A extensive review of the whole field of cerebellar physiology and pathology has brought to light some aspects of its function that have been frequently overlooked, some of which are new and others are very old but long neglected. Many new findings explain old controversies and some observations open new research opportunities that are available only to clinical observers. The purpose of this review is to highlight these features of cerebellar function.

Cerebellar physiology will be discussed under the following headings:

I. The Cerebellum and Somatic Motor Activity
   A. Effect on muscle tone
   B. Effect on phasic reflex activity
   C. Effect on voluntary movement

II. Localization of Function in the Cerebellum

III. The Cerebellum and Sensation

IV. The Cerebellum and Vegetative Functions

V. The Cerebellum and Convulsive Seizures

The material of this paper has been taken in large part directly from our monograph on the cerebellum and much of it from those chapters prepared by Professor G. Moruzzi, who should be given full credit for the work. I wish to express my great indebtedness to him and also to Professor Olof Larsell, who has read this paper critically and assisted in the preparation of the anatomical material.

Before beginning the body of the paper it is appropriate to present Table 1 showing the relationship of the anatomical subdivisions of the cerebellum according to Larsell's classification. The cerebellum, however, has not only a horizontal division identified by Larsell as Lobules I through X with their related hemispheral extensions designated as HII through HIX but also a longitudinal division. These are particularly important in regard to the efferent connections from the cerebellum and have been shown recently to have great functional significance. These longitudinal divisions are designated as medial, intermediate and lateral zones. It should be noted that while the anterior lobes of some subprimates do not extend beyond the intermediate zone, in primates the anterior lobe has very definite extensions into the lateral zone.

I. THE CEREBELLUM AND SOMATIC MOTOR ACTIVITY

A. Effect on muscle tone

The fact that modifications of sensory and vegetative mechanisms were usually not observed by those who studied animals after ablation experiments indicates conclusively that the regulation of somatic motor activity is the most conspicuous and essential of all the functions of the cerebellum. Its relation to muscle tone has been one of the most confusing and controversial aspects of cerebellar physiology for over a half century. By postural tone we mean the muscular function which Sherrington called the "maintenance of attitude" which in antigravity muscles is concerned mainly with the maintenance of a standing posture. However, other than antigravity muscles have tone and the work of Rossi and others showed that there is a cerebellar control of this muscle tone also. Postural tone is, therefore, a more inclusive
### Table 1

**Representation of the lobes of the cerebellum**

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* Cerebellar terminology is presented in tabular form. Those terms frequently applied to the folial pattern of lower animals are shown on the left and on the right the terms applied to the human cerebellum. In each category the scheme of numerical designations proposed by Larsell is included. Please note that while Lobule II can be readily homologized in all species including man, it is a part of the lingula of human terminology and a part of what has been called the lobulus centralis in subprimate animals. Also note that the lateral Lobules HIV and HV in the human extend well into the hemisphere. The position of the lobules of the posterior lobe, so far as their position in respect to the medial, intermediate and lateral longitudinal divisions, are less well defined at the present time.
term than antigravity tone and they should not be used synonymously. *Extensor hypertonia* in antigravity muscles results from either acute or chronic ablations of the avian cerebellum provided the lesions are bilateral. However, *extensor hypotonia* has been confirmed by all investigators who have made total or unilateral cerebellar ablations in primates. It is in the observations of subprimate mammals that controversies have arisen concerning the influence of the cerebellum on muscle tone.

The Dutch school of physiologists 39, 40, 94 denied that hypotonia was found in subprimate mammals but their negative experiments concerned exclusively the effects of total cerebellectomy. Unilateral lesions of the cerebellum or of its nuclei in decerebrate cats result in changes in tone which are much more complex and result from an imbalance of tonic vestibular and labyrinthine reflexes released by cerebellar lesions. The effect of unilateral lesions can be completely different from lesions of the same parts performed in a bilaterally symmetrical fashion (Fig. 1). 59, 90, 126 Moruzzi and Pompeiano 59, 90 showed that the distribution of extensor tone was reversed when even the rostral or caudal parts of the fastigial nuclei were destroyed unilaterally in decerebrate cats.

Bremer 11 gave a lucid interpretation of the evolution of the cerebellar regulation of postural tone. He held that postural extensor mechanisms are tonically inhibited through bulbo-spi nal relays by the paleocerebellum; whereas, a tonic facilitatory influence is exercised by the neocerebellum on the cerebral cortex. These views were confirmed by Botterell and Fulton 7, 8 when cerebellar lesions were performed extensively in primates including the chimpanzee.

More recently a syndrome strikingly similar to Luciani’s atonia ensues when the whole 69 or the rostral part 3, 4 of one fastigial nucleus is chronically destroyed in the otherwise intact cat and if this chronic lesion is confined to the caudal half of one fastigial nucleus, the hypotonia is found on the contralateral limbs. 3, 4

In summary, the difference between lower mammals and primates is related mostly to the greater importance in primates of the lateral nuclei and of cerebellocerebral relations in the maintenance of supporting tonus. In consequence, extensor hypotonia occurs even after bilateral cerebellar lesions in these species. How much asymmetrical nuclear lesions play in the hypotonia so prominent in man and other primates remains to be seen by extension of these experiments of isolated nuclear ablations in cats to the monkey and other primates.

FIG. 1. Diagrammatic representation of the effects on the postural tone of the forelimbs produced by isolated lesions of the cortex of the medial part of the anterior lobe of the corpus cerebelli and of the fastigial nuclei. The lesions are marked in cross-hatch. MC = medial cortex of the anterior lobe; F = fastigial nuclei; R = reticular formation; CFT = corticofastigial tract; FBT = fastigio-bulbar tract; RST = reticulospinal tract; PG = pectoral girdle and brachial spinal cord.

A. Orientation diagram showing bilateral moderate extensor tone of the decerebrate cat. B. Ipsilateral increase in the extensor tone and contralateral decrease after unilateral ablation of the cerebellar cortex. C. Reversal of the tonic effect, with ipsilateral flexor rigidity and contralateral extensor rigidity, when the fastigial nucleus is destroyed on the same side as the cortical ablation. D. Marked accentuation of the postural asymmetries of C produced by ablation of the remaining portion of the medial anterior lobe cortex. E. Strong bilateral extensor accentuation produced by bilateral ablation of the medial part of the cortex of the anterior lobe and both fastigial nuclei.

Reproduced from Sprague and Chambers 28 (Fig. 4).
The alterations of muscle tone and the asymmetrical phasic reflex described by Italian neurophysiologists are not generally known in this country. Technically, these experiments consist of localized destructions of small and superficial parts of the cerebellar cortex. These effects have been found in dogs, rabbits and guinea pigs. If a dog is secured with its back on the animal board and the head and trunk lying symmetrically along the sagittal line, the position of the four legs will be symmetrical as soon as the typical passive attitude is assumed. If a small lesion of Crus I is then made, the symmetry will be lost and the ipsilateral foreleg generally will appear more flexed. This phenomenon was called by Rossi "postural asymmetry" (Fig. 2). It was also found that bilateral cortical excision of the motor cortex or even thalamic transection neither prevented nor abolished this postural asymmetry but it did disappear following intercollicular decerebration. It was also not abolished by acute or chronic labyrinthectomy. The same phenomenon was observed following local application of chloroform and cocaine. These tonic asymmetries disappeared only following a dose of curare which was significantly greater than that required to abolish the antigravity tonus of decerebrate rigidity which was shown by many workers to be selectively abolished by subparalytic doses of curare. This together with other evidence shows that this tonus is in some way different from extensor hypertonus and is not dependent on the myotatic and labyrinthine reflexes concerned with maintenance of standing posture. Rossi, as long ago as 1927, suggested that this tonus may be related to a central regulation of intrafusal muscle fibers, a field of investigation which recently has been more fully investigated and which will be discussed below.

B. Effect on phasic reflex activity

The cerebellum is less involved here than in either the regulation of tone or in the control of voluntary movement. Dusser de Barenne was struck by the normality of the scratch reflex. Swimming, which is a reflex activity in lower animals, is relatively little affected by cerebellotomy as opposed to activities that depend on maintenance of the standing posture. However, all labyrinthine reflexes, both static and phasic, are modified by the cerebellum. Furthermore, the phasic postural reactions so carefully and completely examined and defined by Rademaker, including the supporting reactions elicited from tactile and proprioceptive receptors, are exaggerated. The hopping and plac-

![Fig. 2. Postural asymmetry following unilateral ablation of Crus I. The time is 28 days after superficial ablation of the left Crus I. The dog is lying supine and shows clear-cut flexion ipsilaterally to the cerebellar lesion. Reproduced from Rossi (Fig. 19).](image)
ing reactions are at first lacking and later delayed following cerebellectomy and tendon reflexes are exaggerated for prolonged periods in the subprimate species.

Following ablation of Crus I, in the dog or in the thalamic cat, phasic responses to faradization of the nasal septum were found by Rossi to be performed asymmetrically. Di Giorgio found similar imbalance in the phasic reflex movements of the hind legs in rabbits following electrical stimulation of the genital region when unilateral lesions of Crus II were performed. Asymmetrical walking and swimming movements were observed by Simonelli in the thalamic cat following acute ablation of Crus I. Rossi and Di Giorgio found that deep lesions of Crus I and Crus II and lobulus paramedianus, without involvement of the nuclei, affected the execution of Rademaker’s reflexes in the dog.

C. The effect on voluntary movement

There is no better place to study the effects of cerebellar lesions on voluntary motor activity than in an analysis of the fundamental defects in man following cerebellar lesions. This has been done best by Gordon Holmes. In addition to the symptoms attributed to hypotonia, which is a conspicuous part of the deficiency in primates and particularly in man as indicated above, he noted a mild degree of asthenia and fatigability of the muscles, abnormalities in rate, regularity and force of voluntary movement and, finally, an alteration in certain associated movements. Movements are initiated more slowly. Their speed varies, sometimes faster, sometimes slower than in normal limbs. They are usually less forceful and the exertion of force is jerky or intermittent and finally there is also a marked slowness in beginning and effecting relaxation.

Bremer attributed these defects to a withdrawal of the facilitatory influence exerted by the cerebellum on the cerebral cortex and he also stated that a lack of the cerebellar support to the inhibitory mechanisms could also explain the failure to arrest voluntary movement promptly. These essentially clinical observations would be the correlate of Rossi’s classical stimulation experiments showing the facilitatory influence of the cerebellum on the motor area of the cerebral cortex. Other data, however, show that cortically induced movements may be inhibited by cerebellar stimulation at spinal levels and that inhibitory impulses arising in the vermal areas of the anterior lobe also impinge upon the cerebral cortex itself. It would appear that this regulation of voluntary movement may occur in many different ways and at all levels of nervous integration: cortical, brain stem and spinal cord.

II. LOCALIZATION OF FUNCTION IN THE CEREBELLM

The problem of a localization of function in the cerebellum is one of particular interest to clinicians because it is an organ with a cortical structure of considerable size which conceivably could have within the complex number of its lobes and fissures a representation of the various parts of the body. While there is general agreement in all quarters, in both the clinic and the laboratory, that there is a homolateral relation between the lateral parts of the cerebellum and the corresponding extremities, the problem of any more precise topographical localization within the cerebellum has been the object of a great deal of laboratory and clinical pathological investigation during the last sixty years.

Points of view beyond this general agreement of homolaterality vary widely. Gordon Holmes stated in 1917, “no local lesion affects only or exclusively one limb or portion of a limb.” Opposed to this point of view have been a great number of other workers who, following Bolk’s comparative studies, attempted to locate specific topographical regions or parts of the body in specific areas or subdivisions of the cerebellum.

In reviewing the literature on the early experimental work which seemed to support such a parcellation, one finds a great deal of inconsistency in the effects reported to occur after local lesions. The first indication that all might not be well with the experiments which quickly followed the publication of
Bolk's important work in 1906 came in 1908 when Binnerts, in Winkler's laboratory, carried out histological studies on the animals operated upon by van Rynberk in Rome from 1904 to 1907. He showed that the extent of the lesion was far greater than one might have anticipated from gross inspection and that van Rynberk's symptoms of cerebral asymmetry for lobulus simplex, ipsilateral forelimb dysmetria for Crus I and alterations in the musculature of the trunk for lobulus paramedianus occurred only whenever deep lesions had been made. Simonelli and Rothmann confirmed and extended these observations and demonstrated extensive vascular damage to the deep nuclei when the lesions grossly appeared to be purely cortical. Another source of error is the fact that superficial damage from exposure of the cerebellar folia alone may occur. Finally, methods of observation capable of detecting minimal alterations in tone and movement need to be used. Bilaterally symmetrical lesions are not capable of detecting these minor abnormalities as was rightly pointed out by Manni. The difficulties and failures should not deter one from studying the effect of well-planned ablations and some modern experiments with lesions of isolated cerebellar lobules which have avoided these
errors are now appearing in the literature.16,17,33,77–79

Bremer’s work on the inhibitory function of the “paleocerebellum” started a new approach to the experimental analysis of the function of the cerebellum and particularly to what we choose to call a functional localization within the cerebellum rather than a topographic localization which had occupied earlier physiologists. Ingvar’s concept of the division of the cerebellum into vestibular, spinal and corticocerebellar parts was illuminating (Fig. 3). The anatomical facts that most strikingly feature this functional division of the cerebellum are that each of these three divisions receives its afferent connections and sends out its efferent pathways to the same part of the nervous system.

The vestibular areas, for example the flocculonodular lobe, the uvula and lingula, receive direct and secondary vestibular cerebellar fibers. Efferent fibers from these lobules go directly to the vestibular nuclei.32 Likewise, the lobules that receive direct afferents from the spinal cord, principally the medial parts of the anterior lobe of the corpus cerebelli, the pyramis and uvula, send their efferents back out via the fastigial nucleus to the reticular formation and back down to the spinal cord. Finally, the lobules dominated by corticopontocerebellar connections, namely, the lateral parts of the anterior lobes and the whole of the posterior lobes of the corpus cerebelli, send their efferents back to the cerebral cortex through dentate, thalamic connections. There is considerable overlapping within these subdivisions (Fig. 4) but in general these anatomical facts stand out.

The intermediate zones particularly have an admixture of spinal and pontocerebellar afferent connections and are considered a functional entity by Chambers and...
Sprague. These authors have emphasized, on the basis of ablation experiments, a functional organization into medial, intermediate and lateral zones: the medial being concerned with tone, posture, locomotion and equilibrium of the entire body; the intermediate with movement, tone and posture of individual movements of the ipsilateral limbs; while the lateral zone "is involved in the same skilled and specially organized movements of the ipsilateral limbs without any apparent regulation of their posture and tone."17

The longitudinal parcellation has been presented by Chambers and Sprague as opposing what these authors chose to call the lobular theory of cerebellar localization which has been correlated by most previous workers with the afferent cerebellar connections. The two concepts are probably not mutually exclusive in the writer's opinion. The emphasis on this longitudinal or zonal organization is to be commended. Chambers and Sprague have, however, erred in insisting on a functional unity of the medial zone. As was pointed out by Dow and Moruzzi, "Chambers and Sprague (1955a and b) have not performed ablations limited to the vestibular parts of the cat cerebellum, but following observations of the behavior of animals with lesions of the pyramis, uvula and nodulus (lobules VIII, IX and X of Larsell) plus secondary fastigial nuclear damage, have noted a marked resemblance to the effects of anterior lobe lesions. They have claimed, therefore, that there is little justification for a differentiation of the various parts of the vermis—a point of view which is incompatible with the findings in the primate cerebellum. Their own protocols, so far as the differences between lesions in the folium and tuber vermis (lobules VI and VII of Larsell) and the anterior and posterior parts are concerned, contradict their conclusions as to the physiological unity of the vermis."

The vestibular part was shown to be a functional entity by ablations restricted to the flocculonodular lobe in primates. This syndrome is exemplified in humans by the titubating gait without ataxia of the individual movements of the extremities in children with medulloblastomas which take origin at the base of the nodulus.

The corpus cerebelli, a part of the cerebellum that far overshadows the flocculonodular lobe in mammals, shows a functional division in which the anterior lobe and more particularly its medial division shows itself to be primarily concerned with the regulation of postural reflexes. Stimulation of this area produces predominantly relaxation of the extensor rigidity of the homolateral forelimb in the decerebrate preparation and ablations, particularly in the dog and cat, producing a release of all the postural mechanisms that characterize the cerebellar ataxia state seen in the dog as studied by Rademaker after total cerebellectomy. The corresponding clinical syndrome in man is less well established for this division but it appears to be exemplified by the cortical cerebellar atrophies which selectively involve the anterior lobe of the corpus cerebelli and adjacent portions of the superior surface of the organ. Here disturbances of gait are the earliest and most conspicuous abnormalities, probably because of the early involvement of the anterior lobe in which are located those parts particularly responsible for the cerebellar control of antigravity postural reflexes.

The posterior lobe, together with the lateral expanses of the anterior lobe, forms the third functional division. Lesions here in man produce the symptoms of cerebellar deficiency so classically described by Gordon Holmes in his masterful study of the effects of injuries of the cerebellum. These are the lesions that produce hypotonia, the weakness or asthenia of limb movements and the disorders of rate, range and speed of muscular contraction which clinicians refer to collectively as the cerebellar ataxia of voluntary movement. This concept of the three functional divisions of the cerebellum which correspond to the three main afferent inputs to the cerebellar cortex does not mean that many cases of cerebellar disease are necessarily confined to these functional subdivisions, in fact, even
the illustrations chosen may involve combinations of all three areas.

Recently evidence suggesting a topographical localization within the cerebellar cortex has again appeared. It began with the observation by Snider and Stowell in 1942, reported in detail in 1944, that cerebellar responses from tactile stimulation of various parts of the body produced electrical discharges in more or less distinct areas of the homolateral anterior lobe and lobulus simplex in the lobulus paramedianus on both sides. Dow had previously noted the effects of single-shock electrical stimulation of peripheral nerves in the decerebrate cat without anesthesia and had been struck, not by the localization of the effects but by the widespread nature of the response throughout the spinal part of the cerebellum and by the similarity of the response, no matter if the forelimb or hindlimb nerves were stimulated. Combs found that even with physiological stimulation the topographical local responses could be found only if the animal were anesthetized with Nembutal and were not demonstrable in the unanesthetized cat.

That it is possible to demonstrate a topographical relationship with certain methods of study there can be no doubt. The same pattern, tail, lower extremity, upper extremity and face from lowest to highest folia of the anterior lobe with a reversal on the lobulus paramedianus was found by Adrian for the anterior lobe in response to contralateral cerebral cortical stimulation in 1943 and these were extended and confirmed by Hampson and Snider and Eldred (Fig. 5). A similar pattern has been found by stimulation experiments and by ablation experiments in the cat.

Bremer has pointed out a difference between the somesthetic areas of the cerebral cortex and those lobules of the anterior lobe of the corpus cerebelli that receive a projection from the various parts of the body. In the cerebral cortex a stimulus to the arm has no effect on a subsequent stimulus to the leg in their respective somesthetic reception areas, while in the cerebellum there is a very striking effect on the testing response by a conditioning volley which results from a stimulus in a remote area of the body or even by a “click” stimulus. These observations demonstrate convergence of various...
afferent connections to the cerebellum. This would agree with Dow’s observation on the striking similarity of the wave form of the response from point to point throughout the anterior lobe, regardless of whether the upper or lower extremities were stimulated.

In 1942, when stimulating the cerebral cortex, Dow attempted to show not how restricted an area would be excited from the cortical stimulation but to map out the extent of cerebellar activation from a local cerebral stimulation. To do this electrical stimuli were used which, while anatomically localized, were many times threshold strength. Conditioning of the responses from stimulation of either arm or leg areas of the cat’s cerebral cortex by each other was demonstrated when a response was being studied at a common point on the cerebellum. The level at which this conditioning effect was produced was not determined but it was shown that the effect was not caused by spread of current. The fact that both Curtis and Dow were able to show such widespread effects in the cerebellum from stimulation of a single cortical point is as significant a finding as the fact that with weaker stimulation and with the use of anesthetics or by leading the afferent volley in the white matter, one can demonstrate topographical parcellation of the cerebellar cortex in certain areas. While widespread cerebellar action potential in the monkey was evoked when areas 4 and 6 and the postcentral gyrus were stimulated, the stimulation of association areas produced action potentials that were definitely greater in the lateral and posterior lobulus, such as the lobulus ansiformis and lateral parts of the lobulus paramedianus. Indeed, no low threshold responses were found when leading from the culmen and pyramis, except when stimulating in the sensory-motor cortex while responses in the lobulus ansiformis were picked up following low threshold stimulation in the parietotemporal and frontal association areas. This relationship was quite clear with a technique which, for practical purposes, was unsuccessful in demonstrated topographic relationship. This observation is particularly striking when one recalls that it is not the cerebral cortex as a whole that is so greatly enlarged in man but rather the “association areas” which have assumed this great size. It is also these lobules of the cerebellum that seem to be related to the association areas which in man have also grown out of proportion to the rest of the cerebellum.

In summary, evidence seems very clear that there is a functional localization respecting the afferent projection of vestibular, spinal and corticocerebellar projection and perhaps some difference between the sensory-motor cortex and the association cortex. There is also very great evidence for a longitudinal parcellation into vermian, intermediate and hemisphere zones as has been emphasized by Chambers and Sprague with distinct roles for each of these divisions closely related to the nuclear outflow from the cerebellum. The emphasis of recent years on the somatotopic localization seems overdrawn. Dow and Moruzzi have concluded, “There seems no doubt that the somatotopic arrangement is by far less pronounced on the cerebellar than on the cerebral cortex and it would be seriously misleading to expect that the different cerebellar areas should be separated by sharp borders, as are those of the Rolandic zone.”

III. THE CEREBELLUM AND SENSATION

The demonstration of a variety of sensory connections to the cerebellum involving exteroceptive sensory fibers, hearing and sight, as well as proprioceptive and vestibular sensation, has aroused new interest in the possible role of the cerebellum in sensation. That vestibular and proprioception were not the only impulses from the periphery, with more or less direct connections to the cerebellum, was indicated as soon as electrical recording of cerebellar action potentials in response to afferent stimulation was made. Stimulation of the saphenous nerve, which is cutaneous in distribution, results in a cerebellar potential that was still present after all reflexes had been abolished by large doses of curare. Using more physiological stimuli several workers observed that the cerebellum was readily affected by exteroceptive stimu-
The somatotopic distribution of afferent projections within anterior lobe and lobulus simplex has already been discussed and was the same regardless of whether pure tactile stimulations or mixed exteroceptive and proprioceptive stimuli were applied. Exteroceptive projections were found, moreover, on the pyramis, lobulus paramedianus and on some folia of lobulus ansiformis.

Snider and Stowell should be credited with the discovery that auditory and visual systems are represented within the cerebellar cortex, although a few occasional observations of this kind had been reported previously by Gerard, Marshall and Saul. Adequate controls and the strict localization of the response showed that the response could not be attributed to spread of bioelectrical impulses from neighboring extracerebellar structures, to proprioceptive reverberation or to occasional exteroceptive stimulation. The conclusion was drawn that auditory impulses are relayed by brain-stem pathways, probably through tectal neurons, to their projection areas within the cerebellar cortex which is located in the lobulus simplex and tuber vermis (Larsell’s lobules VI, HVI and VII). Another important observation was that the auditory areas coincided very closely with the cerebellar zone yielding responses to a flash of light. The visual responses differed from the auditory ones by much longer latencies and by their greater sensitivity to barbiturates. Practically all the experiments had to be performed under chloralose anesthesia. Adequate controls indicated that retinal impulses were relayed to the cerebellar cortex, probably through tectal neurons. Gastaut, Naquet, Roger and Badier suggested that photic responses reached the cerebellum only under abnormal conditions. Although undoubtedly distorted and magnified by chloralose anesthesia, Fadiga, Pupilli and von Berger showed that responses of lobules VI and VII to photic stimuli were present also in the unanesthetized cat and should be considered a normal phenomenon.

The fact that such a variety of sensory modalities have a more or less direct connection to the cerebellum in itself might suggest a more extensive function for the cerebellum than simply the control of muscular activity. Gordon Holmes, whose work on the effects of acute cerebellar lesions in man is classical in clinical observations, stated in 1939 concerning this subject: “In man even extensive lesions of the cerebellum involve no form of conscious sensation.” This conclusion is widely accepted by most physiologists and clinicians today.

It should be pointed out, however, that not all clinicians shared these views. Lotmar, Maas, Goldstein, Goldstein and Reichmann, Reichmann and Panzé all have reported disturbances in the appreciation of weights in patients with cerebellar disorders. Holmes himself stated in his original description of cerebellar deficiency in man in 1917 that when “identical weights were placed in his two hands, his eyes being closed, the patient frequently did not recognize that they were equal and in almost every case stated that the heavier was in the affected hand.” He was unable, however, to discover any alteration in the accuracy of discrimination between two weights and, in his more detailed analysis of these observations in 1932, he believed that this tendency to overestimate the weight of objects held in the affected hand might be ascribable to the asthenia of the limbs and the toneless state of the muscles “owing to which the proprioceptive nerve endings within them may be less easily excited when they contract or are subjected to strain by the resistance of raising the weighted limb.” Holmes’ explanation, however, will not account for the observations of Lotmar, Maas and Goldstein whose patients underestimated weights held in the affected hand and Goldstein insisted that ability to discriminate the difference between weights was poorer in the affected hand. Goldstein claimed that the localization of tactile stimuli often was wrong in the affected side, that slow, passive movements were properly evaluated only when the excursion was greater than on the normal side. He even claimed abnormal responses to visual and auditory stimuli.

A review of animal experiments which
Some aspects of cerebellar physiology have been made in the past which might possibly shed some light on this problem. Would necessarily start with the observations of Renzi, reported in 1863 and 1864, whose views were so unorthodox that it is easy to see why they have been neglected for almost one hundred years. Renzi spoke of the cerebellum as the organ of centrifugal innervation of sensation. He observed that fear reactions to visual stimulation and arousal by tactile stimulation were reduced in birds contralateral to an acute cerebellar lesion and that in guinea pigs responses to auditory stimulation were reduced following cerebellar ablations. While adequate anatomical controls were never exercised by physiologists of this era, it is of particular interest that Chambers and Sprague reported in anatomically well-controlled experiments in cats that there was "a great reduction in startle responses to loud noises, lack of attention to noises which had preoperatively aroused quick investigation, following bilateral cortical ablation of tuber and folium." It is, therefore, conceivable that Renzi's contention that the cerebellum had a centrifugal innervation which was concerned with the phenomenon of sensory attention may not be as farfetched as would have been thought a few years ago.

Another old observation which has recently had some confirmation is that of Russell in 1895. While describing the results of removing one cerebellar hemisphere in the dog, he stated that in the first few days "the animal may take notice of cold water dropped onto all the other extremities or to the painful clip applied to any of these and yet take no notice of either of these stimuli when they were directed to the posterior extremity on the same side as the lesion." Here again Chambers and Sprague have observed a "marked increase in threshold to nociceptive stimuli of ipsilateral limbs and trunk following dentate destruction." These observations may not necessarily represent a defect in conscious sensation for they could be the result of an acute withdrawal of a tonic facilitatory influence exerted by the cerebellum in the motor cortex which might bring about the temporary disappearance of a conditioned response without affecting necessarily conscious sensation. There is some reference in recent Russian literature to alterations in visual sensation in humans following cerebellar injuries but insufficient details of the experimental procedures are presently known to allow any critical evaluation of these reports.

One place where the cerebellum may exert an influence on sensation and which has been the object of a great deal of electrophysiological study concerns the gamma efferent innervation of the intrafusal fibers of the muscle spindles. This has been shown to be influenced by stimulating the cerebellum and by ablatting or cooling some of its parts. Granit and Kaada recorded the efferent discharge of the gamma neurons from the ventral roots. They also studied the afferent discharge of the muscle spindles as they lead from isolated A type fibers of the dorsal roots properly identified by the techniques described in detail by Granit and his associates. They demonstrated that the afferent discharge from the muscle spindle in the gastrocnemius muscle was augmented during stimulation of the lateral part of the anterior lobe and decreased and even at times blocked during stimulation of the medial part. They found the gamma efferent discharge to be also inhibited by stimulation of the medial part of the anterior lobe. Eldred observed changes when the nuclei and brachium conjunctivum were stimulated and Granit, Holmgren and Merton found that cooling the anterior lobe silenced the spindle discharge and rewarming restored the original afferent discharge (Fig. 6).

One must, however, not draw the conclusion, even from these experiments, that this necessarily means an influence on conscious proprioceptive sensation. As Granit has pointed out and Mountcastle, Covian and Harrison, as well as McIntyre have shown, with the technique of evoked potentials, the nuclear bag afferents project onto the cerebellum only and that other sense endings so situated as to escape cerebellar control appear to be the ones that reach the cerebrum.

Some disorganization of this mechanism of
gamma neuron function may be responsible for the results of Sjöqvist and Weinstein\textsuperscript{117} who could not find evidence of a disturbance of weight discrimination in trained monkeys after cerebellar lesions and only transient disturbances following severing of the medial lemniscus. However, when both medial lemniscus and cerebellar lesions were made “there was a marked permanent loss in general proprioceptive function and ability to discriminate weight.” It would be of interest to see how cerebellar deficiency prevents recovery after injury of the medial lemniscus. It was assumed by Sjöqvist and Weinstein\textsuperscript{117} that the cerebellothalamocortical pathways were essential for the recovery. However, it would be most interesting to see what the effect on the recovery from lemniscus interruption would be when the outflow from the superior cerebellar peduncle was not interrupted but when the gamma neuron regulation of the muscle spindle was disorganized by a fastigial lesion.

Finally, one other bit of experimental evidence which points toward a way the cerebellum might function in the sensory sphere. Hagbarth and Kerr\textsuperscript{84} experimenting on curarized cats found that stimulation of the anterior vermis blocked the transsynaptic response of the ventral column of the spinal cord following single-shock electrical stimulation of a spinal nerve root (Fig. 7). They also found interference with the cortical response to this stimulation and that this recovered later than the second sensory neuron did. This suggested to these authors that the sensory conduction had probably been interfered with not only in the spinal cord but also in high centers. These effects could be reproduced by repetitive stimulation of the bulbar or midbrain reticular formation and several regions of the central cortex but not from cerebellar areas other than the anterior vermis. Snider and Sato\textsuperscript{122} have described either inhibition or facilitation, depending on the time intervals, of the cortical response to click stimulation when the sensory stimulus was preceded by a single short stimulation of the “auditory” area of the cerebellum.

In any consideration of the role of the cerebellum in sensation, one must remember that in all other areas where its function has been more thoroughly investigated and certainly better understood, the cerebellum always exercises only a measure of control on a neural mechanism in all instances capable of its own independent activity. It will,
therefore, be expected that any cerebellar influence on sensation will be to control or influence a sensory mechanism capable of functioning to a greater or lesser degree independently of the cerebellum. The task which presents itself now is to define how and to what extent the cerebellum influences sensory experiences which recent electrophysiological studies have given an hitherto unsuspected role in cerebellar physiology.

The last years have seen a truly remarkable but nevertheless quite disproportionate growth of our knowledge of the cerebellum. The functional anatomy of the afferent and efferent projections has been the field that gained the greatest advantage from the introduction of electronic methods. The results obtained so far should be controlled, however, with experiments performed along different lines. It is likely that important facts were missed in previous ablation experiments and in the routine clinical observations because the observers were not prepared to look for these unexpected functional relationships and, therefore, no adequate tests were developed to bring out these deficiencies. It is certainly true that for an analysis of sensory phenomenon man remains our best experimental animal. How this clinical material can be brought into our understanding of neurophysiology remains to be seen. One immediately thinks of the illuminating work of Bender and his associates on the sensory function of the cerebral cortex where the team of neurologist and experimental psychologist yielded important information. Whether or not a similar approach could produce equally significant results in an analysis of cerebellar function remains to be seen.

IV. THE CEREBELLUM AND VEGETATIVE FUNCTIONS

No attempt will be made here to discuss in detail the experimental evidence for a cerebellar influence on vegetative function. This has been completely documented by Dow and Moruzzi. Moruzzi has convincingly demonstrated that stimulation of the anterior lobe of the cerebellum has an inhibitory effect on vasopressor cardiovascular reflexes. Zanchetti and Zoccolini observed outbursts of sham rage to follow cerebellar stimulation in the region of the fastigial nucleus. Moruzzi also noted an inhibitory effect of anterior lobe stimulation on respiration, especially if it was performed during a period of excessive hyperpnea.

A number of workers have obtained results that indicate some relation between the cerebellum and endocrine glands. The work of Wiggers is probably the most interesting. He found changes in both fasting blood-sugar levels and in glucose tolerance curves following ablations of the uvula. Kaplan had
previously reported changes in the glucose tolerance curves in dogs following vermian lesions. Less convincing evidence of a cerebellar control of body temperature and basal metabolism has been noted by some authors.

Pupillary responses to electrical stimulation have been reported by many workers beginning with Ferrier's report in 1876. Chambers described both mydriatic and myotic responses. Chambers and Sprague also described changes in pupillary size following both cortical and nuclear lesions.

The only clear-cut evidence of an influence of the cerebellum on the digestive system is the observation by Bard et al. that the nodulus was essential to the production of motion sickness in dogs.

Chambers is the only author to demonstrate with certainty the cerebellar origin of stimulation effects on micturition in unanesthetized cats. These were obtained from the deep nuclei and adjacent white matter mostly in the rostral portion of the roof nuclei. Chambers and Sprague also noted in histologically well-controlled experiments that the bladder was hypotonic following lesions in these areas. Gall's incorrect hypothesis concerning the cerebellum and sex functions remains of only historical interest. The trophic lesions of skin and muscles described by a number of authors following cerebellar lesions have never been proven to be the result of these ablations. Wang and Brown, however, have shown an inhibition of the galvanic skin reflex by stimulation of the anterior lobe of the cerebellum.

V. THE CEREBELLUM AND CONVULSIVE SEIZURES

The relationship between certain neuropathological conditions of the cerebellum and myoclonic epilepsy dates from an initial clinical observation by Hammond in 1867, followed by Hunt's description of dyssynergia cerebellaris myoclonica. Hodskins and Yakovlev, in an extensive work, pointed out a significant relationship between cerebellar atrophy and myoclonic epilepsy in a neurological survey of 300 epileptic patients. Christophe and Rémond found the spike and wave pattern characteristic of the myoclonic epilepsies in a case of dyssynergia cerebellaris of Ramsay-Hunt.

Russell showed that the myograms of the extensor muscles involved in generalized clonic convulsions produced by absinth were very much greater on the side of a recent or chronic unilateral cerebellar ablation. While the mechanism of this cerebellar influence on convulsive seizures has never been adequately worked out, his results, as well as those of Meyers, were so striking as to demand further investigation by modern methods of research. Cooke and Snider noted that electrically induced cerebral seizures could be blocked by stimulation of the cerebellar cortex or the fastigial nucleus. Iwata and Snider have observed that the seizure patterns of the cerebral cortex induced by strong hippocampal stimulation can be stopped by faradization of the cerebellum.

Clark described some prolonged motor effects of cerebellar stimulation in unanesthetized-unrestrained cats subjected to electrical stimulation of the cerebellum through chronic implanted electrodes. These he called cerebellar seizures and stereotyped patterns of movement were described lasting from 5 to 15 minutes after the intensive stimulation of a single point on the cerebellar surface. These effects were also duplicated by mechanical stimulation and in one animal by a small abscess under an implanted electrode. Chambers, Clark and Ward and McDonald have made important contributions to these unusual observations.

An important opportunity to investigate these observations would be to extend Pool's observations on the effect of electrical stimulation of the human cerebellum in unanesthetized patients, recording both the subjective and objective results. This method has proven of great value in the understanding of cerebral epilepsy in the hands of Penfield and his associates but it has never been attempted in a systematic way on the cerebellum. Neurosurgeons have a unique opportunity to make some important observations here.
CONCLUSION
The cerebellum remains in many respects a mysterious organ. We are still far from understanding what characterizes the influence exerted by the cerebellum on other neural structures. We can say that its function is always in relation to some other nervous mechanism. Such words, however, as "regulation," "control" or "supervision," useful as they may be in any attempt to give a tentative explanation of our results, may create the wrong impression that we know what is going on within the cerebellum. Indeed the same words are used when we attempt to describe the influence exerted by the reticular formation on the spinal cord or cerebral cortical mechanisms. We know that this great mass of neurons is not merely the system to which these terms could be applied. The main problem of cerebellar physiology is to learn how so many different functions are integrated within the complex folial pattern of the cerebellar cortex and its underlying deep nuclei. There is much information needed before we shall fully understand how this organ carries out its unique functions.

REFERENCES
28. DI GIORGIO, A. M., and MENZIO, P. Azione tonica cervelletto nell’animale deafferentato (arti an-
108. van Rynberk, G. Le problème de la localisation
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dans le cervelet. Arch. int. Physiol., 1907, 5: [127]–[128].


119. SNIDER, R. S., and ELDRED, E. Cerebral projections to the tactile, auditory and visual areas of the cerebellum. Anat. Rec., 1948, 100: 714.


