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Microstimulation of the Supplementary Motor Area (SMA) in the Awake Monkey*

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Summary. The supplementary motor area of three *Macaca fascicularis* was mapped using intracortical microstimulation (ICMS). Both forelimb and hindlimb movements were evoked using currents of 30 μA or less. However, thresholds for evoking movements were higher than those in the primary motor cortex. Proximal motor effects predominated, but distal joint movements were also elicited. Forelimb points were clustered in mesial cortex of area 6, anterior to the precentral hindlimb and tail region. Distal joint effects were located deep in the cortex, intermingled with proximal effects. Hindlimb responses which were less spatially localized, were found both ventral to the forelimb area, in the dorsal bank of the cingulate sulcus, and in mesial cortex, well anterior to area 4. No movements of facial muscles were elicited.

Injections of HRP were made into the spinal cord at the cervical level in two animals and the lumbar level in the third one. An area of labelled cells was seen in mesial area 6 which corresponded closely to the region from which ICMS effects were elicited. No movements were evoked from the anterior portions of the fundal region of the cingulate sulcus which were also labelled.

Key words: Supplementary motor area – Microstimulation – Pyramidal tract – Primate

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Introduction

The supplementary motor area (SMA) was first described on the basis of electrical stimulation experiments (see Penfield and Welch 1951, for an historical review). This region was mapped by Penfield and Welch (1951) in awake monkeys and man and by Woolsey et al. (1952) in anesthetized monkeys. According to both groups, prolonged surface stimulation of mesial area 6 anterior to the primary motor cortex (MI), from the dorsal surface down to the dorsal bank of the cingulate sulcus, produces discrete movements of body segments similar to those evoked in area 4 but at higher thresholds. Whereas Penfield and Welch reported a rather disjunctive arrangement of evoked movements, Woolsey et al. described a discrete somatotopical organization in which the whole body musculature was represented in an ordered rostro-caudal sequence. In man, both Penfield and Welch (1951) and Talairach and Bancaud (1966) found no evidence of such a clear-cut somatotopy. As has been pointed out (Penfield and Welch 1951; Wiesendanger et al. 1973), the results of prolonged surface stimulation of the SMA at high intensities may be difficult to interpret, because of the possibility of excessive current spread and synaptic transmission of excitation to the primary motor area.

However, a renewed interest in the SMA has arisen with the discovery of the involvement of this area during the performance of motor task and with more precise knowledge about its anatomical relationships (cf. reviews by Humphrey 1979, and by Wiesendanger 1981). In particular, newer anatomical techniques have confirmed a close reciprocal relationship of the SMA with MI (Matsumura and Kubota 1979; Muakkassa and Strick 1979). Furthermore, it has now been firmly established that the primate SMA has a substantial population of cor-

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ticospinal neurones which project to both cervical and lumbosacral levels of the cord (Biber et al. 1978; Murray and Coulter 1981).

In light of this evidence of a projection from SMA to the spinal cord, we asked whether SMA might then be microexcitable. If so, this would provide some evidence for a close coupling between SMA and spinal motor centers. Secondly, it was expected that the use of microstimulation, together with the labelling of corticospinal cells by retrograde tracer techniques in the same animals, might disclose the details of somatotopical organization in this area.

In the following, we describe a small region in medial area 6 from which both forelimb and hindlimb muscles were activated by microstimulation. This region corresponded well with the area of medial cortex containing labelled cells following injections of horseradish peroxidase (HRP) into the spinal cord.

Methods

Data from three *Macaca fascicularis* monkeys are presented here. Each animal was prepared for chronic microstimulation using standard techniques. The SMA was exposed, with the dura intact, and a stainless steel chamber (25 mm i.d.) and head fixation device were cemented to the skull. Following a recovery period of at least 1 week, daily microstimulation sessions were begun. The monkey was seated in a primate chair, with its head secured in a semi-chronic headholder (D. Kopf). The exposed cortex was systematically mapped on a 1 mm grid using either epoxy-coated stainless-steel or glass covered tungsten microelectrodes (exposed tips abouth 15 μm). The stimulus was a train of 12 constant current cathodal pulses of 0.2 ms duration at 330 Hz. In each penetration, searching stimuli of 30 μA (occasionally up to 50 μA) were applied every 250 μm to a depth of 10 mm. The nature and threshold of evoked responses were examined by at least two observers, employing visual observation of overt movements, palpation of muscles and, sometimes, intramuscular electromyographic recordings (EMG). An arbitrary value of 30 μA was accepted as the maximum threshold intensity for the evoked movements included in these results. This was both to avoid the effects of noxious currents (Asanuma and Arnold 1975) and to facilitate comparison with previous studies. A typical session lasted for a maximum of 2 h, after which the monkey was returned to its cage.

After completion of the mapping, the animals were anesthetized with pentobarbital and a laminectomy was performed. Large, rapid injections of HRP (Boehringer, grade I, 30% in equal quantities of Tris-buffer, pH 7.3 and KCl) were made bilaterally into the lateral portions of the cervical or lumbar cord to disrupt as many fibers as possible. In two animals, the injections were made at the cervical level to attempt to label a maximum number of corticospinal cells (case 80–130: 2 μl HRP in each side, segments C3–C4; case 80–151: 1 μl HRP in each side, segments C4–C6). The third animal (80–49) was injected bilaterally in segments L3 to L5 with 1 μl HRP.

After survival periods of 3, 4, and 3 days, respectively, two electrodes were inserted using the same coordinate system as for the microstimulation tracks and left in the brain to serve as marking tracks for later reconstruction. The animals were then deeply anesthetized and perfused, first with physiological saline, then with 1,5% glutaraldehyde and 1% paraformaldehyde. After perfusion the brain was removed and the relevant portions were placed in a sucrose-buffer solution for 24 h. Coronal sections (case 80–130) or sagittal sections (cases 80–151 and 80–49) were cut at 50 or 100 μm intervals. Alternate sections were reacted with tetramethyl benzidine (Mesulam 1978) and counterstained with neutral red or thionin. Labelled corticospinal cells were plotted on outline drawings of selected sections by means of a pantograph system. The border between areas 4 and 6 was established from the same sections as judged mainly from the disappearance of the Betz cells and other criteria described by Brodmann (1903), von Bonin (1944), and Bucy (1935). The anterior border of area 4, as described by these authors, is more rostral than that of Vogt and Vogt (1919) who included some of anterior area 4 in their area 6aα. In the present study, we adhered to the convention of the first group of authors and included in area 4 the sometimes scattered islands of Betz cells in front of the continuous line of giant pyramids. It was therefore important to compare serveral neighbouring sections in order to obtain a consistent 4/6 border. This border served as a reference plane in caudo-rostral direction. The depth alocations were based on the microdrive readings in the protocol, taking into account tissue shrinkage. The term 'medial cortex' as used in this study includes all parts of areas 4 and 6 near the midline. It is further subdivided in 'dorsolateral cortex', 'mesial cortex' (facing the falx), and superior bank of cingulate cortex.

Results

Microstimulation Effects

In all three monkeys, overt muscle twitches were evoked from the SMA in both forelimb and hindlimb muscles with microstimulation at intensities of 30 μA or less. The microexcitable region was continuous with that of MI and extended up to 7 mm anterior to the 4/6 border. Microstimulation effects were seen throughout the full dorsoventral extent of mesial cortex and in the dorsal bank of the cingulate sulcus. However, these microexcitable regions were very small and "patchy". Often, the vertical extent of one positive region in a track was as small as 250–750 μm, with areas above and below which were negative with currents of up to 50 μA.

Figure 1 shows an example from one animal of all the microstimulation tracks in one particular sagittal plane which passed through the cortex of the mesial surface of the brain. The dots indicate the points in each track where movement could be evoked with a stimulus intensity of 30 μA or less. Each horizontal dash marks the point of lowest threshold for each particular movement. The presence of two or more contiguous low threshold points in the same track and involving the same body part implies a change from one type of movement to another (i.e., toe extension to toe flexion).

Tracks in which forelimb movements were evoked are located up to 7 mm anterior to the 4/6

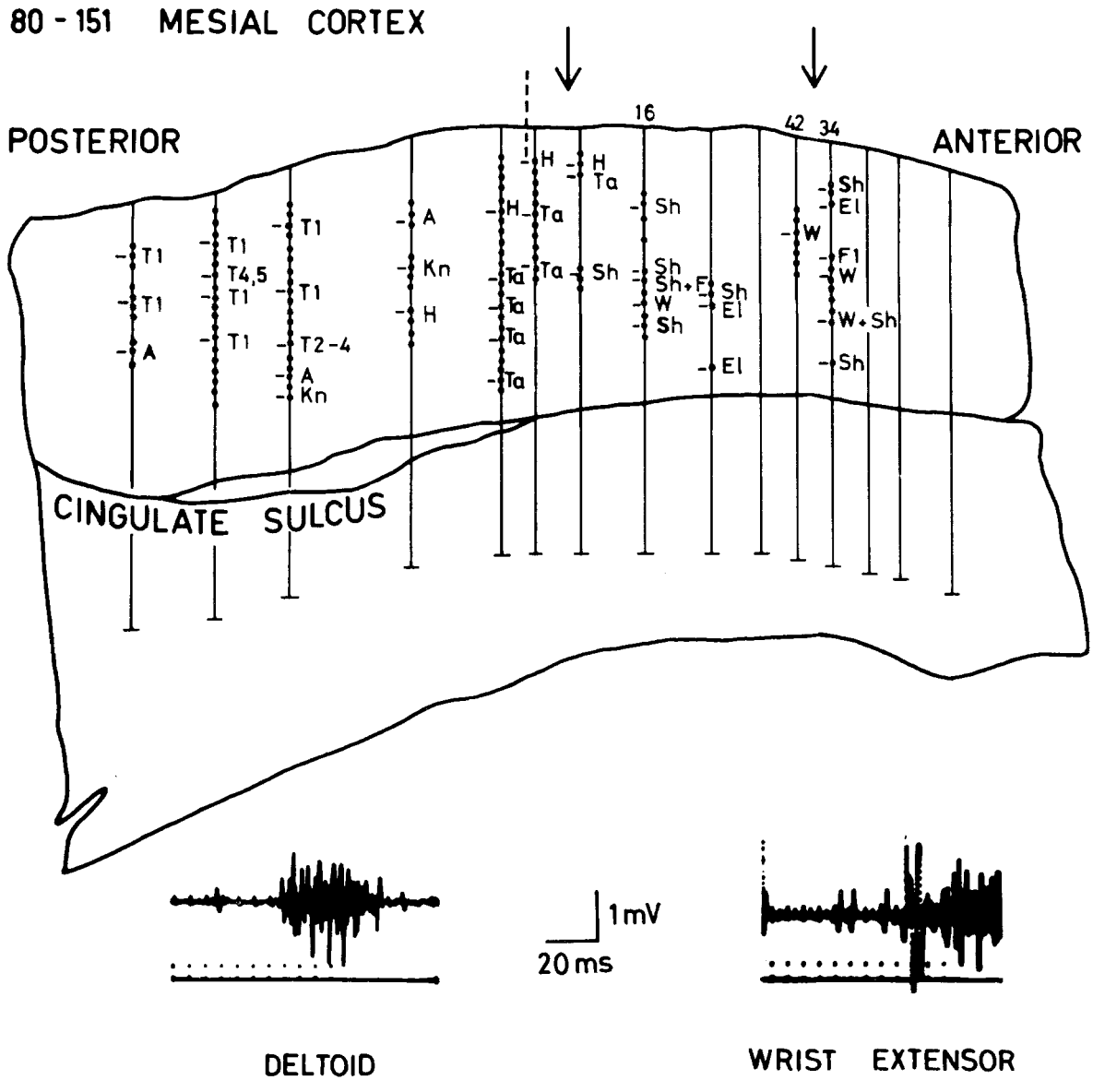

Fig. 1. Evoked movements with thresholds of 30 μA or less in mesial cortex of monkey 80–151. Each low threshold point is indicated by a dot with the lowest threshold point for each movement marked with a dash. Abbreviations: *Sh* – shoulder, *El* – elbow, *W* – wrist, *Fl–5* – fingers 1–5, *H* – hip, *Kn* – knee, *A* – ankle, *Tl–5* – toes 1–5, *Ta* – tail. The dotted line marks the area 4/6 border. Arrows indicate the anterior planes of the two marking tracks (positions of these with respect to cortical surface landmarks are shown in Fig. 2A). Scale: 6 mm between arrows. Insets: EMGs evoked by ICMS (superimposed sweeps). Deltoid EMG was recorded in track 16 at the first low threshold shoulder point, using 25 μA stimulation (threshold 16 μA). Wrist extensor activity was evoked in track 42 with 30 μA. The threshold for movement was 17 μA (the lowest in the track)

border (dotted line in Fig. 1). Movements were observed at both proximal (shoulder and elbow) and distal (wrist and finger) joints. Two examples of evoked forelimb EMG activity are shown at the bottom of Fig. 1.

Maps of all the ICMS evoked movements from two monkeys are shown in Figs. 2C and 3C. The cortical surface has been represented as a two dimensional plane, having been "unfolded" at points d, e and e' as shown in part B of each figure. This representation conforms to that of Woolsey et al. (1952). Very low threshold points for evoked movement extended for long distances into the white matter. (Threshold currents for activating fibers can be as low as, or lower than, those for cell bodies (Asanuma et al. 1976)). However, only those low threshold points which were in the gray matter or just at the lower edge were included on the maps.

In area 4 mesial cortex, considered as part of MI, were found low threshold points for hindlimb proxi-

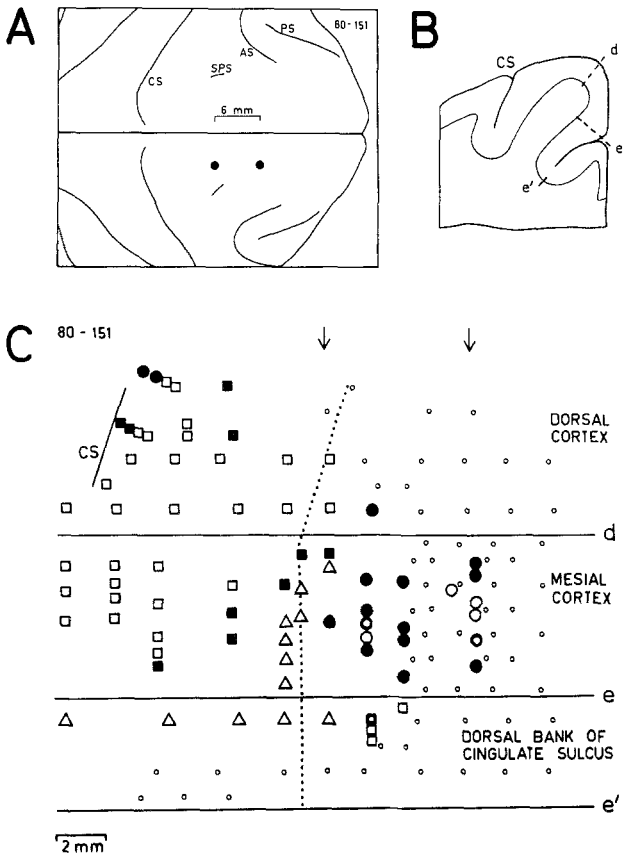

Fig. 2A–C. Map of low threshold evoked movements for monkey 80–151. **A** Positions of marking tracks (dots) with respect to cortical surface (drawn from photograph). Abbreviations: *CS* – central sulcus, *SPS* – superior precentral sulcus, *AS* – arcuate sulcus, *PS* – principal sulcus. **B** Coronal section through precentral cortex showing points of "unfolding", d, e, and e', to obtain the two dimensional map of the cortex shown in **C**. **C** Proceeding from the top of the diagram, the dorsal surface of the cortex is represented first, from lateral to medial, followed by mesial cortex and then the dorsal bank of the cingulate sulcus. Arrows indicate the anterior positions of the marking tracks. The dotted line represents the area 4/6 border. Symbols: hindlimb proximal ■ and distal □ joints; forelimb proximal ● and distal ○ joints; tail △; negative points °

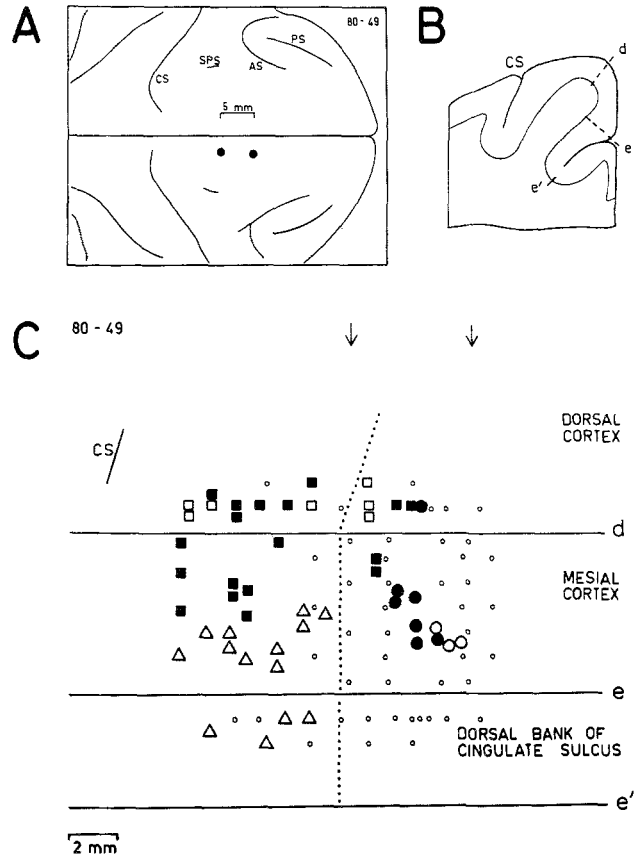

Fig. 3A–C. Map of low threshold evoked movements for monkey 80–49. Details as for Fig. 2

mal muscles (all three cases) and distal muscles (two cases; 80–49 was less extensively explored in this region). The tail representation formed the anterior border of this region and extended into the dorsal bank of the cingulate sulcus. No hindlimb evoked responses were seen in this latter area, below the MI hindlimb region. The shift from tail to forelimb representations in mesial cortex corresponded closely with the cytoarchitectonic transition from area 4 to area 6 in all three animals.

From the SMA, the forelimb segment most commonly activated was the shoulder, although discrete movements of wrist and fingers were evoked at thresholds as low as 14 μA in monkey 80–151 and 15 μA in 80–49. In the third monkey, no area was found with thresholds for distal effects of less than 40 μA. In both animals illustrated, the distal forelimb region appeared to be relatively deep in the mesial cortex. Monkey 80–151 (Fig. 2C) had proximal muscle zones both above and below the distal ones.

Movements were evoked by ICMS in the hindlimb less frequently than in the forelimb from the SMA. Both proximal and distal hindlimb muscles were activated by stimulation in the dorsal bank of the cingulate sulcus, ventral to the forelimb region (Fig. 2C). Other hindlimb responses were evoked from area 6 mesial cortex caudal and dorsal to forelimb regions (Fig. 3C). On the dorsal surface of the cortex, but still in area 6, hindlimb movements could also be evoked with stimulation of 30 μA or less (Figs. 2C and 3C). However, this area is continuous with the hindlimb region of area 4, so it is not clear whether it is actually part of SMA or MI.

No responses were evoked in muscles of the face or head from the area sampled. Of particular interest was the finding that movements about non-contiguous joints of a limb, such as shoulder and finger

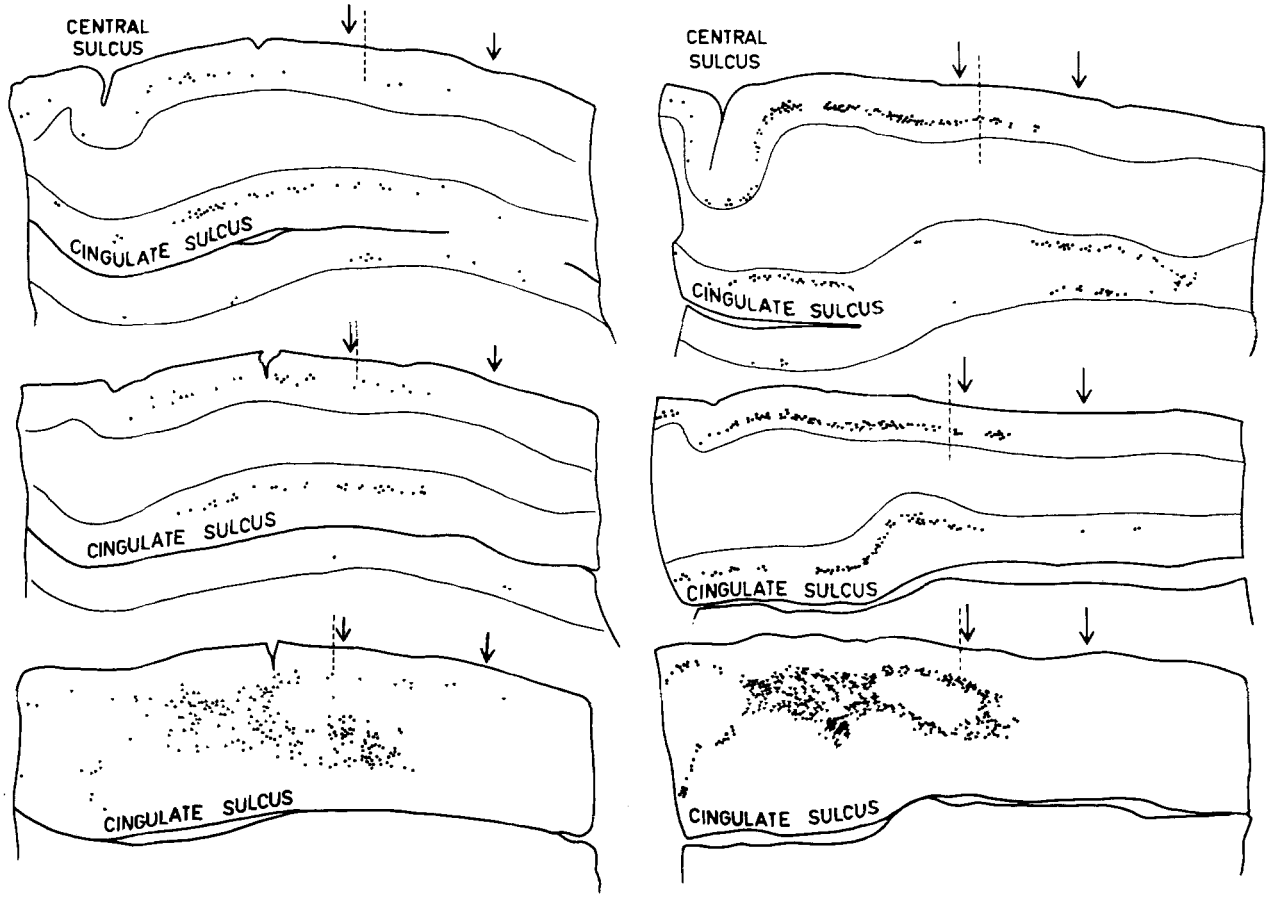

Fig. 4. HRP-labelled cells following injection in cervical (*left*) and lumbar (*right*) spinal cord. Representative sagittal sections from medial (*bottom*) to more lateral (*top*) planes. Posterior to the left, anterior to the right. Dotted lines represent area 4/6 border. Arrows indicate positions of marking tracks as shown in Fig. 2A, C for monkey 80–151 and Fig. 3A, C for monkey 80–49

joints, were occasionally elicited simultaneously, and exhibited the same thresholds of activation. In Fig. 1 are two such tracks, 16 and 34, where shoulder and finger or wrist movements were evoked together with the same threshold of 19 μA in one case, and 14 μA in the other.

The currents just threshold for evoking movements from the SMA were generally higher than those in area 4. The lowest thresholds for forelimb effects in SMA were 16 μA (monkey 80–130), 14 μA (80–151) and 15 μA (80–49). In contrast, in MI more than one third of the proximal hindlimb, distal hindlimb and tail movements had a minimum threshold of 10 μA or less. The thresholds were as low as 2.5 μA for proximal hindlimb, 1.2 μA for distal hindlimb and 1.7 μA for tail effects.

Anatomical Results

In Fig. 4 are shown the positions of labelled cells following the HRP injections into spinal cords of two of the animals used in the microstimulation study. For both cervical (left) and lumbar (right) injections, many small and medium sized filled cells were found in area 6 in the dorsal cortex, mesial cortex and dorsal bank of the cingulate sulcus. Cells were also seen in the ventral bank of the cingulate sulcus, in area 24 B of the cingulate gyrus, but they were fewer in number.

Labelled cells in the two cervically injected animals (80–151 and 80–130, not illustrated) were observed up to 6 or 7 mm anterior to the 4/6 border in mesial cortex, and even further in both banks of the cingulate sulcus. Following the lumbar injection, HRP-filled cells in mesial cortex extended well into area 6, but apparently not as far anteriorly as cells labelled by the cervical injection. However, with both cervical and lumbar injections there were numerous labelled cells extending up to 10 mm rostral to the 4/6 border, in upper and lower banks of the cingulate, especially in the region of the fundus (see Fig. 4, top section, right side). In all three animals, it was observed that the microexcitable area

of SMA in the mesial cortex corresponded closely to the region containing corticospinal cells labelled with HRP. However, motor effects were not elicited in the rostral labelled region of the dorsal bank of the cingulate, or at any rostro-caudal level in the ventral bank of the cingulate sulcus. Microexcitable regions and HRP-labelled areas can be seen by comparing Figs. 2 and 3 with Fig. 4, left and right sides, respectively. In each case, the arrows indicate the anterior levels of the marking tracks.

Discussion

This report presents the new finding that a discrete region of mesial area 6 which is within the SMA as defined by Penfield and Welch (1951) and Woolsey et al. (1952) is microexcitable. This region of low threshold evoked movements also contains cells which project directly to the spinal cord. Previous attempts to microstimulate in the SMA have produced negative results. Palmer et al. (1981) attributed their negative findings to the fact that the animals were anesthetized. It appears that stimulation effects from the SMA are more susceptible to the level of anesthesia than those from MI (Penfield and Welch 1951). Smith (1979) and Wise and Tanji (1981), however, microstimulated in the awake monkey with no effect. It should perhaps be stressed that the microexcitable regions, as revealed in this study, were quite small and extensive mapping was required to find them.

The body representation in the SMA based on the evoked movements reported here differs in some details from previous findings. The mesial cortex of area 6, anterior to the MI hindlimb and tail region showed a major clustering of forelimb related points. Distal forelimb responses were deep in the cortex, and intermingled with proximal responses. This organization resembles more that of Penfield and Welch (1951) than that of Woolsey et al. (1952). The latter group described a clear progression of representation from digits in the dorsal mesial cortex, extending on to the dorsal surface, to proximal muscles in ventral mesial areas and the dorsal bank of the cingulate sulcus.

The hindlimb representation reported here was apparently less extensive and more disjunctive than that of the forelimb. This may reflect a bias in sampling since the dorsal bank of the cingulate sulcus was less extensively explored than the mesial cortex. In the stimulation experiments of Penfield and Welch (1951) hindlimb related responses were concentrated in the dorsal bank of the cingulate in area 6, ventral to the forelimb region, but scattered in mesial cortex as well. Contrary to the somatotopic map of Woolsey et al. (1952), the present study and the two latter ones found no evidence of a hindlimb representation ventral to MI in the dorsal cingulate.

The facial muscles were not activated by ICMS in the SMA. This was also in agreement with results of Penfield and Welch (1951), obtained with surface stimulation. On the basis of autoradiography, Künzle (1978) found no evidence for an SMA projection to the facial, motor trigeminal or hypoglossal nuclei which could explain the lack of stimulation effects. However, this question needs further study.

In the mesial cortex and dorsal cingulate, the area from which movements were evoked contained a moderately dense population of corticospinal cells. Labelling from both cervical and lumbar injections was more sparse in the dorsal cingulate anterior to the excitable zone, as well as in the ventral bank of the cingulate where no movements were evoked. Although the microstimulation results reported here do not support Woolsey's concept of a somatotopical rostro-caudal sequence of face, forelimb and hindlimb representation, they nevertheless revealed a spatially distributed but caudal concentration of hindlimb points. This is in line with the recent retrograde tracing study of Murray and Coulter (1981).

The question may arise whether current spread or physiological spread of excitation may blur the picture of a possibly intricate somatotopic organization. The diameter of the sphere of effective current spread for direct activation of cortical elements has been estimated to be about 400 μm for cell bodies and 1,000 μm for axons (from various sources as reported by Ranck 1975). The effective spread by synaptic activation is larger (Stoney et al. 1968; Jankowska et al. 1975). However, the extremely small and "patchy" distribution of the low threshold points in this study rather suggests that the effects of ICMS were focal and did not spread widely.

The microexcitability of the SMA indicates the possibility of a close coupling between SMA and spinal motor nuclei. This coupling, however, is not as tight as that of area 4, as judged by the higher thresholds observed for SMA evoked movements. The possibility of an involvement of the primary motor cortex in these effects evoked from the SMA is, of course, not ruled out, and this problem remains to be clarified. In fact, according to Penfield and Welch (1951), excision of the primary motor area in the monkey abolishes the hand movements elicited by stimulation of SMA, whereas proximal movements remain, but at a higher threshold.

In light of the observation of movements of the wrist and fingers evoked at microstimulation intensities, it appears likely that the function of area 6 is

not limited to the control of proximal muscles, even though proximal effects are predominant. Indeed, recent studies in the behaving monkey have demonstrated the presence of cells in SMA whose firing is related to movements of distal segments (Smith 1979; Brinkman and Porter 1979; Tanji and Kurata 1979; Wise and Tanji 1981). These results along with anatomical evidence of projections from the SMA to both motor cortex and spinal cord (see Introduction) indicate that SMA may act in parallel with as well as serial to the motor cortex in controlling movement. Studies have reported increased local cerebral blood flow in SMA (and therefore, presumably, neuronal activity) during the planning of movement (Orgogozo and Larsen 1979; Roland et al. 1980). Both a readiness potential presumed to be generated in SMA (Deecke and Kornhuber 1978) and activation of single units have been observed at intervals before the onset of movement (Smith 1979; Tanji et al. 1980; Wise and Tanji 1981). These data, together with the present results, can be considered to be consistent with a tentative hypothesis that the SMA is involved in controlling the excitability of motoneurones in anticipation of a forthcoming command from the motor cortex to begin movement.

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