typing is difficult in free-to-move animals but effective stimuli fell into four categories: hair bending or brushing, light tapping of hairy or glabrous skin, deep pressure (i.e. palpating muscle bellies, foot pads, tendons, etc.) and manipulation of joints. Cells responding to the first category are presumably being driven from cutaneous receptors whilst those responding to one or both of the third and fourth categories are presumably responding to input from deep (i.e. subcutaneous) receptors. Some cells responded to only one stimulus category (most often light tapping) but many responded to more than one category as for example when discharge was elicited by tapping or by brushing hairs and a clear additional discharge was provoked by joint manipulation. It is assumed that such incremental responses imply convergence of input from cutaneous and deep receptors.

For 112 cells the adequate stimulus could be established with some confidence. The findings are presented in Table 1. Over-all, 41 % of cells had superficial receptive fields (i.e. responded to hair movement and/or light taps), 29 % had deep receptive fields and the remaining 30 % (mixed) were driven by both deep and superficial inputs.

Table 1 also shows the distribution after dividing the cells into two categories: those in which the receptive field was confined to or included the foot (distal) and those driven from more proximal areas but not from the foot (cf. Armstrong & Drew, 1984*b* and see below). Cells with superficial (i.e. probably cutaneous) receptive fields amounted to 58 % of 'distal' cells whilst unequivocally deep receptive fields totalled only 12 %. The remaining 30 % responded to various combinations of deep and cutaneous stimuli. The findings for cells with 'proximal' fields are in marked contrast. None responded selectively to brushing of hairs, only 13 % to light tapping and only 4 % to both hair movements and light tapping. Joint manipulation however, was the effective stimulus for no less than 45 % and palpation for a further 8 %. Thus, only 17 % responded selectively to superficial stimuli whilst 53 % had deep receptive fields. Clearly, these proportions indicate that the majority of 'distal' cells received superficial inputs whilst the majority of 'proximal' cells received deep inputs. Note, however, that the proportion showing deep/superficial convergence was the same.

TABLE 1. Proportions of cells responding to different stimuli

Effective stimulus	All cells (%)	'Distal' cells (%)	'Proximal' cells (%)
Superficial			
Brush hairs	3	5	0
Light tap	25	34	13
Hair and tap	13	19	4
Deep			
Palpation	7	6	8
Joint manipulation	20	3	45
Palpation & joint manipulation	2	3	0
Mixed			
Tap & palpation	4	6	0
Tap & joint manipulation	21	15	30
Hair & joint manipulation	3	5	0
Hair & tap & joint manipulation	1	2	0
Tap & palpation & joint manipulation	1	2	0
Total	100	100	100

Based on 112 neurones with forelimb receptive fields (see text). 'Distal' fields are those restricted to or including the foot. 'Proximal' fields are those not including the foot.

TABLE 2. Representation of forelimb

A. Different zones and combinations of zones

Zones of forelimb	Sensory (%)	Motor (%)
1	29	1
1+2	12	0
1+2+3	10	0
1+3	4	3
2	11	8
2+3	4	12
2+3+4	0	2
2+4	0	3
3	13	15
3+4	5	20
4	7	36
6	5	0

B. Over-all representation of each zone

1	39	3
2	26	18
3	26	37
4	9	42

C. Number of zones included in receptive field or of joints moved by stimulation

One	63	60
Two contiguous	22	31
Three contiguous	11	2
Two non-contiguous	4	7

A shows percentage occurrence of neurones with the receptive field locations indicated (sensory) and the percentage of sites at which stimulation caused movement involving that location (motor). 1, digits; 2, wrist; 3, elbow; 4, shoulder; 6 widespread including forelimb. B shows over-all percentage representation of different limb zones in receptive fields and in movements. Based on 121 neurones and on stimulation at eighty-seven locations.

Receptive fields: size and location

Receptive fields which included the forelimb varied considerably in size. Distal fields were often very small (e.g. restricted to one or two toepads or digits) and only occasionally extended much beyond the wrist. Proximal fields were usually larger so that, for example, some units responded to passive movements of two joints and to taps delivered to both upper arm and forearm (see Fig. 5 for examples).

When the limb was divided into four 'zones', i.e. foot, wrist and lower forearm, elbow (including lower part of the upper arm) and shoulder (numbered 1–4 respectively) some cells had receptive fields confined to a single zone whilst in other cases the field included part or all of two or more zones. The frequency distribution of fields in the different zones and combinations of zones is shown in percentage terms in Table 2A in the sensory column. Note that 41 % (29 plus 12) of cells had fields confined to foot or foot and wrist, whilst only 12 % (5 plus 7) had fields confined to shoulder or shoulder plus elbow. This predominance of distal inputs is emphasized further when the data are re-categorized to show the percentage representation of each of zones 1–4 among the receptive fields (Table 2B). It is noteworthy that for both methods of categorization there was no difference between groups in regard to the proportion of cells which were p.t.n.s nor were fast-axon and slow-axon p.t.n.s differentially distributed between groups.

The sensory column of Table 2C shows the frequency of occurrence of cells with receptive fields including one, two and three zones. Note that a small proportion of receptive fields (4 %) was discontinuous. These are the cases in the 1 plus 3 category in Table 2A.

Cortical topography for responses to peripheral afferent input

Because the sites of insertion of all electrodes were recorded (see Methods) the location of the peripheral receptive fields could be correlated with the distribution of the electrodes and the results are shown by filled or open circles in the maps of Fig. 3. The four categories of receptive field location already used have been supplemented to include cells with hind limb fields (category 5), with widespread fields (category 6; cf. Table 2A and see Fig. 3 legend) and with no detectable field (category 7). The maps show the locations of the cells in each of the seven categories and in each combination of categories encountered. For example map 2 includes cells excited only from the region of the wrist whilst map 1 plus 3 includes cells excited from the foot and also from tissues associated with the elbow. Note that some electrodes recorded more than one cell (cf. Armstrong & Drew, 1984*a*, *b*) and this accounts first for the small clusters of points in some maps and secondly for the fact that some loci are represented in more than one map.

Several interesting findings emerge from Fig. 3. First, cells with hind limb fields are confined to the posterior sigmoid gyrus (approximately half being in buried cortex; open circles). Secondly, although the distributions for the four different forelimb 'zones' show considerable overlap, there is nevertheless an obvious tendency for more proximal regions of the limb to be represented further medially in the cortex. Thus, most cells excited from the foot (category 1) are in the coronal gyrus whilst most in the wrist category (category 2) are near the junction of this gyrus with the

sigmoid gyri. The elbow (category 3) is represented in all three gyri whilst cells driven from the shoulder (category 4) are mainly in the anterior sigmoid gyrus. Finally, cells unresponsive to peripheral stimulation occur in the hind limb area and also in the forelimb area where their distribution is similar to that for shoulder-related (category 4) neurones.

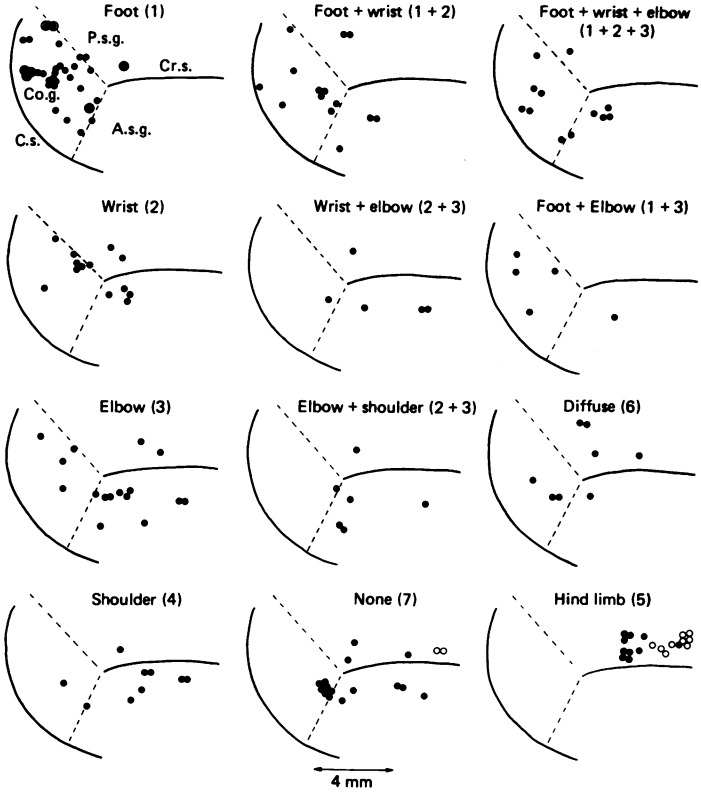

Fig. 3. Distribution in pericruciate cortex of cells with differently located peripheral receptive fields. In each map circles show neurones responding to natural stimulation within the part of the body shown by the heading. Note some loci feature in more than one map because the corresponding electrode recorded more than one cell with different receptive fields. As in Fig. 1 open circles in the maps for hind-limb-related cells and for cells without receptive fields represent neurones buried in posterior wall of cruciate sulcus. Abbreviations as in Fig. 1.

Cells with input only from the digits were mainly along the lateral margin of the electrode distribution in the coronal gyrus suggesting that within the foot area there may be a finer somatotopy not revealed by Fig. 3.

Fig. 3 includes separately the distributions for cells responding to stimulation in more than one 'zone' (e.g. foot plus wrist, wrist plus elbow, etc.) but a better impression of the over-all distribution of input from each part of the forelimb is obtained from Fig. 4 in which each map shows all cells with receptive fields *including* (but not necessarily restricted to) each of the four zones (cf. Table 2B). Each distribution extends over a substantial portion of the explored cortex (cf. Fig. 1*A*)

but nevertheless the representation of successively more proximal parts of the limb gradually shifts successively further medially so that the foot and wrist distributions centre on the coronal gyrus whilst that for the shoulder is almost confined to the sigmoid gyri.

That the large area covered by each electrode distribution in Figs. 3 and 4 is not a consequence of pooling the results from different brains is shown by the encircled

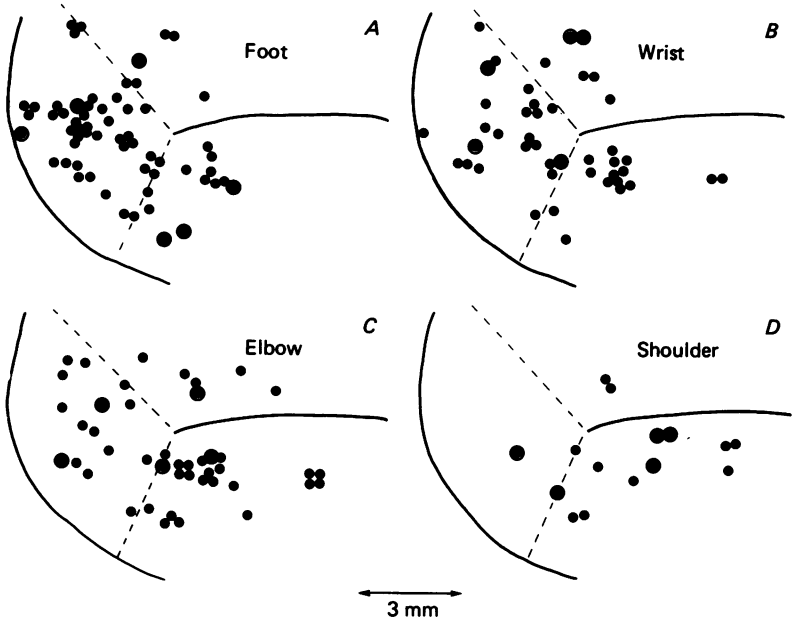

Fig. 4. Representation in pericruciate cortex of cells responding to peripheral input from different parts of the contralateral forelimb. Filled circles in *A*, *B*, *C* and *D* indicate cells whose receptive field included the part of the limb shown by the heading (irrespective of whether or not input was also received from other parts of the limb). In each map the encircled loci represent neurones from a single animal (different in each case).

loci in the 'foot' map of Fig. 3 and in each map of Fig. 4. In each case these widely scattered points represent cells encountered in a single experiment (different in each case).

No distinction has been made in Figs. 3 and 4 between cutaneous and deep receptive fields but in fact no relationship could be established between cell location and stimulus type other than the predominance already noted for superficial inputs amongst 'distal' fields and deep inputs amongst proximal fields. As a result, cutaneous inputs predominated in the lateral part of the coronal gyrus and deep inputs in the lateral parts of the sigmoid gyri.

Micro-organization of responses to somatosensory input

Histology revealed that the electrodes did not undergo gross movements during the recording period (see Armstrong & Drew, 1984*a*) so it is very probable that cells

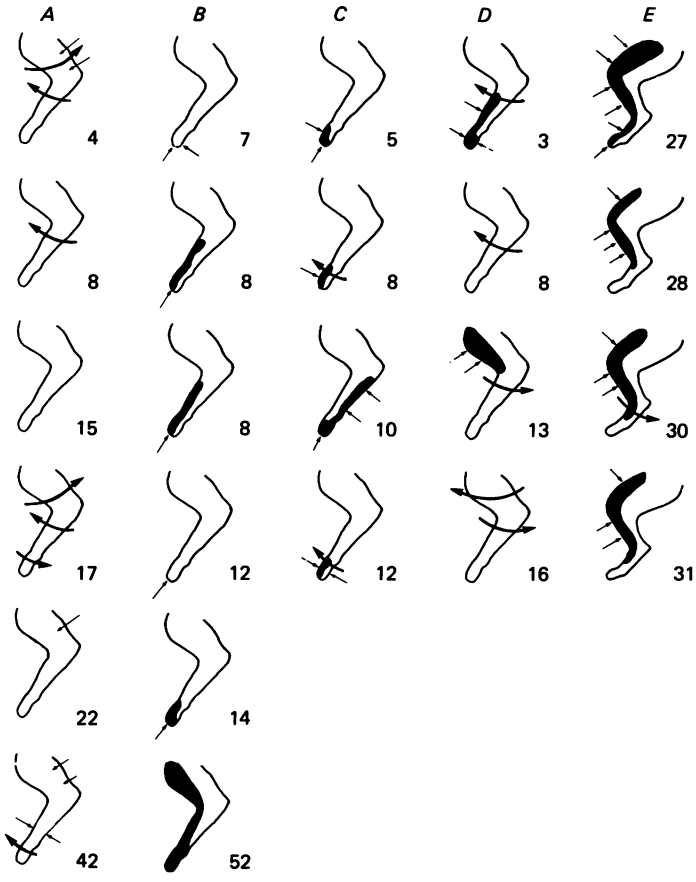

Fig. 5. Receptive fields for neurones recorded via the same micro-electrode. *A–E* show results for five different wires; electrodes *A* and *B* each recorded six neurones; *C*, *D* and *E* each recorded four neurones. Numbers indicate the days on which the units were recorded after operation on day 0. Figurines show lateral views of the contralateral forelimb (*A–D*) and hind limb (*E*). Filled areas are those over which brushing of hairs was an effective stimulus. Small arrows indicate light taps, large curved arrows imply passive movement of the joint above the arrow.

recorded via the same electrode were closely juxtaposed within the cortex. It is therefore of interest to compare the receptive fields of such cells.

Forty-three electrodes recorded more than one neurone and of these twelve recorded three cells, five recorded four cells, one recorded five cells and two recorded six cells; the remaining twenty-three recorded two cells each.

Note that two or more cells from ten of these electrodes were studied during locomotion; their locomotor-related discharges and receptive fields were described by Armstrong & Drew (1984*b*).

There was an overwhelming tendency for cells recorded via a single electrode to have similar receptive field locations. In some cases all cells were related to a single limb zone and only in four of the forty-three cases did the cells fail to have at least one zone in common. The similarity did not, however, extend to stimulus type: a

single electrode could yield some cells responding only to superficial input and others only to deep.

Illustrative results for five electrodes which recorded four or more cells are shown in Fig. 5; electrodes *A*, *B*, *C* and *D* recorded cells with fields on the contralateral forelimb whilst for *E* the fields were on the contralateral hind limb. Electrode *A* recorded two cells for which the receptive field was confined to tissues around the elbow (days 8 and 22) and for three other cells the field included the elbow (days 4, 17 and 42) but also involved shoulder (day 4), wrist (day 42) or both these areas (day 17). One cell (day 15) had no discernible receptive field. Electrodes *B* and *C* both recorded cells with more restricted receptive fields. Five of the cells from electrode *B* had receptive fields confined to foot (days 7, 12 and 14) or foot and wrist (the two cells of day 8). The remaining cell (day 52) was excited from tissues associated with both elbow and shoulder but again the receptive field included foot and wrist. Electrode *C* recorded three cells excited from foot and wrist and one from foot only (day 5). For electrode *D* all four cells shared input from the elbow but in one case (day 3) excitation was also produced from foot and wrist and in another (day 16) from the shoulder. Finally, the similarity between the cells from electrode *E* is especially striking, all were excited by cutaneous stimuli delivered to the leading edge of the hind limb with in one case (day 30) excitation also from passive ventroflexion of the ankle.

Efferent topography

In all, intracortical stimulation was applied via 280 of the micro-electrodes in twelve of the animals (see Methods). At intensity 35 μA movements were evoked from ninety-nine of these electrodes distributed across the pericruciate cortex. Effective and ineffective electrodes were inter-mingled apparently randomly and not all electrodes which yielded single units proved effective, nor were electrodes which failed to yield units always ineffective. However, all except two of the effective wires yielded multi-unit activity and since wire tips lying in the subcortical white matter showed neither single nor multi-unit activity (see Armstrong & Drew, 1984*a*) we conclude that the tips of the effective electrodes lay in the grey matter. Forelimb movements were evoked from eighty-seven electrodes and hind limb from twelve electrodes. The over-all distribution of effective electrodes is shown in Fig. 1*B*.

At the stimulus current routinely used (35 μA) 60 % of the forelimb movements were at a single joint but the remainder involved two or occasionally three joints (e.g. retraction of the arm might be combined with elbow extension or protraction with elbow flexion and wrist dorsiflexion). Usually, however, one movement was strongest and when intensity was decreased to threshold this movement persisted. Thresholds ranged from 5 to 35 μA but most were 10–25 μA and the frequency distributions of different thresholds were similar for shoulder, elbow and wrist movements. Hind limb movements were usually flexions which frequently involved ankle, knee and hip or two of these three joints.

Table 2A (motor column) shows the percentage of sites at which 35 μA stimulation yielded movements confined to each particular forelimb zone (i.e. digits, wrist, elbow or shoulder; simple movements) and each combination of zones (compound

movements) whilst Table 2B shows the over-all frequency with which different joints were moved either alone or in combination with other joints. Shoulder movements were commonest, and digit movements rarest, a striking reversal of the receptive field findings (cf. sensory column in Table 2A and B). Table 2C shows the relative frequency of simple movements and of compound movements. Occasionally the movement involved two non-adjacent joints, for example wrist and shoulder.

TABLE 3. Evoked movements before and after pyramidectomy

	Before		After	
Electrode	Movement	$T(\mu A)$	Movement	$T(\mu A)$
1	Elbow extension	25	Elbow extension	240
2	Elbow extension + wrist dorsiflexion	20 12	Elbow extension + wrist dorsiflexion	500
3	Wrist dorsiflexion	9	Wrist dorsiflexion	350
4	Wrist pronation	30	Digit dorsiflexion	300
5	Elbow flexion	30	Elbow flexion	300
6	Abduction	11	Abduction & retraction + wrist dorsiflexion	100 70
7	Protraction & abduction	27	Retraction of forelimb & elbow flexion	100
8	Protraction + wrist dorsiflexion	35	Elbow flexion + wrist dorsiflexion	250
9	Retraction	15	Retraction	550
10	Ankle dorsiflexion + knee flexion	8	Ankle dorsiflexion + knee & hip flexion	75

Results from one animal. T, threshold current.
Note electrode 10 was in medial posterior sigmoid gyrus.

Table 3 shows an example of the stimulation findings in one animal in which ten of the implanted electrodes gave movements at 35 μA or less; six produced movements at one joint and four gave more complex movements which in three cases (electrodes 2, 8 and 10) involved two different joints. Table 3 also shows the threshold currents for each electrode and the effect of complete unilateral pyramidectomy on the responses (see Methods). Though movements were still evokable and usually involved the same joint or joints, thresholds were greatly elevated indicating that movements observed previously were dependent on the integrity of the pyramidal tract. Similar findings were made in all pyramidectomized animals.

Cortical topography for evoked movements

When all electrode locations yielding similar movements were plotted onto one cortical diagram, maps were produced analogous to those for unit recordings in Figs. 3 and 4.

For electrodes yielding movements restricted to a single joint the results are shown by the circles in Fig. 6*A*, *B*, *C* and *D* which relate to movements at wrist, elbow, shoulder and hind limb respectively. Only one electrode gave a movement confined to the digits and this is indicated by the open circle in Fig. 6*A*.

Inspection of Fig. 6 reveals first that wrist movements were evoked from only seven

electrodes and six of these were confined within a restricted area on the coronal gyrus (Fig. 6*A*). These electrodes were from five different experiments so that the relatively close grouping suggests that the pooling of results does not result in excessive blurring of the electrode distributions. Secondly, elbow movements were obtained from twelve electrodes scattered across the coronal gyrus and the lateral parts of the sigmoid gyri (Fig. 5*B*). For shoulder movements (Fig. 6*C*) the position is markedly different in that most of the loci were in the rostral part of the coronal gyrus or the adjoining

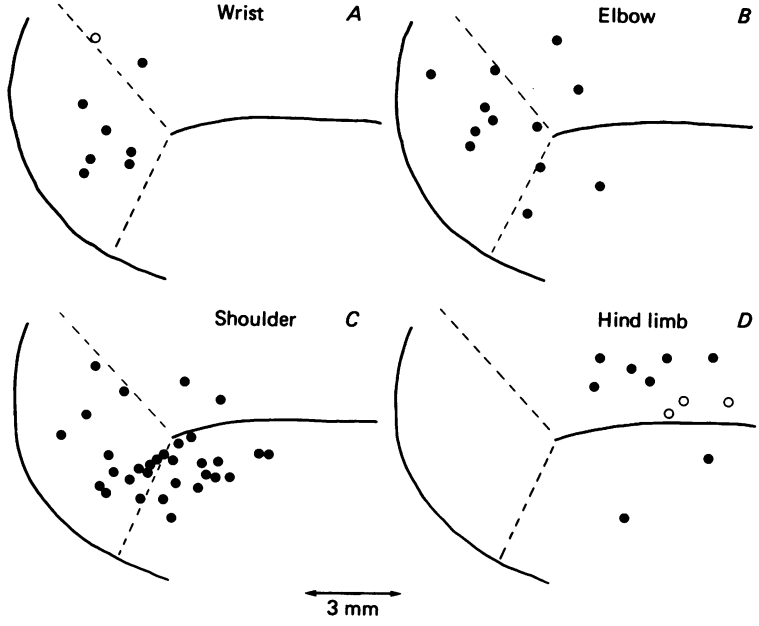

Fig. 6. Distributions of electrodes from which movements confined to one particular part of the contralateral forelimb or to the contralateral hind limb were evoked by intracortical stimulation at intensity 35 μA. *A*, movements confined to digits (one electrode, open circle) or to wrist (filled circles). *B*, *C*, movements confined respectively to elbow, shoulder. *D*, movements confined to hind limb (open circles are electrodes inserted more deeply to reach posterior wall of cruciate sulcus; cf. Fig. 1.

part of the anterior sigmoid gyrus. Finally, hind limb movements (Fig. 6*D*) were obtained only from the medial part of the posterior sigmoid gyrus and from two medially placed loci on the anterior sigmoid gyrus.

Maps were also prepared which included all loci from which movements at a particular forelimb joint were obtained, whether alone or in combination with movements at other joints (cf. the procedure for receptive fields in Fig. 4). The results for wrist, elbow and shoulder are shown in Fig. 7*A*, *B* and *C* respectively. For the wrist (Fig. 7*A*) the procedure considerably increases the number of loci represented, a feature which reflects the high frequency with which wrist movements were evoked in combination with movements at other joints. That the expansion of the wrist distribution is not an artifact of pooling is shown by the wide separation between the four encircled points. These represent effective loci from a single animal. Elbow

movements (Fig. 7*B*) were obtained from within the same part of the coronal gyrus which yielded wrist movements but there is a very noticeable medialwards extension of the electrode distribution to include the lateral parts of both sigmoid gyri. Finally, Fig. 7*C* demonstrates that for shoulder movements the effective area extends still further medially and the number of effective loci on the sigmoid gyri exceeds that on the coronal gyrus.

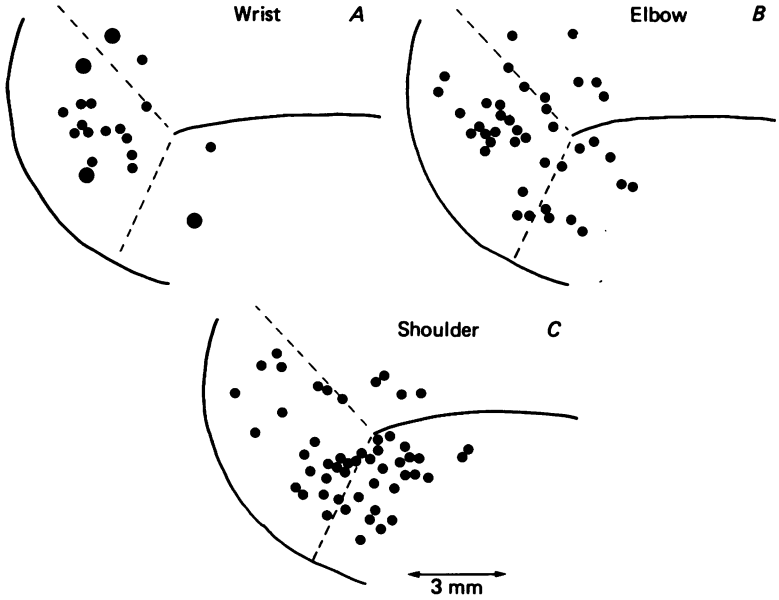

Fig. 7. Distributions of all electrodes from which a particular part of the forelimb was moved either alone or in combination with other joints. *A*, *B* and *C* are for wrist, elbow and shoulder movements respectively. Stimulus intensity 35 μA throughout. Encircled points in *A* were from a single experiment (see text).

In Figs. 6 and 7 the electrode distributions include all loci relating to each joint irrespective of the direction of the evoked movement. For the wrist, for example, pronations and ventro- and dorsiflexions are all included. Maps were therefore prepared which distinguished different directions of movement and examples are shown in Fig. 8. Fig. 8*A* shows dorsiflexions (filled circles) and ventroflexions (open circles) of the wrist. Ventroflexions were obtained infrequently but it is noticeable that the three effective loci are closely spaced at the lateral margin of the main concentration of loci giving dorsiflexion. Similarly in Fig. 8*B* elbow extensions (open circles) were obtained infrequently and from points fringing the extensive distribution for flexions (filled circles).

For shoulder movements the results were different because although adduction of the limb was not observed, abduction, protraction and retraction were all evoked frequently and each from electrodes throughout the over-all area for shoulder movements. This may be verified for retraction and abduction by inspection of Fig. 8*C* and *D* respectively (cf. Fig. 7*C*). Here again the widespread nature of the distributions is not an artifact of pooling because in each case the widely scattered encircled points distinguish results obtained from a single experiment.

Topography for threshold movement

A generally acknowledged difficulty for the interpretation of maps such as those in Figs. 6, 7 and 8 relates to uncertainties regarding stimulus spread within the cortical tissue. Physical spread of current has been investigated by Stoney, Thompson & Asanuma (1968) and from their findings it seems likely that 35 μA stimuli might directly excite all cortical efferent neurones within a sphere of radius at least 150 μm

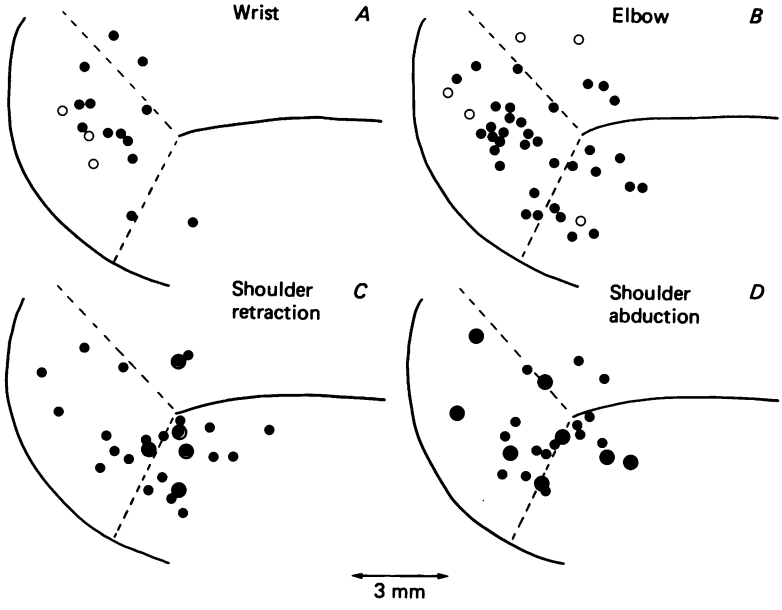

Fig. 8. Electrode distributions evoking particular directions of movement at particular joints of contralateral forelimb. Stimulus intensity 35 μA throughout. *A*, filled circles, dorsiflexions of wrist; open circles, ventroflexions. *B*, filled circles, elbow flexions; open circles, elbow extensions. *C*, retraction at shoulder; encircled loci were from one experiment. *D*, abduction at shoulder; encircled loci were from one experiment. Note that the movements were evoked alone from some loci and in combination from others.

and some (i.e. the more excitable) cells within a radius of *ca.* 250 μm. However, recurrent axon collaterals of cortical efferent neurones may also be stimulated (Asanuma, Arnold & Zarzecki, 1976) and cortical efferent neurones may be discharged trans-synaptically via direct excitation of cortical interneurones and/or the terminal portions of thalamocortical afferent fibres (Asanuma, 1975; Jankowska, Padel & Tanaka, 1975).

No real solution to such problems is yet available (see Phillips & Porter, 1977 for extensive discussion) and in these circumstances it is of interest to determine whether the localizations are much changed if stimulus intensity is lowered to near-threshold, when spread of excitation is presumably minimized. Just suprathreshold currents in the present experiments normally evoked single movements and the localization then evident is shown in Fig. 9*A*, *B* and *C* for wrist, elbow and shoulder movements respectively. Unfortunately threshold stimuli were not delivered to all loci but nevertheless comparison with the corresponding maps in Figs. 6 and 7 shows that

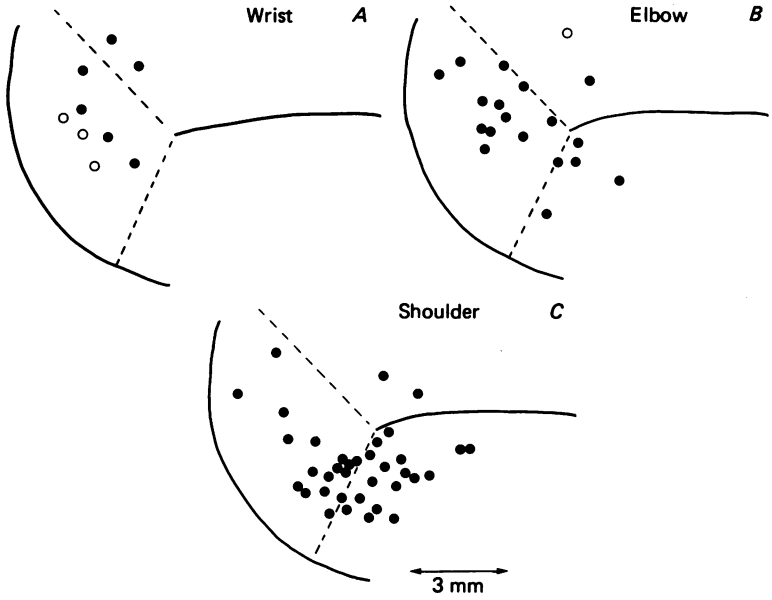

Fig. 9. Distributions of electrodes evoking movement at particular joints of the forelimb when threshold currents were employed. Currents ranged from 5 to 35 μA but most were 10–20 μA. *A*, filled circles, dorsiflexions of wrist; open circles, ventroflexions. *B*, filled circles, flexions of elbow; open circle, extension of elbow. *C*, shoulder movements (includes abduction, retraction and protraction).

the over-all somatotopical pattern remained unaltered. For movements at progressively more proximal joints of the forelimb the electrode distribution underwent the same kind of gradual but progressive medialwards shift as was evident for 35 μA stimuli.

Comparison between the receptive field and movement topographies

Comparison of the sensory and motor localizations was undertaken in two ways.

First the maps in Fig. 4 (sensory) and in Fig. 7 (motor) were compared. Such comparison reveals a number of differences which may conveniently be listed:

(1) For the wrist (compare Fig. 4*B* and Fig. 7*A*) the receptive field distribution clearly extends further medially (i.e. onto the lateral parts of both sigmoid gyri) than the motor.

(2) For the elbow (compare Fig. 4*C* and Fig. 7*B*) a similar difference is evident: seven cells with receptive fields including the elbow zone are well medial to any electrodes which yielded movements including the elbow.

(3) For the shoulder (compare Fig. 4*D* and Fig. 7*C*) the receptive field distribution again extends further medially on the anterior sigmoid gyrus, and in addition only one cell in the coronal gyrus had receptive field including the shoulder zone although shoulder movements were quite frequently evoked from the coronal gyrus.

In summary, this comparison reveals clearly that the movement maps for the forelimb show a systematic lateral displacement relative to the corresponding receptive field distributions. Moreover, it may be noted that this displacement

remains evident if the distributions for cells with receptive fields restricted to a particular zone of the limb (Fig. 3) and for movements restricted to a single joint (Fig. 6) are compared or if the comparison is made using threshold movements (compare Fig. 9 with Figs. 3 and 4).

A second method of comparing the receptive field and the movement localizations was to compare the receptive fields of cells recorded via an individual microwire with

TABLE 4. Sensory representation of forelimb zones at electrodes yielding movements at different joints

	Percentage representation			
Zone	All electrodes	Shoulder movement	Elbow movement	Wrist movement
Foot	40	27	46	59
Wrist	23	25	22	23
Elbow	29	36	27	18
Shoulder	8	12	5	0
Total	100	100	100	100

Based on sixty-seven neurones with forelimb receptive fields recorded via thirty-nine electrodes at which 35 μA stimulation yielded forelimb movements. First column of numbers indicates the relative frequency with which different limb zones are included in the receptive fields of all sixty-seven neurones. Shoulder, elbow and wrist columns express the relative frequency for those cells recorded via electrodes at which the evoked movement included shoulder, elbow and wrist respectively.

the movements evoked at 35 μA via the same electrode. As already noted not all electrodes yielding cells also evoked movements (and vice versa) but nevertheless there were thirty-nine electrodes which evoked forelimb movements and also recorded cells. The latter totalled seventy-seven of which three had wide receptive fields, seven had no receptive field and sixty-seven had receptive fields confined to the forelimb.

Among these last the number of times each of the four limb zones featured in a receptive field was determined and each total was expressed as a percentage. The results are shown in the left hand column of Table 4. Comparison with Table 2 B shows incidentally that the percentage representation of the different zones was very similar to that for all cells indicating that in this respect the sixty-seven cells were a representative sample. The procedure was then repeated after dividing the cells into three subgroups according to whether their respective electrode yielded a movement including shoulder, elbow or wrist. The results are shown in the three remaining columns of Table 4. Inspection shows that the percentage representation of the wrist is unchanged across the Table indicating that this part of the limb is an equally important source of afferent input irrespective of which joint is included in the evoked movement. For the other zones, however, the findings are different. The foot becomes progressively more often represented as the movement involves progressively more distal joints and an equally obvious, but opposite, trend is evident for elbow and shoulder, indeed no shoulder inputs were found for those cells recorded via electrodes evoking wrist movements.

In general, therefore, the importance of distal inputs increased and that of proximal

inputs declined as the evoked movements involved progressively more distal joints. This finding agrees precisely with the previous demonstration that the pericruciate cortex displays two somatotopical arrangements, one somatosensory and one motor, each showing considerable overlap and with the latter shifted laterally relative to the former. Moreover, this agreement exists despite the fact that the electrode-by-electrode comparison avoids any topographical distortions which might arise when comparison is made between electrode distributions derived by pooling results from a number of animals.

DISCUSSION

Peripheral receptive field organization within motor cortex

Representation of hind limb

Many fewer cortical neurones had hind limb than forelimb receptive fields (22 as compared with 115) because most electrodes were implanted in 'forelimb' motor cortex. Hind-limb-related neurones were in fact entirely confined to the medial part of the posterior sigmoid gyrus and although most were buried in the posterior wall of the cruciate sulcus some were from the convexity of the gyrus and the over-all distribution as projected onto the cortical surface is in excellent agreement with the area from which movements of the contralateral hind limb were obtained in the awake cat by Nieoullon & Rispal-Padel (1976).

Representation of forelimb

Cells responding to inputs from the contralateral forelimb were widely scattered throughout the coronal gyrus and the lateral parts of both sigmoid gyri and evidence has been presented that this widespread distribution did not arise as an artifact of pooling results from different brains.

Among these cells 40 % had 'probably cutaneous' receptive fields, 30 % responded only to deep inputs and the remaining cells appeared to receive convergent input from both deep and superficial receptors. These findings are closely comparable with those of Baker *et al.* (1971) whose data from awake cats indicate that taking anterior and posterior sigmoid gyri together *ca.* 35 % of neurones responded to hair movement and/or light touch, 40 % to joint movement or palpation and 20 % to both deep and superficial stimuli. By comparison, Brooks *et al.* (1961*a*) found in locally anaesthetized paralysed cats that 56 % of neurones received cutaneous inputs and 22 % responded only to deep inputs (i.e. joint movements) and Sakata & Miyamoto (1968) found in free-to-move cats that 61 % of cells received cutaneous input and 32 % responded to joint movement. Our study (and that of Baker *et al.* 1971) differs from these two latter principally in the smaller proportion of cells classed as 'cutaneous' and this in turn reflects our inclusion of a substantial category receiving deep/superficial convergence. Admittedly, stimulus typing can be difficult in free-to-move animals but we nevertheless believe that the apparent convergence was usually real. It may be noted that in monkeys Wiesendanger (1973) has demonstrated such convergence by electrical stimulation of cutaneous and muscle nerves and Lemon (1981*a*) has found that 12 % of cells receiving input from hand and fingers are excited by natural stimuli both to the skin and to deep tissues.

Regarding cutaneous inputs we confirm (cf. Brooks *et al.*1961*a*) that relatively few cells are excited by movement of hairs: light taps were much more effective and were also very effective when applied to glabrous skin. The proportion of cells responding to light tactile stimuli was considerably higher among cells with 'distal' as opposed to 'proximal' receptive field and this recalls the finding in the monkey that although 'joint' cells outnumber 'cutaneous' when the receptive field is above the wrist, the reverse is true for neurones excited from the hand and fingers (Lemon, 1981*a*, *b*).

Receptive fields ranged in extent from part of a single digit to tissues associated with two or three joints and our neurones therefore spanned the 'local-field' (<8 cm^2) and 'wide-field' categories of Brooks *et al.* (1961*b*). Like these workers and like Baker *et al.* (1971) we found both that some fields were discontinuous and that proximal fields were larger. However, we found very few cells with fields extending across the mid line of the body and in this respect our findings are closer to those of Asanuma *et al.* (1968) and Sakata & Miyamoto (1968).

There is substantial evidence (e.g. Welt *et al.* 1967; Brooks & Stoney, 1971) that the cat motor cortex contains radial columns of cells in which most neurones have overlapping receptive fields. Our results agree with those of Sakata & Miyamoto (1968) in suggesting that this type of organization remains apparent in the free-to-move animal: cells recorded via the same electrode showed a strong tendency to display receptive fields in the same zone of the limb. However, the similarity did not extend to stimulus type and here also our findings are consistent with the previous studies.

Over-all afferent topography

Previous single unit studies in the cat have not been particularly concerned with establishing an over-all somatosensory topography and our results in this field are therefore of particular interest.

Briefly, each 'zone' of the forelimb, i.e. foot, wrist, elbow, shoulder, was represented in a wide area of cortex so that the four representations overlapped rather heavily. Nevertheless, there was a clear tendency for progressively more proximal parts of the limb to excite cell populations centred progressively further medially in the pericruciate area. This was evident despite the fact that the lateral edge of the coronal gyrus was sampled rarely and the medial portion of the forelimb area relatively infrequently (see Fig. 1*A*).

This heavily overlapping somatotopic pattern may be compared with recent results obtained in monkeys where a patch of motor cortex receiving input from the hand and fingers lies on the rostral bank of the central sulcus and is accompanied by a succession of progressively more rostro-medial areas crescentic in shape and related to wrist, elbow or shoulder (Wong *et al.* 1978; Lemon, 1981*a*, *b*). These crescents overlap quite heavily although a part of the hand/finger area is not overlapped by any other zone. In the present study likewise there were a few cells in the lateral-most part of the coronal gyrus which were excited only from the forepaw (see Fig. 6*C*). The cortical area involved was small but it reached the lateral boundary of the electrode distribution and it may therefore extend further laterally. The somatotopical pattern of peripheral input to motor cortex thus seems to be organized on the same

general lines in cat and monkey. The overlap between limb zones appears to be greater in the cat but to some extent this may reflect a degree of 'blurring' due to our need to pool results from different animals.

Localization of movements evoked by intracortical stimulation

With the exception of two electrodes in the medial part of the anterior sigmoid gyrus all the microwires which evoked movements of the contralateral hind limb were in the medial part of the posterior sigmoid gyrus and *mutatis mutandis* all movements evoked from this area were confined to the hind limb. This agrees well with the results of Nieoullon & Rispal-Padel (1976) who studied movements evoked in awake cats by longer trains of stronger pulses (up to 100 μA) delivered via larger electrodes. We did not study hind limb movements in detail but we agree that they were usually flexions, often involving the whole limb.

All other movements involved the contralateral forelimb and/or shoulder and the over-all area of cortex involved again agrees well with the maps of Nieoullon & Rispal-Padel (1976) for forelimb movements. Unlike these workers we observed no movements restricted to back, neck or face, but our electrodes did not reach the (rostrally located) areas corresponding to these parts. Regarding the forelimb, we concur that a somatotopic pattern is detectable and this was found both with 35 μA stimuli and with threshold currents. Moreover we agree in many details despite the different stimulus parameters in the two studies. Thus, although movements of the claws and digits were infrequent in the present experiments, when found they were evoked only from the lateral part of the coronal gyrus. It is therefore possible such movements might have been commoner had our electrode distribution extended further laterally. Regarding movements of the wrist, the agreement is excellent and both studies also show that elbow movements are evoked from an area which includes the wrist area but extends further medially. The only marked discrepancies relate to movements at the shoulder. First, the shoulder representation of Nieoullon & Rispal-Padel (1976) extended further medially in the anterior and posterior sigmoid gyri (but we inserted only a small number of electrodes into these regions). Secondly, our shoulder area extended considerably further onto the coronal gyrus. This difference may reflect the difference in stimulus parameters or perhaps a difference between the method of observing movements. Thresholds for movement are dependent on posture and shoulder movements observable when the limb hung free were sometimes undetectable when the animal was standing or lying down. Another difference was that in our study shoulder thresholds were as low as those for wrist and elbow movements. The manner in which intracortical stimulation acts on the cortex remains debatable (see Results), so it is reassuring that the over-all topography for movement scarcely changed when threshold movements were studied.

Nieoullon & Rispal-Padel (1976) did not distinguish between different movements evoked at the same joint but at 35 μA our areas yielding wrist ventroflexion and dorsiflexion were largely separate, the latter being considerably the larger. By contrast, abductions, retractions and protractions at the shoulder were each obtained from electrodes throughout the wide area yielding shoulder movements. The situation for the elbow was rather similar to that for the wrist in that extension was obtained only from a few laterally placed electrodes whilst flexion was obtained from a much

wider area. This finding apparently differs from that of Larsen & Yumiya (1979) who found elbow extension well represented among the movements evoked in cats tranquillized with ketamine. In other respects their results (obtained with an array of eight electrodes) appear compatible with ours and with those of Nieoullon & Rispal-Padel (1976).

The results of pyramidectomy establish that the integrity of the medullary pyramid is necessary for the movements evoked by stimuli of 35 μA or less. It is therefore probable, though not proven, that cortico-spinal volleys were a major factor in evoking the movements.

Relationship between the receptive field and movement topographies

Both in terms of peripheral input and in terms of evoked movement the wrist, elbow and shoulder were widely represented in the cortex and there was extensive overlap between their representations. Nevertheless, there was a distinct tendency for each population of movement loci to centre further laterally than the population of neurones with receptive fields in the corresponding limb zone. This principle was confirmed by a direct comparison of the sensory and motor responses evoked via the same electrode, which demonstrated that the more distal the joint the greater is the input from the foot and the less the input from the shoulder.

Here it may be noted that a sensori-motor comparison for some individual electrodes has previously been made by Sakata & Miyamoto (1968) who concluded that cutaneous receptive fields were usually related to movements elicited in muscles proximal to the fields whilst deep fields were usually related to movement evoked at the same joint. Relevant findings have also been reported by Asanuma *et al.* (1968) who concluded that 'the cortical efferent zone for a given muscle appears to receive proprioceptive input mainly from the distal joint involved in the action of that muscle' and that 'in general, a given efferent zone receives cutaneous inputs predominantly from skin regions which lie in the pathway of limb movement produced by contraction of the muscle to which the zone projects'. Though Sakata & Miyamoto (1968) partially disagree on this last point (they observed an *aversive* relationship between cutaneous receptive field and direction of evoked movement) it is clear that in relation to the over-all somatotopy of input–output relations all three studies agree quite well. However, as regards any extrapolation of the results to normal cortical mechanisms of movement control it should be remembered that all three studies are subject to the limitation that electrical stimuli are unlikely to excite cortical neurones in their natural patterns and combinations.

We thank L. Gregory for technical assistance, C. Makepeace for photography, A. Lear for typing and Action Research for financial support. T. Drew was supported by the Medical Research Council of Great Britain.

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