ON THE MOTOR FUNCTIONS OF THE CEREBRAL CORTEX OF THE CAT¹

JOSEPH DUERSON STOUT

From the Laboratory of Physiology of the George Washington University

The results of the early experiments to determine the localization of the cerebral motor areas, by means of electrical stimulation were far from consistent. Some of the discrepancies may be accounted for on the ground of differences of experimental methods, but that other factors may be present has generally been lost sight of. Franz has recently shown that when a number of hemispheres are investigated by the same stimulation method considerable variations are discovered. These variations are chiefly: (1) Differences in the absolute amount of the stimuable areas; and (2) differences in the relative extents of the stimuable areas for individual segments (for the fore and hind limbs which he investigated). In the more highly developed brain of the monkey, on which he worked, and in man, such variations are, he has shown, indicated by the activities of the individual animals. In those animals in which the nervous system, and especially the cerebrum is simple, the routine and partly unvarying nature of the reactions suggests that there may be less variation in motor cerebral control. Franz has demonstrated what others had previously suggested, that the greater complexity of the brain in higher animals is associated with a greater variation in motor control.

¹ The investigation of the motor areas of the cat's brain was made because this animal is being generally utilized in experiments on the nervous system (cf. especially Sherrington's studies of reflexes), because of the ease with which it can be handled, because its general behavior is less complex than that of the monkey, and more variable than that of the rabbit and other rodents, because this animal has been used in a number of previous experiments and its capacity of learning (the possibility of motor adjustments) has been investigated, and because the motor area of the animal has not been carefully mapped out.

DESCRIPTION OF THE CAT'S BRAIN

The accompanying diagram (fig. 1) illustrates the principal features of the anterior part of the cat's brain, and, as far as they refer to the present work, they may be described as follows: The approximate measurements of the cerebrum are: antero-posteriorly, 5 cm.; transversely, 4 cm.; and vertically, 3 cm. The sulcus cruciatus occupies a prominent position on the anterior portion of the superior surface, extending outwards from the median line about 5 mm. On the mesial surface of the hemisphere, it extends backwards and slightly downwards for

FIG. 1. Appearances of cat's brain from (a) the lateral aspect, (b) the superior aspect, and (c) the mesial aspect. C.C., corpus callosum; S.M., supra-marginal gyrus; S.Cr., crucial fissure; F.So., supraorbital fissure; L.O., olfactory lobe; F.Rh., rhinal fissure; F.L., lateral fissure; C.A., compensatory ansate fissure; F.Cor., coronal fissure (adapted from Wilder and Gage).

the same distance. When the posterior bank is lifted backwards, the cortical structure, extending into the sulcus, is seen to have approximately the shape of a quadrant of a circle, the outer boundary curving downwards, backwards, and inwards from the superior surface to the mesial surface of the hemisphere. An artery is invariably found on the surface of the hemisphere at the junction of the margins of the sulcus, but with care the posterior bank of the sulcus may be lifted back, leaving the artery on the anterior bank, with slight injury and little hemorrhage. About 7.5 mm. in front of the crucial sulcus is the deep depression, marking the union of the olfactory and frontal lobes. The olfactory lobe is parallel to and extends downwards from the

median fissure and on the under surface of the hemisphere it almost meets the optic chiasm. Its outer margin, the fissura rhinalis, curves downwards, then gradually outwards, and reaches the supraorbital fissure. The latter begins 5 mm. underneath the middle of the crucial sulcus, and is directed downwards, and backwards, to meet the fissura rhinalis. (The description of other features of the cat's brain will be found in Wilder and Gage.)

Running parallel with the superior margin of the hemisphere, and about 5 mm. from it, is the fissura lateralis (*F.L.*), extending from the posterior portion of the superior surface forwards to a point about 7.5 mm. above the outer end of the crucial sulcus, then turning sharply inward toward the inner end of the crucial. At the point where it changes its direction, the ansate fissure arises and extends outwards and forwards for about 2.5 mm. At or near the outer end of this fissure the fissura coronalis starts and travels in a semi-circular course around the outer end of the crucial sulcus, having a radius of about 0.5 cm. from the end of the crucial. A small dimple, sometimes a short fissurette as it is called by Campbell, is found at a point about equally separated from the outer half of the sulcus cruciatus and the fissura lateralis. This it is that Campbell believes to be the "homologue of Rolando," i.e., the upper half of the fissure of Rolando, although it may be stated that this belief is not in keeping with the physiological findings of the present work. When distinguishable as a fissure, it is called the compensatory ansate fissure.

Histologically, Campbell and others have found that the so-called motor area contains fiber and cell arrangements, which map it off rather sharply from surrounding areas. Campbell's studies have led him to conclude that the motor area in the cat may be represented as in the accompanying figures (fig. 2). He describes this area as follows:

On the mesial surface, the area is confined to a small portion of the marginal gyrus, situated immediately behind the sulcus cruciatus, and it is worthy of mention that it does not reach quite to the hinder extremity of the sulcus. In a frontal view, the close relation to the sul-

cus cruciatus is better displayed. Then, anteriorly, the area extends downwards and outwards, to be limited in turn by the upper extremity of the orbital and the anterior extremity of the coronal sulcus. Laterally, the sulcus coronalis constitutes a bar, transverse sections showing that formation reaches to the floor of, but not beyond, the sulcus. Posteriorly, the field meets the post-crucial or sensory area medially, across the hinder line of the sigmoid gyrus, and it is most important to observe that the boundary line is constantly related to a shallow depression, placed equidistant from the cruciate and ansate sulci. This depression varies in representation in different brains and even in opposite hemispheres. It may appear as a short transverse fissurette, or merely as a dimple, but it is never entirely absent, and I have little doubt that it is the equivalent of a fissurette better developed in other animals and known as the *Compensatory Ansate*.

FIG. 2. Motor area of cat's cerebrum (cross-hatched), as differentiated by cyto- and myelo-architectonic methods (adapted from Campbell).

He makes further reference to the homology of this fissure.

There have been few satisfactory descriptions of the physiological conditions existing in the brain of the cat, which are available for the study of the motor control. The most satisfactory accounts are those published by Ferrier in 1886 and by François-Franck in 1887.

Ferrier made numerous investigations of the motor area in the cortex of the cat. In stimulation experiments he used the induced current of sufficient strength to cause "a pungent but quite bearable sensation when the electrodes were placed on the tip of the tongue." He states that

Though it is obviously advisable to use no stronger current than is sufficient to produce a definite result, the measure of the intensity of

the stimulus to be employed in each case is the degree of definite and decided localization of effects uniformly obtainable.

The results of Ferrier's experiments may be summarized as follows: Stimulation of the median area—the posterior portion of the sigmoid gyrus—is followed by movements of the hind limb; stimulation of the region immediately anterior to the posterior extremity of the coronal fissure, by movements of the fore limb; stimulation of the area immediately internal to the anterior extremity of the coronal fissure, by movements of the

FIG. 3. Motor areas of the cat's cerebrum, determined by Ferrier (adapted). 1, advance of the hind leg; 4, retraction and adduction of the fore leg; 5, elevation of the shoulder, flexion of the fore arm and paw, sometimes clutching or grasping action of the paw, with protrusion of the claws; 7, elevation of the angle of the mouth and cheek, with closure of the eye; 8, retraction with some degree of elevation of the angle of the mouth, and drawing downward and forward of the ear; 9, opening of the mouth and movements of the tongue; 13, eye-balls moved to the opposite side; 14, pricking of the ear and eyes turned to the opposite side; 15, elevation of the lip and torsion of the nostril on the same side; 16, divergence of the lips.

fore limb and shoulder. Of the remaining lateral and superior regions of the cortical surface, stimulation of that portion, lying between the posterior halves of the lateral and the supra-Sylvian fissures, results in movements of the eyes and head. Stimulation of the region adjacent to the anterior extremity of the supra-Sylvian and extending to the coronal fissure results in movements of the mouth, tongue, lips, ear and paw. It is interesting to compare the results with those obtained in the present work. For purposes of comparison a diagram of Ferrier's localizations is here given (fig. 3).

The opinions of various investigators as to the equivalent in the brain of the cat of the fissure of Rolando in the brain of man and the higher monkeys, have varied considerably from time to time. To quote from Ferrier:

The crucial sulcus has been regarded by some as the homologue of the fissure of Rolando. Others (Meynert, Pansch) regard the coronal fissure as the true homologue; while Broca finds it the prae-Sylvian sulcus, or sulcus bounding the gyrus formed by the anterior extremities of the lower three external convolutions.²

Ferrier discards the prae-Sylvian sulcus and the crucial sulcus, but is inclined to accept the coronal fissure as the Rolandic analogue. This is contrary to the later opinion of Campbell, as has been indicated above, but the criteria of Campbell and of Ferrier are, it should be noted, not the same, the former depending upon anatomical examination, while Ferrier has taken the physiological point of view. The conclusions of Ferrier in this regard are to be compared with the results which are reported in later sections of this paper.

François-Franck has not definitely located the various points on the cortex which he stimulated other than to describe them as points for the movement of the crossed fore limb, etc., so it is necessary to deal with his results in some cases with much reserve in comparing them with the results from definitely located points.

Methods

The animals used were adult cats. Each was first anaesthetized in a box and while unconscious strapped to an animal holder. Anaesthesia was then maintained throughout the experiment with the A. C. E. mixture.³ In the animals first operated upon, two $\frac{1}{2}$ -inch trephine openings were made in the skull and the openings were then enlarged with bone forceps, backward and to the front and side. By this method difficulty was ex-

² D. Ferrier. *Functions of the Brain*. 2d edit. 1886, p. 346.

³ This is a mixture of 1 part alcohol, 2 parts chloroform and 3 parts ether, frequently used in animal experiments and sometimes as an anaesthetic for man.

perienced in exposing the anterior areas without considerable shock and hemorrhage, and in other animals the first trephine opening was made in the glabellar region, as far forwards as possible, without taking in the orbital margins. This exposed the upper portions of the two frontal bony sinuses. A second opening was then made in the median line sufficiently posterior to clear the posterior wall of the sinuses. The button, when removed, did not tear the vascular sinus, but considerable bleeding from the bone and small vessels followed. This was usually stopped with hot sponges and, if much blood appeared to be lost, the animal was given from 5 to 15 cc. of salt solution subcutaneously. The openings were enlarged with bone forceps on all sides and the plate of bone between the frontal bony sinuses and the brain cavity was removed. After all hemorrhage had been stopped, by means of hot sponges and bone wax, and the animal had rested a few minutes, the dura was slit and laid back, thus exposing the cerebral surface of one side. The brain tissue was kept moist and warm by frequent applications of cotton sponges, wet in warm salt solution. Bipolar stimulation was used in most experiments, monopolar in a few. The former method was found most convenient.

Stimulation was applied from an inductorium by means of platinum electrodes with the center of the points about 1.5 mm. apart. The secondary coil was kept at such a distance from the primary that the stimuli were supraminimal, but not maximal. After twenty or thirty tests, each stimulus being approximately two seconds in length, at intervals of one or two minutes, the brain was covered with warm, moist sponges and allowed to rest for a quarter of an hour.

The use of methods for keeping the body temperature at a normal line was found necessary. For this purpose the animal was kept throughout the tests on a metal box containing a lighted electric lamp, and when observations of reactions were not being made the animal was covered with cloths.

LOCALIZATION AND LIMITATION OF THE MOTOR AREA

The first series of experiments was conducted with the object of locating the boundaries of the motor field of the cat's cerebral cortex. For this purpose twelve animals gave results of comparative value, although the details for all animals are not given in the present paper. All cases are omitted in which the experiments were not completed to the desired point, but the results in these omitted cases do not differ, except in minor detail, from those that are recorded here. The results indicate that the motor area is confined laterally to that portion of the cortical surface between the two coronal fissures and the median line. It extends posteriorly to the anterior extremity of the fissura lateralis, and anteriorly to a line about 0.5 cm. above the upper extremity of the olfactory lobe. It occupies both banks of the crucial sulcus, and, anteriorly to the crucial sulcus, it extends over to and upon the median surface of the hemisphere about 0.5 cm. The region thus marked off is fairly constant in different animals, and the stimulation of similarly located areas of it in the successive animals led to the production of movements which, in their general nature, are similar. These motor reactions are, for the purpose of study, divided into four groups, according to the portions of the body involved, and the location on the cortex of the points from which they were initiated was mapped out. These groups are (1) hind limb, (2) trunk and tail, (3) fore limb, and (4) head and neck.

Total extents of motor area

Cat 8 was the first one to offer sufficient results to be satisfactorily considered in this classification. The motor field of the right hemisphere extended from the fissura lateralis to a line 0.5 cm. above the superior margin of the olfactory lobe, and from a line 0.5 cm. from the median line outward, almost to the fissura coronalis. The movements of the hind limb were obtained from stimulation of the whole of this area, with the exception of a narrow strip on the outer side and a small area anteriorly. Movements of the trunk and tail were few in num-

ber and these were obtained only from the middle third of the field. Movements of the fore limb, which were numerous, followed stimulations within a field almost co-extensive with the field for hind limb movements. Movements of the head and neck were from stimulations of a field lying almost entirely in front of the crucial sulcus and at the outer part of the motor field.

Cat 9, right hemisphere. The motor field extended as a whole over an area similar to that of cat 8, and in addition reached the median line. The central portion of the field, lying posterior to the sulcus cruciatus, gave upon stimulation almost exclusively movements of the hind limb. Movements of the trunk and tail were initiated by stimulation of two small areas close to the median line. The larger of these areas is at the posterior portion of the motor field and the other on the posterior bank of the crucial sulcus. All movements of the fore limb were obtained from stimulation of a large area in front of the crucial sulcus. Movements of the head and neck were obtained from stimulation of two areas, a small area at the anterior portion of the motor field, near to the median line, and a large area posterior to the outer end of the crucial sulcus.

Cat 10, both hemispheres. The right hemisphere presented two distinct fields, one extending about 0.5 cm. in each direction from the sulcus cruciatus and to the median line. This gave upon stimulation only movements of the hind limb, except within a small area anterior to the outer end of the sulcus, which gave movements of the fore limb, trunk and tail. Movements of the head and neck were initiated by stimulation of a small field, extending from the upper end of the fissura rhinalis, almost to the median line. The left hemisphere of this animal presented an arrangement quite similar, except that the area for the hind limb extended further posteriorly.

Cat 11, left hemisphere. The total motor field extended from the middle third of the coronal fissure to the median line and from a line about 0.5 cm. above the upper end of the olfactory lobe to the anterior extremity of the fissura lateralis. Movements of the hind limb followed stimulation within an area ex-

tending from the median line to the outer end of the crucial sulcus and from the end of the fissura lateralis to a line 0.5 cm. anterior to the crucial sulcus. The fore limb movements were from an area with the same antero-posterior boundaries, but lying in the outer half of the motor field. The trunk and tail movements were from a narrow strip of the cortex, extending within the posterior part of the hind limb area. The head and neck movements were obtained from stimulations within a triangular area lying close to the median line, its apex at the inner end of the crucial sulcus and its base on a line 0.5 cm. posterior to the upper end of the olfactory lobe.

Cat 12, right hemisphere. All reactions were obtained from a crescent shaped area, about the sulcus cruciatus, the horns of the crescent extending forward. The area about the crucial sulcus, when stimulated, gave movements of the hind limb. The base of the outer horn gave movements of the fore limb. The portion of the field lying internal to the anterior end of the coronal fissure and the portion lying between the median line and the upper end of the fissura rhinalis gave movements of the head and neck.

Cat 14, left hemisphere. The extent of the stimuable area was almost identical with that of the field for cat 11, except at its inner boundary, which did not reach quite to the median line. The fore limb field extended from the middle third of the coronal fissure almost to the median line, and from a line half way between the anterior end of the fissura lateralis to a line 0.5 cm. above the upper end of the olfactory lobe. The area for the head and neck movements did not reach the median line, but was limited to an area about the superior end of the fissura rhinalis. The hind limb field, and that for the trunk and tail, had almost exactly the same location as the same fields in cat 11.

Cat 15, left hemisphere. The motor field was along the crucial sulcus, extending from the median line almost to the coronal fissure. Movements of the hind limb were from stimulations applied to the inner four-fifths of this field and movements of the fore limb from stimulations applied to the outer four-fifths

of the field. The portion of the field extending between the upper end of the fissura rhinalis and the outer half of the crucial sulcus gave movements of the head and neck only.

Summary. To make a generalized account of the fields, the total stimuable areas have been combined, and also the separate areas for the anatomically segmental movements, for the hemispheres of all animals (figs. 4, 5, 6, 7, and 8). It is found that the motor field as a whole, figure 4, extends from the anterior end of the fissura lateralis anteriorly to a line about 0.5 cm. above the olfactory lobe, and from the fissura coronalis inwards to the median line. In front of the crucial sulcus it extends over the median margin, a short distance on the median surface of the hemisphere. The areas for the movement of the several body segments are not distinct but overlap, the stimulation of the posterior one-fifth of the field giving almost entirely movements of the hind limb and tail, stimulation of the anterior, inner portion almost entirely movements of the head and neck. Between these areas the fields overlap, but it may be said that the cortical representations, for the different body areas, occupy the following fields:

(1) Movements of the hind limb (fig. 6), a field about four-fifths the size of the entire motor area and extending from the median line almost to the fissura coronalis, and from a line, slightly internal to the anterior end of the fissura lateralis, to a line half way from the sulcus cruciatus to the upper extremity of the olfactory lobe. This field is almost hexagonal in shape and only touches the median line adjacent to the sulcus cruciatus. The larger portion of this field is posterior to the sulcus cruciatus. (2) Movements of the trunk and tail (fig. 8), small scattered areas lying within the posterior portion of the hind limb field. (3) Movements of the fore limb (fig. 7), an octagonal shaped field almost as large as the hind limb field, and extending from a line half way between the anterior end of the fissura lateralis and the sulcus cruciatus anteriorly, to the upper end of the fissura rhinalis and laterally from the fissura coronalis to within a short distance of the median line. It approaches nearest to the median line anterior to the sulcus cruciatus, and from there

rapidly recedes anteriorly and posteriorly. (4) Movements of the head and neck (fig. 5) are obtained from stimulation of several fields, lying almost entirely within the anterior inner

FIGS. 4, 5, 6, 7, and 8. Combined areas for movements in the cat's cerebral cortex. Each diagram is a composite of results obtained by stimulating the cortices of four hemispheres. The crucial sulcus is indicated in the diagrams by the heavy cross line. Figure 4 shows the combined area for all animals for the two hemispheres. Figure 5 shows the combined areas for movements of the head and neck. Figure 6 shows the areas for the hind limb. Figure 7 shows the areas for the fore limb. Figure 8 shows the areas for the trunk and tail.

quadrant of the motor area. The representation for these movements is richest at the anterior extremity of the precrucial area, adjacent to the median line. This area is almost entirely for movements of this type. It extends posteriorly to the crucial

sulcus and over on the adjacent median surface of the hemisphere, about 0.5 mm.

In cats 15 and 16 that portion of the cortex lying on the banks of the crucial sulcus was exposed either by cutting away one bank or by lifting the posterior bank backward. The surface thus exposed was in extent approximately one-third the size of the motor area lying on the exposed surface of the hemisphere. Stimulation of it gave results which were in every way similar to those obtained by stimulation of the exposed motor area previously described, and the movements, which were elicited, prove this area to be functionally merely an infolding of the cortical surface, for they involve the same body areas as the adjacent surface cortex. In addition there was a particularly rich representation for movements of the head and neck, especially for the tongue, lips, jaws, throat and eyes. The number of non-stimulable areas distributed among the stimulable areas, in the exploration of these banks, indicates that the results were true stimulations of the motor cells and not due to overflow of current into contiguous tissue. A fuller account of these fields will be given in a subsequent section and will there be illustrated by diagrams.

AREAS FOR DIFFERENT SEGMENTAL MEASUREMENTS

Figures 9 to 16 show graphically the distribution of the areas in the brains of the different animals upon which the tests were made; and the composite of localization in those animals on which complete series were obtained is given in figure 4. As has been noted above, the results on other animals, in which the exploration of one hemisphere was thought not to be sufficiently complete, are not included, because it is not sure that the results would have been strictly comparable. The results were plotted on diagrams of a size approximately 5 diameters of the original brains and from the enlarged diagrams the illustrations of the present work were reduced.

In these figures the longitudinal sulcus and the crucial sulcus are represented by heavy black lines, the other fissures by

lighter lines. The areas for movements of the body segments are dealt with as if they extended in straight lines mostly, but in this respect the figures are necessarily diagrammatic.

The reproduced illustrations are slightly larger than the original brains, and in the figures the fissural variations are shown.

Figures 9 to 12 show the respective distributions in cats 8, 9, 10 and 12 of the areas of the right hemispheres for the four anatomical groups which have been made, and figures 13 to 16 give similar results for the left hemisphere of cats 10, 11, 14 and 15 respectively. Figure 4 shows the total superficial area obtained by the summation of the areas in all animals. In each of the figures 9 to 16 are shown the distributions of the fields for head and neck, fore limb, hind limb and trunk and tail. The results, which are graphically represented, show a great amount of variation in location of the motor responsive cortex in the hemispheres of different animals. For one animal, cat 10, of which both hemispheres were investigated, a similar deviation was found (compare figs. 11 and 13). These variations are apparently greater than the gross anatomical variations in fissural arrangement, and the great differences in the relative sizes and overlappings of areas are readily noted.

The figures representing the combined fields (figs. 4 to 8) are not to be interpreted as the average field, but solely as the widest distribution of areas in which stimuli were found to result in movement in the animals which were sufficiently investigated. The compactness or solidity of the areas for the fore and hind limbs is in marked contrast with the wide and isolated distribution of the areas for the head and neck and the trunk and tail. In the individual hemispheres similar diffusion or separation of the areas was sometimes found, as is shown in figures 10, 12, 15, and 16.

Considering the field for the head and neck, on the right cortices, it is seen that in cat 8, figure 9, the field is slightly external to and mainly anterior to the outer end of the crucial sulcus. In cat 9, figure 10, it is again external to the end of the crucial sulcus, but not entirely posterior to it. In cat 10, figure 11, it

is at the anterior extremity of the motor field, near the median line, and about 0.5 cm. posterior to the upper part of the olfactory lobe. In cat 12, figure 12, it is in two portions, one near the anterior end of the coronal fissure and the other anterior to the inner end of the crucial sulcus, extending over the margin of the hemisphere onto the median surface. On the left cortices, the field for the head and neck is found as follows in the various animals. Cat 10, figure 13, a very small area about 0.5 cm.

FIGS. 9, 10, 11, 12, 13, 14, 15, and 16. The illustrations show the extent of the cortical areas in the hemisphere of the individual cats over which movements of different segments were obtained. The parts inclosed by the full line show the areas for trunk and tail; those inclosed by circles show the areas for the head and neck, the dotted lines inclose the areas for the fore limb, and the lines of dots and dashes show the areas for the hind limb. The figures 9, 10, 11, and 12 give results from the right hemispheres of cats 8, 9, 10, and 12, respectively; figures 13, 14, 15, and 16 give the results from the left hemispheres of cats 10, 11, 14, and 15.

In the figures, posterior is above, anterior is below; the left hemisphere is at the right of each figure, and the right hemisphere is at the left. The lines represent certain fissures. These are lettered in figure 9 as a key, the designations being as follows: A, longitudinal fissure; B, crucial fissure; C, olfactory lobe; D, lateral fissure; E, coronal fissure.

above the superior extremity of the olfactory lobe. In cat 11, figure 14, a very large area, extending from the anterior extremity of the coronal fissure to the inner end of the crucial sulcus and a short distance onto the median surface of the hemisphere and forward to within 0.5 cm. of the upper part of the olfactory lobe. In cat 14, figure 15, a moderate sized area, half way between the crucial sulcus and the olfactory lobe.

The fore limb field is likewise subject to considerable variation, though less than the head and neck field. On the right the following distribution is found. Cat 8 (fig. 9), a very large field, including practically all of the motor field demonstrated for this animal, and extending from the anterior angle of the lateral fissure to the upper end of the supraorbital fissure, from the middle of the crucial sulcus almost to the coronal fissure. Cat 9 (fig. 10), a small field immediately anterior to the crucial sulcus and extending almost to the median line. It is to be noted that this is the only animal in which the fields for the fore and hind limbs do not coincide at some point in their extent. Cat 10 (fig. 11) a small area immediately anterior to the outer half of the crucial sulcus. Cat 12 (fig. 12), a moderate sized field embracing both banks of the crucial sulcus and extending outward and forward to the coronal fissure. On the left cortices the fore limb field is as follows: Cat 10 (fig. 13), a small field lying between the anterior end of the coronal fissure and the posterior end of the supraorbital fissure. Cat 11 (fig. 14), a very large field extending from the posterior four-fifths of the coronal fissure to the middle of the crucial sulcus. Cat 14 (fig. 15), from the middle third of the coronal fissure inward to a line 0.5 cm. from the median line, and lying mostly in front of the crucial sulcus. Cat 15 (fig. 16), a narrow zone lying along the banks of the crucial sulcus and extending from the coronal fissure almost to the median line.

The fields for the hind limb are located as follows: Right cortices, cat 8 (fig. 9), from the anterior angle of the lateral fissure to a line half way between the crucial sulcus and the upper end of the supraorbital fissure, from the middle of the crucial sulcus to within 2 mm. of the posterior third of the coronal

fissure. Cat 9 (fig. 10), posterior to the crucial sulcus and extending from the median line opposite the anterior end of the fissura lateralis to a line half way between the outer end of the crucial sulcus and the posterior end of the coronal fissure. Cat 10 (fig. 11), a large field extending from the anterior end of the lateral fissure to the anterior end of the coronal fissure and from the median line to a line slightly external to the outer end of the crucial sulcus. Cat 12 (fig. 12), an area restricted to the bank of the crucial sulcus. On the left cortices the localizations are as follows: Cat 10 (fig. 13), a large area extending from the anterior angle of the lateral fissure to a line half way from the crucial sulcus to the olfactory lobe, and occupying the middle two-thirds of the area between the median line and the coronal fissure. Cat 11 (fig. 14), an area similarly located to that of cat 10. Cat 14 (fig. 15), from the anterior angle of the lateral fissure to a line 0.5 cm. above the olfactory lobe and from a line slightly external to the median line to a line continued forward from the body of the lateral fissure.

The fields for the trunk and tail may be said in a general way to occupy scattered areas mainly posterior to the crucial sulcus, but there is considerable variation in the different animals. The localizations in the individual animals, on the right side, are as follows: Cat 8 (fig. 9), an area posterior to the outer end of the crucial sulcus and extending almost to the middle of the coronal fissure. Cat 9 (fig. 10), two small areas, one immediately posterior to the inner end of the crucial sulcus and the other extending from the median line outward to the anterior end of the lateral fissure. Cat 10 (fig. 11), a small area immediately anterior to the outer end of the crucial sulcus. On the left side, the localizations are as follows: Cat 10 (fig. 13), none. Cat 11 (fig. 14), a narrow zone extending from the median line outward to a line drawn forward in continuation of the body of the lateral fissure and lying half way between the anterior portion of the lateral fissure and the crucial sulcus. Cat 14 (fig. 15), two small areas, one immediately anterior to the outer end of the crucial sulcus and the other midway between the anterior portion of the lateral fissure and the outer half of the crucial sulcus.

The comparison of the extent of the motor field as demonstrated by the present work, and the extent of the motor field as demonstrated by the methods of Campbell, brings out the following differences. The motor field, as given by Campbell, is bounded posteriorly by the ansate fissure. In the present work the motor field extends farther posteriorly to the point where the lateral fissure bends inward (sometimes outward). Campbell's field then approaches the inner end of the crucial sulcus and passes over onto the median surface of the hemisphere immediately posterior to the inner end of the crucial sulcus. In the present tests motor reactions were obtained by the stimulation of the area between the angle of the lateral fissure and the median line in many of the animals, although in a few the stimuable area did not reach quite to the median line posteriorly. In all animals there was a stimuable area internal to that portion of the lateral fissure lying anterior to the ansate fissure. No reactions were obtained from stimulation of the median surface of the hemisphere, posterior to the crucial sulcus, except in the case of cat 16, where a narrow stimuable area was found immediately adjacent to the posterior bank of the opened crucial sulcus. It did not reach to the margin of the hemisphere. Reactions were obtained from the stimulation of a narrow strip of cortex within the median line, anterior to the crucial sulcus, though, according to the description of Campbell, the motor area only extends to that portion of the median surface of the hemisphere lying posterior to the crucial sulcus. Anteriorly and laterally the extent of the motor field, as found in the present tests, is identical with the extent mentioned by Campbell.

MOTOR AREAS LYING WITHIN THE CRUCIAL SULCUS

The results obtained from the stimulation of the banks of the crucial sulcus, either after separation by lifting the posterior bank backwards or after the removal of the posterior bank, correspond with those which have been described for the superficial cortical areas.

The difficulties encountered in the investigation of the functions of the banks of the crucial sulci are considerable, owing

FIG. 17. Giving graphically the results of the stimulation of the usually concealed parts of the cortex within the crucial sulcus. The kinds of movements are indicated by small geometrical marks, the explanations of which are given below the figures. A shows the results obtained on the posterior bank of the right crucial sulcus of cat 16; B shows the results on the posterior bank of the sulcus on the left side, and C those on the anterior bank of the left side of the same animal. D shows the results of the stimulation of the anterior bank of the left crucial sulcus of the left side of cat 15.

both to the somewhat inaccessible position of the tissue and to the location of an artery of considerable size between the two lips of the sulcus, or, as it appears on inspection, in the sulcus. The removal of this artery is frequently followed by troublesome hemorrhage, but the results on two animals were sufficiently good to record.

Stimulations applied to that portion of the posterior bank lying immediately internal to the visible margin of the crucial sulcus resulted, in cat 16, on the left side, mainly in flexions of the crossed hind limb. Stimulation of the inner portion of this bank resulted mainly in movements of the eyes and pupils. Stimulations of the outer margin resulted in movements of the tongue, eyes, nictitating membranes, pupils, mandible and flexions of the hind limb. Stimulations of the portion of the field farthest removed from the surface resulted in movements of the eyes, nictitating membranes and lips. These results are shown in figure 17B.

The only results obtained from the posterior bank of the right crucial sulcus of this animal (fig. 17A) were from stimulation applied to the region immediately internal to the margin of the crucial sulcus and along that portion of the median surface immediately adjacent. The stimulation of the former area resulted in movements of the mandible, lips, tongue and neck. Stimulation of the latter area resulted in movements of the lids and tongue and flexion of the fore limb.

The anterior bank of the left crucial sulcus of cat 16 gave the following results (fig. 17C). Stimulation of that portion of the field lying immediately internal to the margin of the crucial sulcus resulted in movements of the eyes and neck from the inner half of the field, and, in addition to these, dilatation of the pupils, movements of the mandible, retraction of the tongue and flexion of the fore limb. Stimulations of the inner margin of the field, adjacent to the median line, resulted in dilatation of the pupils, movements of the lids, retraction of the tongue, and movements of the neck and nictitating membranes. Stimulations of the outer margin of the field resulted in dilatation of the

pupils, movements of the eyes, lids, nictitating membranes, retraction of the tongue, and movements of the head on the neck.

The anterior bank of the left crucial of cat 15 gave the following results (fig. 17D). Stimulation of the region lying immediately within the visible margin of the crucial sulcus, resulted in dilatation of the pupils, retraction of the tongue, movements of the lips. Stimulation of the outer margin of the field resulted in retraction of the tongue, movements of the lids, mandible, lips and flexion of the fore limb. Stimulation of the middle portion of the field resulted in movements of the eyes and mandible, retraction of the tongue and flexion of the fore limb.

The order of mention of the various types of movement following stimulation of the banks of the crucial sulci is the order of the frequency of their actual occurrence.

CHARACTERS OF MOVEMENTS FROM CORTICAL STIMULATION

The results obtained from the stimulation of the cortices of cats 8, 9, 10, 11, 12, 14 and 15 were analysed as to the types of the movements produced and the points on the cortex from which each type of movement originated. The accompanying table (table 1) gives a list of these movements and figures 18 to 61 illustrate the cortical locations for each type. Four right and four left hemispheres are included.

The total number of successful stimulations of the eight hemispheres was 467. Of these 154, or 33 per cent, were of the right, and 313, or 67 per cent, were of the left cortices. The number of the successful stimulation for each animal was as follows: right hemisphere—cat 8, 34; cat 9, 39; cat 10, 39; cat 12, 42; left hemisphere—cat 10, 31; cat 11, 99; cat 14, 131; cat 15, 52. It was found that a total of 903 segmental movements (i.e., movements relating to single segment) of all types resulted from these stimulations, of which 306, or 34 per cent, were from the right, and 597, or 66 per cent, from the left cortices. The number of these movements for the individuals was as follows: right—cat 8, 95, or 2.79 individualized movements per stimulation; cat 9, 70, or

TABLE 1
Analysis of movements from stimulation of the cerebral cortex

NUMBERS OF FIGURES AND TYPES OF MOVEMENT	RIGHT HEMISPHERE					LEFT HEMISPHERE					GRAND TOTALS
	Cat 8	Cat 9	Cat 10	Cat 12	Totals	Cat 10	Cat 11	Cat 14	Cat 15	Totals	
18 Depression shoulder.		2		1	(3)			7	1	(8)	11
19. Adduction fore limb				1	(1)					(0)	1
20. Lifting shoulder		2			(2)			2		(2)	4
21 Adduction fore limb		3			(3)		1	3		(4)	7
22. Inward rotation fore limb		1			(1)		1	4		(5)	6
23. Outward rotation fore limb		2			(2)		2	2		(4)	6
24. Retraction elbow	15	4	5		(24)	18	27	7		(52)	76
25. Forward extension fore limb.	3		4		(7)	1	5	11	4	(21)	28
26. Flexion fore knee.	6	2		1	(9)	10	23	10		(43)	52
27. Extension fore knee.	6		4	3	(13)	1	6	15	6	(28)	41
28 Rotation fore limb	2	1		1	(4)		2			(2)	6
29. Flexion fore ankle	6	4		1	(11)	1	1	18	2	(22)	33
30. Extension fore ankle	4	2	4	7	(17)	1	8	16		(25)	42
31. Flexion toes fore foot.	3				(3)			3		(3)	6
32. Extension toes fore foot.	2	2		7	(11)		5	4	1	(10)	21
33. Adduction thigh	2			8	(10)			1		(1)	11
34. Inward rotation thigh				2	(2)					(0)	2
35. Outward rotation thigh.		4		1	(5)					(0)	5
36 Flexion thigh	1	6	1		(8)	1	6	6	1	(14)	22
37. Extension thigh	6	2			(8)			3		(3)	11
38. Flexion hind knee	12	10	10	9	(41)	7	22	41	24	(94)	135
39. Extension hind knee.	1			1	(2)		1	1		(2)	4
40. Flexion hind ankle	8	6	20	3	(37)	19	23	40	35	(117)	154
41. Extension hind ankle	2		2	1	(5)		1	7		(8)	13
42. Rotation hind ankle	1	2	1	1	(5)		8		4	(12)	17
43. Flexion hind toes	4	5	3	1	(13)	4	13	8	1	(26)	39
44. Extension hind toes	1	2	1	1	(4)	3	4	2		(9)	13
45. Eye movements		1	2	8	(11)		9	2	1	(12)	23
46. Lid movements					(0)		4			(4)	4
47. Lip movements.	1		4	1	(6)		3	4	1	(8)	14
48. Jaw movements.		3			(3)		6	2		(8)	11
49. Face movements		1		2	(3)	1	1			(2)	5
50. Retraction tongue	1	3		2	(6)		2	4		(6)	12
51. Extraction tongue					(0)			2		(2)	2
52 Throat movements					(0)		6			(6)	6
53 Head bent to side			1	2	(3)					(0)	3
54 Head turned to side			2		(2)					(0)	2
55. Head forward				4	(4)		1	3	2	(6)	10
56. Head backward	1		4		(5)	3		5	2	(10)	15
57. Depression of tail			1		(1)		2	2		(4)	5
58. Lifting of tail		3			(3)			3		(3)	6
59. Sideward movement of tail.		2	2		(4)			8		(8)	12
60. Unanalyzed movement		4			(4)		2			(2)	6
61. Movement of trunk					(0)			1		(1)	1
Total number of movements	95	70	72	69	(306)	42	173	280	102	(597)	903

1.79 per stimulation; cat 10, 72, or 1.85 per stimulation; cat 12, 69, or 1.64 per stimulation: left—cat 10, 42, or 1.36 per stimulation; cat 11, 173, or 1.75 per stimulation; cat 14, 280, or 2.14 per stimulation; cat 15, 102, or 1.96 per stimulation. Summarizing, there were from the right cortices a total of 154 successful stimulations and a total of 306 movements, or an average of 1.99 movements per stimulation, and from all left cortices a total of 397 successful stimulations and a total of 597 movements, or an average of 1.91 movements per stimulation. Combining the figures for the two sides, there were a total of 467 stimulations with a total of 903 movements, or an average of

TABLE 2

Analysis of the motor results from the stimulation of the cortices of cats 8, 9, 10, 11, 12, 14 and 15

	RIGHT					LEFT					TOTAL RIGHT AND LEFT
	Cat 8	Cat 9	Cat 10	Cat 12	Total right	Cat 10	Cat 11	Cat 14	Cat 15	Total left	
Total successful stimulations	34	39	39	42	154	41	99	131	52	313	467
Total movements produced	95	70	72	69	306	42	173	280	102	597	903
Average number of movements per stimulation.	2.79	1.79	1.85	1.64	1.99	1.36	1.75	2.14	1.96	1.91	1.95

1.95 movements per stimulation. This indicates the complexity of the cortical motor relations, but shows an approximate similarity in the complexity of results for both hemispheres. Referring to the results for the individual animals, it is seen that the relation of movement to stimulation, as shown by the figures for the average number of simple movements following the various stimulations, is subject to considerable variation in the different individuals. The only animal presenting results from two hemispheres is cat 10. A marked variation is found in the results from the two sides of this brain, for while the right gave an average of 1.85 movements per stimulation, the left gave an average of only 1.36 movements per stimulation.

For further analysis we may consider the movements of flexion

and extension of the joints of the fore and hind limbs, including the hip, but excluding the shoulder owing to complexity of the movements of this latter joint. From stimulation of the eight cortices there was a total of 441 flexions, of which 122 were from stimulation of the right side and 319 from stimulation of the left side. Comparing these with the total number of movements of all types, the flexions are 40 per cent of the activity for the right cortices and 53 per cent for the left. There was a total of 145 extensions from the eight cortices, of which 60 were from the right side and 85 from the left. Comparing these with the total number of movements of all types, from these cortices, we see that the extensions are 20 per cent of the total activity of the right and 14 per cent of the activity of the left cortices. Average for the two sides 16 per cent.

Combining the two sets of figures we find that of the total number of movements of all kinds, following stimulation of the right cortices, a total of 60 per cent is either flexion or extension of some one of the joints considered, and of the left cortices a total of 65 per cent is either flexion or extension of these joints. The flexions are slightly over three times as numerous as are the extensions, being twice as numerous on the right side and nearly four times as numerous on the left side. In cat 10 the flexions were 47 per cent of the activity of the right cortex and 76 per cent of that of the left; average for the two sides, 58 per cent. The extensions were 17 per cent on the right, and 12 per cent on the left; average for the two sides 15 per cent. Flexions and extensions together were from the right cortex 64 per cent and from the left cortex 88 per cent, for the two cortices an average as compared with the total activity, of 74 per cent.

In tables 1, 4, and 5 the first columns show the numbers of the diagrams which refer to the other data on the corresponding lines on these tables. The remainders of the tables are almost self-explanatory.

The study of the actual distributions of the cortical points, the stimulation of which results in the production of various types of body movements, brings out several interesting facts.

TABLE 3

Summary of movements of the fore and hind limbs

MOVEMENTS	RIGHT HEMISPHERE					LEFT HEMISPHERE					TOTAL RIGHT AND LEFT
	Cat 8	Cat 9	Cat 10	Cat 12	Total right	Cat 10	Cat 11	Cat 14	Cat 15	Total left	
Total movements from cortex	95	70	72	69	306	42	173	280	102	597	903
Fore limb											
Total shoulder movements	23	9	9	2	43	1	27	56	12	96	139
Total fore knee movements	12	2	4	4	22	1	16	38	16	71	93
Total fore ankle movements	12	7	4	9	32	2	11	34	2	49	81
Total movements toes fore foot	5	2		7	14		5	7	1	13	27
Total movements fore limb	52	20	17	22	111	4	59	135	31	229	340
Percentages	55	29	24	32	36	10	34	48	31	38	38
Hind limb											
Total hip movements	9	12	1	11	33	1	6	10	1	18	51
Total hind knee movements	13	10	10	10	43	7	23	42	24	96	139
Total hind ankle movements	11	8	23	5	47	19	32	47	39	137	184
Total movements toes hind foot	4	6	5	2	17	7	17	10	1	35	52
Total movements hind limb	37	36	39	28	140	34	78	109	65	286	426
Percentages	39	51	54	41	46	81	45	39	64	48	47

The protocols of the experiments performed on cats 8, 9, 10, 11, 12, 14, and 15 were analysed, and a list was made of all movements of a certain types, such as flexion of the fore knee, extension of the hind knee, etc. In this consideration the complex activities were analysed into their components, as far as was possible, and the resultant simple movements are dealt with individually. Forty-four such types of simple movement had been recorded. A diagram of the locations of the motor points for each of these types of movement was made. These diagrams are presented in figures 18 to 61. Each one of these diagrams is a composite map of the localization of points which gave certain movements in the animals which have been dealt with. There were eight cortices, four right and four left. The principal features in the motor region are given as in the previous

diagrams. The dots indicate the locations of the areas on the several hemispheres which, on stimulation, gave rise to the movement under consideration. The numerals in parentheses placed immediately without the anterior end of the coronal fissure represent the total number of such movements from the

TABLE 4
Comparative frequency of movements of the various joints

MOVEMENTS	RIGHT HEMISPHERE					LEFT HEMISPHERE					TOTAL RIGHT AND LEFT
	Cat 8	Cat 9	Cat 10	Cat 12	Total right	Cat 10	Cat 11	Cat 14	Cat 15	Total left	
Fore limb											
<i>Shoulder</i>											
18. Depression		2		1	3			7	1	8	11
19. Adduction fore limb				1	1					0	1
20. Lifting of shoulder		2			2			2		2	4
21. Abduction fore limb	3				3		1	3		4	7
22. Inward rotation fore limb		1			1		1	4		5	6
23. Outward rotation fore limb	2				2		2	2		4	6
24. Retraction of fore knee	15	4	5		24	18	27	7	52	76	76
25. Forward extension fore limb . .	3		4		7	1	5	11	4	21	28
Total shoulder movements . .	23	9	9	2	43	1	27	56	12	96	139
<i>Fore knee</i>											
26. Flexion of fore knee	6	2		1	9		10	23	10	43	52
27. Extension of fore knee	6		4	3	13	1	6	15	6	28	41
Total fore knee movements	12	2	4	4	22	1	16	38	16	71	93
<i>Fore ankle</i>											
28. Rotation fore ankle	2	1		1	4		2			2	6
29. Flexion fore ankle	6	4		1	11	1	1	18	2	22	33
30. Extension fore ankle	4	2	4	7	17	1	8	16		25	42
Total fore ankle movements . . .	12	7	4	9	32	2	11	34	2	49	81
<i>Toes of fore foot</i>											
31. Flexion toes fore foot	3				3			3		3	6
32. Extension toes fore foot	2	2		7	11		5	4	1	10	21
Total movements toes fore foot	5	2	0	7	14	0	5	7	1	13	27
Total movements for fore limb.	52	20	17	22	111	4	59	135	31	229	340

TABLE 4—Continued

MOVEMENTS	RIGHT HEMISPHERE					LEFT HEMISPHERE					TOTAL RIGHT AND LEFT
	Cat 8	Cat 9	Cat 10	Cat 12	Total right	Cat 10	Cat 11	Cat 14	Cat 15	Total left	
Hind limb											
Hip											
33. Abduction of thigh	2			8	10			1	0	1	11
34. Inward rotation of thigh. .				2	2					0	2
35. Outward rotation of thigh . .		4		1	5					0	5
36. Flexion of thigh	1	6	1		8	1	6	6	1	14	22
37. Extension of thigh	6	2			8			3		3	11
Total hip movements	9	12	1	11	33	1	6	10	1	18	51
Hind knee											
38. Flexion hind limb	12	10	10	9	41	7	22	41	24	94	135
39. Extension hind knee	1			1	2		1	1		2	4
Total hind knee movements.	13	10	10	10	43	7	23	42	24	96	139
Hind ankle											
40. Flexion hind ankle	8	6	20	3	37	19	23	40	35	117	154
41. Extension hind ankle	2		2	1	5		1	7		8	13
42. Rotation hind ankle	1	2	1	1	5		8		4	12	17
Total hind ankle movements.	11	8	23	5	47	19	32	47	39	137	184
Toes of hind foot											
43. Flexion toes hind foot	4	5	3	1	13	4	13	8	1	26	39
44. Extension toes hind foot.... .		1	2	1	4	3	4	2		9	13
Total movements toes of hind foot	4	6	5	2	17	7	17	10	1	35	52
Total movements of hind limbs . .	37	36	39	28	140	34	78	109	65	286	426
Summary											
Total movements of all types. . .	95	70	72	69	306	42	173	280	102	597	903
Total movements of fore limb. . .	52	20	17	22	111	4	59	135	31	229	340
Total movements of hind limb . .	37	36	39	28	140	34	78	109	65	286	426
Per cent for fore limb	55	29	24	32	36	10	34	48	30	38	38
Per cent for hind limb	39	51	54	41	46	81	45	39	64	48	47

four cortices The larger numerals correspond with those given in table 1, in which are enumerated the different types of movement, and the actual number of each type resulting from the stimulation of the brain of each animal as well as the totals.

TABLE 5

Comparative frequency of flexions and extensions of the joints of the limbs

MOVEMENTS	RIGHT HEMISPHERE					LEFT HEMISPHERE					TOTAL RIGHT AND LEFT
	Cat 8	Cat 9	Cat 10	Cat 12	Total right	Cat 10	Cat 11	Cat 14	Cat 15	Total left	
26 Flexion fore knee....	6	2		1	9		10	23	10	43	52
29. Flexion fore ankle	6	4		1	11	1	1	18	2	22	33
31. Flexion toes fore foot	3				3			3		3	6
Total flexion fore limb.	15	6		2	23	1	11	44	12	68	91
36. Flexion thigh	1	6	1		8	1	6	6	1	14	22
38. Flexion hind knee	12	10	10	9	41	7	22	41	24	94	135
40. Flexion hind ankle	8	6	20	3	37	19	23	40	35	117	154
43. Flexion toes hind foot	4	5	3	1	13	4	13	8	1	26	39
Total flexion hind limb	25	27	34	13	99	31	64	95	61	251	350
Total flexions both limbs.	40	33	34	15	122	32	75	139	73	319	441
27. Extension fore knee	6		4	3	13	1	6	15	6	28	41
30. Extension fore ankle	4	2	4	7	17	1	8	16		25	42
32. Extension toes fore foot	2	2		7	11		5	4	1	10	21
Total extensions fore limb	12	4	8	17	41	2	19	35	7	63	104
37. Extension thigh	6	2			8			3		3	11
39. Extension hind knee	1			1	2		1	1		2	4
41. Extension hind ankle	2		2	1	5		1	7		8	13
44. Extension toes hind foot		1	2	1	4	3	4	2		9	13
Total extensions hind limb.	9	3	4	3	19	3	6	13		22	41
Total extensions both limbs	21	7	12	20	60	5	25	48	7	85	145
Total movements of all types.	95	70	72	69	306	42	173	280	102	597	903
Percentage of extensions of fore and hind limbs.	22	10	17	29	20	12	14	17	7	14	16
Percentage of flexions of fore and hind limbs	42	47	47	22	40	76	43	50	72	53	49

It is seen that there is considerable variation in the distribution, not only of the stimuable points in the composite map for the two sides, but even for the location of the general fields on the two sides. To a certain degree, the locations of the fields on the two sides do correspond for certain types of movement, but

for many of the types the fields on the two sides appear to have little relation to each other. An excellent example is given in figure 28, which shows the locations for rotation of the fore limb. On the left cortex, the field for outward rotation is adjacent to and external to the outer end of the crucial sulcus, while on the right side it is close to the anterior angle of the lateral fissure. The field for inward rotation of the fore limb, figure 22, is shown to be adjacent to and external to the end of the crucial sulcus on the left side, and near the upper end of the supraorbital fissure on the right side. The field for flexion of the toes of the hind foot, figure 43, on the right side, is in the region adjacent to the crucial sulcus, on the left in the region about the anterior end of the lateral fissure. The field for movements of the mandible, figure 48, is, on the right side, between the outer end of the crucial and the anterior end of the lateral fissure, on the left side it is internal to the upper end of the supraorbitalis. The field for retraction of the tongue, figure 50, has a distribution on the two sides similar to that for the movements of the mandible. The field for sideward movements of the tail, figure 59, is, on the right, immediately posterior to the inner end of the crucial sulcus and immediately anterior to the outer end, but on the left it is between the outer half of the crucial and the anterior limb of the lateral.

On the other hand, for certain types of movement, the cortical fields are quite symmetrically placed on the two sides. The following examples of such symmetrically placed fields may be mentioned: The field for retraction of the elbow, figure 24, occupies, on the right and left sides, the area bounded by the coronal, supraorbital and anterior limb of the lateral fissure. The field for extension of the fore knee, figure 27, from the middle of the crucial sulcus on both banks to the coronal fissure, in a wedge shaped area. The field for flexion of the toes of the hind foot, figure 43, adjacent to the crucial sulcus on both banks and to the anterior limb of the lateral fissure. The field for movements of the eye, figure 45, internal to the supraorbital fissure. The field for movements of the lips, figure 47, same as for movements of the eyes.

FIGS. 18 TO 31

The very wide distribution of the fields for certain types of movements is at once noted on inspection of the diagrams. For example, the field for flexion of the hind knee, figure 38, occupies

FIGS. 32 TO 41

practically the posterior three-fifths of the entire motor field on the left and the posterior two-fifths of the total motor field on the right. Flexion of the hind ankle, figure 40, is obtained from numerous points scattered thickly over the entire motor

field on either side. Retraction of the elbow, figure 24, is obtained from a field bounded by the coronal and supraorbital fissures and by the anterior limb of the lateral fissure.

FIGS 42 TO 51

The great number of points producing reactions of certain kinds and the wide distribution of such points on the cerebral surface probably indicate the frequent demand for that particular type of movement in the daily life of the individual and the

FIGS. 52 TO 61.

FIGS. 18 TO 61. These figures show the location of the individual points on the right and left cortices, each figure representing results from eight hemispheres. The complex movements were analyzed for this purpose into component segmental terms. For description of the method see the text. The movements are tabulated in table 1, to which reference is to be made for the determination of the kinds of movements which are localized in the diagrams. The large figure with each illustration is that referring to the diagram (and to a corresponding number in the first columns of tables, 4 and 5), the smaller figures in parentheses give the total number of movements of the particular type in the four hemispheres stimulated.

In the figures, posterior is above, anterior is below; the left hemisphere is at the right of each figure, and the right hemisphere is at the left. The lines represent certain fissures. These are lettered in figure 18 as a key, the designations being as follows: *A*, longitudinal fissure; *B*, crucial fissure; *C*, supraorbital fissure; *D*, lateral fissure, *E*, coronal fissure.

frequent combination of such types of movement in the production of certain forms of activity, which are in constant demand in the individual's reaction to his complex environment.

ANALYSIS OF THE RESULTS OBTAINED FROM STIMULATION OF THE
EXTRA-MOTOR CORTEX

In each of the animals studied investigation was made of results of irritations of other portions of the cerebral cortex, lying outside of the boundaries of what we believe to be the true motor field. These extra-motor fields are the readily approached anterior, superior and lateral aspects. It was found that usually there was no response from stimulation with the ordinary strength of current for a moderate time. With an increased strength of current, or with an application for a longer time, a total of fifty-nine responses was obtained. From study of these the following observations are made:

1. A stronger current or longer application was required than for stimulation of the motor cortex.

2. The latent period of the movement, when a movement was obtained, was always longer than for cortical motor stimulation. Frequently the latent period was three or four times as long as that of movements resulting from the stimulation of the "primary" motor cortex.

3. As far as inspection could determine, the movements which were produced were as functionally perfect as were movements produced by stimulation of the motor cortex.

4. The movements involved more restricted portions of the body musculature than did movements from motor cortex stimulation, and they frequently were of a so-called vegetative nature, that is they involved mechanisms whose activities are for the carrying on of respiration, or jaw and tongue movements, such as are encountered in mastication.

5. When analysed, the fifty-nine responses were found to include a total of seventy-three simple movements, of which only twenty-eight involved the contra-lateral side of the body alone, one the homolateral side alone, and thirty-four involved

FIG 62. The location of cortical areas outside of the crucial area which give motor results on prolonged or strong stimulation. Areas of circles correspond with movements of respiration acceleration, those of dots with respiration inhibition. The area of horizontal lines gave movements of the hind leg and tail. The area marked with crosses gave movements of the face. The area indicated by broken lines opposite the crucial sulcus gave movements of the fore leg.

In the figure, posterior is above, anterior below. The fissures are lettered as follows: A, longitudinal fissure; B, lateral fissure; C, supra-Sylvian fissure; D, crucial fissure.

both sides. This is a very high percentage of bilateral activity and can indicate either that the extra-motor areas are functionally in connection with the motor areas of both sides of the brain, in other words are bilateral in their control, or that the mechanisms which are involved are so intimately bilateral that control may be present in both sides of the cerebrum. The general distribution of the stimuable extra-motor areas is given in figure 62.

TABLE 6
Summary of movements obtained from extra-motor stimulations

	CONTRA- LATERAL	HOMOLAT- ERAL	BILATERAL
Eye movements	10	1	8
Pupil changes.			7
Fore foot movements	12		
Hind foot movements	5		
Hind knee movements..... .	1		
Face movements..... .			3
Lip movements			4
Jaw movements			2
Tail movements			2
Ear movements..... .			1
Changes of respiration:			
Stoppage:			
Inspiratory			5
Expiratory..... .			0
Hastening or deepening.. . . .			2
	28	1	34

Figure 62 is a diagram presenting a record of the combined results obtained from the stimulation of the extra-motor regions of the cortices of cats 19, 20, 21, 24, 25, 26, and 27. The hemisphere investigated in each case, except that of cat 19, was the left, and since the results obtained from the investigation of cat 19 were similar to the results from the other animals they were included in the composite diagram of the left cortices of the other animals for the purpose of simplification. The areas represented in this diagram indicate only the total extent of the fields from which the various types of movement were initiated

by stimulation of the seven hemispheres. No attempt has been made to present the average field or to indicate the differences in the animals, which in this respect were very great.

The results of these tests may be compared with the results reported by Ferrier. It is seen that there is considerable similarity in the two series of results. For example, the field for the eye movements is almost coextensive in the two diagrams. Movements of the face region are from an area similarly located in the diagrams, immediately external to the anterior portion of the lateral fissure, though considerably more extensive according to Ferrier than is indicated by the present results. Ferrier's results from stimulation of the true motor region are, so far as they are given, identical with those here obtained.

Of the regions here referred to as "extra-motor," that lying adjacent to and between the longitudinal portion of the lateral and supra-Sylvian fissures give movements of the eyes in both Ferrier's and my experiments. Certain movements of respiration, which are found from stimulation of the banks of the supra-Sylvian region, are not mentioned by Ferrier. In both series, the region lying between the posterior portion of the coronal fissure and the anterior extremity of the supra-Sylvian fissure gives movements of the face area. Ferrier obtained no movements of the hind limb from the region external to the posterior portion of the coronal fissure, while in the present series of experiments such responses were frequently obtained. Ferrier secured a very extensive exposure of Sylvian area, and obtained motor responses of the lips, mouth and nose by stimulation in that region. No attempt was made in my experiments to expose this region and consequently a comparison cannot be made other than to say that the extra-motor field for these movements ran from the coronal fissure outward in such a direction that if further exposure had been made it seems probable that Ferrier's results would have been confirmed.

The probable reason for the consideration of these areas as truly motor by Ferrier, was his failure to recognize and distinguish between what we believe, as a result of careful and more recent histological and physiological methods, is a true motor

field, and what we believe are areas influencing the true motor fields. In the present series of experiments, note was taken of the comparative strengths of current and durations of stimulation needed in the various areas investigated. It was found, as previously mentioned, that from stimulation of points on the cortex outside of the sigmoid area either a longer application or a stronger current, or both, was required to obtain motor reaction than for successful stimulation of the sigmoid or true motor areas.

THE EFFECT OF SIMULTANEOUS OR SUCCESSIVE STIMULATIONS AT
A MOTOR AND AN EXTRA-MOTOR POINT ON THE
CEREBRAL CORTEX

On the brains of three animals there was investigated the effect of stimulating a point in the motor region of the cortex and, without discontinuing this stimulation, of adding a second stimulation at some point on the extra-motor cortex. A kymographic record was taken of the responses, and the following observations made: If a current of moderate strength is applied to the motor areas, and this stimulus be continued for a time, a clonic discharge is manifested in the appropriate muscles. If, while continuing stimulation at the point within the motor cortex, another current of similar strength is applied to some point in the extra-motor cortex, the clonus is at once steadied to a tonus (see figs. 63 and 68). Removal of the first current, while continuing the second current, is at once followed by commencing relaxation of the muscles involved, but the relaxation is very much retarded by the presence of the extra-motor stimulation (see fig. 65). In the relaxation following the removal of the stimulus to the motor region, when this stimulus has alone been applied, there is usually a slight tendency to after-movement. The after effect is likewise present, but to a less degree, when an extra-motor stimulus is kept applied, during the relaxation stage (see fig. 63).

The extra-motor stimulus, judging from these results, is able to exert a steadying influence on the motor discharge, such as

would tend to make the movement more constant in its nature. It was unable, in the strength used, either to initiate movements of its own or to maintain activities initiated by direct stimulation of the motor cortex.

Examples of the myograms obtained by the above given methods of stimulation of the motor and extra-motor cortex, are presented in figures 63, 64, 65, 66, 67, 68, and 69.

FIGS. 63, 64, 65, 66, 67, 68, and 69. Curves showing the effects of stimulating a "motor" point and the simultaneous or successive stimulation of a point within the so-called "extra-motor" region. The figures have been reproduced from tracings of the kymograph records. The broad black parts of the lower two lines of each figure show the time of application of the stimulus to the motor area (indicated by m) and to the extra motor region (indicated by em). For description of the results see the text

The extra-motor regions investigated with regard to the effect of applying a stimulus to a point within them simultaneously with the application of a similar stimulus to some point on the motor cortex were those areas lying internal to the anterior half of the main limb of the lateral fissure and external to the ansate fissure in cat 36, and a similar location on the brain of

cat 37. From the stimulation of each of these fields positive motor results were obtained, though differing considerably, both in degree and in nature, for even successive tests of the same pair of points in the motor and extra-motor regions.

While in general the results have exhibited only controlling or steadying action by the simultaneous extra-motor stimulation, it should be mentioned that some of the results indicate the possibility, or even probability, of an augmenting influence by the addition of such an extra-motor stimulus. An example of such effect is presented in the tracing of the myogram for the stimulation applied to two such points on the cortex of cat 36, as shown in figure 67.

There is frequently a retardation of the muscular relaxation when there is present, or there is added, an extra-motor stimulation during the period immediately following the discontinuance of the stimulus to the motor cortex (figs. 63, 64, and 65). The addition of the extra-motor stimulus also frequently results in a decrease of clonic activity, resulting from the continuance of a motor stimulus (figs. 63, 66, and 68). The addition of, or the presence of, an extra-motor stimulus was never found to cause an abnormal continuance of activity initiated by a stimulation applied to a point within the motor cortex, although it was usually able to cause a retardation of the relaxation time, when the motor current was discontinued. In nearly all cases, the curves showed a commencing relaxation immediately following the removal of the motor current, even though a comparatively strong current was applied to some point of the extra-motor cortex.

A satisfactory explanation for the influence of the stimulation of the extra-motor regions, upon the activity of the motor regions, is not at hand. The actual explanation cannot be definitely stated until further work on the nervous system has been done, and until some of the at present imperfectly understood connections are definitely learned. It may, however, be stated that the exertion of an inhibiting, exaggerating, or steadying influence can be accounted for in one of several ways: (a) the extra-motor areas may exert such influence by direct connections with

the motor cortex by associational fibers; (b) there may be mutual connections of the two regions by means of fibers running to the basal ganglia, such as the lenticular, or the caudate nuclei, or the optic thalamus; (c) efferent fibers passing to the cerebellum, from the two regions, may mediate the control there; (d) efferent fibers, from the extra-motor regions, passing into the spinal cord to the spinal cell centers, may be responsible.

It seems most likely that the extra-motor influence is like that of the efferent elements in the spinal cord upon the activity and tonus of muscles, innervated by cells in corresponding spinal segments.

COMPARISON OF THE PERIOD OF LATENCY FROM STIMULATION OF POINTS ON THE CORTEX AND POINTS JUST UNDER THE CORTEX

In three animals stimuli were applied to various points on the cortex within the motor area, and records were made of the reactions. From these there were determined the times between the beginning of the stimulation and the resulting movements, i.e., the latent periods. After these records were made, for each of the points chosen, the cortex at that particular area was removed with a sharp pair of hair-pointed scissors and as soon as the slight hemorrhage was controlled, the tissue underneath was similarly stimulated to determine if there was a change in the duration of this period. The tissue removed was about 2 mm. square and of about the same thickness. The time interval was unfortunately not measured in terms of seconds or parts of seconds, but in terms of vibrations of the primary coil of the inductorium, which was used for stimulation. While it is not certain that this vibration remained constant in all tests, it is certain that it was reasonably constant for the tests on each animal. The comparison of the latencies is, therefore, possible although not in parts of a second. The following table (table 7) gives the results of these tests. On the brain of each animal the number of stimuable points differed, and at times more subcortical than cortical stimuli were given at one point. The table shows the number of stimuli, the aver-

age duration in vibration rate for the cortical and subcortical, and the percentage relations, i.e., the subcortical average divided by the longer cortical.

The results of this part of the work are not conclusive and are given at this time because of their suggestive value, rather than their power of explanation. In comparison with the results here recorded it is of interest to note that in cat 24 the average cortical latent period, in ten tests, was 30.9 vibrations.

TABLE 7
Comparison of latency of movement for cortical and subcortical points

CAT	CORTICAL		SUBCORTICAL		PER CENT SUBCORTICAL
	Number of stimulations	Average latency	Number of stimulations	Average latency	CORTICAL
26	20	10 7 v.	45	6 3 v.	59
27	29	28 5 v.	30	22 1 v.	78
32	44	21 5 v.	51	18 9 v.	88

The table shows that the latency of the subcortical stimulations was approximately 75 per cent of the latency of the stimulations of the cortex. In addition to these relations the following observations were made of the cortical and the subcortical reactions. The amount of current needed for the stimulation of the cortical and of the subcortical tissue was approximately the same. The character of the reactions and the fatiguability of the two tissues was not noticeably different.

It will be observed that the latent periods for the cortical stimulation vary considerably in the different animals, the difference between the shortest and the longest periods being nearly 200 per cent. Similar variations in the latent periods for subcortical stimulations were also found, but a comparison of the results in cats 26, 27, and 32 shows that in every case the average subcortical latency is less than that of the cortical. The table gives the results in percentages and shows that the difference is not the same for all animals, in cat 26 the subcortical latency being about 40 per cent less than the cortical latency, while in cat 32 the difference is only about 12 per cent.

Whether or not the greater delay in cortical stimulation is due

to the extra space or to more synaptic connections which are traversed is not sure, but the great differences would rather indicate the latter condition. One other matter should be briefly considered, viz., the probability that the subcortical tissue may have become more excitable than the cortical, on account of the injury with its resultant loss of blood and washing with normal salt solution. This is a possible explanation for such results, but this explanation is not certainly warranted in view of the similarities in irritability, as measured by current strength necessary to produce a reaction, which were obtained. It should be noted that the subcortical stimuli were given always after the cortical (a condition imposed by the nature of the experiment) and the stimuli, if a fatigue effect for the first tests was present, should have resulted in a longer latent period for the subcortical stimuli. The time of the latent period for subcortical stimuli, even in view of a possible retarding fatigue effect, was shorter and this is a further indication that this is not a casual result. A comparison of the latencies for the corresponding cerebral points, cortical and subcortical, is also instructive with respect to the differences. In a few cases the subcortical latencies were greater than the corresponding cortical, but not frequently.

One further qualification should be made with respect to the method and results. Although an effort was made to stimulate the subcortical tissue immediately below a certain cortical point which was selected, it was (and is) impossible to be certain that this was accurately done. Assuming, however, that the tissue immediately below the cortex was stimulated, it is not possible to say that the fibers for the same overlying cells were stimulated. One fact is, however, especially noteworthy. This is that the subcortical stimulation, as a rule, resulted in a movement of the same muscles as those from the cortical stimulation.

It was noted that in many cases there is considerable after-movement following the discontinuance of the stimulation. This is true both for cortical and subcortical stimulation. Such a result for subcortical stimulation is rather surprising in view of the statement of François-Franck that stimulation of the corona radiata results in motor reactions which cease immediately after

the discontinuance of the stimulation and that stimuli at these points are not followed by after-movement. A condition similar to that mentioned by François-Franck would be expected from stimulation of the subcortical tissue. The absence of it indicates a very close (and perhaps frequent) connection between the cortex and the immediately underlying tissue, a connection even closer than the connection between the cortex and the corona radiata.

The presence of after-movement in the contractions resulting from the stimulation of the subcortical tissues in the cat may, however, be due to the fact that the cat is lower in the scale than the monkeys with which François-Franck worked, and that in the cat the dependence of the lower centers is not so marked. It may then be that the lower centers once set into activity are capable of continuing their motor discharges for a certain time, in the form of after-movement in the cat while in the monkey the dependence of the lower centers is such that they cease activity immediately on the discontinuance of the discharges from the higher centers. This presupposes that the after-movement present from the stimulation of the intact cortex of the monkey is a purely cortical phenomenon. A somewhat similar amount of independence of the cortex and the subcortical parts in the dog, as compared with the monkey, is indicated in the relative ease of recovery of the dog and the relative difficulty of recovery in the monkey after the experimental production of a cortical hemiplegia.

MOTOR REACTIONS FROM STIMULATION OF THE CORPUS CALLOSUM AND THE CORONA RADIATA

Tests of the irritability of the corpus callosum and the corona radiata in cats 18, 21, 26, 27, and 32 were performed as follows: The superior surface of the cortex of the left hemisphere was removed in a long wedge-shaped strip, extending from the occipital pole to the superior end of the supraorbital fissure and from the lateral fissure to a line projected posteriorly from the outermost portion of the coronal fissure. The tissue re-

moved was sufficiently thick to include the roof of the lateral ventricle. This method of approach was adopted in order to secure as complete an exposure of the corpus callosum and corona radiata as possible. By such an approach the corpus callosum was severed antero-posteriorly throughout its whole extent. The portion of the corona radiata laid bare included most of the tissue underlying the motor cortex and a large part of that underlying the extra-motor regions of the superior and lateral portions of the hemisphere.

The tests of irritability were carried out as soon as the hemorrhage, which was sometimes considerable, was arrested by packing lightly with surgical gauze. The same method of recording

TABLE 8

Results of stimulation of corpus callosum. General distribution of stimuable areas, the portions of the corpus callosum in the table being related to the movements mentioned

CAT	MOVEMENTS			RESPIRATION	
	Hind limb	Fore limb	Head and neck	Inspiration	Expiration
18		Mid. $\frac{1}{3}$	Ant. $\frac{1}{3}$		
21	Ant. $\frac{1}{3}$	Ant. $\frac{1}{3}$	Ant. $\frac{1}{3}$		
26	Ant. $\frac{1}{2}$	Ant. $\frac{1}{2}$	Ant. $\frac{1}{3}$	Mid. $\frac{1}{3}$	
27		Ant. $\frac{1}{2}$	Ant. $\frac{1}{2}$		Ant. $\frac{1}{3}$
32	Ant. $\frac{1}{3}$	Ant. $\frac{2}{3}$	Ant. $\frac{1}{3}$	Post. $\frac{1}{3}$	M d. $\frac{1}{3}$

results was used as in the tests of irritability of the surface. It may be said that most of the animals used for the investigations of the irritability of the corpus callosum and corona radiata were first used for a short time for the investigation of the surface irritability. The first stimulations applied to the exposed tissue of the corpus callosum were by means of a very weak current, which was gradually increased to an amount just sufficient to produce reaction, an effort being made to use as weak a current as possible to prevent unnecessary fatigue of the tissue.

The accompanying table (table 8) presents the summary of the results from the stimulation of the various portions of the corpus callosum and table 9 gives the summary of results ob-

tained from the stimulation of the corona radiata. In table 8 it is seen that the results from the stimulation of the corpus callosum are fairly constant in the different animals, although the extents of the area for the various types of muscular activity differ slightly from animal to animal. For example, movements of the hind limb resulted from stimulation of the anterior third of the corpus callosum in cats 21 and 32, and from the anterior half in cat 26. Movements of the fore limb resulted from the stimulation of the anterior third in cat 21, from the anterior half in cats 26 and 27, from the anterior two-thirds in cat 32, and from the middle third in cat 18.

The area most responsive to stimulation was the anterior half, although in cats 18, 26, and 32 reactions were obtained from all the structure, excepting the posterior fifth. The richness of reaction from stimulation of the anterior portion is to be accounted for by its nearness to the motor area and the consequent richer supply of fibers passing presumably between the motor areas of the two sides. It is to be noted that the most of the movements produced by stimulation of the corpus callosum were of the muscles of the right side of the body, while the left end of the corpus callosum was exposed. The explanation of this is not clear, but it is probably due to the fact that the fibers producing the reactions are not members of the usual motor efferent system, but are normally used to convey impulses from the left cortex to associated motor mechanisms of the right cortex. It is as yet impossible to say what their actual course is. Further study of the motor cerebral control of the cat is necessary to explain this matter.

The area of the exposed tissue of the corona radiata yielding the most satisfactory results was that portion of the structure underlying the motor cortex and extending posteriorly close to the anterior half of the corpus callosum. This is probably due to the passage of the previously mentioned motor associational fibers from the motor cortex to the corpus callosum, and thence to the other hemisphere. The actual forms of movement produced from the stimulation of the corona radiata were in many cases similar to the activity produced by stimulation of the

immediately overlying motor cells. A second area yielding motor reactions was found under that portion of the cortex in the region extending from the anterior bank of the postlateral fissure outwards and forwards to the superior extremity of the

TABLE 9

Summary of results from the stimulation of the corona radiata. General distribution of stimuable areas

CATS	
Movements of the hind limb	
18	None
21	Close to the under portion of the middle third of corpus callosum, and anteriorly under the post-crucial area
26	None
27	None
32	Close to the anterior third of the corpus callosum
Movements of the fore limb	
18	None
21	Close to the middle third of the corpus, and under all of the surface motor area
26	Under the surface area about the crucial sulcus
27	Same
32	Under the post crucial area
Movements of the head and neck	
18	None
21	Close to the middle third of the corpus, and along the outer margin of the posterior one-third of the exposed field
26	Close to the under surface of all the corpus and under the crucial area
27	Under the inner part of the anterior section of the motor area
32	Under the inner part of the motor area
Movements of respiration	
	Inspiratory:
18	None
21	A few points near the middle third of corpus
26	None
27	Under the anterior portion of the motor field
32	Above the posterior one-third of corpus
	Expiratory:
	None
	Numerous points opposite the middle third of the corpus
	None
	None
	Above the posterior one-third of corpus

ecto-Sylvian fissure. A third and less frequently found field is situated under the region of the surface lying external to the median portion of the supra-Sylvian fissure. The movements obtained from stimulation within these fields were as functionally perfect as movements produced by stimulation of the motor areas of the surface. They involved movements of each side of the body and sometimes of both sides.

From stimulation both of the corpus callosum and of the corona radiata a large number of responses included a change in the depth or rate of the respiratory movements.

GENERAL SUMMARY

Superficial motor cortex. 1. The general area of motor control in the cortex of the cat extends from the fissura coronalis, on either side, to the mid-line, and about 5 cm. over the margin of the mid-line on to that portion of the mesial surface of the hemisphere back of the sulcus crucialis. It extends from a point about 0.5 cm. above the upper margin of the olfactory lobe backwards to the union of the posterior end of the fissura coronalis with the anterior end of the fissura lateralis. It extends well to the bottom of the sulcus crucialis on both banks.

2. The area for control of the hind-limb and tail extends over the posterior three-fourths of this area, being richest in the area from the sulcus crucialis backwards. The area between the ansate fissure and the median line is almost entirely for control of the hind-limb.

3. The area for motor control of the fore-limb includes that between the inner end of the ansate fissure and the sulcus coronalis, back of the sulcus crucialis, and the area immediately in front of the sulcus crucialis extending downwards to the anterior end of the fissura coronalis.

4. The area for control of the neck lies anterior to the sulcus crucialis and downward to a point about 0.5 cm. above the upper margin of the olfactory lobe.

5. The area for the control of the nose, mouth and tongue lies around the superior end of the fissura supraorbitalis. Stimula-

tion of the various points in the area for control of these latter movements give bilateral movements which are well coördinated and purposeful in nature. A similar result is found from scattered stimulations from various places controlling movements of the limbs.

6. The area outside of the fissura coronalis is practically barren of results from stimulation.

Banks of the sulci cruciales. 7. The anterior and posterior banks of the crucial sulci give reactions which are not quite so widespread over the body musculature as are those from stimulation of the surfaces of the hemispheres, but which are coördinated equally as well for those members which they do involve. The anterior bank controls movements of the tongue, mouth, throat, neck, eyes, pupils and fore feet. The posterior bank controls movements of the tongue, mouth, eyes, face and ears and fore and hind limbs.

Variability of motor control. 8. Analysis of the results from stimulation of the cortices of cats 8, 9, 10, 11, 12, 14, and 15 as to the types of movement included in the responses indicates a considerable degree of complexity in the cortical representations for the activities of the muscles. When analysed into their simpler component parts it is found that the average response to each stimulation applied to the right cortex included 1.99 simple movements, and of the left cortex 1.95 simple movements. This is subject to considerable variation in the individual animals, as shown by the results for cat 8, right hemisphere, of 2.79 and for cat 10, left hemisphere, of 1.36 movements per stimulation. It is subject to considerable variation even in the responses from the two hemispheres of the same animal, as shown in the case of cat 10. The average number of simple movements per stimulation of the right cortex of this animal was 1.85; and 1.36 for the left cortex.

9. Comparison of the frequency of the various types of movements of the joints of the limbs indicates that on the right side an average of 82 per cent and on the left side an average of 86 per cent of the total cortical responses were movements of some type of the joints of either fore or hind limb. As to the relative

frequency of the involvement of the two limbs, for the right side an average of 36 per cent, and for the left side an average of 38 per cent of the responses were movements of the fore limb. On the right side an average of 41 per cent and on the left side an average of 47 per cent were movements of the hind limb. This indicates, when the figures are combined, that there is a slightly greater cortical representation for movements of the hind limb than for movements of the fore limb.

10. Considering the frequency of movements, involving the various joints, it is seen that the joint most frequently involved is the right hind ankle (137 movements), and the next most frequent the right hind knee or right shoulder (each 96 movements). The most frequent type of movement is flexion of the right hind ankle (117).

Extra-motor cortex. From stimulation of the readily approachable portions of the cortical surface, outside the boundaries recognized for the motor area, the following conclusions may be drawn:

11. More current or longer application of current is required to produce motor activity than is required for successful stimulation of the motor area.

12. The movements so produced are as functionally perfect as are movements produced by stimulation of the motor area.

13. The latency is always longer with stimulation of these areas.

14. The movements involve more restricted portions of the body musculature, and are most apt to involve activity of such mechanisms as respiration, pupil changes, chewing, etc.

15. About 47 per cent of the movements so produced are bilateral in their distribution and the others contralateral.

16. The stimutable extra-motor field occupies a triangular area whose apex approaches the median line near the center of the fissura lateralis, and whose base extends from slightly external to the center of the fissura coronalis, to the point where the supra-Sylvian fissure bends downward posteriorly. Stimulation of the major portion of this field results in movements of the eyes and pupils. Several small areas along the supra-Sylvian

exert influence on the respiratory movements. The anterior portion of the field, adjacent to the motor field, gives movements of the face, hind leg and fore ankle. These are similar to the results of stimulation applied to the cortex within the adjacent motor field, and it may be thought that overflow of current into the motor cells might have been the cause of such reactions, but the occurrence of motor reactions of the face from the immediately adjacent field tends to discredit this, because the portion of the motor field which controls activity of the muscles of the face does not extend over this portion of the cortex, but is confined to that region lying mainly in front of the crucial sulcus.

Simultaneous and successive stimulation of two different parts of cortex. The application of two stimulations to the cortical surface, one within the limits of the motor field, and the other at some point on the cortex outside of the motor field, discloses the following facts.

17. If the motor current be applied first the muscular contractions usually assume a clonic form. If the extra-motor current be then applied, while continuing the motor current, the clonus is sometimes steadied to a tonus. If the motor current be now discontinued the phase of relaxation at once sets in, but is much prolonged as compared with the relaxation following the removal of stimulation applied to the motor cortex alone.

18. The stimulation of a point within the extra-motor area may be said to cause this area to exert a steadying influence on the motor discharge from stimulation of the motor field, so long as stimulation of the motor area is continued, but when stimulation of the motor field is discontinued the extra-motor stimulation is unable to cause a continuance of the motor discharge at full force for even a brief period. The influence of the extra motor-field is possibly such as to cause the motor discharge to assume a more purposeful nature.

Cortical and subcortical reactions. From comparison of the motor reactions from stimulation of the motor cortex at various points, and the reactions following the removal of small pieces of the cortex at these same points, and subsequent stimulation

of the immediately underlying tissue, i.e., the most peripheral portion of motor corona radiata, the following conclusions may be drawn:

19. The latency from the subcortical point is approximately 75 per cent of the latency of the overlying cortex.

20. The amount of the current needed to excite the subcortical point is not appreciably different with the apparatus used in these experiments.

21. The character of the reactions from the two regions is practically identical. The stimulation of the subcortical point usually reacts in activity of practically the same groups of muscles as does stimulation of the cortical point.

Motor reactions from stimulations of corpus callosum and of corona radiata. The results from stimulation of the exposed end of the corpus callosum may be summarized as follows:

22. The corpus callosum is irritable to electrical stimulation except at its posterior extremity.

23. Stimulation of the anterior one-third results in movements of the hind limb usually of the crossed side, but sometimes of the hind limb of the same side.

24. Stimulation of the anterior half results in movements of the fore limb of one or the other side, usually the crossed side.

25. Stimulations of the anterior four-fifths result in movements of the head and neck, of a bilateral nature.

26. Stimulations applied to the middle two-fourths result in changes of the respiratory activity, usually causing an increase in the intake.

27. The amount of current needed for the stimulation of the exposed tissue of the corpus callosum is practically the same as for stimulation of the surface of the cortex.

28. The movements produced are as functionally perfect as are those produced by stimulation of the cortical surface and are apt to involve several joints in the same manner as do the cortical responses.

The results from stimulation of the structure of the corona radiata, exposed by removal of a long wedge-shaped strip of the cortex, may be summarized by saying that (29) motor reac-

tions followed the application of a moderate strength of current to points widely scattered over the field so exposed. The most productive area was that underlying the motor cortex and adjacent to the anterior portion of the corpus callosum.

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