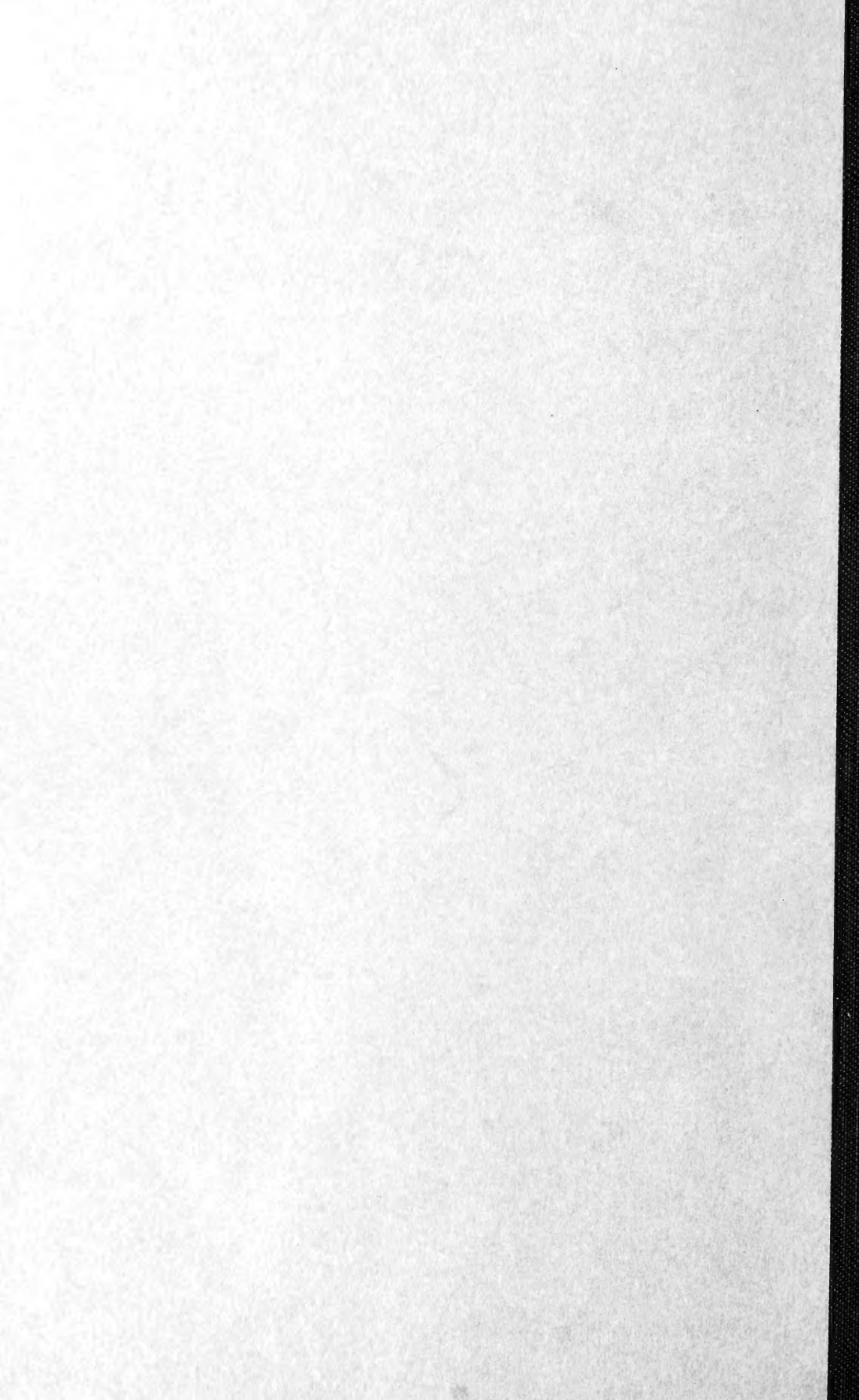




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STUDIES OF CEREBRAL FUNCTION IN LEARNING

V. THE RETENTION OF MOTOR HABITS AFTER DESTRUCTION OF THE SO-CALLED MOTOR AREAS IN PRIMATES *

K. S. LASHLEY, Ph.D.

MINNEAPOLIS

Since the area was first described by Fritsch and Hitzig,¹ the function of the electrostimulable cortex of the cerebrum has been the subject of almost continuous controversy. The experiments were immediately called in question through criticisms of the technic by Dupuy,² Sanderson,³ Carville and Duret,⁴ and others, or by abstruse metaphysical deductions such as were advanced by Hermann⁵ who objected to the motor area as violating the "unity of mind." The work of Ferrier,⁶ Carville and Duret and Hitzig soon established the fact of the electrical excitability of limited areas of the cortex, but immediately a new question arose. Fritsch and Hitzig had considered the excitable zone as motor, if we may translate the expression, "entry of single psychic functions into material" by such a term. In this they were followed by Carville and Duret, who described the motor disturbances following lesions in the area as "paralyse de la motricité volontaire corticale." Ferrier also considered the area as motor. But most of the early work had been done with dogs, and the sensory disturbances which appear in this animal after ablation of the stim-
ulable area were emphasized by Schiff,⁷ Nothnagel,⁸ Munk⁹ and

* From the Department of Psychology of the University of Minnesota.

1. Fritsch, G., and Hitzig, E.: Ueber die elektrische Erregbarkeit des Grosshirns, *Arch. f. Anat. u. Physiol.* 1870, pp. 300-332.

2. Dupuy, E.: Experiment sur les fonctions moteur du cerveau, *Compt. rend. soc. de biol.*, 1888, pp. 1025-1027.

3. Sanderson, J. B.: Note on the Excitation of the Surface of the Cerebral Hemispheres by Induced Currents, *Proc. Roy. Soc.* **22**:368-370, 1874.

4. Carville, C., and Duret, H.: Sur le fonctions des hémisphères cérébraux, *Arch. d. Physiol.* **7**:352-490, 1875.

5. Hermann, L.: Ueber elektrische Reizversuche an der Grosshirnrinde, *Arch. f. d. ges. Physiol.* **10**:77-88, 1875.

6. Ferrier, D.: *The Functions of the Brain*, London, 1876.

7. Schiff, M.: Untersuchungen über die motorischen Functionen des Grosshirns, *Arch. f. exper. Path. u. Pharmacol.* **3**:171-179, 1875.

8. Nothnagel, H.: Experimentelle Untersuchungen über die Functionen des Gehirns, *Arch. f. path. Anat. u. Physiol.* **57**:184-227, 1873.

9. Munk, H.: *Ueber die Funktionen der Grosshirnrinde*, Berlin, 1890.

Hitzig,¹⁰ who interpreted the disorders of movement variously as due to the loss of muscular and cutaneous sensitivity or to the loss of kinesthetic images of the movements to be performed.

Following the suggestion of Tamburini, Luciani and Seppili¹¹ advanced the view that the motor areas contained somesthetic projection fibers as well as motor elements, and developed a theory of the sensorimotor function of the sigmoid gyrus and rolandic areas. In this they were followed by Horsley,¹² Mott,¹³ Dana,¹⁴ Rothmann¹⁵ and many others.

De Barenne,¹⁶ in particular, has demonstrated the existence of marked sensory disturbances in the cat after application of strychnin to an area which widely overlaps the stimuable area, and the general correctness of Luciani's view for the stimuable areas of lower mammals does not seem open to question, although there may be some doubt as to whether the motor functions of the cortex in these forms are comparable with those of primates.

Recent more critical work with primates, however, shows that in them a further specialization has occurred with the development of the fissure of Rolando as a line of demarcation between centripetal and centrifugal projection areas.¹⁷ The work of Schäfer,¹⁸ Mills,¹⁹ Grün-

10. Hitzig, E.: Physiologische und klinische Untersuchungen über das Gehirn, Berlin, 1904.

11. Luciani, L., and Seppili, G.: Die Funktion-Localization auf der Grosshirnrinde, Deutsche Ausgabe, Leipzig, 1886.

12. Horsley, V.: On the Analysis of Voluntary Movement, 19th Century **29**:857-870, 1891.

13. Mott, F. W.: The Sensory-Motor Functions of the Central Convolutions of the Cerebral Cortex, J. Physiol. **15**:464-487, 1893-1894.

14. Dana, C. L.: A Study of the Functions of the Cortex of the Motor Area of the Brain, J. Nerv. & Ment. Dis. **21**:761-785, 1894.

15. Rothmann, M.: Ueber die elektrische Erregbarkeit der Zentralwindungen, Monatschr. f. Psychiat. u. Neurol. **32**:489-502, 1912.

16. Barenne, J. G. D. de: Sensory Localization in the Cerebral Cortex, Quart. J. Exper. Physiol. **9**:355-390, 1916.

17. The lack of any persistent paralysis in rodents, carnivora and ungulates after destruction of the stimuable areas and the occurrence of partial paralyses after destruction of parts of the corpus striatum in lower forms suggest that the differentiation of function of precentral and postcentral gyri in primates may be due rather to the acquisition of primitive striate functions by the cerebral cortex than to a division of cortical functions which overlap in lower forms.

18. Schäfer, E. A.: On the Alleged Sensory Functions of the Motor Cortex Cerebri, J. Physiol. **23**:310-314, 1898.

19. Mills, C. K.: The Separate Localization in the Cortex and Sub-Cortex of the Cerebrum of the Representation of Movements and of Muscular and Cutaneous Sensibility, J. Nerv. & Ment. Dis. **38**:595-619, 1901.

baum and Sherrington,²⁰ C. and O. Vogt,²¹ Lewandowsky and Simmons,²² Hoppe,²³ Cushing,²⁴ Franz,²⁵ and Leyton and Sherrington,²⁶ all points to the conclusion that primary excitability is limited to the precentral gyrus and that sensory disturbances rarely result from lesions confined to this area.

These studies have defined the centrifugal function of the cells of the precentral gyrus and have confirmed the view that the area is motor rather than somesthetic, but in spite of the fairly general recent agreement as to the location of "motor" area, there is a wide diversity of opinion concerning the significance of the "motor" function. The area is somehow concerned with the production of movement, but how it acts and what kinds of movement it controls, are still debated points. Ferrier⁶ emphasized the "automatic" character of movements after destruction of the motor areas and held that "All reactions not so (automatically) organized, and still dependent upon conscious discrimination and exercise of attentive volition are effectually and permanently annihilated." Munk²⁷ classified movements according to their somatic distribution and maintained that small unilateral adaptive movements (*Einzelbewegungen*) are permanently lost after destruction of the motor areas. His definition of these movements is by no means clear, but his accounts seem to imply that the movements had been learned, and he denies that a dog can learn to give his paw after destruction of both motor areas. Wagner²⁸ maintained that the chief function of the motor areas is in learning, and that animals deprived of them are incapable of forming any new habits. Bechterew²⁹ also refers to experiments lead-

20. Grünbaum, A., and Sherrington, C. S.: Observations on the Physiology of the Cerebral Cortex of the Anthropoid Apes, *Proc. Roy. Soc.* **72** B:152-155, 1903.

21. Vogt, C., and Vogt, O.: Zur Kenntnis der elektrisch erregbaren Hirnrindengebiete bei den Säugetieren, *J. f. Psychol. u. Neurol.* **8**:277-456, 1907.

22. Lewandowsky, M., and Simmons, A.: Zur Physiologie der vordern und hintern Zentralwindung, *Arch. f. d. ges. Physiol.* **129**:240-254, 1909.

23. Hoppe, H. H.: A Critical Study of the Sensory Functions of the Motor Zone (Pre-Rolandic Area): More Especially Stereognosis, *J. Nerv. & Ment. Dis.* **36**:513-527, 1909.

24. Cushing, H.: A Note Upon the Faradic Stimulation of the Postcentral Gyrus in Conscious Patients, *Brain* **32**:44-54, 1909.

25. Franz, S. I.: Variations in Distribution of the Motor Centers, *Psychol. Monogr.* **19**:80-162, 1915.

26. Leyton, A. S. F., and Sherrington, C. S.: Observations on the Excitable Cortex of the Chimpanzee, Orang-Outan and Gorilla, *Quart. J. Exper. Physiol.* **11**:135-222, 1917.

27. Munk, H.: Ueber die Fühlspähren der Grosshirnrinde, *Sitzungsber. d. Berlin Akad. Wiss.*, 1892, 679-723; 1893, 759-781; 1894, 823-833; 1896, 1131-1159.

28. Wagner, V.: Discussion in *Neurol. Zentralbl.* **24**:1022, 1905.

29. Bechterew, W. v.: Die Funktionen der Nervencentra, *Jena* **3**, 1911.

ing to the same conclusion. He states that after removal of the motor centers associative motor reflexes are lost. "With unilateral destruction of the motor region in dogs the associative motor reflex may be elicited in the homolateral fore-leg, but in the contralateral fore-leg the reflexes learned earlier are forever lost and can not be reestablished even after a number of conditioning associations (p. 1551ff.)." Gierlich³⁰ also supports this view of the exclusive motor function of the stimulable areas.

In opposition to these results, several writers have reported the acquisition of habits after the destruction of the motor areas or of the pyramidal tracts. Starlinger³¹ trained a dog to give his paw after total destruction of both pyramidal tracts. Rothmann³² observed learning in a rhesus monkey in which one precentral gyrus had been extirpated and the pyramidal tract of the other had been sectioned in the cervical region. Franz and Lashley³³ and Lashley³⁴ found learning ability in the rat unaltered by total destruction of the stimulable cortex. This result has been confirmed by Jellinek and Koppányi.³⁵

In the contradiction of evidence here, we must favor the positive results. Failure to learn may be due to any one of a number of factors in addition to specific destruction of tissue, and a single positive case with certain destruction of the motor area is sufficient to discredit any number of negative findings such as are cited by Bechterew and Munk. It seems quite certain that the formation of conditioned motor reflexes is possible in the absence of the electrostimulable cortex, but this fact fails to reveal the normal function of the area in the performance of complex activities. Both Rothmann and Brown³⁶ seem to believe that in the intact animal the motor areas form the chief centrifugal path for complex adaptive reactions and that when learning occurs in their absence it is to be considered as due to vicarious function of other

30. Gierlich, N.: Ueber Symptomatologie, Wesen, und Therapie der hemiplegischen Lähmung, Wiesbaden, 1913.

31. Starlinger, J.: Die durchschneidung beider Pyramiden beim Hunde, Neurol. Zentralbl. **14**:390-394, 1895.

32. Rothmann, M.: Ueber die physiologische Wertung der cortico-spinalen (Pyramiden) Bahn, Arch. f. Anat. u. Physiol. (Physiol. Abt.) pp. 217-275, 1907.

33. Franz, S. I., and Lashley, K. S.: The Retention of Habits by the Rat After Destruction of the Frontal Portion of the Cerebrum, Psychobiol. **1**:3-18, 1917.

34. Lashley, K. S.: Studies of Cerebral Function in Learning, Psychobiol. **2**:55-135, 1920.

35. Jellinek, A., and Koppányi, T.: Lernfähigkeit gehirnverletzter Ratten, Anzeiger d. Akad. d. Wiss., Wien, 1923, No. 17.

36. Brown, T. G.: Studies, XXVII. 6. The Motor Activation of Parts of the Cerebral Cortex Other Than Those Included in the So-Called "Motor" Areas in Monkeys, Quart. J. Exper. Physiol. **10**:103-143, 1916.

parts rather than as an expression of their normal function. On the basis of Brown's work and of clinical evidence, however, Monakow^{36a} is inclined to minimize the importance of the pyramidal areas for "voluntary" movement. He suggests that "We must give up or essentially modify the view that the precentral convolution alone conducts impulses to voluntary movement. It is probable that the pyramidal areas serve less for the execution of voluntary movements than for the inhibition of the kinetic functions of spinal coordination. Their function seems to be in the class of reflex activity." Lashley³⁷ has reported the survival of visuomotor habits after the complete destruction of the stimuable area and serious injury to the caudate and lenticular nuclei³⁸ and has suggested that the primary function of the stimuable area is the reflex regulation of postural and kinetic mechanisms. Similar results have since been obtained for the stimuable cortex with problem-box and maze habits.

Thus we find in the literature claims that the electrostimulable cortex is motor, that it is sensory, that it is sensorimotor, that its motor function is exercised through the storing of images of movement, that it is the final common path for all voluntary movements, and that it is a reflex center not primarily concerned with voluntary activity.

Much of the literature on the function of the electrostimulable cortex, as on cerebral localization in general, presents an inextricable tangle of physiologic fact and psychologic speculation. The long controversy between Goltz, Munk, and Hitzig was largely due to their inability to grasp each other's psychologic theories, and recent progress in psychology tends to invalidate much of the cerebral localization which was based on older conceptions of mental faculties.

Images have fallen into disrepute, and even the psychologists who still deal with them deny that kinesthetic imagery has any demonstrable relation to the initiation of movement (Thorndike³⁹). The conception of volitional activity is too vague to have any scientific value. At best it represents an indefinite distinction between more or less complexly conditioned activities, and the conception of conditioned reflexes leaves the distinction without significance. The "will" has been largely discarded in psychology, although it is still in good standing in neurologic discussions. Such a statement as that the stimuable cortex is not

36a. Monakow: See footnote 57.

37. Lashley, K. S.: Studies of Cerebral Function in Learning. The Motor Areas, *Brain* **44**:255-286, 1921.

38. When these experiments were reported, I believed that the lesions were largely confined to the caudate nuclei. Dr. J. B. Johnston has since called my attention to the fact that the caudate nucleus in the rat comprises only a narrow median band in the corpus striatum and that the lesions reported actually included a considerable portion of the lenticular nucleus.

39. Thorndike, E. L.: The Mental Antecedents of Voluntary Movement, *J. Philos., Psychol. and Sc. Meth.* **4**:40-42, 1907.

motor, but "psychomotor," means no more than that the pyramidal cells excite patterns of spinal motor cells rather than individual cells. It contributes nothing to our understanding of cerebral function. In the present state of psychologic science, we can not do better than follow the dictum of Bubnoff and Heidenhain,⁴⁰ "Es will uns überhaupt scheinen als müste die Untersuchung der physiologischen Prozesse in dem Gehirn von den jene Vorgänge begleitenden Bewusstseinsvorgängen möglichst absehen, wenn es sich um eine Deutung physischen Geschehens handelt," and rigidly exclude from neurologic discussion every subjective concept which cannot be translated into objective terms.

There is no evidence for the localization of any "mental function" in any part of the cerebrum. All that can be concluded from the existing evidence is that the conducting pathways concerned in particular kinds of behavior lead from receptor to effector through certain cerebral areas. Cerebral motor localization is a problem of the origin and function of the centrifugal neural impulses of the cortex. Their "volitional" or "automatic" character can be defined only in terms of their complexity of organization and their relative importance in the total motor integration or kinetic melody, and until so defined the terms are meaningless. The "reflex" conception of cerebral function, although still a theory and notably inadequate to account for all the phenomena of cerebral function because of oversimplification in its formulations,⁴¹ is too well supported by evidence on nerve conduction and analogy with spinal functions to be disregarded in favor of any speculations concerning the localization of "psychic" functions.

STATEMENT OF PROBLEM

Stated objectively, three mutually incompatible theories concerning the function of the precentral gyrus are to be found in the current literature. They are: 1. This area is the only centrifugal outlet from the cerebral cortex for complexly integrated movements or for movements acquired as a result of training (voluntary movements or conditioned reflexes). 2. In the intact animal, the Betz cells are the principle centrifugal paths, but some neural impulses of like function may descend by extrapyramidal tracts, and these tracts may assume vicariously all the functions of the motor area. 3. The motor area is a part of the mechanism functioning in the regulation of tonus and posture and is not directly concerned in conditioned reflex activity.

40. Bubnoff, N., and Heidenhain, R.: Ueber Erregungs- und Hemmungsvorgänge innerhalb der motorischen Hirncentren, *Arch. f. d. ges. Physiol.* **26**: 137-200, 1881.

41. The data on direct adaptation of unpracticed organs to the solution of problem-boxes presented later in this paper seem wholly inexplicable in terms of simple conditioned reflexes.

The first of these views is definitely ruled out by the evidence cited above for habit formation after destruction of the areas. The evidence for the second and third views, as applied to primates, is inconclusive, although a considerable mass of evidence derived from the cerebral paralyses seems to support the second. The validity of this evidence will be considered after the experimental data are presented.

A simple test of the hypotheses is possible. If after total destruction of the precentral areas an animal shows undiminished ability to carry out activities of all degrees of complexity, acquired before the operative destruction, this will be conclusive evidence that the lesion did not destroy any part of the conditioned reflex arcs involved in the activities, and, as a corollary, that these arcs do not traverse the motor areas. Loss of the conditioned reflexes following the lesion with their later reestablishment through training will support the second view, that the pyramidal cells of the precentral region are the principal efferent paths involved in habitual movements.

Such a test was made with the rat and gave unmistakable evidence against the participation of the motor areas in the activities of the simple maze and visual discrimination box (Franz and Lashley,³³ Lashley³⁷). Since the publication of that report, the results have been confirmed for a complex maze and the "double-platform box." As the rat shows no paralysis after lesions to the stimulable areas alone, it is not possible to generalize from it to higher forms which do develop a paralysis. I have therefore repeated the tests in a series of experiments with monkeys.

EXPERIMENTAL METHODS

The paralysis which follows lesions to the precentral gyrus in monkeys necessitates a modification of the technic used with the rat. The general procedure was as follows: The animals were trained in rather simple manipulative acts involving a new and easily recognizable pattern and sequence of movements. They were then kept without practice for about two months, at the end of which time their retention of the habits was tested. This gave a measure of the normal loss to be expected from disuse of the habits over a period equal to that required for recovery from cerebral paralysis. After these *preliminary retention tests*, the motor areas were destroyed. The animals were then kept without further practice in the habits until the paralysis was so far improved that they were judged capable of making the movements required. They were then given a final series of retention tests (*post-operative retention tests*) and brought to necropsy.

Training Methods.—For training, the familiar problem-box method was used. The animals were confined in a large cage, 5 by 5 feet, to

the floor of which a small problem-box containing food was bolted. Three problem-boxes were used:

1. Pull box. The animal must reach through a circular hole, 2 inches in diameter, grasp and pull forward a rod which passed transversely 3 inches behind the hole. This released the lid of the box, which was thrown open by a spring.

2. Crank box. The animal must grasp and turn a crank projecting from the front of the box. The crank handle described a 6 inch circle. It offered a resistance of about 200 gm. at all points of the circle. It was set at "one o'clock" and must be turned counter-clockwise through 270 degrees, at which point it released the lid of the box. The lid was thrown back by a spring.

3. Hasp box. The animal must open an ordinary gate hasp, closed with a wooden plug inserted loosely through the staple, withdrawing the plug and lifting the hasp from the staple, over which it would fall again if released. He must then raise the lid of the box and hold it open while he reached in for the food.

Five trials a day were given with each box; the time spent in each trial was recorded, and detailed notes were made as to the use of right or left hand and the exact method employed in opening the boxes. Training was continued until the latches were released in a stereotyped manner without random movements. Several interruptions of training occurred lasting from one to several weeks, so that the learning curves do not represent the rate for continuous training.

In addition to the problem-box habits, each animal was trained to pick out cubes of banana from among cubes of wood of similar size and appearance. The cubes were scattered in irregular order under a sheet of glass supported 2 inches above the floor of the cage. They were placed about 6 inches back from the edge so that the animals had to reach under the glass to get the cubes, which they could see but could not distinguish by odor.

Operative Technique.—Destruction of the motor areas was made under ether anesthesia, with aseptic precautions. The region of the precentral gyrus was exposed by trephining and identified by electrical stimulation. The opening was enlarged by bone-forceps until the precentral gyrus and surrounding areas were exposed. Arm, leg and face areas were verified by stimulation, and the limits of the excitable area determined. The entire area was then undercut by thermocautery to a depth of about 6 mm. To avoid injury to the longitudinal sinus, a median bridge of bone, 1 cm. in width, was left intact. In one specimen the leg area of this region was undercut by passing the cautery diagonally mediad and downward until the resistance of the falx was felt, then cutting longitudinally across the gyrus. The dural flaps were then replaced and the wound closed. In the cases reported below the wounds healed without infection.

Retention Tests.—The animals all showed marked paralysis after operation. This cleared up gradually, and the retention tests were given about two months after the operation. (Numbers 1 and 3, v.i., recovered somewhat more quickly than is usually the case when the lesion is restricted to one hemisphere.) In the postoperative retention tests, the animals were placed singly in the large cage with each of the latch boxes in turn. The time required to open the boxes was noted, and the methods were recorded in detail for comparison with methods employed in learning and in the preliminary retention tests.

Verification of Lesions.—When the tests were completed, the operative fields were again exposed and explored by electrical stimulation. Excitable points found were mapped. The brains were then removed, fixed in 10 per cent. formaldehyd, and sketches made under a camera lucida. Serial sections of the region of the lesions were then prepared. Camera drawings of these were made and the lesions reconstructed from them.

PROTOCOLS

NUMBER 1.—This was a small male cebus, trained on the crank box, pull box and hasp box. The skull was trephined and opened on both sides in front of the precentral gyrus. The openings were extended backward to the fissure of Rolando. The leg, arm and face areas were located by electrical stimulation and destroyed by cautery. Cauterization extended beyond the stimuable area except in the median line. The wound was covered with mica and closed.

On the following day, there was a partial paralysis of both sides with great spasticity. Coordinated walking movements were possible, but there was great weakness of the legs. The arms were extended toward food. He could not grasp with his left hand. Partial grasping with the right hand appeared, but there was inability to raise food to the mouth. He recognized a banana, and made efforts to grasp it. The arms were usually hyperextended.

Four days later, he moved clumsily, his arms and legs spread out frequently, letting him fall prone. He grasped with his right hand, but was unable to hold food or lift it to his mouth. He ate by thrusting his mouth against the bread. He was well oriented in the room. Two weeks before operation he had learned to slip out of the crack as the door was opened and to run into an adjoining room. He did this twice on the fourth day. He had a tendency to stay near a cage containing other monkeys and to hide under it when pursued. There was marked tremor after slight effort.

Ten days after operation, he stood and walked without falling, fumbled in grasping, but was able to hold food in the right hand or to lift it to his mouth.

Thirty-five days after operation, he climbed and ran accurately, picked up small pieces of banana with the right hand without noticeable clumsiness, and made quick movements in efforts to catch flies. Retention of the problem-box habits was tested at this time.

The average time per trial in each day's practice (five trials daily) is given in Table 1 for each of the problem-boxes. This is followed by the average time per trial on each day of the preliminary retention tests, and similarly for the postoperative retention tests.

TABLE 1.—Average Time in Seconds Per Trial Consumed in Opening Each Problem-Box in Each Day's Practice of Training, Preliminary Retention Tests and Postoperative Retention Tests

Training Tests			Preliminary Retention Tests		
Pull Box	Crank Box	Hasp Box	Pull Box	Crank Box	Hasp Box
136.6	206.2	135.2	1.6	3.2	44.4
5.4	390.0	34.4	3.0	1.6	81.8
1.8	47.2	10.0	2.4	11.0	14.0
2.0	12.8	18.0	1.2	2.4	
1.6	4.6			5.6	
1.2	3.8			2.6	
2.4	10.8			2.7	
2.0	27.6				
2.2	2.6				
1.6	4.8				
	6.0				
	1.8				
	2.8				
	1.6				
	2.2				
	2.6				
			Postoperative Retention Tests		
			Pull Box	Crank Box	Hasp Box
			2.8	63.6	31.0
			2.2	7.4	57.6
				4.4	
				3.8	

Tests for visual discrimination were made. There was no error in 100 trials. At all times following the operation the animal was oriented in the cage and room and, with the exception of the motor disturbance, gave no indication of any deterioration.

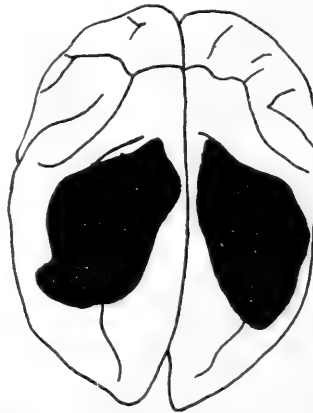


Fig. 1.—Extent of lesions in animal No. 1. Reconstructed from camera sketch and serial sections.

Extent of Lesions.—The areas destroyed are shown diagrammatically in Figure 1 and in sections in Plate 1.

Left Hemisphere: Medial, the lesion began about 1 mm. behind the end of the fissure of Rolando and extended forward to the level of the knee of the corpus callosum. The cortex of the precentral gyrus was destroyed to within 2 mm. of the edge of the longitudinal fissure, but that of the median surface was uninjured. Caudad, the lesion extended slightly onto the postcentral gyrus but did not involve all of the cortex within the fissure of Rolando. Laterad, it extended to the upper border of the operculum. The parts of the stimulative area left intact were the paracentral gyrus, the cortex within the fissure of Rolando and the lateral part of the face area included on the operculum.

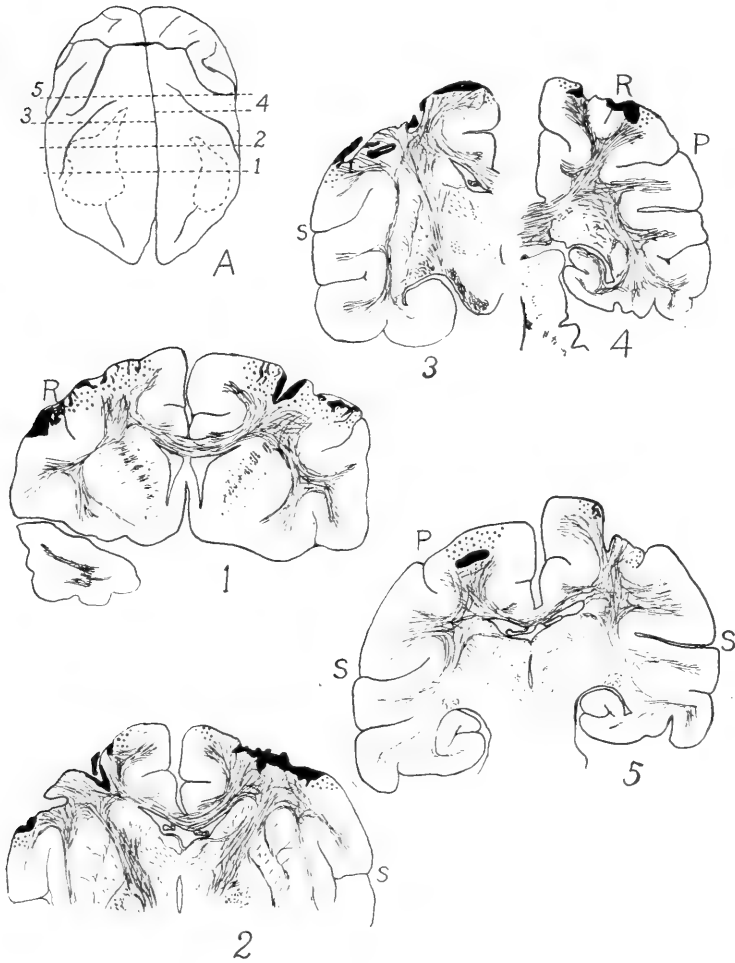


Plate 1.—Fig. A: Outline of the dorsal aspect of the cerebrum. The broken areas outlined indicate the extent of dural adhesions. The transverse broken lines show the level of the sections designated by the corresponding numbers.

Figs. 1 to 5.—Camera sketches of sections showing extent of lesions. Blood clots and scar tissue are indicated in solid black. Obviously degenerated cortex is marked with coarse stippling. R, fissure of Rolando; S, fissure of Sylvius; P, parieto-occipital fissure.

Right Hemisphere: The lesion was similar to that on the left but slightly more extensive. The cortex within the rolandic fissure was destroyed, and the lesion extended farther over the operculum.

After destruction of almost all of the arm areas of both sides and of most of the areas of the legs and face, this animal, on recovery from paralysis, showed perfect retention of visual and motor habits acquired before injury. Except for the paralysis and later spasticity, no significant change in his behavior could be noted.

NUMBER 2.—This was a small male cebus too wild for training at the beginning of the experiments. The motor area of the right hemisphere was exposed, the arm, face and leg areas identified and cauterized to a depth of 5 mm., caudad to central fissure, laterad and cephalad to a line 5 mm. beyond the limits of the excitable area.

Following operation, the left leg and arm were not used. The leg was hyperextended and gave some support to the body in standing or sitting, but made no stepping movements. No movements of the hand could be elicited. This complete paralysis of the left hand persisted for two weeks.

Four weeks after operation, the left leg was used almost normally. The left arm could be used to support the animal's weight, but tended to become rigid in hyperextension, and the left hand could not be used for grasping.

Eleven weeks after operation, the paralysis had almost disappeared; the left hand was somewhat clumsy but could be used in grasping food. It was not used when the right hand was unrestrained.

Training on the problem boxes was begun at this stage of recovery. During the next three months, the problems were learned and retention tests given.

Seven months after the first operation, the left motor area was exposed and similarly explored and destroyed. Paralysis of the right arm and leg followed. It appeared to be as complete as that of the left side following the first lesion. It improved more rapidly, however. Six weeks after operation the right hand was used to pick up food, and, although still somewhat spastic, was judged capable of manipulating the latch boxes. Retention tests were therefore begun. The average time per trial for successive groups of five trials in training, preliminary retention tests, and postoperative retention tests are given in Table 2. Visual discrimination was unaffected by the operation.

TABLE 2.—Average Time in Seconds Per Trial Consumed in Opening Each Problem-Box in Each Day's Practice in Training, Preliminary Retention Tests and Postoperative Retention Tests

Training Tests			Preliminary Retention Tests		
Pull Box	Crank Box	Hasp Box	Pull Box	Crank Box	Hasp Box
24 hrs.*	126.0	102.2†	2.2	28.8	8.8
24 hrs.*	105.0	111.0†	2.0	1.6	6.4
2,520 sec.	16.0	235.0			
24 hrs.*	5.2	184.4			
366 sec.	7.8	19.6			
2.5	7.4	16.0			
1.4	1.4	53.6			
4.5	1.2	6.0			
20.4	2.8	6.6			
1.6					
			Postoperative Retention Tests		
			Pull Box	Crank Box	Hasp Box
			9.8	14.8	102.5
			3.6	11.4	93.4
			1.2	7.2	35.4
					60.6
					22.8
					15.4

* Failed to open box while under observation and was left in the cage over night.
 † Time with hasp left unfastened.

The short time required for opening the boxes in the postoperative retention tests gives clear evidence for some retention of the habits. Much of the delay apparent was due to the weakness and clumsiness of the right hand. With each problem-box the attack in the postoperative retention tests was directly on the latches. The methods employed were at first those used before operation, and the movements were definitely adapted to solving the problems, although lacking force and accuracy; for example, efforts were all directed to turning the crank counter-clockwise.

The weakness of the right arm led to a surprising readjustment on the part of this animal. The operation on the right hemisphere made the left arm weak and spastic during training. In all of the trials of training and preliminary retention tests the left arm was used only as a prop, and the left hand was *not once* used in manipulating the latches of any of the boxes. After the second operation, the right hand was much more affected than the left, which had largely recovered, and an almost immediate shift to the left hand in opening all of the boxes occurred.

Pull Box: Postoperative retention tests. Trial 1: Fumbled in hole with right hand, removed hand, peered into hole; again inserted right hand and again pulled lever; twenty-seven seconds.

Trial 2: Right hand, fairly accurately, seven seconds.

Trial 3: He fumbled with right, then inserted left, grasped lever and pulled; seven seconds.

Trial 4: He inserted left hand at once; three seconds.

Trial 5: Left hand used at once; five seconds.

The right hand was used only four times in the succeeding forty trials.

Crank Box: Trial 1: He grasped the crank with his right hand at once and turned counter-clockwise. The crank stuck in the third quadrant. He pushed at it feebly, gave up, returned to the attack from the side of the box and pulled it through final segment; 160 seconds.

Trial 2: He grasped the crank with the right hand. Apparently, he was unable to move it. He grasped it with both hands and swung it around; twenty-five seconds.

Trials 3, 4 and 5: He used only the right hand and turned with difficulty moving to side of box and exerting direct pull instead of his former transverse rotary movement.

Trial 6: He grasped with the left hand and turned counter-clockwise; six seconds. All later trials were made with the left hand only.

Hasp Box: On the first three days of the postoperative tests, he pulled out the plug and disengaged the hasp promptly with his right hand, but lacked strength to lift the lid. He gave up after a few attempts with his right hand.

On the fourth day, he drew out the plug and disengaged the hasp with his right hand, then lifted the lid with his left foot. It fell back as he attempted to reach the food. He lifted it again with his left hand, climbed to the edge of the box, bringing his right side against the lid, so holding it up while he grasped the food with his left hand. On the second trial, he lifted with the left hand and held it up with his left hand, inserting his head for the food. In

all later trials, he lifted the lid with his left hand, sometimes holding it back with his left knee or with his head while reaching into the box with his left hand, or with the left hand while reaching with his head. On the eighth and all later trials, he pulled the plug with his left hand and used the right only as a prop.

Throughout the retention tests his activities were centered on the plug, hasp, and lid. He never attempted to lift the lid until the hasp was disengaged. When the lid was raised the next acts seemed definitely directed to holding it up, and though clumsy, the movements were clearly not random.

EFFECTS OF SUBSEQUENT DESTRUCTION OF THE CORPUS STRIATUM

A broad bladed cautery was next passed through the old lesion into the corpus striatum and drawn back and forth through this nucleus. The wound was closed, and the animal was kept under observation until his death eight days later.

On recovery from anesthesia, the animal showed marked spasticity of the left side. The left arm was usually hyperextended, although in walking or clinging to a perch the arm and leg assumed a normal posture. The left side was very weak, and when he walked the arm and leg frequently collapsed suddenly. He took food with his right hand and placed it in his mouth. When I held a bit of food, he drew my fingers to his mouth with the palm of his left hand, but without closing the fingers, which remained hyperextended.

On subsequent days, he used both right and left hands in walking, climbing and grasping food. The left side was spastic and very weak but capable of a variety of fine adaptive movements. The right side showed a coarse tremor, and athetoid movements of the left arm appeared when the right was used. There was marked paralysis of the pharynx. He kept his mouth stuffed with food or shavings but was unable to swallow.

At no time was the paralysis as marked as after the destruction of the cortex. Indeed the condition showed no resemblance to hemiplegia, but, except for the pharyngeal paralysis, was essentially that described by Wilson⁴² for lesions of the striate nucleus without involvement of the pyramidal tracts. The possibility that the recovery from the initial paralysis was due to vicarious functioning of the striate nucleus seems thus definitely to be ruled out. The animal did not recover sufficiently for retention tests after this operation, but his behavior when released in the laboratory showed that his general orientation was unaffected.

42. Wilson, S. A. K.: An Experimental Research Into the Anatomy and Physiology of the Corpus Striatum, *Brain* **36**:427-492, 1913.

When given an egg, he made efforts to break it by pounding it on the floor, as he had done before the operation, and in the performance of this habit both hands were used.

Extent of Lesions.—The extent of the destructions is indicated in Figure 2 and sections through the area are shown in Plate 2.

Right Hemisphere: The lesion extended cephalad from the median end of the central fissure to the middle of the superior frontal gyrus, bordering the longitudinal fissure but leaving the cortex of the median surface of the hemisphere intact. Caudad it invaded the postcentral gyrus and completely obliterated the fissure of Rolando. Laterad it extended well onto the operculum. Only the paracentral gyrus and the lateral portion of the face area remained intact.

The second operation destroyed all of the caudate nucleus and the greater part of the lenticular, leaving only the posterior end of the putamen intact.

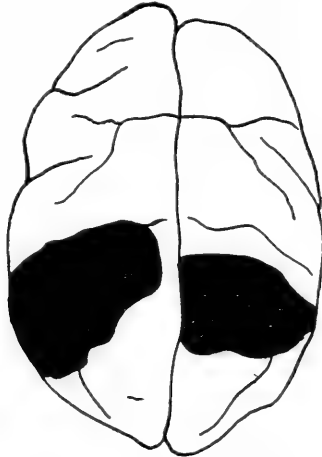


Fig. 2.—The extent of the lesions in animal No. 2. Reconstructed from camera sketch and serial sections. The posterior border of the left precentral gyrus escaped injury.

Left Hemisphere: The lesion was less extensive than that on the right. It began 5 mm. in front of the median end of the central fissure and extended to the frontal lobe. All of the cortex of the median surface to the callosomarginal fissure was destroyed. The posterior edge of the precentral gyrus remained intact, for a width of about 5 mm.

In this animal, practically all of the precentral gyrus of the right hemisphere was destroyed. He was then trained in manipulative movements of the right hand. This was followed by partial destruction of the left precentral gyrus. On recovery from paralysis, he gave clear evidence of retention of the habits but owing to spasticity of the right hand, made a direct transfer of the habits to the left hand. The right precentral gyrus was almost completely destroyed, whereas a rather large proportion of the left precentral gyrus escaped injury, but in spite

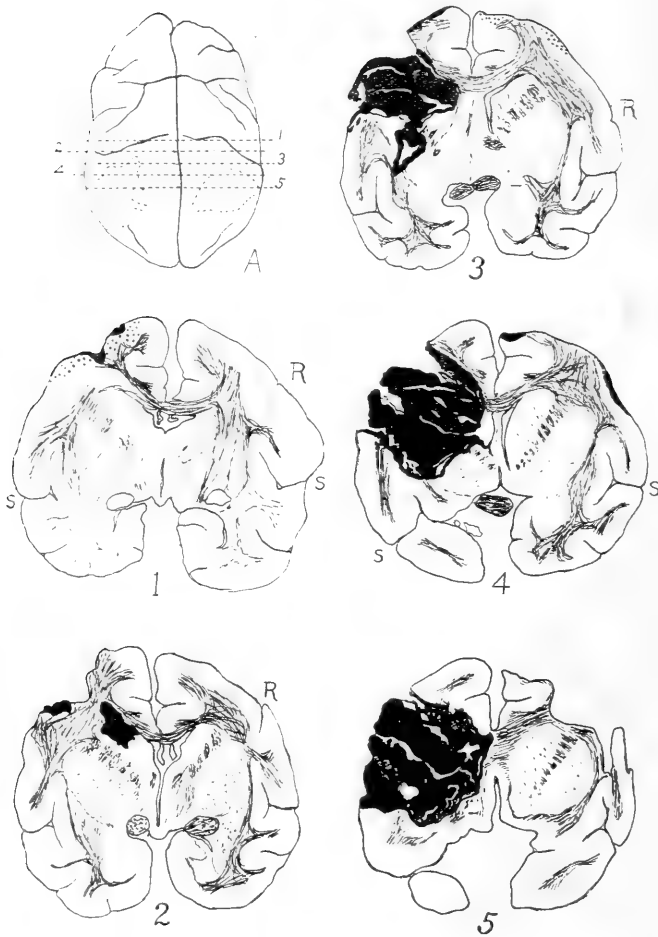


Plate 2.—Fig. A: Outline of the dorsal aspect of the cerebrum. The broken areas outlined indicate the extent of dural adhesions. The transverse broken lines show the level of the sections designated by the corresponding numbers.

Figs. 1 to 5.—Camera sketches of sections showing extent of lesions. Blood clots and scar tissue are indicated in solid black. Obviously degenerated cortex is marked with coarse stippling. *R*, fissure of Rolando; *S*, fissure of Sylvius; *P*, parieto-occipital fissure.

of this, the animal shifted to the use of his left hand in opening the problem-boxes. Subsequent destruction of the greater part of the corpus striatum did not produce a recurrence of the hemiplegic symptoms.

NUMBER 3.—This was a large female rhesus trained on problem-boxes and visual discrimination. After retention tests, the motor areas of both sides were exposed, mapped and cauterized. Following the operation the legs and left arm were completely paralyzed. The right arm made clumsy pawing movements. Twelve hours after operation, the animal walked a few feet with staggering gait, then collapsed with arms and legs widely extended, and for several days made no further efforts to walk. The following day she grasped a grape with her right hand and brought it to her mouth after several unsuccessful trials. The movements were clumsy and slow.

Four weeks after operation she seemed sufficiently recovered for retention tests, although still showing a general clumsiness and marked weakness of the left limbs.

The average time per trial for successive groups of five trials in training, preliminary retention tests and retention tests after operation is given in Table 3. Visual discrimination was unaffected by the operation.

TABLE 3.—Average Time in Seconds Per Trial Required for Opening Each Problem-Box in Each Day's Practice in Training, Preliminary Retention Tests, and Postoperative Retention Tests

Training Tests			Preliminary Retention Tests		
Pull Box	Crank Box	Hasp Box	Pull Box	Crank Box	Hasp Box
68.2	1,595.0	40.4*	1.0	4.2	24.0
2.6	111.8	373.2	1.0	3.8	6.6
1.0	145.4	124.6		1.6	5.0
1.0	304.2	24.2		1.2	3.6
	140.0	17.0		1.0	2.2
	16.8				2.8
Postoperative Retention Tests					
Pull Box	Crank Box	Hasp Box			
1.0	2.2	49.2			
1.0	1.4	9.8			
2.6	1.4	8.4			

* Time with hasp unfastened.

The time required to open the problem-boxes in the postoperative retention tests gives certain evidence of the retention of the habits. An average of 678.8 seconds was consumed in each of the first five trials of training in opening the boxes by the method of random activity. Only 17.5 seconds' average were required for the first five trials of the postoperative retention tests. The methods of opening the pull and crank boxes were the same before and after the operation. The persistent weakness of the left arm called for a change in method of opening the hasp box. Before operation, the animal had used the same method in twenty consecutive trials. The plug was pulled out of the staple with the right hand. The hasp was lifted from the staple with the right hand, turned back against the lid, and then transferred to the left hand. The lid was lifted with the left hand and the right hand

thrust into the box for the food. In the postoperative retention tests, the left hand was not used at all. She first lifted the lid with her right hand, then released it and attempted to grasp the food with the same hand, but the lid falling back prevented this. On the first trial, she finally held the lid back with her right hand, inserted her head in the box and took the food in her teeth. On the second trial, she thrust her head against the lid after raising it with the right hand and so held it open while the hand was inserted in the box. The same method was used on the third and fourth trials. On the fifth trial, she attempted to hold up the lid with her left foot and finally succeeded in this after overbalancing twice. In all later trials, she released the lid and allowed it to fall against her right arm as this was thrust into the box. These

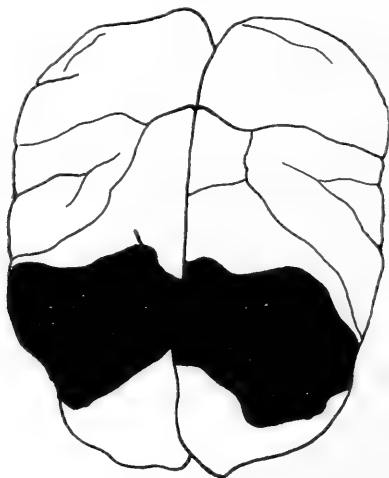


Fig. 3.—The extent of the lesions in animal No. 3. Reconstructed from camera sketch and serial sections. Practically the whole of both precentral gyri destroyed, including the paracentral gyrus and cortex within the central sulcus.

various acts were carried out with definite adaptation to the contour of the box and had none of the elements of random pulling and thrusting which characterize the initial stages of learning. As in the case of Number 2, there seemed to be an immediate adaptation of movements to opening the box, which had not been employed at any time in the previous practice.

Extent of Lesions.—The injured areas are shown in Figure 3 and sections in Plate 3.

Right Hemisphere: The lesion began at the posterior median end of the central fissure and included practically all of the precentral gyrus. On the median surface, all of the cortex above the callosomarginal fissure was destroyed. Practically all of the gyrus within the rolandic fissure was involved. Laterad,



Plate 3.—Fig. *A*: Outline of the dorsal aspect of the cerebrum. The broken areas outlined indicate the extent of dural adhesions. In a preliminary examination, the left hemisphere was cut through along the longitudinal dotted line. The sections of its two halves are therefore from somewhat different levels. The transverse broken lines show the level of the sections designated by the corresponding numbers.

Figs. 1 to 5.—Camera sketches of sections showing extent of lesions. Blood clots and scar tissue are indicated in solid black. Obviously degenerated cortex is marked with coarse stippling. *R*, fissure of Rolando; *S*, fissure of Sylvius; *P*, parieto-occipital fissure.

the lesion included the upper half of the operculum. At most, only the lateral facial area escaped destruction.

Left Hemisphere: The lesion was almost coextensive with that on the right. More of the paracentral gyrus was destroyed and somewhat less of the operculum.

After practically complete destruction of both precentral gyri, this animal gave evidence of perfect retention of visual habits and habits of manipulation. Direct adaptive changes in behavior were made to compensate for weakness of the left arm.

DISCUSSION OF EXPERIMENTS

After extensive lesions to the precentral gyri of both hemispheres, each of the animals studied gave clear evidence of the retention of patterns of movement which had been acquired before the operative destructions. Evidence of this retention was obtained from a comparison of the time required for opening the problem boxes in initial training with that for the postoperative retention tests, from the restriction of reactions in the postoperative retention tests to the catches of the problem boxes, and from the persistence of individual peculiarities of opening the boxes.

The average time required by all animals for opening each box in the first five trials of training was 584⁴³ seconds. An average of only 30.7 seconds was required in the first five trials of the postoperative tests. The animals all failed the hasp box in the preliminary training until first trained without the plug in the staple. In the postoperative tests, they all opened this box promptly with the hasp closed by the plug. At the beginning of the postoperative tests, each animal (except Number 3 with the hasp box) used the same hand or hands for each part of the manipulation as he had before the operation, and attacked the latches in his former manner, although the methods of attack were modified rapidly to compensate for the persistent motor difficulties. All the animals showed perfect retention in the visual discrimination test.

These results establish conclusively that the cerebral areas destroyed were not essential to the performance of the habits studied, and observations on the general behavior of the animals following recovery from the paralysis justify the further conclusion that the areas are not essential to the performance of any type of complex adaptive or habitual activity.

Four possible explanations of the results must be considered:

1. In no case did the operation destroy the entire precentral gyrus of both sides. The parts remaining intact may have contained a suffi-

43. This does not include the failures with the hasp box or the times when Number 2 was left in the cage over night.

cient number of fibers previously integrated in the habit to produce the conditioned reflexes, in spite of the great destruction of other fibers of equivalent function. Such a possibility is supported by data on other functional areas in which the various parts seem equipotential (Franz,^{43a} Lashley³⁴) and by the apparent equipotentiality of parts of the motor area revealed by electrical stimulation (Lashley⁴⁴), but several facts speak strongly against this explanation.

Partial destructions usually entail a certain confusion in the performance of all the functions of an area, which seems to exceed anything of the sort noted in these animals.⁴⁵

In Number 3, the destruction on both sides was so nearly complete that only a part of the face areas could have remained functional. If we attempt to explain the survival of habits as being due to the activity of undestroyed parts of the motor area, we must assume that a part of the face area is capable of performing all the functions of the entire motor cortex—an assumption which is as far from the accepted views of localization as is the denial of all habit function to the motor areas.

2. It might be urged that in the recovery from the motor paralysis, the vicarious functions assumed by other areas included the movements involved in the problem-box habits; that the habits were relearned during the period of recovery from paralysis. The habits, however, consist of particular patterns of movement associated with the stimuli presented by the latch boxes. During the postoperative period, there was no occasion for the animals to reacquire these particular patterns of movement and no opportunity for the movements to be associated with the latch boxes.

3. The long controversy concerning the sensorimotor function of both the precentral and postcentral gyri suggests that the two may both include centrifugal cells for the performance of habits. The literature cited in the first part of this paper seems to establish the differential function of the two areas, however, and the lack of paralysis after lesions to the postcentral gyrus makes the hypothesis untenable.

43a. Franz, S. I.: On the Functions of the Cerebrum: The Frontal Lobes, *Arch. Psychol.* 1907, No. 2, pp. 1-64.

44. Lashley, K. S.: Temporal Variation in the Function of the Gyrus Precentralis in Primates, *Am. J. Physiol.* **65**:585-602, 1923.

45. I am collecting data on this question at present. The evidence is not complete, but there is indication that, e. g., any extensive but incomplete destruction of the visual areas of both hemispheres in the rat is followed by inaccuracy of brightness discrimination, with great variability from day to day, such as has been reported by Franz in 1916 for aphasia, yet without any complete loss of any phase of the visual function. Such loss as appeared in the motor habits of the monkeys was almost certainly ascribable to the simple motor weakness, and gave no indication of an apraxia.

Nañagas⁴⁶ found a few islands of large pyramidal cells in the postcentral gyrus, but the great mass of them was restricted to the precentral. Finally, Brown³⁶ reported that the destruction of the postcentral gyrus did not abolish learning ability or interfere seriously with habits formed before the operation in the chimpanzee.

4. The only remaining possibility seems to be that the electro-stimulable areas do not include the centrifugal elements of conditioned reflex arcs of any sort. (It is of course possible that they contain some such elements, but these cannot comprise any significant proportion of the total number of centrifugal cells, since their destruction leaves the habits completely unaffected.) In this, the experiments confirm for primates the results previously reported for the rat. The neural impulses involved in conditioned reactions do not pass from sensory projection areas to the precentral gyrus and thence to lower centers, but must be conducted by centrifugal cells lying outside of the pyramidal system. In the rat, the evidence points to the view that the centrifugal fibers of the sensory projection area itself are primarily involved in this motor function, since the destruction of any fourth of the cerebrum exclusive of the visual areas does not affect the performance of visual habits.⁴⁷ Whether or not the same lack of important transcortical conduction holds true for the monkey is questionable in view of the greater proportionate development of the transcortical association tracts in this animal, but it seems established that the "motor areas" are not concerned in the initiation of habitual movements.

THE CORPUS STRIATUM AND VICARIOUS FUNCTION

All recent students of the question agree that recovery from cerebral paralysis is not due to the assumption of the function of the destroyed motor cortex by the corresponding area of the opposite side. On the contrary, the simultaneous destruction of the areas in both hemispheres seems to be followed by a rather more rapid recovery than follows the destruction of either alone. The fact has been noted by Grünbaum and Sherrington²⁰ and by Wagner²⁸. It was apparent in the slower recovery of Number 2 from the first operation than from the second. The

46. Nañagas, J. C.: *Anatomical Studies on the Motor Cortex of Macacus rhesus*, *J. Comp. Neurol.* **35**:67-96, 1922.

47. Experiments now in progress, which indicate that extensive fronto-parieto-temporal lesions may also abolish visual habits without producing a general deterioration of learning ability, indicate that a mass action of the cerebrum is also somehow involved, but they do not seem to invalidate the conclusion that the efferent fibers of the sensory projection area are primarily concerned in the subcortical initiation of movements associated with the receptor for that area.

explanation is probably to be found in the forced practice which diplegia imposes on the paralyzed limbs (Odin and Franz⁴⁸).

Other restricted cerebral areas have also been rather definitely excluded from participation in the vicarious function of the stimulable areas, by the work of Leyton and Sherrington²⁶ (Lashley⁴⁹). Luciani⁵⁰ has suggested that recovery may be due to the activity of the corpus striatum, which has homologies with the stimulable cortex. This was tested in animal Number 2 of the present series by destruction of the right striatum after recovery from diplegia. Hemiplegic symptoms did not recur, so that we may conclude that the recovery had not been due to the vicarious activity of the striate nucleus.

THE FUNCTION OF THE ELECTROSTIMULABLE AREAS

The conclusions which may be drawn from these experiments are wholly negative. They seem to prove that the precentral gyrus does not include the efferent paths for learned activities; in the current localization terminology, it is not the center for "voluntary movements," as is almost universally assumed. But if this is true, what is the significance of the movements elicited by electrical stimulation? How may we interpret the cerebral paralyses, and why do they especially affect the finer manipulative movements? A number of lines of evidence may help to answer these questions and clear up the function of the precentral gyri.

The Postural Function of the Stimulable Areas.—Many investigators have pointed out the similarity between the movements elicited by cortical stimulation and "voluntary movements." I am convinced that this is an error due to contrasting these movements with those which are elicited by stimulation of motor nerves or spinal cord. In the latter cases, the movements are wholly incoordinated, whereas the movements following cortical stimulation involve synergic groups of muscles. But in all cortical stimulation experiments which I have seen, the movements have been slow and rather massive, i. e., chiefly involving the larger musculature of the limbs. When smaller segments are moved, the movements are never coordinated as they are, for example, in grasping small objects. They never show the fineness of gradation and accuracy of adjustment which is characteristic of the movements of the intact animal. This has been observed by various investigators and interpreted as showing that the finer adjustments are integrated

48. Odin, R., and Franz, S. I.: On Cerebral Motor Control: The Recovery from Experimentally Produced Hemiplegia, *Psychobiol.* **1**:33-50, 1917.

49. Lashley, K. S.: Studies of Cerebral Function in Learning. Vicarious Function After Destruction of the Visual areas, *Am. J. Physiol.* **59**:44-71, 1922.

50. Luciani, L.: *Human Physiology*, London **3**, 1915.

at some higher level and imposed through it on the motor area. But there is no direct evidence that this is the case. The movements following excitation are far more like the gross changes of posture which one may observe in the intact animal—the raising of an arm preparatory to snatching at food, bracing against a pressure, or the like. It seems significant that coordinated movements of the eyes are among the most easily elicited movements on electrical stimulation (although their stimuable points lie outside of the precentral areas), and that these movements in the intact man or animal are almost always a reflex fixation (postural adjustment) called out directly by extero-stimulation and, in fact, can not be accurately performed in the absence of such stimulation, as with lids closed.

Wilson⁵¹ has pointed out the similarity of the contractures in cerebral paralysis to the postural reflexes of decerebrate rigidity, and from this it seems certain that a part of the function of the stimuable areas is the regulation of these spinal and cerebellar postures. It seems rather probable that the movements obtained on electrical stimulation are only a further exhibition of this postural activity and are unrelated to the finer coordinations of conditioned motor reflexes, or motor habits.

The Dynamic Function of the Stimuable Areas.—The condition following lesions to the precentral gyrus or internal capsule, even in man, should be described rather as an enormous difficulty in making movements than as an absolute paralysis of movement. The degree of paralysis varies somewhat from day to day. Excitement seems to increase motor control (Minkowski,⁵² Lashley³⁷), and the paralysis may in part or wholly disappear during emotional disturbance, only to recur when the disturbing situation is past. If we may judge from the tonic condition of the muscles, there must be in excitement a general facilitation of lower motor centers which temporarily reinstates cerebral control. Further, if this is the case, in the intact animal in the absence of emotional stimulation cerebral control must likewise be conditioned by some such facilitation derived from the precentral gyrus. The work of Brown⁵³ and of Leyton and Sherrington²⁶ has shown that stimulation of the motor area does facilitate the centrifugal paths of other

51. Wilson, S. A. K.: On Decerebrate Rigidity in Man and the Occurrence of Tonic Fits, *Brain* **43**:220-268, 1920.

52. Minkowski, M.: Etude physiologique des circonvolutions rolandique et pariétal, *Arch. Suisse de Neurol. et Psychiat.* **1**:389-459, 1917.

53. Brown, T. G.: Studies in the Physiology of the Nervous System. XXV. On the Phenomenon of Facilitation. 4. Its Occurrence in the Subcortical Mechanism by the Action of Which Motor Effects Are Produced on Artificial Stimulation of the "Motor" Cortex, *J. Physiol.* **9**:131-145, 1915; also Footnote 36.

areas, either at cortical or subcortical levels, since stimulation of the precentral gyrus renders the otherwise inexcitable postcentral gyrus excitable for corresponding movements.

After partial recovery from cerebral paralysis, the most prominent symptom is the weakness of the formerly paralyzed limbs. The greater part of their repertoire of movements may be restored, speed may be nearly normal, but only a slight force can be exerted, and fatigue occurs readily. What is lacking in this condition is not an adequate integration of the motor impulses, but a sufficient mass of neural impulses to maintain muscular activity. This may be ascribed either to a reduction in the number of functional nerve cells, or to inadequate facilitation. The ready fatigability is evidence for the latter.⁵⁴

There is evidence that the withdrawal of facilitation derived from other sources will produce similar weakness and fatigability and a tendency not to use the affected parts. Thus Munk⁵⁵ has shown that denervation of a limb has such effects, and Sherrington's⁵⁶ work has demonstrated that they are due to the withdrawal of impulses derived largely from the denervated muscles.

The importance of such facilitating systems has been emphasized by a number of recent investigators (Monakow,⁵⁷ Wilson,⁴² Sherrington,⁵⁸ Tournay,⁵⁹ Hunt⁶⁰). The general conception of these investigators is of a series of hierarchies of motor reflexes, all exerting a facilitating influence on the final common path. These involve at least the following elements.

54. The all or nothing principle of nerve and muscle activity requires the assumption that strength of muscular contraction is dependent upon the number of motor fibers involved and the rate of succession of propagated disturbances. Piper's work (*Elektrophysiologie menschlicher Muskeln*, Berlin, 1912) indicates that fatigue involves a decrease in this rate rather than a reduction in the total number of muscle cells activated.

55. Munk, H.: Ueber die Folgen des Sensibilitätsverlustes der Extremität für deren Motilität, *Sitzungsber. d. Berlin Akad. Wiss.*, pp. 1038-1077, 1903.

56. Sherrington, C. S.: *The Integrative Action of the Nervous System*, London, 1911.

57. Monakow, C. von: *Aufbau und Lokalisation der Bewegungen beim Menschen*, Ber. über d. iv. Kongress f. exp. Psychol. in Innsbruck, 1910.

58. Sherrington, C. S.: Postural Activity of Muscle and Nerve, *Brain* **38**: 191-234, 1915.

59. Tournay, A.: Conception actuelle des grande fonctions motrice, *J. de Psychol.* **17**:904-930, 1920.

60. Hunt, R.: The Static and Kinetic Systems of Motility, *Arch. Neurol. & Psychiat.* **4**:353, 1920.

1. Excitation of the motor cells supplying a muscle by impulses derived from the receptors in the muscle itself (Sherrington⁵⁶).

2. Long spinal reflexes from synergic muscles (Sherrington,⁵⁶ Magnus⁶¹).

3. Other proprioceptive and general exteroceptive facilitation whose central mechanism is as yet rather obscure (Yerkes,⁶² Richter⁶³).

4. Vestibular and proprioceptive influences exerted through the mechanisms of the cerebellum.

5. Probably facilitation derived from thalamic mechanisms in emotional excitement (Head⁶⁴).

6. Kinetic influences of obscure origin integrated in the corpus striatum (Wilson,⁴² Hunt⁶⁰).

Interference with any of these mechanisms is able to produce a change in the excitability of the final common path, and in the intact organism it seems certain that every act involves the participation of all of them, both by excitation and inhibition.

These considerations make it possible to form a tentative hypothesis concerning the function of the precentral gyrus. Its demonstrated facilitating effects, and its lack of direct participation in the conditioned reflex arc seem to throw it into a class with these other postural and tonic systems. Cerebral paralysis, is, I believe, to be interpreted as showing that a normal function of the stimuable cortex is to supply a substratum of facilitating impulses which act in some way to render the final common paths excitable by the more finely graduated impulses, descending from the cortex by extrapyramidal paths and producing the finer shades of adaptive movement. In other words, impulses descending from the precentral gyrus do not initiate the finer adaptive movements through the lower motor neurons, but only "prime" these cells so that they may be excited by impulses from other sources. The source of this activity and the probable interrelations of the stimuable areas with other parts of the motor system and with sensory projection areas present problems too complex for discussion here. Unquestion-

61. Magnus, R., and de Kleijn, A.: Die Abhängigkeit des Tonus der Extremitätenmuskeln von der Kopfstellung, *Arch. f. d. ges. Physiol.* **145**:455-548, 1912. Magnus, R.: Welche Teile des Centralnervensystems müssen für das Zustandekommen der tonischen Hals- und Labyrinthreflexe auf die Körpermuskulatur vorhanden sein? *Arch. f. d. ges. Physiol.* **159**:224-250, 1914.

62. Yerkes, R. M.: Inhibition and Reinforcement of Reactions in the Frog, *J. Comp. Neurol. & Psychol.* **14**:124, 1904.

63. Richter, C. P.: A Behavioristic Study of the Activity of the Rat, *Comp. Psychol. Monogr.* **1**:1-55, 1922.

64. Head, H.: *Studies in Neurology*, London, 1920; Release of Functions in the Nervous System, *Proc. Roy. Soc.* **92** B:184-209, 1921.

ably, the areas receive excitations from other parts of the cerebrum⁶⁵ and it is probable that all parts of the kinetic system⁶⁶ are capable of mutual influence. Postural facilitation and inhibition may themselves be habitual responses, but the present experiments indicate that they are rather generalized and not independently organized for each specific manipulative habit.

Recent work in general tends to emphasize the complexity of neural functions. We must hesitate to ascribe an exclusive or precise function to any neural structure, for the evidence points rather to the view that observable behavior is always the product of the interaction of many neural systems and that the function of any system is dependent on its temporary physiologic relation to other systems. This is particularly true of the finer adaptive responses of the intact animal which are subject to inhibition and facilitation by innumerable factors. Their execution depends on preparatory postural adjustments, emotional and other dynamic facilitation, as well as integration of impulses from many exteroceptors.⁶⁷ The total mass of excitation is effective both through the specific efferent patterns activated and also through the general dynamic effects which alone are incapable of producing the overt motor reactions elicited. The experiments reported here indicate that the electrostimulable areas are rather more concerned with the maintenance of excitability and the regulation of postural reflexes than with the excitation and control of finely integrated adaptive movements.

65. I have made several attempts to isolate the area from other parts of the cortex by circumsection but have not yet been successful. The literature on this point is conflicting. Marique (*Brain* **8**:536-538, 1885) reported the same results from circumsection as from excision of the area. Exner and Paneth (*Arch. f. d. ges. Physiol.* **44**:544-555, 1889) found similar results but were inclined to ascribe them to interference with the blood supply of the area. Schäfer (*Jour. Physiol.* **26**:23-25, 1901) reported one case of complete circumsection without paralysis. He does not report histologic examination of the lesion, however, and in view of the difficulty of the operation there is not sufficient evidence that the isolation was complete.

66. In this discussion, I have disregarded the important conception of static and kinetic functions advanced by Hunt (*Arch. Neurol. & Psychiat.* **4**:353, 1920) because the evidence does not show clearly to which of his systems the electrostimulable cortex is to be referred. The postural influences of the area would indicate a static function. What I have called the dynamic or "priming" function is rather a kinetic function, but is more primitive than the activities implied in Hunt's conception of the neokinetic system.

67. The statement that every act of the intact organism involves the participation of every neuron within the central nervous system is probably no more of an exaggeration than are the extreme theories of precise localization of function or of isolated conditioned reflex paths.

SUMMARY

The greater part of the precentral gyrus of both hemispheres was destroyed in monkeys which had been trained previously in habits of manipulation and visual discrimination. When the animals recovered from paralysis, it was found that they showed perfect retention of these habits. From this it is concluded that the so-called motor areas are not directly concerned with the performance of complex learned activities. The motor impulses of conditioned reflexes must descend from other areas of the cerebral cortex than the precentral gyri, and the latter cannot be regarded as the source of impulses to "voluntary movements."

Destruction of the corpus striatum subsequent to recovery from diplegia produced only the usual symptoms of striate lesion without recurrence of the symptoms of cerebral paralysis. Recovery from paralysis was therefore not due to vicarious function of this nucleus.

The evidence for considering the precentral gyrus as a part of the kinetic mechanism for reflex control of spinal posture and for maintenance of excitability of lower motor centers is summarized.

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