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NEUROLOGICAL DEFICIENCIES AFTER ABLATION OF THE PRECENTRAL MOTOR AREA IN *MACACA MULATTA*[1]

BY

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SINCE 1869 when Hughlings Jackson (1931, p. 59) defined the cerebral cortex anterior to the central sulcus as serving "in the motor aspect of mind," many investigators have studied the frontal lobes in an effort to determine the anatomical and functional divisions of the so-called "motor" cortex.

Recent re-examination of the motor areas of the frontal lobes in the monkey has defined by electrical stimulation the two distinct somatotopically organized precentral and supplementary motor areas (Woolsey and Settlage, 1950; Woolsey *et al.*, 1950, 1952). Fig. 1 shows the localization of the areas.

Since these motor areas do not coincide with any previous definition of the "motor" cortex, it was decided to investigate the effects of placing lesions according to these maps. In this paper the results following removal of the precentral motor area will be presented; subsequent papers will describe the effects of ablation of the supplementary area and the results of lesions involving both precentral and supplementary motor areas.

METHODS

Materials

Four fully grown adult and four adolescent monkeys (*Macaca mulatta*) were subjected to precentral motor ablations. Precise lesions

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were made and these monkeys were studied in detail for typical deficiencies. We were mainly interested in the post-operative motor status of the extremities. Hence the limb motor areas were ablated sparing the face areas, since other experiments demonstrated that removal of the face area did not add any additional deficit to that of the limbs. The face areas were always damaged slightly, in order to make certain that the arm areas were entirely destroyed. The accuracy of the lesions was determined by stimulation at the time of operation, often by re-estimulation at successive operations, and by gross examination after autopsy of the animals that were sacrificed. A study of thalamocortical relations was made on these specimens (Akert, 1954). Marchi studies were done on the brain-stem and spinal cord (Barnard, 1953).

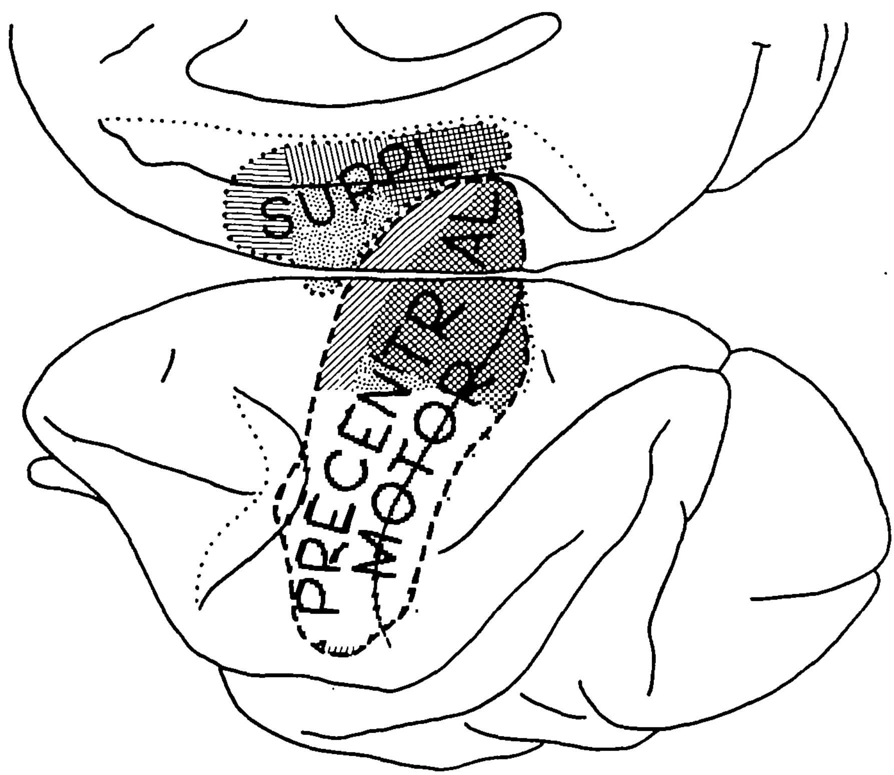

FIG. 1.—The extents of the precentral and supplementary motor areas of the monkey on the medial and dorsolateral aspects of the hemisphere. Each area is redivided into four smaller areas to represent localization of parts of the body; cross-hatching for hind-limb, dots for fore-limb, hatching most lateral in precentral motor and most anterior in supplementary area for face, and remaining two hatched areas for trunk musculature. The light dots parallel to the sulci for most of their distance designate the bottoms of the three sulci.

Surgical Procedures

All operations were performed under surgical anæsthesia induced with pentobarbital sodium given intraperitoneally. Since the validity of experimental data involving the nervous system depends upon the accuracy with which lesions are made, special attention was given to the details of surgical technique. The operations were accomplished under careful asepsis by Dr. Clinton N. Woolsey.

Usually a free bone-flap was turned, which was replaced and held in position with sutures placed through very small drill holes. The dura was so incised that its closure could be made entirely over the lesion except at the ends of the incisions. This minimized the formation of adhesions over the surrounding tissue allowing subsequent operations to be easily performed. Lesions were made with the aid of a binocular loupe, and special care was taken to preserve the chief afferent and efferent vessels to the remaining tissue.

Motor cortex ablations were performed according to the precentral and supplementary motor maps (fig. 1) but were usually preceded by cortical stimulation with monopolar type electrode (indifferent on abdomen) to delimit the exact boundaries of the lesion in each animal. The aspiration technique of cortical removal was used because it possesses definite advantages over the cautery or blunt dissection techniques. The benefits are : preservation of a clear operative field, better control of bleeding, minimal trauma to adjacent cortex, and removal of tissue inaccessible to ordinary instruments by using aspiratory tips of correct shape and size. Special precautions were taken in removing the precentral hind-limb area to avoid damaging the supplementary area, and care was taken to go only as deep as the cortex toward the white matter thus aiming to spare all fibres from the supplementary hind-limb area.

Methods of Examination

Post-operatively the animals were examined every other day for the first week and were subsequently tested at approximately weekly intervals until the time of reoperation or of death. The examining chair consisted of a wooden V back chair, which could be clamped to the side of a table, and into this each monkey was strapped leaving all limbs free for examination.

Cage behaviour, unusual patterns of walking, righting reactions, and posture assumed in the examining chair were the general observations noted. The distribution of muscle tone was examined by passive movements of the extremities and by observation of the positions assumed by joints distal to those moved. Tendon reflexes were examined with a rubber reflex hammer in the usual manner. Abdominal reflexes were examined by pricking lightly the skin of the abdominal wall, and plantar reflexes were elicited by stroking the plantar surfaces of the feet with a blunt instrument, beginning at the heel and proceeding to the base of the toes. The degree of atrophy following the lesions was approximately determined by taking limb measurements at seven standard positions in each fore- and hind-limb. These measurements were taken pre-operatively and then at specific intervals during the post-operative period. By calculating the cross sectional areas from the measured circumferences, the percentage of decrease at each position could be determined. The grasp reflex, more correctly termed in the monkey the "hanging reflex," was tested by determining the length of time that an animal would hold on to a bar or the examiner's index fingers with his hands or feet. The placing and hopping reactions were routinely tested.

Results

Table I lists the monkeys which had the precentral limb areas removed and gives the sequences of the operations in each animal. The results from these experiments will be summarized under major headings.

Table I.—Sequences of Operations of the Precentral Motor Limb Areas

*Animal No.**	*Name*	*Sex*	*Wt. Kg.*	*Operation No.*	*Operation Date*	*Date of Last Observation*	*Lesions*
50–10	Peter	M	6·7	1	4.2.50		Left precentral fore-limb area.
			7·9	2	17.5.50		Right precentral fore-limb area.
			8·7	3	11.8.50		Left precentral hind-limb area.
			9·0	4	5.10.50	24.11.50	Right precentral hind-limb area.
50–70	Oscar	M	7·5	1	16.6.50	25.10.50	Bilateral precentral fore-limb area.
50–74	John L.	M	8·4	1	27.6.50		Bilateral precentral fore-limb area.
			10.0	2	30.11.50	10.8.50	Bilateral precentral hind-limb area.
51–30	Hope	F	3·7	1	28.5.51	29.6.51	Left precentral fore-limb area.

*These numbers were the laboratory serial numbers; the number before the hyphen referred to the year in which the animal was operated upon the first time. Each animal retained the same number throughout its existence in the laboratory.

General observations.—In each instance deficits were observed only in the limbs contralateral to the lesions. No ipsilateral motor deficiencies were detected. In monkeys 50–10 and 50–74 additional removal of the hind-limb areas after recovery from previous complete fore-limb area ablations yielded no additional impairment of the upper extremities. There seemed to be definite somatotopic localization of the precentral motor area, and these ablational data are contrary to the opinion that every part of the motor cortex exerts some control over all parts of the body musculature. No sensory deficit was detected in any of the animals. There was good localization to cotton stimulation.

Cage behaviour.—Brief summaries after certain operations in two monkeys will serve to illustrate the typical deficiencies.

A description of monkey 50–10 after his first operation, *ablation of the left precentral fore-limb area,* follows. A few hours post-operatively, while he lay on his right side attempting to right himself, the right fingers formed a tight fist, and this elbow flexed strongly. For five days the right fore-limb usually hung pendant, except for semiflexion of the lateral digits at the first and second interphalangeal joints. On the second day the monkey in the adjacent cage threatened him. He immediately shook his cage with the left hand and also placed his right hand in the side of the cage bending the elbow 90 degrees. The monkey in the next cage reached across and touched his right fingers. Instead of removing this hand from the cage, he seemed to hold on tighter and fought vigorously with the left hand. On the sixth day he rubbed the right side of his face with the back of the right hand, and accompanying the movement there was elevation and retraction of the shoulder with maximal flexion of the elbow. After a week, movements, such as elevating the shoulder to empty the food pouch and grasping the cage, were frequently noted in the right fore-limb. After two weeks he picked up small pieces of food by apposition of the right thumb and index finger. Manipulation of the fore-arm was accomplished to orient fingers properly to the mouth. Movements were slow but precise; the slowness constituted a permanent deficit. After three weeks slowly executed grooming movements were present in the right hand. Although he used the abnormal right upper limb, up to the time of the next operation (over three months post-operatively) it was not used as often as the left. If both hands were free, the left was preferred in taking food held directly in front of him. If food was offered from the right, generally the right hand accepted it. If a piece of food was large, however, the left hand took the food from the right and transferred it to the mouth. Initially only the left hand grasped a whole apple, but soon both hands held the apple. Often, however, he released the grasp of the right hand. He did not elevate the right shoulder as often as the left in emptying his food pouch, and frequently the left hand emptied the right pouch. No deficit was demonstrable in the left upper extremity or in either hind-limb.

The following observations were made on monkey 50–10 after his third operation, *removal of the left precentral hind-limb area.* No deficit was observed in the left lower extremity. On the second day the right foot did not place on the bar, but the right knee and hip flexed at right-angles in the air with ankle plantar flexed and toes extended. On the fifth day he placed this foot on the bar, but it tended to slip off after once placed. Right toes only occasionally flexed around the bar; his hind-limb assumed a flexed posture with no rotation of the thigh. His right foot was always placed secondarily to the left when he climbed upon the bar, and even after maximal recovery the right toes grasped about half as frequently as the left ones. There was no additional impairment of the upper extremities. A preference for the right hand persisted. He groomed not only himself but the monkey in the next cage, but the fingers remained slow. Although he accurately placed his fingers at the edge of his dressing, he could not remove the bandage from his head; he merely picked at it for hours.

After his first operation, *bilateral removal of the precentral fore-limb area,* monkey 50–74 showed the following findings. For a week both upper extremities remained pendant most of the time, except for slight flexion of the fingers at the metacarpophalangeal and first interphalangeal joints. On the second day he flexed his elbows and grasped the cage with both hands. On the third day he once emptied the right food pouch with the back of his right hand. In the third week his right hand transferred food to his mouth in clawlike fashion. After three months he slowly took raisins by apposition of the right pollex and index finger, and if one insisted, he used the left hand in a clawlike manner. After four months he could appose the thumb and index finger of the left hand. Both hands remained slow, and there persisted definite preference for the right hand. Often he took food with the mouth directly. The left hind-limb moved a little more slowly than the right for five days.

After a second operation, *bilateral removal of the precentral hind-limb area,* monkey 50–74 had the entire precentral limb areas ablated bilaterally. On the first day he sat on the floor of his cage and both lower limbs were flexed except for the toes which were extended. By the fourth day he sat on his bar, placed his feet on the wires of the side of the cage, and at times flexed his toes. After a month he reached maximal recovery. He remained slow in the use of all limbs and his fingers were used in an awkward manner. Figs. 4A, B, C, and D depict postural attitudes assumed in his cage, whereas fig. 4E demonstrates an upright standing position.

Chair posture.—If the fore-limb was involved, it was placed occasionally on the arm of the chair as early as the second day. After maximal recovery the affected upper extremity did not place on the arms of the chair as constantly as in normal animals. Often the fore-limb hung pendant, but with maximal recovery the fingers usually grasped the chair. If the hind-limb area was removed the opposite lower extremity usually remained pendant with toes extended for about a month. After six weeks the involved hind-limb placed and grasped the chair part of the time. Fig. 4F of monkey 50–74 illustrates a typical posture in the examining chair after maximal recovery from bilateral precentral fore- and hind-limb area lesions. Although the tonus was difficult to distinguish from that present in a normal relaxed monkey, certain differences in posture were noted. Whereas the normal monkey places both feet constantly on the chair and holds on by flexing all toes, he only placed his feet about half the time—sometimes one, then the other, and less frequently both simultaneously. Likewise, the hands were not placed on the arms of the chair as constantly as in normal animals. He often assumed a normal posture, but it was not continually maintained.

Tonus.—An immediate hypotonia occurred in the extremities contralateral to the precentral lesions. The limbs, however, were never completely limp. For about a week the fingers of the affected hand assumed semi-flexed postures and after passive extension resumed this position like weak springs. Gradually approximately normal tonus became present, and no permanent hypertonia resulted from the precentral motor lesion.

Tendon reflexes.—Initially the tendon reflexes were less active in the affected limb than observed in the normal extremities. The triceps and finger jerks, usually within two weeks, entered a moderate hyperactive phase, without clonus, lasting five to seven months. Biceps-jerk was difficult to obtain in these animals. The reflexes of the lower extremities gradually returned to normal with generally no period of hyperactivity.

Abdominal reflexes.—After removal of the abdominal representations, the reflexes opposite the lesion were absent for two weeks. The reflexes were impaired for an additional two to four weeks, after which interval the abdominal reflexes appeared normally active.

Plantar reflexes.—The plantar reflex, in the foot opposite the precentral hind-limb area ablation, showed a permanent motor deficit. The normal plantar response usually initially consists of extension of the toes and dorsiflexion of the ankle as one begins stroking the heel, and as the stimulus proceeds to the base of the toes, there follows flexion of the toes, inversion of the foot, and frequently flexion of the knee and thigh in a withdrawal response. Initially after the precentral hind-limb lesion only slight twitching and apposition of the first and second toes was observed. Within two to four weeks the reflex reached maximal recovery and consisted of apposition of all toes. The withdrawal response involving the entire lower extremity seldom accompanied these reactions; instead the hand reached down to remove the stimulus.

Pupils.—In monkey 50–10 after the first operation the left pupil was 0·5–1·0 mm. larger than the right for ten days. After his second operation the left pupil measured 4 mm. in diameter while the right was 3 mm., but after two weeks pupils were equal. In each instance after the other operations on these monkeys the pupils were equal.

Atrophy.—Standard measurements in the fore-limb were taken: just beneath the belly of the deltoid muscle or over the greater mass of the triceps; over the largest portion of the biceps; above the elbow; below the elbow; wrist; and at the level of the metacarpal bones, with and without the pollex. In the hind-limb measurements taken were: thigh

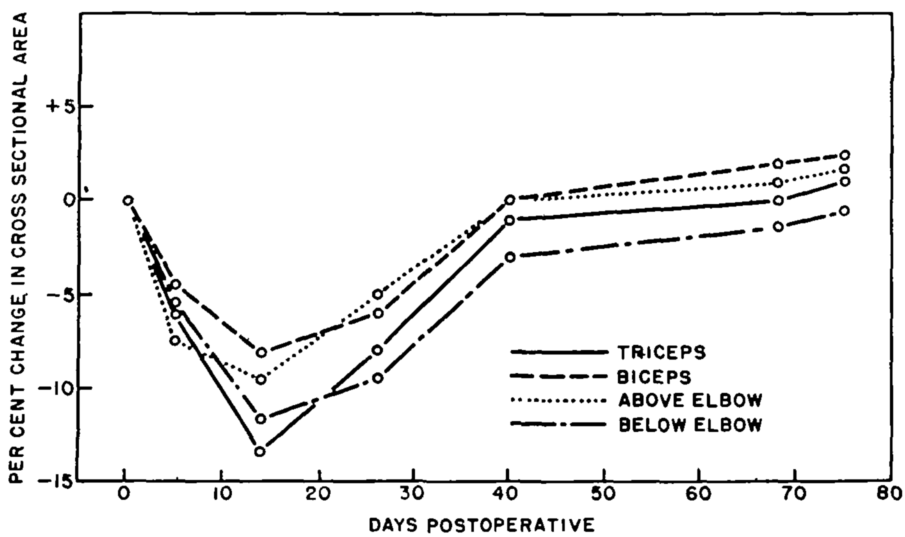

FIG. 2.—Post-operative atrophy of right fore-limb in monkey 50–10 after first operation.

at level of symphysis; above knee, below knee; over the largest bulk of the calf muscles; ankle; and at the level of the metatarsal bones, with and without the hallux. Atrophy occurred in the contralateral extremity after a precentral limb area lesion. It correlated with the impaired function of the limb and reached a maximum of about 10 per cent after two to four weeks but subsided after five to six weeks. The four positions showing significant decrease in cross sectional area for monkey 50–10 following his first operation of removal of the left precentral fore-limb area are plotted in fig. 2. Fig. 3 is illustrative of atrophy of the

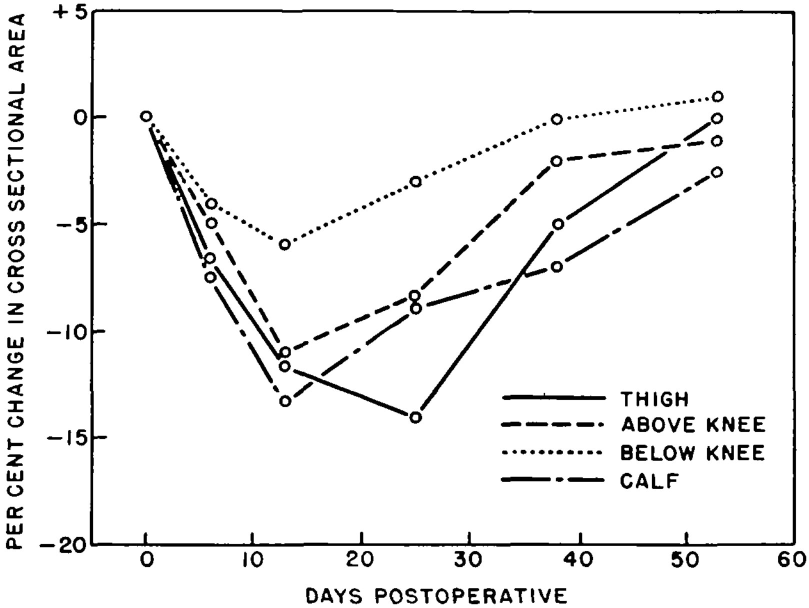

FIG. 3.—Atrophy of right hind-limb in monkey 50–10 following his third operation.

hind-limb and shows the four positions demonstrating significant changes in monkey 50–10 following the third operation of ablation of the left precentral hind-limb area.

Grasp reflexes.—The hanging reflexes were absent in these animals following each operation with one exception. In monkey 50–74 there were grasp reflexes present in the hands after his second operation, bilateral removal of the precentral hind-limb area. The right hand had a grasp lasting five seconds, while the left involuntarily grasped six to seven seconds. The reflexes persisted until the time of the next operation and were most likely due to minimal damage to the supplementary finger areas.

Placing and hopping.—Initially following either unilateral or bilateral lesions of the precentral limb areas, placing and hopping reactions were absent in the extremities contralateral to the limb areas ablated. If an adjacent limb area was damaged, there also occurred temporary impairment of the reactions in the involved extremity. Within one to three weeks after removal of a precentral limb area, placing and hopping were present in the abnormal limb. The reactions were permanently hypermetric with a larger displacement than normal required to initiate a response. Hopping was performed faster forward and laterally than medially and backward. Hopping and placing were accurately performed but were *slower* and *less delicate* than normal, throughout the post-operative interval. Often the digits of the involved upper or lower extremity fanned. The hind-limb frequently hopped in a steppage-like gait, and often the toes flexed at right-angles at the first interphalangeal joints. Excitement of the animal always enhanced the responses. After maximal recovery from his second operation monkey 50–74 hopped forward with the hind-limbs and left fore-limbs 6–8 per meter, while the right upper extremity usually made 9–10 hops for the same distance. Normal monkeys usually hop 12–15 steps per meter.

Verification of lesions.—In five succeeding operations monkey 50–10 was completely decorticated and the precentral lesions were verified. From gross inspection and stimulation of the cortex adjacent to the lesions, no representation for the fore- or hind-limb was found. In animal 50–70 the precentral hind-limb area and part of the supplementary area were removed bilaterally at a second operation. From inspection and stimulation, the precentral fore-limb area lesions were as intended. In monkey 50–74 upon removal of the parietal lobes at two successive operations, data were obtained to account for the difference in performance of the hands. On the left near the bottom of and limited to the wall of the central sulcus was found a small strip of cortical tissue belonging to the precentral fore-limb area, which yielded fore-limb movements upon stimulation. It was 10 mm. in its mediolateral extent and 3 mm. in the ventrodorsal direction. All the left precentral hind-limb area had been removed, and on the right the lesions were complete. In animal 51–30 the ablation was determined to be complete from gross inspection of the lesion at autopsy.

Simultaneous with the observations of the neurological disturbances Hamuy (1951) studied retention and performance of skilled movements in these animals. One test was concerned with the ability of the monkey to catch peanuts as they rolled down an inclined plane, which was partitioned into 3 alleys 15 inches long, whose slope could be adjusted.

The animal did not know before any trial in which alley the peanut would be placed, and he was required to catch each peanut by the time it reached the bottom of the slide, or it fell out of reach. At the lowest angle at which the inclined plane could be set the animals were able to catch only approximately 25 per cent of the number which a normal animal could pick up, and failed entirely when the angle was increased, although normal animals still succeed.

To supplement Hamuy's results a simple test was devised to evaluate the speed of these monkeys when objects of food remained stationary. On a clipboard raisins were arranged checker-board style, and these were always presented in front of the animal at approximately the same level as the height of the arms of the examining chair. Fig. 5 shows such a testing arrangement. Raisins were selected because they demonstrated fine movements of the fingers. Usually between 20 and 40 raisins were placed on the board; the best number was arrived at after many trials. Too many caused the animal to stop at intervals to chew up a mouthful; too few did not give an accurate representation due to initial time loss in starting. The time it took the animal to pick up the raisins was recorded by a watch with a second hand. One hand at a time was strapped behind the animal to obtain values for each hand. This test was run on many normal monkeys, and they averaged 0·5 to 0·7 second for each raisin. These animals, after complete removal of the precentral fore-limb area averaged from 1·4 to 1·7 seconds per raisin, having *approximately half* the speed of normals. No additional deficit was observed in the fore-limbs after the precentral hind-limb area lesions.

Since ablation of a complete precentral limb area resulted in no significant spasticity in the contralateral affected limb, additional experiments were performed to determine if small lesions in one of the precentral limb areas would produce hypertonia. The fore-limb area was chosen because with its removal there is less possibility of damaging the supplementary motor area than with ablation of the precentral hind-limb area.

In three animals, 50–65, 51–42, 51–61, similar small unilateral removals were made in the hand–finger area. Fig. 6 shows the extent of the lesion in monkey 51–42. The first two monkeys were kept for four weeks and the third for six weeks before autopsies were performed. Little abnormality was detected in the animals, and after recovery from the anæsthetic the hand contralateral to the lesion was used almost as well as the normal hand. In 50–65 and 51–42 the triceps and finger jerks on the side opposite the operation were hyperactive within two days and continued so throughout the survival periods, and in 51–61 the tendon reflexes were essentially the same as pre-operatively. No increased resistance to passive movements developed.

A fourth experiment in monkey 51–44 (20.7.51; male; wt. 8·1 kg.; Nick) consisted of bilateral removal of Hines' "strip" area rostal to the precentral hand area. On the first day little abnormality in cage behaviour was observed. Tonus was approximately normal, and no increased resistance developed. No abnormal posture such as elevation of the shoulders resulted. Tendon reflexes were difficult to obtain, as they had been pre-operatively. For a week there was slowness in the hopping reactions of the upper extremities on forward and lateral displacements. Also the placing responses were slowly performed when the backs of the hands were touched. This indicated impairments in protraction and abduction of the shoulders. After eight months his shoulders were not used as frequently as normal to empty his food pouches, but often the hands were used instead.

These experiments demonstrate that *lesions restricted to the precentral motor area, regardless of their size, produce no significant increased resistance to passive movement of the extremities.*

Discussion

Since the precentral motor area differs from previous definitions of the "motor" area, an attempt will be made to relate these results to currently accepted data on ablation derived from removals of the histologically mapped "motor" (area 4) and "premotor" (area 6) areas. First a résumé will be given of the extent of the precentral motor field in relation to the cytoarchitectural maps of Brodmann and the Vogts by which former experimental lesions were placed. The anterior boundary of Brodmann's (1909) original map of area 4 in the monkey appears to correspond closely with the rostral boundary of our precentral area. The rostral boundary of the Vogts' (1919) area 4, on the other hand, is situated more posteriorly, and the precentral motor field includes (in addition to) their areas 4*a*, 4*b*, and 4*c*, and probably their entire 6*a*α on the dorsal and lateral surfaces of the hemisphere. Likewise, the part of 6*a*α on the medial aspect of the hemisphere from which movements of the vertebral column, tail, and anus were obtained, belongs to the precentral area. The posterior boundary of the precentral field is the bottom of the central sulcus and agrees with the boundary of area 4 as described by both authors. Medially the precentral area extends only to the dorsal lip of the sulcus cinguli. Previous ablations, however, involving the "motor" hind-limb areas continued to the bottom of the cingulate sulcus and removed the supplementary as well as the precentral hind-limb representations.

After a precentral ablation an immediate hypotonia and impairment of voluntary movements resulted in the contralateral limbs. Fulton and Kennard (1934; Kennard and Fulton, 1933) reported similar results and obtained flaccid paresis in the affected extremities after extirpation of Vogt's area 4. Hines (1937) after removal of area 4 posterior to the strip area, likewise, found immediately a rather complete paralysis with hypotonia. Our results, obtaining essentially no increased resistance to passive movement, are consistent with those of Tower (1940) who produced hypotonic paresis by section of the medullary pyramids. Since this paresis was greater than we observed in our animals, it might be attributed to interruption of fibres originating not only from the precentral but from other areas of the cortex.

Following a precentral lesion the hypotonia merged gradually into a state of approximately normal tonus. Similar results were described by Fulton and his collaborators (Fulton and Kennard, 1934; Fulton, 1935; Fulton and Jacobsen, 1935; Fulton and Viets, 1935) after removals of Vogt's area 4 and by Hines (1937) after lesions in the posterior part of Brodmann's area 4. After ablation of the precentral representations for trunk and extremities, movements recurred as soon in the distal as in the proximal joints. Differences in the results found by previous workers seems to be associated with their definition of the anterior boundary of area 4. Since Vogt's area 4 includes little of the precentral representations for the proximal limbs, Fulton and Kennard (1934) obtained greater paralysis of the distal joints with ablation of area 4 probably because mainly centres for distal joints were removed. The proximal centres were excised when Fulton and his colleagues ablated the "premotor" area. Hines (1937) after removal of Brodmann's area 4 found that the opposite limbs did not initiate independent movements but only followed movements of the normal extremities. She probably obtained greater paralysis than we did because of some involvement of the supplementary motor area.

A possible reason why finer movements of the fingers returned after a precentral fore-limb ablation, and not after lesions of Vogt's area 4, may be related to the surgical methods employed. With careful use of the suction method injury to the surrounding cortex is minimal. Formerly cortical operations were performed by blunt dissection or with the electrical cautery and either method could easily damage adjacent cortex. With removal of area 4 by cautery, damage could have occurred to the adjacent postcentral digital area. After long-standing bilateral ablation in adult monkeys of the precentral and supplementary motor areas, we found that isolated movements of the digits occur upon stimulation of the digital area of the postcentral gyrus (Woolsey *et al.*, 1952). Furthermore, our results after ablation demonstrated that this *postcentral motor system contributes significantly to motor function after complete precentral lesions* (Travis and Woolsey, 1953). Additional removal of the parietal lobes after a previous bilateral precentral motor lesion produced a much more incapacitated preparation. After many months the animal was still unable to feed himself with his hands. These experiments indicate a possible explanation of why the observation that finer movements of the digits recur, may disagree with those of previous authors. By closely checking with electrical stimulation we attempted to make sure that the entire precentral fore-limb area was removed.

Since fine movements of the fingers returned after removal of the precentral fore-limb area, means of determining the persisting deficits were devised. The impairment of ability to make fast adjusting movements was clearly demonstrated in the peanut slide test used by Hamuy. The method of timing the rate at which small stationary objects of food, such as raisins, could be picked up from a board was a simple but useful test in analysing continuous movement for several minutes, for most of the animals were co-operative. The animals demonstrated *approximately half* the speed of a normal monkey when no time limit was imposed upon them.

The hopping and placing reactions served as another means of studying permanent impairments. The responses were performed in a retarded, hypermetric manner and the reactions improved with excitement. After ablation of the precentral area the best hopping responses occurred upon forward and lateral displacements. Thus it seems that these two hopping reactions are less dependent upon the precentral motor cortex than is hopping in other directions. Woolsey and Bard (1936) localized the cortical areas which controlled the placing and hopping reactions in *Macaca mulatta*. They determined that unilateral ablation of Brodmann's area 4 produced enduring loss of the contralateral reactions, except labyrinthine and visual placing which became only deficient. Since the authors stated that less extensive lesions of area 4 produced only permanent deficiencies, it seems evident, in view of our results, that removal of Brodmann's area 4 included in addition to the precentral field the entire supplementary limb areas. The fact that defective hopping and placing reactions are still present after unilateral and bilateral precentral lesions indicates that the supplementary area likewise plays an important part in the control of these postural reflexes.

Just as stimulation of the precentral field yielded movements in the contralateral limbs, the motor disturbances after removal of this area were present only in the limbs opposite the lesion. Leyton and Sherrington (1917), experimenting on chimpanzees, orang-utans, and gorillas, found that ablations of the arm area of the second hemisphere causes no added paresis of the ipsilateral arm. Bucy and Fulton (Bucy, 1933; Bucy and Fulton, 1933), however, evoked ipsilateral responses in monkeys by stimulating a restricted area about the superior precentral sulcus. The level of anæsthesia may explain why we observed no ipsilateral limb movements upon stimulation of the precentral motor area. From their ablational results Bucy and Fulton also concluded that an ipsilateral motor area existed in monkeys. This was based on the findings that an animal with bilateral removal of areas 4 and 6 was totally incapacitated, whereas if either area 4 or 6 was left intact in one hemisphere the animal was capable of moving all extremities. We have reported, however, that adult monkeys can walk, climb, and feed themselves after bilateral ablation of areas 4 and 6 (Travis and Woolsey, 1952).

Although our precentral area lesions included the "ipsilateral area" about the superior precentral sulcus, no observable ipsilateral deficits resulted. This does not prove that an ipsilateral area does not exist; it only indicates that if ipsilateral representations are present, their functions are probably small.

In these ablations involving the precentral motor cortex, we did not confirm the findings of Ades and Raab (1946), who reported bilateral compensation after unilateral lesions of area 4 such that if area 4 of the remaining hemisphere is removed after a suitable delay (three to four months) none of the signs of pyramidal injury appear. Although this time interval was allowed to elapse in early experiments, the contralateral paralysis following the second lesion was as severe as in the limbs opposite the primary ablation.

If the precentral fore-limb area was removed completely at an initial operation and the contralateral upper extremity was permitted to reach its maximal recovery, ablation of the hind-limb area on the same side as the original lesion yielded no additional impairment in the upper extremity. Thus these observations lend no support to the view that all parts of the motor cortex exert *some* control over all parts of the body musculature. Similar results were obtained by Leyton and Sherrington (1917, p. 207) who stated "neither the ablation nor excitation methods gave any evidence that the remaining part of the arm area had taken on the functions of the ablated hand area." Recently Glees and Cole (1950) concluded from small subsequent motor lesions that remaining adjacent cortical areas developed the ability to control the functions of previously ablated tissue. Since the authors did not remove, even at their first operation, all of the thumb area as judged by our motor map, it is not surprising that thumb movements were obtained later upon restimulation of the adjacent cortex. One would expect an additional deficit on removing this surrounding tissue. After small area 4 lesions, their animals did not reach their pre-operative skill, indicating a deficit from small removals. Our results suggest that if the thumb representations were entirely ablated at a primary operation the permanent impairment in the thumb should be as great as if the complete precentral motor area were removed. Kennard (1942) from experimental data and Bucy (1949) from clinical cases concluded that ablation of the arm area alone had less effect on arm function than if arm and leg areas were both removed. *These results were probably due to either incomplete removal of the precentral fore-limb area or involvement of the supplementary fore-limb area upon ablation of the precentral hind-limb.*

The complete inability to obtain any permanent hypertonia was an important finding. However, post-operatively certain reflexes were temporarily hyperactive though not clonic. Fulton and Viets (1935) reported after motor area ablations in monkeys that some of the reflexes (knee and biceps jerk) became hyperactive although the limbs remained flaccid. Following a lesion of the precentral fore-limb area usually a semiflexion of the fingers occurred for approximately a week following the operation, and the digits returned to this flexed posture after passive extension. Since springlike action of the fingers is observed in normal anæsthetized animals, this posture is considered normal in a state of great voluntary impairment. Under some definitions of spasticity, the temporary increased tendon reflexes and flexor posture of the fingers would probably be included. However, the degree of this transient spasticity was slight and most unimpressive in comparison with the strong results obtained after other lesions, so the conclusion that spasticity does not appear to be an effect of ablating the precentral motor area alone is not significantly altered.

The atrophy resulting in this series of experiments supports the disuse theory. The correlation between impairment of motor function and the time of greatest atrophy was close, and with the return of volitional movements the atrophy disappeared. Fulton (1936), after removing area 4 in chimpanzees, obtained an atrophy of over 50 per cent. This is larger than we obtained in monkeys after precentral lesions perhaps because Fulton, with ablation of area 4, probably removed part of the supplementary area. Alternatively there may be a considerable species difference.

Richter and Hines (1934) produced a transient hanging reflex by unilateral or bilateral lesion of upper area 6. Since ablations restricted to the precentral motor area yielded no grasp reflex, one can assume that removal of portions of area 6 not included in the precentral motor area may be responsible for producing an involuntary grasp.

In summary, it was our goal to determine the maximal recovery obtainable in these animals, and from the impairments that remained to define the deficits characteristic of a precentral motor area lesion. In Hughlings Jackson's writings is found the following statement concerning recovery of function (1931, p. 149): ". . . it will be inferred that recovery follows not because other units take on duties they never had before; but because these units having in health closely similar duties to those of the unit destroyed, they can act nearly as well for the duties of both." After maximal recovery the functional deficits which persist can be attributed to the area destroyed. Recovery may be nearly complete, but in the words of Marion Hines (1929, p. 484), "In just that difference between complete and 'practically' complete lies the material for the final analysis of the function of the motor cortex."

Summary

These experiments were concerned with a reinvestigation of the function of the "motor" cortex studied in eight *Macaca mulatta*. Since the precentral motor area was defined as a functional unit that does not coincide with previous definitions of the "motor" cortex (Woolsey and Settlage, 1950; Woolsey *et al.*, 1952), this study was undertaken to determine the results of ablation of this area alone. The following conclusions were reached.

(1) Precentral motor area lesions resulted in immediate severe voluntary impairment, hypotonia and diminished tendon reflexes in the extremities contralateral to the ablations; no ipsilateral deficits were observed.

(2) Partial recovery of motor performance followed, and movements reappeared as soon at distal as at proximal joints; detectable impairments persisted at both.

(3) Within two to twelve weeks the animals were able to pick up small stationary objects by apposition of thumb and index finger, but

after maximal recovery this manœuvre was accomplished with only approximately half normal speed.

(4) No significant spasticity developed. In the arms the triceps and finger jerks passed through a transient phase of moderate hyperactivity.

(5) Placing and hopping reactions returned after one to three weeks in the affected limbs, but they were performed persistently in a retarded, hypermetric manner. The responses were enhanced with excitement of the animal.

(6) The abdominal reflexes on the side contralateral to the lesion were diminished for four to six weeks following the operation, but after this interval they appeared as active as normal.

(7) The plantar reflex consisted of apposition of all toes instead of the normal active flexion of the toes and frequent withdrawal of the entire hind-limb.

(8) Atrophy of about 10 per cent appeared in the limbs opposite the lesion during the period of greatest disuse and completely subsided after maximal recovery of motor function was achieved.

(9) No grasp reflexes were obtained, although the lesions included Vogt's dorsal and part of the medial area 6$a\alpha$.

(10) These experiments do not support the concept that all parts of the motor cortex exert *some* control over all parts of the body musculature.

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PLATE XV

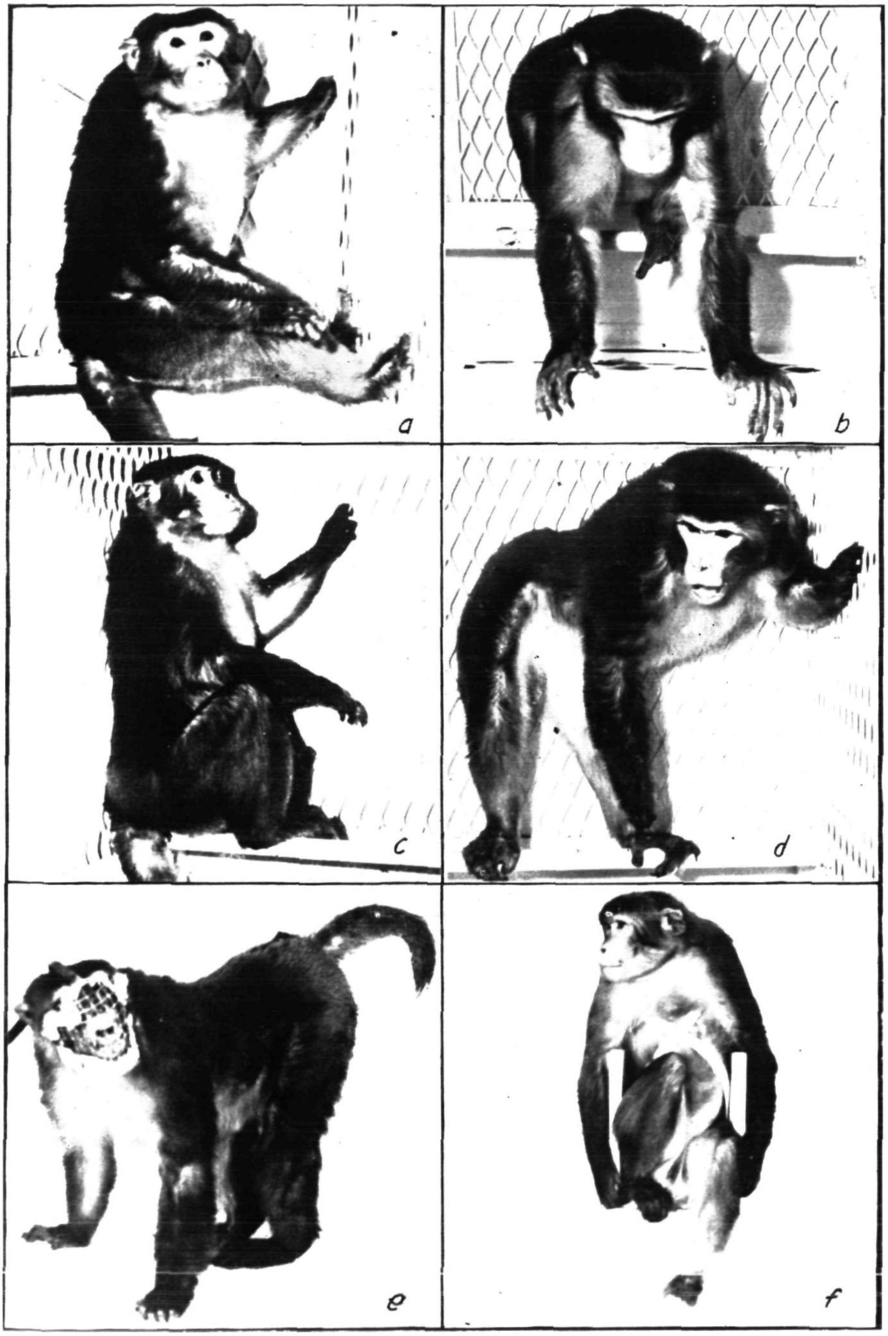

FIG. 4.

To illustrate article by Ann Marie Travis.

FIG. 5.—Monkeys 50–10. An animal picking up raisins from a clipboard. Time values were compared with the speed of normal animals.

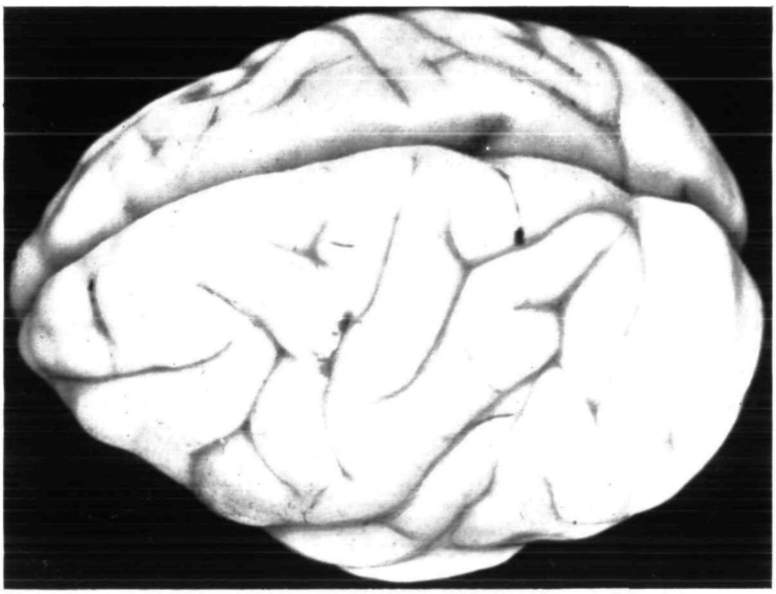

FIG. 6.—Extent of lesion in monkey 51–42.

To illustrate article by Ann Marie Travis.

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LEGEND

PLATE XV

FIG. 4.—Monkey 50-74 nine months following his second operation which completed the removal of the precentral limb areas bilaterally.

A. Maintains balance on bar of cage by grasping cage with only one hand. Grooming posture of right hand frequently observed. Note ability to completely extend the lower extremities and to grasp the wires of the cage with toes of feet.

B. Attempt to escape from cage. Hind-limbs are flexed while fore-limbs are nearly completely extended. Notice particularly the extension and slight fanning of the fingers.

C. Sitting on bar with lower limbs flexed in a similar to normal posture with no rotation of the thighs. Although the right hand was faster in performing than the left, he more frequently grasped the cage with the left hand.

D. Threatening observer. This illustrates his ease in balancing when standing upon bar of cage. The digits of all extremities are flexed. Flexion of the toes is significant in that animals with combined precentral and supplementary area lesions seldom flex the toes. He is able to flex or extend the elbows as evidenced by the posture of the upper extremities. No abnormal elevation of shoulders present.

E. Erect standing posture. Swaying of back probably due to his great weight and not significant of the lesion. Fingers of one hand are flexed while in the other they are extended.

F. A typical posture assumed in the examining chair. Observe the relaxed posture of upper limbs and flexed position of fingers as he holds on to the arms of the chair. Whereas a normal monkey keeps both feet constantly placed, this animal may place both simultaneously but more frequently just places one foot at a time. Toes of both feet are flexed.