

The cerebellum : its functions, diseases and encephalic interrelations / Charles K. Mills, M.D., LL.D., Emeritus Professor of neurology in the Medical School of the University of Pennsylvania, Philadelphia.

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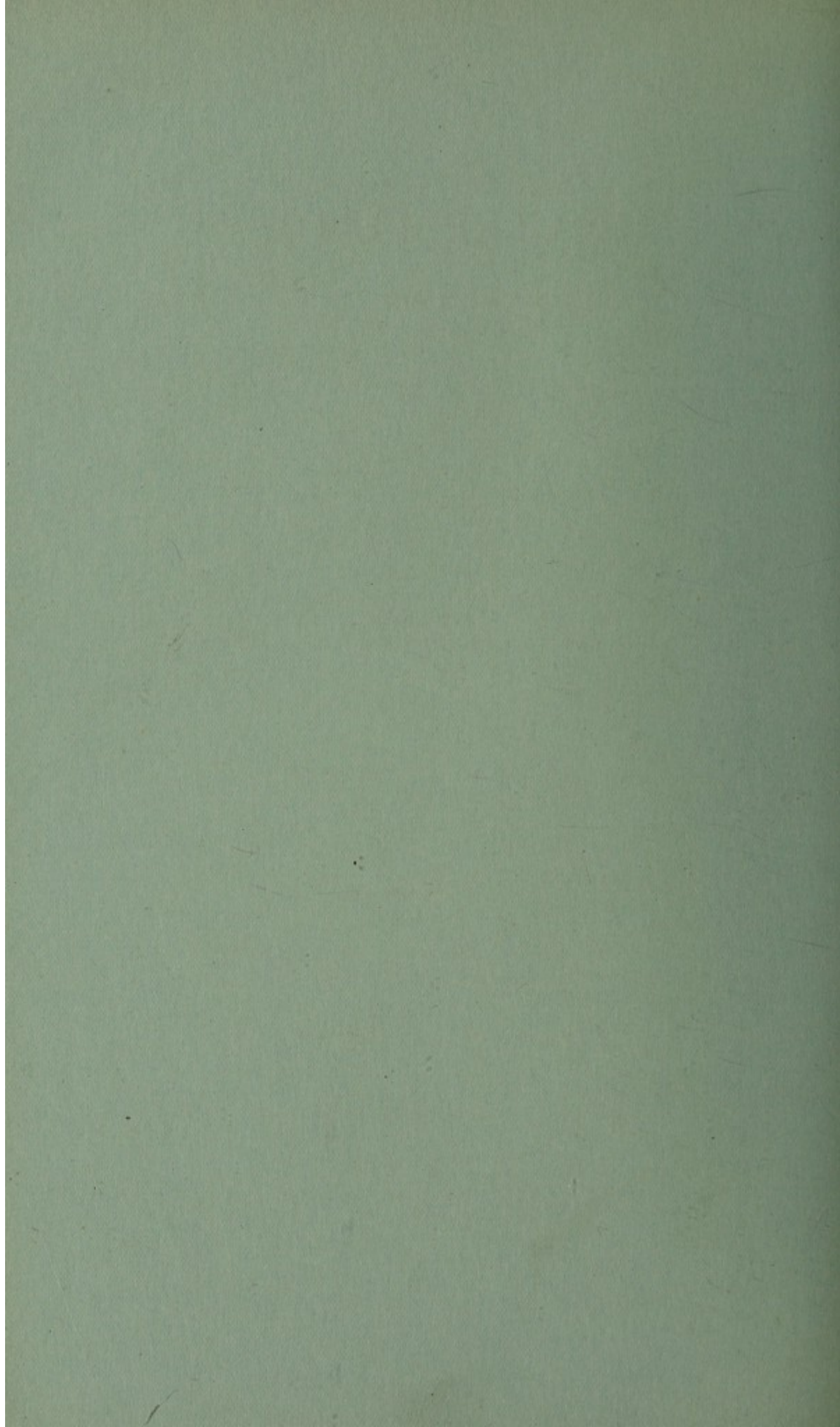
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PHILADELPHIA

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THE CEREBELLUM

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INTERRELATIONS *

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One of my earliest clinicopathologic publications was an article concerning a large hemorrhage into the thalamus in which, besides giving the symptomatology of the disease, I also recorded the macroscopic observations found at necropsy. A well marked tract of degeneration extended from the thalamus to the inferior olive.¹

Tilney² and others have shown the connections between the inferior olive and the cerebellum.

The parietal lobe is of importance in any consideration of the symptomatology of the cerebellum, as one of the mistakes occasionally made is that of confusing conditions of this lobe with disease of the cerebellum.

By a neurophysiologist as able as Lewandowsky,³ the cerebellum has been described as an organ of muscular sensibility. The reason for this and similar mistakes is not hard to see. Loss of muscular sense from disease of the parietal lobe or of the thalamus or from the sensory tracts coming from the spinal cord to the cerebellum or the thalamus gives motor symptoms which at first sight resemble cerebellar disorders of motility. A patient with disease of the parietal lobe uses his arm and leg in an ataxic or disorderly manner, because he does not comprehend the position of the limbs, whereas in cerebellar ataxia, no loss of sensation is present. I shall not, however, go in detail into the well settled question of the differential diagnosis between parietal and cerebellar disease.

* Read at the Fifty-Third Annual Meeting of the American Neurological Association, Atlantic City, N. J., May 24, 25 and 26, 1927.

1. Mills, C. K.: Hemorrhage into the Right Optic Thalamus and Small Cyst in the Right Corpus Striatum; Also in the Same Case, a Large Cyst in the Left Corpus Striatum, Phila. M. Times 9:268 (March 1) 1879.

2. Tilney, Frederick: The Relation of the Inferior Olive to Cerebellar Activity, Proc. Assoc. for Research in Nerv. & Ment. Dis., December, 1926. Also Tilney and Riley: Form and Functions of the Central Nervous System, ed 2, New York, Paul B. Hoeber, 1923, p. 422.

3. Lewandowsky: Die Functionen des zentralen Nervensystems, Jena, 1907.

In 1882, I became a visiting member of the staff of the Pennsylvania Training School for Feeble Minded Children at Elwyn. My attention was soon called to a boy known in the school as the "whirling dervish." A few years after I made my first examination of the boy, he died of what was supposed to be tuberculous meningitis, but unfortunately necropsy was not made.

Many, if not most of us, have at times seen a dog or perhaps a cat, engaged in the interesting experiment of pursuing his tail. In doing this it is noticeable that his body assumes a curved or crescentic appearance, the incurvature being toward the side of the movement. In this effort the animal's movements become faster and faster.

To the ordinary observer such a procedure is probably an object of amusement, but to the student of brain phenomena it calls to mind the labyrinthine mechanism and the medipenduncle of the cerebellum of which the animal seems to be able to make use, not only without any disturbance of his animal mentality and without any physical inconvenience, but with a certain amount of pleasure in the sport.

The spectacle also calls to mind to one familiar with the literature of the East, the stories of Mohammedan whirling dervishes or fakirs. These dervishes, it is said, pirouette or revolve on one heel used as a pivot. They probably attain great facility in their performances through training from their early childhood to adult life. The whole performance is after all a cerebrocerebellar one.

It is not improbable, although by no means certain, that the Elwyn boy who died of tuberculous meningitis may have had a small tuberculoma in the pons or cerebellar medipenduncle.

Tilney and Riley,⁴ in their book on the "Forms and Functions of the Central Nervous System," report the case of a boy, 4 years of age. In this case, there was paralysis of the left internal and right external recti muscles of the eyes giving rise to left lateral gaze, which produced a right conjugate deviation. The symptoms in the whirling boy to whom I referred were different, and I refer to the case only because Tilney and Riley found on necropsy a tuberculoma the size of a pea on the right side of the pons as the one lesion to account for the pontocerebellar symptoms.

At the meeting of the American Neurological Association of June, 1881, at which I was elected a member, I presented a paper recording a case of tumor of the pons causing conjugate deviation of the eyes and rotation of the head.⁵ The tumor was situated in the left upper quarter of the pons. It was in the body of the pons the anterior and posterior surfaces of which retained their integrity.

4. Tilney, F., and Riley, H. A.: *Forms and Functions of the Central Nervous System*, ed. 2, New York, Paul B. Hoeber, 1923, p. 397.

5. Mills, C. K.: Tumor of the Pons Varolii with Conjugate Deviation of the Eyes and Rotation of the Head, *J. Nerv. & Ment. Dis.* 8:470 (July) 1881.

Conjugate deviation of the eyes and of the head is an early symptom in many cases of apoplexy of the cortex or subcortex of the cerebrum producing hemiplegia. In these cerebral cases, as shown by the studies of Vulpian,⁶ Flourens,⁷ Ferrier,⁸ Priestly Smith⁹ and others, the conjugate deviation is usually toward the side of the lesion in the hemiplegic cases. If, however, the lesion is irritative causing convulsion, for instance, the conjugate deviation will be away from the side of the lesion or, in other words, toward the side of the convulsions. In pontile cases, the conjugate deviation is toward the side of the paralysis if the lesion is situated in the cephalic portion of the pons. In pontile cases also, conjugate deviation is away from the side of the lesion and toward the side of the paralysis if the lesion is in the caudal portion of the pons, but deviation does not invariably occur.

In a paper by me, contributed to *Brain* in 1880, was included the account of a case of tumor of the pons, in which rotatory movements toward the left took place during a convulsive attack.¹⁰ I witnessed one of these seizures in which, although the spasmodic attack was general, the patient's right side was more affected than the left. With the patient lying on his back the spasm had the effect of lifting up the right side of his body and causing him to work over toward the left as if the patient were trying to get on his face in this direction, but before getting altogether on his left side, he would fall backward again, when the same curious lifting rotatory movement would be repeated.

This case had a number of other interesting features, but I dwell on the rotatory movements because of the situation of the tumor, and the associated softening were such as to involve the pontile nuclei and medipeduncle of the cerebellum on the left.

The case recalled the experiments by Schiff¹¹ in which he cut the left cerebellar medipeduncle which resulted in causing the animal to exhibit a rotatory movement toward the side of the lesion as in the case of the tumor I recorded.

I have recorded a number of cases, clearly indicating the part played by the pons in the interrelations of the cerebrum and the cerebellum and

6. Vulpian: *Leçons sur la physiologie du système nerveux*, 1866, cited in Ferrier: *Functions of the Brain*, ed. 2, London, Smith, 1886.

7. Flourens: *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, ed. 2, 1842.

8. Ferrier, D.: *The Functions of the Brain*, ed. 2, London, Smith, 1886.

9. Smith, Priestly: *Reflex Amblyopia*, *Ophth. Rev.*, May, 1884; cited in Ferrier's *Function of the Brain* (footnote 8).

10. Mills, C. K.: *Five Cases of Disease of the Brain, Studied Chiefly with Reference to Localization*, *Brain*, January, 1880.

11. Schiff, M.: *Lehrbuch der Physiologie des Menschen*, Lahr, Schauenburg, 1858-1859.

emphasizing the thesis that in order to understand the cerebellum it is necessary to comprehend the evolution of as well as much else concerning the various regions of the brain. The frontal, parietal, occipital and temporal lobes all have anatomic connections with the cerebellum which is also intimately associated in its activities with both the mesencephalon and the diencephalon.

On Feb. 23, 1882, I exhibited at the Philadelphia Pathological Society the brain of a negro who had died in my wards.¹² The negro had committed a murder nearly thirty years before. He was tried, convicted and sentenced to death, but the governors of the state would not sign the warrant for execution. He was pardoned five years before his death, two or three years subsequent to the appearance of paralysis of the left side.

The right hemisphere of the cerebrum, especially in the motor region, was much atrophied as was also the left hemisphere of the cerebellum. A hard, brownish-black nodule or small tumor was found isolated in the upper portion of the pons to the right of the median line. This probably involved not only the pontile nuclei but also by compression or directly, the pyramidal tract.

I presented a paper at the meeting of the College of Physicians of Philadelphia, May 4, 1910.¹³ This paper included the record of a patient whom I saw in consultation. About six months before she came under observation, she had had an attack which rendered her right side somewhat paretic. She had a continuous coarse tremor in the right arm which she held slightly flexed at the elbow. She had lost the sense of position and passive movements in the right arm and leg. Tactile discrimination and the spatial sense were also markedly affected, and she had astereognosis in the right hand. The right pupil was somewhat larger than the left.

I concluded that the lesion was near the nucleus ruber, where the superior cerebellar peduncle passes into the brain stem. It is probable that the loss of muscular sense and of astereognosis were due to lesion of the tracts entering the thalamus from below.

The case was an example of the so-called Benedikt's syndrome. It might be said, in connection with the report of this case, that the region of the cephalic ends of the superior cerebellar arm and the floor of the sylvian aqueduct is a fruitful eponymic soil. Besides the name of Benedikt, names like those of Weber, Millard-Gubler, Westphal, Perlia,

12. Mills, C. K.: The Brain of a Negro Murderer, Phila. M. Times **12**:575 (May 20) 1882.

13. Mills, C. K.: Hemichorea, Hemiataxia, Hemiparesis, and Dilated Pupil Probably Due to a Lesion of the Superior Cerebellar Peduncle, Tr. Coll. Phys. Phila. **32**:136, 1910.

Spitzka, Siermerling, Kahler and Pick, Spiller and others are associated with particular syndromes occurring in this limited area.

The floor of the aqueduct is a continuation of the floor of the fourth ventricle, and therefore, in Hughlings Jackson's scheme, it belongs to the lowest or spinal level. In this floor or just cephalad of it are located the nuclear representations of the subdivision of the movements of the third and fourth nerves. It therefore follows that restricted lesions may give a variety of symptom pictures.

Perlia located a nucleus in the middle line in the floor of the iter, which nucleus acts in the control of convergence of the eyes. The center of convergence has been the object of particular study by Dr. W. G. Spiller,¹⁴ who not long since presented a paper on this subject.

At the meeting of the American Neurological Association in 1912, I reported a case with necropsy of which I had previously recorded the clinical symptoms.¹⁵ The symptoms were ataxia of the upper and lower extremities on one side and on the other side deafness and paralysis of the emotional expression in the face and loss of the senses of pain, heat and cold over the entire half of the body.

At the necropsy the macroscopic examination revealed a destructive lesion involving the left dentate nucleus and the cerebellar cortex above this nucleus including also the superior cerebellar peduncle. Degeneration was also evident to the naked eye in the right nucleus ruber which body was much smaller than the left ruber.

At this meeting a detailed record of the microscopic observations was made by Dr. Spiller. These conditions threw light on the functions of the cerebellum and its physiologic relations both to the cerebrum and to the spinal cord. Branches of the superior cerebellar artery supplying the dentatum, cerebellar folia, and superior arm were obliterated. Tracts of degeneration proceeded in both directions through the brachium conjunctiva.

This case was of importance as showing the relations of the superior region of the cerebellum to the nucleus ruber and spinal cord, and also the relation of the cerebellum to the thalamus by way of the prepuncle.

An article on "The Diagnosis of Tumors of the Cerebellum Especially with Reference to Their Surgical Removal" was contributed by me to the *New York Medical Journal*, Feb. 11 and 18, 1905.¹⁶ The

14. Spiller, W. G.: Ophthalmoplegia Internuclearis Anterior; A Case with Necropsy, *Brain* **47**:345 (Aug.) 1924.

15. Mills, C. K.: Preliminary Notes on a New Symptom Complex Due to Lesion of the Cerebellum and Cerebello-Rubro-Thalamic System, *J. Nerv. & Ment. Dis.* **39**:73 (Feb.) 1921.

16. Mills, C. K.: The Diagnosis of Tumors of the Cerebellum Especially with Reference to Their Surgical Removal, *New York & Phil. M. J.* **81**:261 (Feb. 11) and 324 (Feb. 18) 1905; also in the *Phil. Hosp. Rep.* **4**:15, 1905.

article also appeared in the *Philadelphia Hospital Reports*, volume 4, 1905, accompanied by contributions of Drs. Frazier, de Schweinitz, Weisenburg and Lodholz on various aspects of cerebellar disease and cerebellar physiology. This article was republished as a small monograph entitled "Tumors of the Cerebellum"¹⁷ and was followed by another volume on "Tumors of the Cerebrum."¹⁸

My paper in the cerebellar volume was founded largely on personal experience in the wards for nervous disease in the Philadelphia General Hospital and in the neurological and surgical department of the hospital and in the neurological and surgical department of the hospital of the University of Pennsylvania. At this time I did not altogether recognize that synergy was the one great function of the cerebellum, a fact which soon became apparent to me.

In recent years, the cerebellum as the particular organ or subdivision of the brain concerned with synergy has been most emphasized by Babinski,¹⁹ Babinski and Tournay,²⁰ and Rothmann,²¹ although this idea really goes back many years.

Ferrier in his work on "The Functions of the Brain" traces the history of the knowledge of the physiology of the cerebellum as first determined by Magendie,²² Flourens, Vulpian, Weir Mitchell²³ and others. The experiments of these investigators indicated a loss or disturbance of the power of coordinating or harmonizing movements when the cerebellum or a large part of it was experimentally extirpated.

In determining that synergy is the special function of the cerebellum, the use of moving pictures has proved of convincing value.

I first became aware of the value of moving pictures for the demonstration of nervous phenomena, normal and abnormal, by the oppor-

17. Mills, C. K.: With Drs. Frazier, de Schweinitz, Weisenburg and Lodholz; *Tumors of the Cerebellum*, Philadelphia, E. Pennock, 1906.

18. Mills, C. K.: With Drs. Frazier, de Schweinitz, Spiller and Weisenburg; *Tumors of the Cerebrum*, New York, A. R. Elliot, 1905.

19. Babinski, J.: De l'asynergie cérébelleuse, *Soc. de Neurol.* 7:684 (Nov. 15) 1899; Hémiasynergie et hémitremblement d'origine cérébello-portuberantielle, *ibid.* 9:422 (April 30) 1901; Asynergie et inertie cérébelleuse, *ibid.* 14:685 (July 15) 1906.

20. Babinski, J., and Tournay, A.: Les symptômes des maladies du cervelet et leur signification, *Tr. 17th International Congress of Medicine*, London, sect. 11, part 1, p. 51, 1913.

21. Rothmann, M.: The Symptoms of Cerebellar Disease and Their Significance, *Tr. 17th International Congress of Medicine*, London, sect. 11, part 1, p. 59, 1913.

22. Magendie, F.: *Mémoire physiologique expérimentale et pathologique*, 1828, cited in Ferrier's *Function of the Brain* (footnote 8).

23. Mitchell, S. Weir: *Researches on the Physiology of the Cerebellum*, *Am. J. M. Sc.* 57:320 (April) 1869.

tunities which I had in 1888 of observing the experiments made by Muybridge and Dercum on locomotion in the lower animals and in man. This work of Muybridge undoubtedly laid the foundation of cinematography.

Professor Edward Muybridge,²⁴ who was an enthusiastic student of the subject of animal locomotion, was engaged in 1888 by Dr. William Pepper, then Provost of the University of Pennsylvania, to pursue a research on animal locomotion under the supervision of a commission appointed by the trustees of the University. A small book was published comprising articles by Professor W. Dennis Marks on "The Mechanisms of Instantaneous Photography," by Dr. Harrison Allen on "Materials for a Memoir on Animal Locomotion" and by Dr. Francis X. Dercum "A Study of Some Normal and Abnormal Movements Photographed by Muybridge."

With Dr. T. H. Weisenburg I began a series of investigations which finally led to the publication of the paper on "Cerebellar Symptoms and Cerebellar Localization, Including Kinematographic Observations on Cerebellar Phenomena."²⁵ It became clear to me that moving pictures could be used not only for teaching purposes but as a method of investigation. The opportunities to enlarge the views of the motor disturbances and the time given to dissect more thoroughly the luminous picture presented, enabled the observer to obtain a truer idea of the character of cerebellar symptoms.

The outcome of the kinematographic studies of cerebellar cases was the adoption of the theory previously expressed by Ferrier, Babinski and others that synergy was the fundamental function of the cerebellum and that cerebellar symptoms local or general, simple or compound were expressions of asynergy.

I have carefully read several of Hughlings Jackson's papers on the cerebellum, but from these it seems to me impossible to arrive at a satisfactory conclusion regarding his views.²⁶ In one of the cases reported, owing to the closure of the sylvian aqueduct, extensive hydrocephalus resulted, causing enormous enlargement of the head and even

24. Muybridge, E.: *Animal Locomotion—The Muybridge Work at the University of Pennsylvania*, Philadelphia, J. B. Lippincott Company, 1888.

25. Mills, C. K., and Weisenburg, T. H.: *Cerebellar Symptoms and Cerebellar Localization, Including Kinematographic Observations on Cerebellar Phenomena*, J. A. M. A. **63**:1813 (Nov. 21) 1914.

26. Jackson, J. Hughlings: *Cases of Tumor of the Middle Lobe of the Cerebellum; Cerebellar Paralysis with Rigidity and Occasional Tetanus-Like Seizures*, Brain **29**:435, 1906; *Case of Tumor of the Middle Lobe of the Cerebellum, Cerebellar Attitude; no Tetanus-Like Seizures, General Remarks on the Cerebellar Attitude*, Brain **29**:440, 1906. Jackson, J. H., and Russell, Risien: *A Case of Cyst of the Cerebellum, Weakness of Spinal Muscles; Death from Failure of Respiration*, Brit. M. J., Feb. 24, 1894; also in collected papers.

separation of the sutures. As revealed by necropsy, the case was undoubtedly one of disease of the base of the middle lobe, but the symptoms present resulted from both the primary involvement of the cerebellum and the secondary effects of the lesion.

The second case was also a tumor and cyst of the inferior surface of the vermis, which must have exerted great pressure on the pyramidal tracts. Jackson speaks of the resulting condition as one of paralysis. It was in reality a mixture of asynergy from destruction of the cerebellar folia and paralysis from pressure on the pyramidal pathway. Jackson seems to recognize this fact in the reference which he makes to the investigations of Ferrier and Turner,²⁷ the practical outcome of which was that synergy was the primary cerebellar function.

In one case reported by Jackson and Risien Russell,²⁸ the patient placed face downward was unable to lift his body from the floor hardly more than one half as far as a normal person of about the same age and strength. The account of this case reminds me of a moving picture of one of the patients on whom a similar experiment was tried. The inability exhibited in such an experiment is due to the loss of power to regulate the movements required and not simply to the loss of energy or paralysis in its technical sense.

At the neurological research meeting in New York in December, 1926, some valuable records were made of experimental lesions of the cerebellar nuclei and the tracts of degeneration produced by these lesions. A tendency was shown, following Horsley and Clarke,²⁹ to hold that it is necessary to determine only the reactions of the deep nuclei to obtain the key to the functioning of the cerebellum. Investigations of the deep nuclei are, of course, of much importance, but one must search the cortical folia of the cerebellum to obtain a knowledge of its specific functions just as one must look to the convolutions of the cerebral cortex if one would unravel the functions of the cerebrum.

The main deep nuclei of the cerebellum—dentate, emboliformis, globosus, fastigial and vestibular—are places of anatomic and physiologic concentration and integration of the centers of the cerebellar cortex. I do not believe it is correct to infer as Horsley and Clarke and MacNalty and Horsley³⁰ have done, that the large volume of

27. Ferrier, D., and Turner, A.: A Record of Experiments Illustrative of the Symptomatology and Degeneration Following Lesions of the Cerebellum and Its Peduncles, Phila. Tr. Roy. Soc., 1895, vol. 105; cited in Ferrier's Functions of the Brain (footnote 8).

28. Jackson and Russell (footnote 26, third reference).

29. Horsley, V., and Clarke, R. H.: Structure and Functions of the Cerebellum Examined by a New Method, Brain **31**:45 (May) 1908.

30. MacNalty, A. S., and Horsley, V.: On the Cervical Spinobulbar and Spino-cerebellar Tracts and on the Question of Topographical Representation in the Cerebellum, Brain **32**:237 (Nov.) 1909.

purely cerebellar tissue known as the folia has no distinct function except that of receptors. It is not beyond likelihood that the cerebellar laminae, evidently arranged so as to increase the amount of functional material, are designed to receive, transform and transmit the impressions conveyed by the spinocerebellar tracts to the cerebellar nuclei.

The theory of Horsley and Clarke and their followers calls up a memory of many years ago. When Hughlings Jackson, Ferrier and others were beginning to present a train of phenomena which indicated the existence of centers in the motor cortex, Brown-Séquard³¹ at first challenged this view, and asserted that the phenomena of motion produced by the electrical irritation of the cortex were the result of transmission of the current to the spinal and bulbar centers of the neuraxis. This view was supported by Dupuy³² and others but soon had to give way to the overwhelming evidence in favor of centers in the cortex.

It is true that a relatively stronger current is required to produce cerebellar cortical phenomena than one for the elicitation of cerebral response. I am as firm a believer in cerebellar localization as I am in the localization of centers and areas in the cerebrum. Cerebellar centers, however, have distinct points of difference from those of the cerebrum. The synergic movements of the cerebellum are compound and therefore a little more difficult to elicit.

In one of my cases in which operation was performed I faradized the exposed folia in order to determine positively whether the operation was on the correct side of the brain, some doubt having arisen regarding this matter. The faradization with a weak current produced movements in the limbs on the side on which the operation had been performed.

DISCUSSION

DR. FRANCIS X. DERCUM, Philadelphia: I do not think that this paper should go without some discussion. It is in keeping with what Dr. Mills has done in other fields of neurology, and, further, his observations, results and conclusions are in keeping with what the morphology of the subject teaches us.

He spoke, among other things, of the labyrinth and of the rôle that the labyrinth plays in coordination. In order to interpret the labyrinth we must turn our attention to the fields of general biology and comparative anatomy. Like other organs, it did not spring into existence suddenly. It is exceedingly probable, as I pointed out in a paper published in the *American Naturalist* in 1879, that the semicircular canals were originally developed from the lateral line system of primitive fishes. The lateral line system of fishes, I may recall to your minds, consists of a series of nerve hills which are practically identical in structure with the maculae acusticae of the semicircular canals. These nerve hills are found at frequent intervals situated in long tubes or canals which extend in single lines

31. Brown-Séquard: Entre-croisements des conducteurs servant aux mouvements volontaires, Arch. de physiol. norm. et path. **1**:218, 1889.

32. Dupuy, E.: The Rolandic Area Cortex, Brain **15**:190, 1892.

longitudinally along the body of the fish; hence the name "lateral line" system. On the head, branches of this system extend over the supra-orbital, infra-orbital and mandibular areas. Occasionally, some of these nerve hills, especially on the head, are exposed or merely protected in shallow grooves, though this is the exception; the usual and almost universal condition is one in which the nerve hills are included in tubes which are in every way analogous to the semicircular canals. These tubes are formed by the grooving or involution of epidermal structures and the coalescence of the opposing edges with the resulting formation of canals. It is exceedingly probable that the semicircular canals of the labyrinth were originally portions of the lateral line system which became deeply submerged and gradually acquired a position below the base of the skull. This becomes the more probable when one reflects that the petrous portion of the temporal bone in which the semicircular canals are embedded is really not a part of the vertebrate endoskeleton, but is in reality ectoskeletal in origin; a surviving portion of an ancient ectoskeletal structure which in due course became incorporated with the base of the skull. We should call to mind also the fact that not all of the fishes have their semicircular canals, for the myxines—the hag fishes—have but one and the lamprey eels have only two. The function of the nerve hills of the lateral line system of fishes is probably to act as exteroceptors for coarse waves or vibrations in the water; perhaps they have other functions as well, such as the transmission of the varying pressures of different depths; but it would seem that the transmission of the impacts of coarse waves or vibrations is their principal or outstanding function, while it would be logical to conclude that the reception of impacts of a higher rate of vibration is the function of the semicircular canals. Coupled with the reception of coarse vibrations by the lateral lines there is necessarily a difference in the intensity with which the impacts impinge on the various portions of the lateral line system dependent on the direction from which the waves come. Intensity of impression and direction appear, therefore, to be indissolubly connected. In other words, the facts justify the conclusion that the lateral line system is intimately related to the spatial orientation of the animal and to its adjustment to its environment. Here, it seems to me, we have indicated the solution of the function of the semicircular canals. In the evolution of the semicircular canals from a primitive lateral line system, the function of the perception of environmental relations has been definitely preserved and in time—in the course of evolution—specialized so that this function has come to be represented by three canals bearing to each other the relations of the three classic planes of space; necessarily at right angles to each other. Thus are fulfilled in a striking manner all of the possible demands of the function of spatial orientation.

In keeping with the view that the lateral line system of fishes and the semicircular canals are primitively a part of one structure is the fact that both the nerves from the lateral lines and from the semicircular canals terminate in the same portion of the medulla; namely, in the acusticolateral area. Further, there is every reason to believe that in this portion of the medulla other impacts arising from the proprioceptors in the muscles, bones and joints, from the interoceptors and proprioceptors of the various viscera are likewise received.

Another interesting fact now presents itself and that is that the cerebellum is developed from this same acusticolateral area. As the demands of adjustment to the environment increase, this area increases in size and complexity. When the aquatic vertebrate becomes terrestrial, when it begins to employ its extremities in crawling and in other forms of terrestrial locomotion—in running, climbing, prehension, erect walking and, in birds, of flying—the increasing intricacies of movement are accompanied by an increase in the size and complexity of the cerebellum.

At the same time that these changes are taking place, great changes in growth and development are also taking place in the telencephalon, the cortex of the cerebrum. The latter develops by the proliferation of intercalary neurons from the distal end of the primitive neural tube, and it is by the continued proliferation of these intercalary neurons that the telencephalon increases in size and complexity. The development of the forebrain from the primitive neural tube and the development of the cerebellum from the acusticolateral area of the medulla go hand in hand. This parallelism is especially evident in the ascending scale of the vertebrates. In birds the final development of the cerebellum greatly exceeds that of the cortex or pallium. This disproportion is due to the special development of the function of flying which is to be interpreted as a highly specialized though limited form of coordination. Further, the motor function in birds is, as in reptiles, largely discharged by the striatum.

The various toning influences to which the voluntary muscles are subject next claim our attention. An analysis of these toning influences reveals them to be of three kinds. The first and most primitive toning influence is derived from the striatum. The second has its origin in the later appearing and usurping telencephalon. These two toning influences act in unison on the voluntary muscles, a balance or equilibrium between the two being maintained. If, however, one of these toning influences is diminished or destroyed by disease, the other acts in excess. For instance, in hemiplegia in which the cerebral cortical innervation has been cut off, spasticity results in the paralyzed arm and leg due to the now unrestrained innervation from the striatum. Similarly, when the striatum and other motor structures of the pale-encephalon—namely, of the brain stem—are cut off, as in paralysis agitans or in the parkinsonian symptom-group of the sequelae of epidemic encephalitis, the muscles likewise become rigid due to the now unrestrained innervation from the motor centers of the cerebral cortex. In addition to these two sources of innervation, there is a third intoning influence derived from the cerebellum.

As indicated in my earlier remarks on the lateral line system, the acusticolateral area in which the cerebellum has its origin, is the recipient of impacts from the receptors in the semicircular canals—in fishes also from the lateral lines—from the proprioceptors in the muscles, bones and joints and from the proprioceptors and interoceptors in the various viscera. All of these impacts are transmitted to the cerebellum in unceasing afferent streams, streams which after ingress to the cerebellar nuclei and cerebellar cortex, give rise to efferent streams which pass by way of the red nucleus down through the cord by way of the rubrospinal tract to the cells of the anterior cornua. By this means a constant intoning influence on the voluntary muscles is maintained. This intoning may vary, may be raised or lowered according to the streams of impacts received from the various receptors, but it never ceases unless the cerebellum is diseased or destroyed. In a sense, the cerebellum keeps every one of the voluntary muscles tense like a violin string. This tension varies according to the play of the cerebral cortical and the striatal innervations. The result is that when a movement is made, as when a limb is flexed or extended, the movement is not sudden or jerky but is a sustained and gradual one. When the forearm is flexed on the upper arm through the action of the biceps, its antagonist, the triceps, does not yield suddenly but remains tense like a piece of India rubber, and the movement of flexion is performed smoothly, uniformly and gradually. In a paper read at the Boston meeting of this association, Dr. Tilney in his experimental investigation of the function of the cerebellum noted the simultaneous contraction of opposing muscles and used the term "co-contraction" in describing this phenomenon. Experimental observation, therefore, confirms the conclusions based on purely

morphologic considerations. Finally, let me again stress the fact that the telencephalon and the cerebellum pursue an almost parallel course in their development. The increasing differentiations in the cerebral motor cortex and the concomitant increasing differentiation in the muscle plates is accompanied necessarily by an increasing differentiation of cerebellar function. In this respect the facts are again in accord with the conclusions of Dr. Mills, namely that there is a corresponding differentiation of structure and therefore of localization of function. In a general sense, this must be admitted to be true. Further, the clinical facts in our possession are in accord with this view. Taking it all in all, the problem of cerebellar function has become more clear than we formerly conceived it to be.

DR. WILLIAM G. SPILLER, Philadelphia: Dr. Mills almost more than any other American neurologist has a mind similar to that of Hughlings Jackson, for he has repeatedly by constructive reasoning come to conclusions which seemed at the time to be lacking in sufficient anatomic, pathologic or physiologic foundation, and yet later developments have shown that his conclusions often were in accordance with facts. It is not easy to discuss a paper which contains the results of an experience of sixty years. Dr. Mills has emphasized especially his belief in the importance of the function of the cerebellar cortex. It is not possible to believe that this considerable structure, rich in nerve cells, has an insignificant function. It is true that electrical stimulation of the cerebellar cortex has given rather unsatisfactory results, but it is known that the striate body does not lend itself to the discovery of its function by electrical stimulation, and it may be that later by other methods, possibly some not yet known and similar to strychnine irritation of the cerebral cortex, we may be able to come to conclusions which are at present impossible.

DR. FREDERICK TILNEY, New York: I want personally to thank Dr. Mills for this reiteration of his faith in the function of the cerebellum, which has been the light in leading all American neurologists. I particularly want to emphasize my belief also in the statement which he has made concerning the great importance of folia in the cortex of the cerebellum which we have been willing to neglect, I think, altogether too much. The idea that the central nuclei (the medullary nuclei of the cerebellum) are the main functional portions of this organ seems to be absolutely unsupported by the best evidence which we have. We must look more and more to the cortex for our interpretations in the functions of this organ. Dr. Mills' views concerning the connections between the neopallium and the pontile nuclei and thus with the cerebellum also stand out as the most hopeful interpretations which we have today in this field.

It was my privilege to preside at the meeting of the Research Association last year, in December, when the subject of the cerebellum was the exclusive topic, and I can confidently say that from a review of all of the evidence presented then and a careful study of the papers in consequence of that intensive study, I feel it certain that we have not advanced our knowledge concerning the function of the cerebellum one particle beyond what Dr. Mills has laid down for us and which we have up to this time been following.

DR. CHARLES K. MILLS. In closing: I simply arise to express my thanks and appreciation for the kind remarks of those who have discussed the paper. I do not think it would be wise to go any further into the matter. My views are expressed in the paper, and, as has been said, have been expressed elsewhere, so I shall simply content myself with thanking the association and those who have discussed the paper for their kindness and consideration.



