Archives of Neurology and Psychiatry

Vol. 4

OCTOBER, 1920

No. 4

THE STATIC AND KINETIC SYSTEMS OF MOTILITY

PRESIDENTIAL ADDRESS

J. RAMSAY HUNT, M.D.
NEW YORK

The subject of motility is one of great interest to scientific men in many fields of investigation. Neurologists, particularly, have always had a peculiar interest in motor function and its disorders, and to neuropathology must be credited much that we know of the underlying neural and muscular mechanisms.

During the last half century our knowledge of this important function of the living organism has made great progress and each decade has marked some new advance in the realm of motion, as well as in the sensory sphere. For these two great functions of the living organism are the pillars on which have been reared those marvellous mechanisms of the central nervous system, the phylogeny of which is the story of all organic life.

The problem of motion and sensation must, therefore, ever remain a living issue in the realm of science, as life itself traverses these two pathways side by side in the slow and imperceptible processes of evolution.

It would carry us too far afield at this time to record the achievements of the many investigators whose names are imperishably linked with the history of motility. This I shall hope to do later when my subject is presented in more extended form. I wish, however, to acknowledge having made free use of this vast accumulation of facts in the conception of the efferent nervous system which I am about to formulate.

This hypothesis is not concerned so much with the elusive intricacies of motility itself, as with the dual nature of its underlying systems.

COMPONENTS OF MOTILITY

I believe that motility consists of two components, each being represented throughout the entire efferent nervous system by separate neural mechanisms, which are mutually cooperative and yet physiologically and

* Read at the Forty-Sixth Annual Meeting of the American Neurological Association, New York, June, 1920.

anatomically distinct. This is true not only of the segmental nervous system but also of the larger integrating and coordinating masses of the brain and cerebellum. Under normal conditions they are inseparable and act in unison, and the harmony of their relation is only disturbed by the dissociation of accident or disease.

One of these components of motility is the movement proper, which is subserved by the *kinetic system*.

The other represents the more passive form of contractility, which we recognize in tonus, posture, attitude, and equilibrium. This static function of the efferent system is subserved by separate neuromuscular pathways, which may be termed the *static system*.

The term static is used here in the same sense as in the physical sciences, where it relates to the laws governing matter at rest and the forces producing equilibrium. I have found no other word which expresses better my conception of this other great function of the efferent system.

THE PHYLOGENY OF CONTRACTILE TISSUE

Before proceeding to a presentation of the evidence on which this conception is based, I would first ask your indulgence while I review briefly the phylogeny of the nervous system in its bearing on the development of movement.

All of those more complicated muscular activities which we study in man have, like every other function of the human organism, a very humble origin. And in order to detect the earliest manifestations of motility we must retrace our steps to the lowest rung of the ladder of life, where the ameboid movements of unicellular organisms allow these minute beings some slight increase in the range of their activities. Even in this lowly form the slow plastic movement is followed by a faint postural or static effort, when the pseudopodium of the cell becomes fixed to some neighboring object by molecular attraction or adhesion. The tiny organism then not only reaps the advantages of movement but the equally valuable effect of postural fixation under new conditions.

For if the power to move in space were not associated with an equal ability to control such movements in terms of posture, attitude and equilibrium, the advantages of motility would be of very doubtful value to the higher organisms.

The next advance in kinetic evolution is the ciliated movement. Here a protoplasmic cell has projecting from its free surface minute fibrils which are derived from the intracellular network of the organism. These cilia are capable of quick rhythmic, to and fro movements quite unlike the slow, plastic transformations of structure which characterize the first protoplasmic efforts of the ameba in the realm of movement.

As one ascends the scale of life, from one phylum to another, there is developed in the course of evolution a more complex contractile substance, the muscular tissue, which is the active agent in producing that great diversity of movement which characterizes animal life. The first development is the unstriated muscle which, according to some authorities, is present as low in the scale as sponges (Parker¹), and is constant in all higher forms. The quality of its movement is slow and plastic. Striated muscle, which represents a higher differentiation of contractile tissue, makes its appearance in worms and mollusks, and constitutes the skeletal musculature of vertebrates. The quality of its movement is quick and elastic.

A very striking illustration of the dual nature of muscle function may be observed in certain of the invertebrates. In bivalved mollusks closure of the shell is affected by the contraction of two distinct muscles, a contractile muscle which is striated, and an arrest muscle which is nonstriated. The rapid movement of closure of the shell is produced by the striated muscle. This is accompanied by a slower contraction of the arrest muscle which becomes firmly fixed as soon as the movement ceases. The arrest muscle thus fixes in posture the closing movement of the shell, which is then able to withstand an enormous degree of pressure before relaxation is induced. A similar division of movement and posturing muscles may also be observed in *Echinus* and *Pecten* and these have separate and distinct sources of innervation (von Uexküll²).

Comparative anatomy shows clearly that the muscular system, like all other structures of the body, is in a state of evolution, adapting itself to the changing conditions of the organism. Development is from the slow movement of the unstriated to the quick movement of the striated muscle fiber. And in man all gradations may be observed from the lowest type of unstriated muscle to the highest type of striated muscle fiber.

Striated muscle contains two substances, both capable of contraction. The one is the disk mechanism of the muscle fiber, which gives rise to the quick movement or the twitch. The other is the sarcoplasm which yields a more plastic form of contraction. It is, I believe, not unlikely that the simple protoplasmic movements of the ameba and the quick rhythmic waves of the cilia are the prototypes of the more elaborate functions of striated muscle.

Marshall,³ after an exhaustive study of the muscles of vertebrate and invertebrate life, has reached certain important conclusions. He

1. Parker: The Reaction of Sponges, *J. Exper. Zool.* **8**:39, 1910.

2. von Uexküll: Studien über den Tonus, *Ztschr. f. Biol.* **44**:269, 1903; *ibid.* **58**:305, 1912.

3. Marshall, C. F.: The Structure and Distribution of Striped and Unstriated Muscle in the Animal Kingdom and a Theory of Muscular Contraction, *Quart. J. Microsc. Sc.* **27**:75, 1888.

believes that the disk mechanism of the muscle fiber is the final product in course of evolution from the primitive intracellular network of the cell. This is represented in the unstriped muscle fiber by the longitudinal fibrillations. He traces from its origin the gradual development of the contractile mechanism and shows its relation to the quality of movement. A movement is slow or quick according to the quality and degree of differentiation of this constituent of the muscle fiber.

A clear conception of the phylogeny of contractile tissue is important to my theory as I do not regard the skeletal muscle mass in man as a mere aggregation of muscle fibers of a standard type, but rather as systems of end organs representing different stages of phylogenic development, and thus corresponding in some measure to similar differentiation in nerve tissue.

I believe that the highest functions of motility are carried out by more highly developed muscle fibers than are the lower forms of movement. For the functions of the efferent nervous system and the muscular system are so closely intertwined that one can scarcely conceive of evolutionary progress in one without corresponding changes in the other, to meet the demands of more elaborate functional activity.

TYPES OF MOTILITY AND POSTURE

Let us now leave the question of muscle tissue and consider, for a moment, the general types of motility in animal life. These are usually divided by physiologists into three groups, reflex, automatic and associated, and isolated synergic movements.

It should be remarked, however, that one group merges imperceptibly into the other and the transition is so gradual that it is difficult to say where one type ceases and the other begins. For as Herbert Spencer pointed out, the progress of evolution is from the most automatic to the least automatic and cessation of automatic activity and the dawn of volition are one and the same thing.

In the lowest forms of life, movement and posture are of a purely reflex character and depend on a primitive reflex arc, which is the functional unit of the nervous system. In higher forms these reflex units are combined and more complicated reflex activities result. These in turn are gradually brought under the control of still higher integrating and correlating centers with corresponding advances in the variety and forms of movement.

There are many extraordinary evidences of reflex action in the lower forms of life, both in the realm of posture and of movement. There are such movements as the reflex of defense, the flight reflex, the turning reflex, that strange reflex of self-mutilation by which an extremity is discarded to escape a threatened danger. There is a disguise reflex characterized by alteration of color, also a tonic reflex

producing a general rigidity and one simulating the posture of death, and many others that have been acquired in the struggle for existence.

In the "automatic and associated group" there are movements of crawling, walking, running, jumping, swimming and flying. These movements are usually bilateral and rhythmic, or alternating and rhythmic, and find their highest expression in vertebrates. All of these movements, reflex as well as automatic, have their corresponding static components, and every cessation of movement is immediately followed by fixation of the contraction in posture.

In the higher mammals and especially in man one encounters a new form of movement which differs from reflex and automatic movements in the quality of individuality and dissociation. Thus, one of the extremities which in reflex and automatic movements plays a fixed rôle as part of a mechanism, becomes capable of isolated and unilateral effort under voluntary control. This form of movement represents an immense advance in the evolution of motility and underlies the development of all skilled movements which have reached such extraordinary perfection in man.

In all of these isolated forms of voluntary movement there is also the element of posture, and it may be stated without fear of contradiction that there is no form of motility from the simple reflex to the most skilled and individualistic type of movement which functions without a corresponding static mechanism.

EVOLUTION OF THE NERVOUS SYSTEM

With the gradual increase in the range of movement and posture in organic life there has been a corresponding development of nerve structure, for every movement is represented as such in the mechanism of the nervous system. As one ascends the animal scale there is an increasing complexity in the arrangement of the central nervous system, due to the development of higher and higher levels of coordination and control. In man and the primates the original simplicity of the segmental neuraxis is quite concealed by the enormous development of cerebrum, cerebellum, and their respective projection systems in the spinal cord.

Hughlings Jackson,⁴ following the philosophic teachings of Herbert Spencer, was the first to grasp the full significance of evolutionary principles as applied to the central nervous system of man. His conception of functional levels, each higher level controlling the activities of the lower centers, stands today, and will, to my mind, continue to dominate all conceptions of nerve functions, psychic as well as

4. Jackson, Hughlings: Croonian Lectures, *Brit. M. J.* 1:660, 703, 1884.

somatic. For in the central nervous system of man is written in terms of functional levels the whole history of the evolution of organic life.

In a general way the central nervous system may be said to represent three great structural and functional divisions. There is a segmental nervous system, which contains the great reflex systems of the neuraxis, a paleo-encephalon which represents the essential sensory and motor mechanism in lower forms, and a neo-encephalon which has its greatest development in man, and subserves the highest functions of motility and sensibility.

It is my belief that these three great functional divisions of the nervous system are related to the three great types of movement and posture enumerated in the foregoing.

In this conception, I regard the cerebellum as the great correlating center for the static functions of motility, in contrast to the corpus striatum and Rolandic area, which I regard as the essential correlating centers for the control of their respective forms of kinetic function. Furthermore, I believe that these systems are represented by special end organs in the skeletal muscles in the same manner as we conceive sensations with their special systems and modes of termination.

THE AUTHOR'S HYPOTHESIS

I will now proceed to a presentation of the evidence on which my hypothesis is based, which, however, on the present occasion, cannot be given in detail but can only be outlined in a very general way. Let us first consider the muscular system, which contains all of the contractile end organs of the efferent mechanism.

The skeletal musculature is composed of striated muscle fiber held together by connective tissue, by means of which the contractile mass performs its functions. The purely anatomic divisions of muscles are of comparatively little importance in the physiology of motion. For as Hughlings Jackson pointed out, "movements not muscles" are represented in the nerve centers and usually a number of muscles participate in any given movement.

We must, therefore, conceive the efferent nervous system, including the muscles, as organized for the execution of a great variety of movements which become more and more numerous and complex as we ascend the scale of life.

As we have seen, each striated muscle fiber is composed of two distinct substances which are now generally recognized by physiologists as subserving different types of motor function. In a general way it is estimated that the disk system constitutes about from one sixth to one half of the total muscle mass, the remaining portion of which is sarcoplasm.

DUAL INNERVATION OF MUSCLE FIBERS

Each muscle fiber contains a motor nerve ending, which is the terminal of a medullated nerve fiber. For many years this was thought to be the sole innervation of the muscle fiber, until Perroncito⁵ and Boeke⁶ demonstrated the existence of another smaller nerve ending in the striated muscle fiber which was shown to be the terminal of a non-medullated nerve.

Boeke expressed the opinion that the motor end plate of the medullated nerve fiber furnished the stimulus for the disk system while the accessory sympathetic terminals were in control of the sarcoplasmic portion of the contractile mechanism, a conception which Mosso had previously expressed in his interpretation of the tonus and twitch components of muscle function. Boeke carried his investigation still further, and in order to prove the independent nature of these two systems, he cut the trochlear nerve in the cat and studied the nerve degenerations in the superior oblique muscle. All of the motor end plates in connection with the medullated nerve fibers were found in various stages of disintegration while the accessory sympathetic nerve endings showed no evidences of degeneration.

One could hardly offer better evidence of the independence of these two systems of nerve endings.

These histologic studies awakened considerable interest in the physiologic world, as Botazzi⁷ had previously enunciated a theory of dual contractility for the muscle of the batrachian heart. In this hypothesis the slow tonic contraction of the sarcoplasm supported and reinforced the quicker movement of the disc system.

It is also interesting that physiologists have detected certain differences in the metabolism of muscles which are probably related to these two forms of activity of the muscle fiber.

Pekelharing⁸ demonstrated the existence of two chemical processes in muscle metabolism. One was related to the disk system, and was characterized by the utilization of nonnitrogenous substances. The other was concerned with the utilization of albuminates and this was possibly dependent on the chemical activity of sarcoplasm. Other experiments have shown that the expenditure of energy of the active

5. Perroncito: Etudes ultérieures sur la terminaison des nerfs dans les muscles à fibres striées, *Arch. ital. de Biol.* **38**:393, 1902.

6. Boeke: Die motorische Endplatte bei den höheren Vertebraten, *Anat. Anzeiger* **25**:193, 481, 1909.

7. Botazzi: The Oscillations of the Auricular Tonus in the Batrachian Heart with a Theory on the Function of Sarcoplasm in Muscular Tissues, *J. Physiol.* **21**:1, 1897.

8. Pekelharing: Die Kreatininausscheidung beim Menschen unter dem Einfluss von Muskeltonus, *Ztschr. f. physiol. Chem.* **75**:207, 1911.

muscle' contraction (tetanus) is far greater than is that of posturing muscle (tonus). This explains the relative unfatigability of the posturing or sarcoplasmic function of muscle. It is certainly significant that muscle fibers consisting of two types of contractile substance should also present two distinct forms of chemical activity.

Another striking confirmation of a dual efferent system is to be found in the researches of Kure, Hiramatsu and Naito,⁹ on the innervation of the diaphragm. These investigators were able to show by animal experimentation that the phrenic nerve conveys the kinetic impulses for this important muscle, while its tonus is received through the splanchnic system of the sympathetic. If the phrenic nerve is cut, the diaphragm is paralyzed but tonus is preserved. When the sympathetic nerve is cut, tonus is lost but motility is unaffected. As the diaphragm performs a relatively simple function it is not surprising that these two systems are dissociated and, as had already been shown by experiments of Boeke, the same is true for the kinetic and static systems of the ocular muscles.

The attempt has also been made to demonstrate a similar dissociation in the innervation of the lower extremities by cutting the trunk of the abdominal sympathetic. This experiment was performed by Dusser de Barenne¹⁰ who claims to have produced a demonstrable loss of tonus in the corresponding muscles. These results, however, have not been confirmed by subsequent observers (Cobb,¹¹ Beritoff,¹² and others) and it appears probable that the sympathetic efferent system of the extremities takes a different route, not passing by way of the vascular system.

As the extremities represent a later phyletic addition to the muscular system, it is possible that the efferent static innervation for these structures may pass to the muscles with the motor nerves. In this connection it is interesting to note that Ransom¹³ has shown the existence of a large complement of nonmedullated nerve fibers in peripheral nerves. Further investigation will be necessary, however, to

9. Kure, Hiramatsu and Naito: *Zwerchfelltonus und Nervi splanchnici*, *Ztschr. f. exper. path. und Therap.* **16**:395, 1914.

10. Dusser de Barenne: *Ueber die Enthirnungsstarre (Decerebrate Rigidity) in ihrer Beziehung zur efferenten Innervation der quergestreiften Muskulatur*, *Folia neuro-biol.* **7**:651, 1913.

11. Cobb: *A Note on the Supposed Relation of the Sympathetic Nerves to Decerebrate Rigidity, Muscle Tone, and Tendon Reflex*, *Am. J. Physiol.* **46**:478, 1918.

12. Beritoff: *Die tonische Innervation der Skelettmuskulatur und der Sympathicus*, *Folia neuro-biol.* **8**:421, 1914.

13. Ransom: *Unmyelinated Nerve Fibers as Conductors of Protopathic Sensation*, *Brain* **38**:381, 1915.

clarify this question and to show any relationship between the non-medullated fibers described by Ransom and the sympathetic terminals of the striated muscle fiber.

The existence of two separate contractile systems in striated muscle fiber is also shown very clearly by the electromyogram. In myotonia congenita, Gregor and Schilder¹⁴ have demonstrated the presence of two distinct contraction waves, the one quick and referable to the disk system, the other slower, more sustained, and of sarcoplasmic origin. A similar dissociation of quick and slow muscle waves may also be produced in the electromyogram of veratrin and creatinin intoxication.

PERIPHERAL MECHANISMS OF TWO SYSTEMS OF MOTILITY

In the theory which I am endeavoring to unfold the disk is to be regarded as the end organ of the kinetic system, and the sarcoplasm as the end organ of the static system, just as we conceive the heat and cold spots or the tactile corpuscles as end organs in their respective sensory spheres. These end organs of the skin have undergone special differentiation on certain parts, and have thus acquired a greater accuracy and refinement of function.

I believe that a similar specialization of function and structure exists in skeletal muscles. By this I would emphasize what perhaps is not generally recognized, that the muscle fiber system, like the nerve fiber system, participates in phyletic differentiation, and that those muscle fibers which subserve the higher functions of neokinesis are more highly specialized than are those which are concerned with paleokinetic function.

According to this conception the corticospinal system and the striospinal system would both be represented by special contractile end organs.

As the striospinal system is older, the muscle fibers subserving this function would be less highly differentiated than those subserving the highest cortical function. Let us see what facts may be derived from histology, and physiology, in support of this point of view. As long ago as 1874, Ranvier pointed out that in muscles there are two kinds of fibers, which he described as pale and dark fibers. The pale fibers are rich in contractile substance and contain comparatively little sarcoplasm. The dark fibers are rich in sarcoplasm with a relatively simple disk mechanism. Both kinds of fibers are found in all muscles in varying degrees.

14. Gregor and Schilder: Zur Theorie der Myotonia, *Neurol. Centralbl.* **32**:85, 1913.

The pale fibers are the quick contracting, and the dark fibers the slow contracting fibers of the physiologists (Pankul¹⁵). And the quickness of a muscle contraction which varies considerably in different portions of the body depends on the relative number and distribution of these two types of fibers. It has also been shown that those muscles which are subjected during the life of the organism to the most constant activity are especially rich in sarcoplasm (Knoll¹⁶).

I believe, therefore, that the more highly differentiated pale fibers are related to the neokinetic system, while the dark fibers are concerned with paleokinetic motility. As the evolution from the lower to the higher movement is gradual, there are transition forms between these two types of fibers.

The skeletal muscles may therefore be regarded as contractile tissue, which bears the imprint of the phylogenetic struggle in the same measure as the nervous system which controls it. Considered as a whole it is the end organ of the efferent system and in its mass are represented the great kinetic and static pathways of the brain and cord.

THE SEGMENTAL NERVOUS SYSTEM AND THE DUAL FUNCTION OF MOTILITY

Let us now consider the segmental nervous system in its relation to a dual function of motility. At this level are represented the earliest centers for movement and posture, and the relative simplicity of its reflex mechanisms has made it an especially attractive field for experimental study. Sherrington,¹⁷ who is the acknowledged authority on the various reflex activities of the nervous system, has reached the conclusion that two types of reflex action may be recognized. There is a reflex movement which he calls the phasic reflex, and a reflex posture which he terms the tonic or postural reflex, and in the realm of reflex action he indicates very clearly the duality of function which I would extend to the whole of the efferent system.

He also has shown in his study of "postural activity of nerve and muscle" that coordination and reciprocal innervation are as much a part of the tonic, or postural, reflex as they are of the phasic reflex mechanism. His experiments on decerebrate rigidity, as well as those of Magnus and Kleijn,¹⁸ show conclusively that innervation and coordination are as important in the realm of posture as in that of movement.

Reflex action is therefore dependent on a peripheral kinetic system which terminates in the disk contractile mechanism. And reflex posture

15. Pankul, in Luciani: *Textbook of Physiology* 3: Chapter 1.

16. Knoll: *Ueber Protoplasmaarme und Protoplasmareiche Muskulatur*, *Denkschr. d. k. Akad. d. Wiss. z. Wien. Math. naturw. Kl.* 58:633, 1891.

17. Sherrington: *Postural Activity of Muscle and Nerve*, *Brain* 38:191, 1915.

18. Magnus and Kleijn: *Die Abhängigkeit des Tonus der Extremitäten muskeln von der Kopfstellung*, *Pflüger's Arch. f. d. ges. Physiol* 145:455, 1912.

is dependent on a peripheral static system which terminates in the sarcoplasm of the muscle fiber. These are the neuromuscular representatives at the segmental level of the kinetic and static pathways of motility.

One function of the peripheral static system is the so-called "lengthening and shortening reactions" of muscles. This intrinsic function of muscle tissue is dependent on postural tonus, by which a muscle may be lengthened or shortened during contraction without corresponding changes of tension. This alteration in postural length without corresponding changes of tension facilitates the easy transition from posture to movement which characterizes motility.

Sherrington has also shown the great importance of this posturing mechanism in hollow viscera, like the bladder, the postural tonus of the muscular walls of this organ allowing considerable changes of volume without increase of the intravesical tension. It has also been definitely established that a similar mechanism exists in the vascular system and in other structures under the control of the autonomic nervous system.

Before leaving the peripheral systems of motility, some mention should be made of the "all or nothing" principle of Bowditch¹⁹ which apparently governs all forms of muscular contraction. His experiments were carried out on the heart muscle of the frog and showed that an induction shock produces a muscle contraction or fails to do so according to the strength of the current. If a contraction is induced, it is the greatest of which the muscle fiber is capable, and there are no gradations with varying strengths of current.

Keith Lucas²⁰ has shown that this principle also applies to the skeletal muscles. Accordingly, the strength of a muscular contraction is not dependent on the strength of the current, but on the number of muscle fibers participating in the contraction. The refinements and gradations of movement are therefore dependent on the number of muscle fibers participating, and not on variations in the strength of the nerve impulse.

CENTRAL PATHWAYS OF TWO SYSTEMS OF MOTILITY

Let us now leave the peripheral mechanisms and pass to a consideration of the central pathways of motility.

In a previous study of paralysis agitans,²¹ I expressed myself as favoring the conception of two great motor systems from brain to

19. Bowditch, in Bayliss: *Textbook of Physiology*, 1919, p. 383.

20. Lucas, Keith, in Bayliss: *Textbook of Physiology*, 1919, p. 383.

21. Hunt: *Primary Atrophy of the Pallidal System: A Contribution to the Functions of the Corpus Striatum*, *Brain* 40:58, 1917; *Arch. Int. Med.* 22:647, 1918.

muscle, one subserving paleokinetic and the other a neokinetic function. The corpus striatum, according to this view, is the paleokinetic center for the control of "automatic and associated movements," and the Rolandic area is the neokinetic center for "dissociated movements" of cortical origin. Their static functions I believe are subserved by other pathways.

It should be remarked, however, that the thalamic portion of the paleo-encephalon is closely associated with the cerebral cortex by afferent and efferent tracts, by means of which paleokinetic motility may be directly controlled from the cortical sphere (cortico-thalamo-striospinal system). This higher control of the striospinal system makes possible a finer differentiation of paleokinetic motility and explains the occurrence of purely involuntary movements of cortical origin. It also bridges the gap between the striospinal and cortico-spinal types of movement and renders the transition from the older to the newer forms of motility a more gradual process.

In striking contrast to the paleokinetic system is the neokinetic system. This is a direct pathway from the cerebral cortex to the spinal cord for the control of isolated synergic movement. It takes its origin in the motor cells of the Rolandic area and passes by way of the pyramidal system directly to the anterior horn cells of the spinal cord, and from there to a special disk representation in muscle subserving the dissociated movements of cortical origin.

These two great motor systems, the pyramidal and extrapyramidal, according to this theory, are both represented in nerves and skeletal muscles. They are in a sense complementary and their independence is only unmasked by the dissociations of disease.

A critical analysis of the symptomatology of pyramidal and extrapyramidal disease (spastic paralysis and paralysis agitans) are strongly corroborative of this hypothesis (Hunt²²).

The central pathways for the control of the static component of motility are, I believe, distinct from those subserving its kinetic function. The essential suprasegmental mechanism for the control of static motility I believe to be the cerebellum. The importance of this organ in the regulation of muscle synergy and tonus and in the maintenance of equilibrium has been recognized by all observers, and yet, notwithstanding years of patient investigation, a certain obscurity still clouds our conception of its function and relation to motility.

DeBoer²³ has recently considered it as the central mechanism for the control of reflex tonus and the sarcoplasmic function of the muscle

22. Hunt: The Existence of Two Distinct Physiological Systems for the Transmission of Motor Impulses in Peripheral Nerves, *Brain* **41**:302, 1918.

23. de Boer: Die Bedeutung der tonischen Innervation für die Funktion der quergestreiften Muskeln, *Ztschr. f. Biol.* **47**:239, 1914.

fiber, and has presented an imposing array of evidence in favor of this hypothesis. Tilney,²⁴ in a comprehensive study of the cerebellum, has enlarged our conception of its synergic function to include the synergic unit. This is represented by a single muscle and its antagonist which contains a "dominant and check mechanism" capable of kinetic and akinetic phases. In this conception both the kinetic and static functions are subserved by the unit of synergy.

While accepting in the main the classic conception of cerebellar synergy as enunciated by Babinski, I would limit this function to a control of the static synergies of motility. The kinetic synergies are controlled by their respective kinetic mechanisms.

Anatomically, the cerebellum has close connections with both the cerebrum and the spinal cord. It receives impulses directly from the spinal cord, which pass to its central portion (vermis), as well as impulses from the cerebral cortex, which pass by way of the pons varolii to the cerebellar hemispheres.

In the cerebellum there are phylogenetic evidences of two great systems, which correspond to similar divisions of the cerebrum. There are a paleocerebellum, or vermian system, and a neocerebellum or hemispheric system.

The efferent cerebellar systems originate in the central nuclei (the dentate, nucleus globosus, emboliformis and fastigii) and traverse the superior cerebellar peduncles.

The older cerebellum stands in relation to what may be termed the *paleo-static system* which controls the static functions of movement of the "automatic and associated type." It takes its origin in the older nuclei of the vermis cerebelli.

The cerebellar hemispheres, on the other hand, regulate the higher postural functions of motility through the medium of a *neo-static system*, which originates in the cells of the dentate nucleus. This is controlled from the cerebral cortex by a special system of fibers passing from the frontal lobe to the pons varolii and thence to the opposite hemisphere of the cerebellum. The frontopontocerebellar system descends in the internal capsule and cerebral peduncle in close association with the pyramidal tracts, and it is interesting to note that both structures, the one subserving the static and the other the kinetic function of motility, receive their myelin sheaths subsequent to birth.

Both of the efferent systems of the cerebellum pass in the superior peduncles to special cellular divisions of the nucleus ruber (nucleus magnocellulatus and nucleus parvicellulatus), from which they descend as separate systems in the spinal cord, a paleorubrospinal system and a neorubrospinal system. I then conceive them as passing in separate systems to the sarcoplasm of the skeletal muscles.

24. Tilney: Functional Significance and Principal Syndrome of the Cerebellum, *Neurol. Bull.* 2:289, 1919.

Before leaving the question of the central pathways, I would say a word in respect to a group of subordinate motor centers which are found scattered in the tegmental region of the brain stem, and usually referred to as prespinal centers of motility.

The prespinal or better supraspinal centers of motility represent a distinctly lower level of phylogenesis than the corpus striatum. They are intercalated in the pathway of the extrapyramidal system, of which they form a part and I believe contain representatives for both the kinetic and the static components of motility. With certain exceptions these cannot be differentiated in the present state of our knowledge. The red nucleus, however, may be cited as an example of a purely static center at the supraspinal level of motility. The manifestations of decerebrate rigidity are probably closely related to this supraspinal static mechanism.

MOTOR MANIFESTATIONS OF DISEASE

I would now pass to a consideration of the efferent system in its relation to symptomatology. Is it possible to recognize the existence of a static and kinetic system in the various motor manifestations of disease?

In the interpretation of such phenomena one should always consider the existence of positive and negative symptoms as differentiated by Hughlings Jackson.²⁵ The positive symptom occurs in lower centers from loss of the inhibitory action of higher centers. Many important motor disturbances are of this order and are referable to secondary functional discharge in lower centers.

In a general way, it may be said that a lesion of the kinetic system causes a disorder of movement, and a lesion of the static system, a disorder of tonus or of posture.

In many of the disturbances of motility both systems participate, although it is usually possible to indicate one or the other as the essential factor involved.

At the segmental level of the nervous system the tendon reflex is a typical example of kinetic function, as is the muscle tonus of static function. Langelan²⁶ has recently shown that tonus consists of two components, a contractile tonus referable to the disk system and a plastic tonus of sarcoplasmic origin. These may also be recognized on direct percussion of the muscle by the quick contractions of myotatic irritability and the more persistent local reactions of the idio-muscular response.

25. Jackson, Hughlings: The Evolution and Dissolution of the Nervous System, *Brit. M. J.* **1**:591, 1884.

26. Langelan: On Muscle Tonus, *Brain* **38**:235, 1915.

A similar division of function is also demonstrable in reflex action, the kinetic system yielding reflex movements, and the static system reflex posture.

Such disorders of motility as paramyoclonus multiplex, myokymia, and fibrillary twitchings are spasmodic phenomena referable to the kinetic spinal mechanism, while myasthenia gravis is a paretic manifestation. The clonus of spastic paralysis and the tremor of paralysis agitans are both of kinetic origin. One is related to the neokinetic, and the other to the paleokinetic system. The more plastic tonicities which are also present in both of these forms of palsy are of sarcoplasmic origin and referable to the static system. Certain well marked differences in hypertonicity which characterize the two disorders I would refer to difference of static and kinetic representation in the skeletal muscle. Huntington's chorea and epilepsy are both of kinetic origin, the former is referable to the striatal and the latter to the cortical level of motility.

Other disorders of motility, referable to the corpus striatum, such as athetosis, dystonia, progressive lenticular degeneration and paralysis agitans, represent different degrees of involvement of its efferent and inhibitory systems. This phase of the subject has been considered in detail in my contributions to the symptomatology of the corpus striatum.²⁷

Rarely, in epilepsy there are seizures which suggest a relation to the static system. These are characterized by unconsciousness and a sudden loss of postural control without convulsive manifestations (static epilepsy).

All forms of myotonia, cerebral, cerebellar, spinal and peripheral, would appear to be of sarcoplasmic origin and referable to the static system. There is also much in favor of the hypothesis that the tonic spasms of cerebellar origin and the tonic rigidity of tetanus are essentially contractile manifestations of sarcoplasm.

The nature of the Bárány reactions to labyrinthine stimulation also indicate, in my opinion, a relationship to static function and the sarcoplasm of muscle. I would recall the slow and quick components of labyrinthine nystagmus. The slow movement is primary and referable to excitation in the static sphere, while the quick movements are secondary, and of kinetic origin.

The relationship of the frontopontocerebellar system to various myotonic phenomena has already been emphasized by Kleist²⁸ and Kinnier Wilson. Mills²⁹ has also considered this question in a discus-

27. Hunt: The Efferent Pallidal System of the Corpus Striatum, a Consideration of Its Functions and Symptomatology, *J. Nerv. & Ment. Dis.* **46**:211, 1917.

28. Kleist: Ueber nachdauernde Muskelkontraktionen, *J. f. Psych. u. Nerv.* **10**:95, 1908.

29. Mills: Muscle Tonicity, Emotional Expression and the Cerebral Tonic Apparatus, *Neurol. Centralbl.* **33**:1266, 1914.

sion of a cerebral tonectic mechanism. Kinnier Wilson and Walshe³⁰ have made the important observation that tumors of the frontal lobe anterior to the motor area may produce myotonia, a peculiar feature of which is the limitation of the disturbance to voluntary movements. Bumke³¹ has also described a family disorder characterized by the occurrence of myotonia with both voluntary and automatic type of movement. It should be remarked that in all of these central forms of myotonia the usual electrical and mechanical evidences of myotonia congenita are absent, which proves the disorder to be of central origin.

These various clinical types of myotonia I regard as corroborative of the conception of a special system for the control of the higher function of static motility.

There is one organic symptom in particular which is closely related to the static function of the cerebellum, and that is the intention tremor. The intention or cerebellar tremor presents the characteristics of a loss of the static components of motility. The coarse tremor movements may be regarded as an effort of the kinetic system to compensate for the loss of the posturing or static functions of the sarcoplasm.

In a movement complex, the kinetic component governs the synergies of the movement itself, but is accompanied by the static function which guides, steadies and reinforces the movement in its course and fixes it in posture when the movement ceases. When this mechanism is disturbed the intention tremor results.

At a meeting of this Association five years ago, I³² described *Dyssynergia cerebellaris progressiva*, an affection characterized by the gradual development of generalized intention tremors. On the basis of pathologic investigations not yet reported, I would refer this disorder to an atrophy of the efferent dentate system through which the cerebellum exercises control of the static system of motility (primary atrophy of the efferent dentate system).

In addition to these various somatic expressions of kinetic and static function, a similar division may be recognized in the mental sphere. Among these may be mentioned catalepsy, catatonia, and certain of the hyperkineses of psychic origin. A psychostatic and psychokinetic representation may therefore be postulated at the psychic level of motility.

This concludes my argument in favor of the two great systems of motility; it is only an outline, and were my time not limited it could be reinforced by many additional facts which would materially strengthen the hypothesis.

30. Wilson and Walshe: The Phenomena of Tonic Innervation and Its Relation to Motor Apraxia, *Brain* **37**:119, 1914.

31. Bumke: Eine familiäre Form von Intentionskrampf *Ztschr. f. d. Neurol. u. Psych.* **4**:644, 1910.

32. Hunt: *Dyssynergia Cerebellaris Progressiva*, *Brain* **37**:247, 1914.

SUMMARY OF HYPOTHESIS

In conclusion, I would restate briefly the general principles underlying this conception of the efferent system. The function of motility, like sensation, is represented by special end organs and neural systems which subserve the various types and modalities of contractile function. Their phylogenesis is in strict accord with the evolutionary hypothesis. From the primitive movement and posture of the lower forms of life to the highest expressions of motility in man, the transition is a gradual one and is recorded in the efferent nervous system of man.

As the animal organism is subject to the mechanical laws of a physical world, two forms of movement, active and passive, have been evolved in the struggle for existence. The one is that passive contractility of the muscular system which maintains the organism in posture and equilibrium and counteracts the forces of gravity and atmospheric pressure. The other is a more active form of contractility by which the organism is enabled to move or change its position in space.

In some invertebrates these two forms of motility are readily distinguished and are subserved by separate muscles. In higher forms these two important functions of muscle tissue are united in the muscle fiber, but are controlled by separate neural systems.

It is therefore possible to trace the evolution of the static and kinetic systems of motility from the lowest to the highest levels of the neural mechanism.