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THE COÖRDINATION OF MOVEMENT

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Normal voluntary movements are accurate in direction, precise in extent, uniform in rate, regular in rhythm, and thrifty in force. This composite quality of movement is called coördination, and movements which lack this quality are called ataxic.

A coördinate movement is the result upon the muscular apparatus of the contraction of a series of muscles in regular order, with regular rhythm, and with appropriate strength. Every muscle which participates, contracts at a rate varying from ten to eighteen contractions per second. As the muscles contract, the tendons are pulled upon, some of the ligaments are strained, others are relaxed, the bones move at the joints, and the skin alters in tension. In this function of coördinate movement of the muscular apparatus, skin, bones, muscles, and joints all share.

Some physiologists formerly assumed that the loss of the function of coördination was attributable to and measurable by the loss of sensibility in one or other of the constituent parts of the muscular apparatus; thus, Leyden specifically emphasized the loss of cutaneous sensibility; Goldscheider, the loss of articular; Frenkel, the loss of muscular; and Dejerine and Egger, the loss of bony sensibility. The function of coördination in so far as it depends upon sensibility must depend upon the sensory impulses

arising from every part of the muscular apparatus, and not upon that of the skin only, or joints only, or muscles only, or bones only. The sensibility of the muscular apparatus must be considered as a whole in regard to the function which it exercises as a whole.

Other investigators, such as Erb, Friedreich, and Charcot, did not accept the hypothesis that sensibility is the basis of coordination and showed that ataxia could occur without sensory loss. Jendrassik and Raymond, recognizing the all-powerful influence of mental control over movement, maintained a so-called psychic theory of ataxia.

All the controversy between the upholders of sensory and of motor theories of ataxia is now at an end. The recent brilliant experimental work of a number of investigators, chief among whom is Sherrington, has revealed to us much of the mechanism by which movement is coordinated, and has shown us the truth that is contained in each of these theories.

In this paper I wish briefly to epitomize our present knowledge of coordination. I shall deal first with the afferent impulses from the muscular apparatus and with their distribution, next with their integration at non-sentient and sentient levels, and lastly, with the initiation and control of efferent impulses, both conscious and unconscious.

Kölliker discovered embedded in muscle, certain fusiform structures which Sherrington later identified as afferent receptors, which respond to the stimuli that arise when a muscle contracts, and which are called muscle spindles. Golgi found in tendons, certain other structures which are obviously designed as receptors of traction stimuli. In ligaments, synovial membranes, and cartilage, analogous receptor structures occur. These receptors are attuned to receive afferent impulses which originate in the muscular apparatus. These afferent impulses underlie the conscious and unconscious control of all movement and are distributed throughout practically the whole central nervous system.

From the muscle spindle, a nerve fiber passes to a cell in the spinal ganglion on the posterior root. The axon of this spinal ganglion cell enters the spinal cord as the posterior root fiber. This fiber divides in the cord into an ascending and a descending branch, each of which gives off many collaterals. One of these collaterals is called the reflex collateral. Traversing the spinal gray

matter from behind forwards, this reflex collateral forms mediately or immediately a synapse with the dendrites of a cell in the anterior horn. The axon of this anterior horn cell is the motor or efferent neuron, and passes to the muscle whence the afferent impulse came, where it terminates in the motor end plate.

From the muscle receptor, stimuli arising in the muscle pass by the afferent nerve, through the cell on the spinal ganglion, through the posterior root, to the posterior horn of the spinal cord, and thence, through the gray matter to the motor cell of the anterior horn which corresponds to that muscle. From this anterior horn cell, along the motor neuron, which terminates in the motor end plate, impulses are discharged which initiate muscular changes. We have now traced an afferent impulse in its transit through a simple reflex arc. But a single detached reflex arc is merely a physiological abstraction. The isolation of a nervous act is scarcely possible. The nervous system responds as a unit to peripheral stimuli.

Continuing to trace the afferent fiber from the muscle receptor, we find the descending branch of the posterior root fiber by means of collaterals is ultimately linked with the anterior horn cells which preside over the destinies of adjacent and allied muscles. Collaterals from the ascending branch are similarly distributed. Afferent impulses which are never sentient are thus allotted among the cells of the spinal cord so as to make possible the reciprocal innervation, reinforcement, inhibition, and irradiation by which reflexes in the same segment are correlated and reflexes in different segments are integrated, so that nervous action is unified. Such correlating effects as the reversal (*Umkehr*) reaction, the relaxation of the antagonists when the agonist contracts; and the activating of synergic muscles, that is, muscles which affect the same bony lever or levers consonantly, are thus rendered possible. These coördinating effects are possible not only because of the distribution of the afferent impulses among the segments of the cord, but also because all efferent impulses leave the cord only by the lower motor neuron, the *final common path* of all motor results of nervous activity.

The ascending branch passes up in the homolateral posterior columns to the nuclei of Goll and Burdach; the fibers from the leg pass by way of Goll, those from the arm, by way of Burdach. In the posterior columns, these fibers are associated with the others

arising from the receptors in the skin over the muscle, from the bone upon which the muscle rests, and from the structures around the joint which the muscle moves. From the cells in the nuclei of Goll and Burdach, a second relay of fibers conveys the posterior column impulses to the cells of the medio-ventral nucleus of the contralateral optic thalamus. The impulses then pass by a third relay of fibers, from the optic thalamus to the cerebral cortex.

Some fibers from the nuclei of Goll and Burdach go, mainly uncrossed, to the middle lobe of the cerebellum. The ascending branch gives off collaterals of which certain go to the cells of the ipsi-lateral columns of Clarke and Stilling. The columns of Clarke and Stilling give origin to the tracts of Flechsig and Gowers, respectively. These tracts form the second relay for the impulses conveyed by the ascending branch collaterals, and end in the cerebellum. The second relay fibers in any series concerned with a function may be anatomically intact, yet physiologically demolished, if the first relay is destroyed; and if the second relay of fibers perish, the first relay is physiologically non-existent, to the extent to which their function is dependent upon the impulses conducted by the second relay. Thus, in tabes, the destruction of the collaterals from the posterior root fiber to the columns of Clarke and Stilling is physiologically equivalent to a lesion of the tracts of Gowers and Flechsig; in Friedreich's ataxia, integrity of the muscle afferent fiber and its collaterals does not avail to procure coördinate action in movement, because there is a lesion of the second relay, the afferent cerebellar, and movement is ataxic to the extent to which coördination depends on the afferent cerebellar impulses. Similarly, a destruction of any relay of fibers must act as a lesion of the preceding and succeeding relays, to the extent that the function of the preceding and succeeding relays is dependent upon that of the injured relay.

The afferent impulses from the muscular apparatus (muscle, tendons, joint structures, bones, and skin) pass, therefore, in part, to the motor cells of the anterior horn of the cord. The impulses belonging to any one segment radiate to other segments. In addition to the segmental and intersegmental distribution in the spinal cord, these impulses go by two paths to the cerebellum. One path runs by way of the collateral, to the columns of Clarke and Stilling, thence to the tracts of Flechsig and Gowers, and ultimately to the cerebellum. The other passes by way of the

dorsal columns, through the restiform body to the cerebellum. This second path to the cerebellum is the lesser in importance. The cerebellar paths are chiefly homolateral.

In addition to the intersegmental and cerebellar destinations, the afferent impulses pass to the optic thalamus, and thence to the cerebral cortex.

Sherrington has differentiated the organism with regard to afferent impulses into three fields: extero-ceptive, proprio-ceptive, and intero-ceptive. The extero-ceptive receptors respond to the stimuli arising from the environment of the organism, and are embedded in the surface layer of the organism. The proprio-ceptive receptors are situated within the organism, and respond to "the changes going on in the organism itself, particularly in its muscles and their accessory organs (tendons, joints, blood vessels, etc.)." The intero-ceptive receptors are situated in the internal surface of the organism, a surface which is usually alimentary in function. Here we are concerned mainly with the impulses arising from the proprio-ceptive receptors.

The correlation of the proprio-ceptive impulses from the muscular apparatus takes place at three distinct levels; first, at the level of the segment to which the muscular apparatus initiating the impulse belongs. At this level, the trophic influence of the anterior horn cell is exerted upon the muscle, and the muscular tone is maintained. The impulses here concerned are wholly reflex and never sentient.

The next level may be said to consist of all the body segments. It comprises the whole musculature with all its proprio-ceptive receptors, including the great vestibular organ of tone, and the cerebellum, "the chief coördinative center, or rather group of centers of the reflex system of proprio-ception." This great mechanism, not only in its entirety, but also in its parts, shows to a superlative degree, the integration of reflex action by which muscular activity is unconsciously coördinated. The single segments are as units in a hierarchy of which the head segment is chief and in which the segments increase in functional importance the nearer they are to the head segment.

At the third, or conscious level, movement may be initiated or inhibited; and may be controlled especially in the general spatial qualities. Arrangements therefore exist for distributing throughout the cord afferent impulses which are never sentient, and

throughout the brain, afferent impulses which may become conscious. When some of the impulses which subserve a function are never sentient and others are sentient, an hypothesis regarding that function, which is based either exclusively upon the impulses underlying the conscious, or exclusively upon those underlying the unconscious part of the function, is obviously untenable. Hence, the so-called sensory and motor theories of ataxia must be abandoned.

So far, thanks chiefly to the wonderful researches of Sherrington, the mechanism of coördinate action is intelligible. But, of the third or conscious level at which the impulses are integrated, we know little. The problems involved belong mainly to the realm of the experimental psychologist.

The path to consciousness via the dorsal columns and the optic thalamus was thought by Egger to be the afferent limb of a reflex which initiates volitional movement. He identified the efferent limb of this higher reflex with the pyramidal tract fiber which passes from the cell in the cortex of the precentral gyrus, through the corona radiata, internal capsule, crus cerebri, pons, and medulla, to the motor cell in the anterior horn of the spinal cord of the opposite side, or to its homologue among the basal nuclei. But this conception of Egger does not explain the mechanism of the psychic power over movement. Sherrington, Head, Rivers, and Holmes have begun the bridging of the gap between the sensory impulse and the sensation which it evokes. Just as Sherrington traced the unconscious reflex integration of activity, so have Head and his collaborators endeavored to trace the synthesis of sensations.

All the afferent impulses reach the spinal cord by way of the afferent or sensory nerve through the posterior root fiber. At the periphery, sensibility may be differentiated into epicritic, protopathic, and deep sensibility. In transit from periphery to posterior root, certain rearrangements take place in the fibers conducting afferent impulses, so that the peripheral nerve may be distinguished as the unit of epicritic sensibility, the posterior root as the unit of protopathic. In the dorsal columns of the cord, yet another rearrangement occurs. The fibers conducting impulses of the same order of sensibility become grouped together. For example, in the cord, no such separation exists as at the periphery between fibers subserving the tactile and pressure elements of

pain; all pain fibers are grouped now together; in the cord, morbid changes affect all forms of painful sensibility together. Similarly, the impulses underlying postural recognition, and spacial discrimination are grouped together and pass in the homolateral dorsal columns. From the nuclei of Goll and Burdach, the second relay fibers pass to the opposite optic thalamus; the impulses underlying recognition of posture and of passive movement are in this transit separated from those dealing with spacial discrimination and the appreciation of form.

After exciting the essential center of the contralateral optic thalamus, sensory impulses pass to the cerebral cortex, by the third relay of fibers, in five main groups. Of these groups, one consists of the impulses which underlie postural recognition and the appreciation of passive movement, and another consists of the impulses upon which spacial discrimination depends. In lesions of the cortex, if any change of sensibility occurs, the recognition of posture and of passive movements is affected; sensations whose origin lies in the distal joints of a limb are more affected than those which arise from proximal joints; the appreciation of movement is usually affected to almost the same degree as the appreciation of posture, and persistence of sensations and hallucinations of movement occur.

The afferent impulses underlying sensations of posture and movement are grouped definitely before they reach the cortex. In the cortex, these impulses are associated to produce sensations. These sensations in our past experience once were conscious, but now are only potentially so. By their association in the cortex with the analogous memory images that compounded former experiences of the same order, perceptions of posture and movement are evoked. Postural perceptions, when fully elaborated, may thus comprise all the visual, motoric, spacial, emotional, and other attributes of posture, although in certain individuals and under certain circumstances, one or other of these attributes may be specially emphasized.

When the whole muscular apparatus is at rest, afferent impulses from it are constantly passing along the three relays of sensory fibers, are constantly exciting images of the posture of the whole body. From the association of present with past postural images, the identity and difference of new postural images are detected. Of the absence or presence, the degree and

quality of change in the myriad of postural images, we are not conscious. Only the intrinsically dominant image or the resultant of several images may reach consciousness. The dominance or lack of dominance of an image is something which may be inherent to that image; for example, an unusual change of posture, a change either unusual in extent or performed at an unusual rate, may command attention; but, as a rule, dominance depends not only upon the inherent qualities of the image, but also upon the state of the associations at the moment that the image arises. In the association sphere we know that the eliciting of one image of a series of images which are habitually associated together tends to elicit the others of that series and not an alien image; that the suppression of one image of a series of images which are habitually associated together tends to suppress the whole series; and that the more associations an image has, the more does it tend to persist and the more difficult is it to suppress. Hence, the fate of the postural image depends upon the success of the competition for attention between that postural image and the images which on its entrance are enjoying conscious attention.

In changing from one posture to another, many of us are conscious only of the initial and final posture. The intermediate postures are unconsciously assumed, although by slowing the rate of change or by arresting the change at intervals, we may become conscious of the series of successive postures which are comprised in the whole change. The images of these successive postures are by practice engraved on our cortex as are the *eingelehrnte reihe* of word, figure, and other associations. Every successive posture awakens images of the preceding and succeeding posture and the one follows the other with mechanical precision, without the guidance of consciousness.

Throughout the investigations of Head and his colleagues, and other workers, the intimacy between the impulses underlying the perception of change of posture and those concerned with movement was always evident. This intimacy is not remarkable, if we consider the genesis of voluntary movement. The infant moves, a certain new posture is assumed, and a desire is fulfilled. Just as in infancy, so in adult life, an hallucinatory (desired) postural image can evoke a motor image which will consciously produce a movement that more or less corresponds to the wished-for posture.

A postural concept is thus from the first associated with a motor image; a motor concept with a postural image. A motor image is an essential attribute of every postural concept; a postural image, an essential attribute of every motor concept. Motor images are a greater aid to postural concepts than are postural images; this is probably the reason why appreciation of posture is more delicate in the large proximal than in the small distal joints. In the same way that postural images are associated, so also are motor images; the awakening of one motor image awakens those habitually associated with it.

But besides the association of postural and motor images, suppression of these images occurs also in the cortex. This suppression may occur unconsciously, as the result of competition between images for attention; and as the result of an inhibitory effect which succeeding psychic acts tend to exert upon their predecessors and which is called retro-activity. It may also occur as the result of a conscious act, of an effect which is initiated in the sphere of the concepts, and which inhibits the associations which lead to perception and reproduction. This conscious suppression may vary in degree, and may exercise a selective power upon all postural and motor images.

In the cerebral cortex, not only do impulses awaken images of movement and posture, not only are these images associated with one another and with other closely allied images of posture and movement, but the result of their association tends to be reproduced as movement.

The motor images are linked with the motor cells in the Rolandic area. From these motor cells axons pass by the pyramidal tract, to the motor cells in the anterior horn and to their homologues among the basal nuclei. Just as the axon of the anterior horn cell is the final common path of all motor activity, so is the pyramidal tract fiber the penultimate common path of psychic activity. The results of innumerable unconscious and conscious associations excite motor images; the dominant of these prevail; stimulate the cells of the motor cortex in a definite order, intensity, and pattern, and the impulses thus awakened pass to the lower motor neurons and excite co-ordinate action.

Just as the postural images which become conscious are merely the dominant among the postural images of the whole

muscular apparatus, so the motor effect which we perceive is merely that of the intrinsically dominant motor image, or the resultant of such images.

The motor action in its various qualities is the resultant of the effects of the motor images which are exciting and inhibiting the activity of the Rolandic area cells at the moment. It has not yet been proved, although it seems feasible, that these cortical motor cells have not only a definite threshold above which they must be stimulated to procure evident action, but also have a latent period within which they remain refractory to stimulation, and thus permit the rhythmic and orderly discharge of the affect of motor images.

Electrical stimulation has shown that the reactions of the motor cortex are very similar to those elicited through the spinal mechanism by reflex stimulation in absence of all cortical influence. The motor reactions of the cortex show reciprocal innervation, and other phenomena, which we have mentioned while dealing with purely reflex movement. The movements excited from the motor cortex are divided by Sherrington into three groups: "In one group, movement evoked from the cortex of one hemisphere seems a fraction of the natural movement, the natural movement requiring in its completeness the corroboration of the symmetrical area of the cortex of the opposite hemisphere. In a second group, instanced by conjugate lateral deviation of the eye-balls toward the opposite side, it is equally obvious that the reactions of symmetrical areas of the right and left cortices are related to one another as antagonistic reactions. In a third group of cases, the reactions of symmetrical cortical areas, right and left, seem neutral to one another. Thus, with the area which yields movement of the thumb, that reaction seems neither to reinforce nor to interfere with the similar reaction evoked from the identical area of the opposite hemisphere."

Till now we have dealt solely with motor responses to peripheral sensations, but movement may occur in response to affective states arising in the course of intellectual processes which are not directly evoked by impulses of peripheral origin. Muscular action is a form of emotional response. No emotion can occur without, in some way, affecting the musculature. Thus, excitement may give rise to gesticulation, anger to trembling, and fear to unsteadiness. The mode of action of these

affective states is not clearly known, but the result is a matter of everyday observation. The emotion acts as a "set," facilitating only concepts of the order characteristic of the prevailing emotion. These concepts in other experiences have exerted active excitory and inhibitory influences upon the primitive engraved images of motor action. The concepts which are allied probably possess allied affects. While such affects are active, the normal automatic association of afferent impulses may be either inhibited or accelerated, and hence the emotional state may be indirectly reflected in movement. Either favorably or unfavorably, the perfection of concomitant movements may be thus influenced; or movements, almost wholly emotional expressions, may occur.

When, owing to functional or organic causes, the elaboration of sensory images is interfered with, the results noted by Head and others upon the perception of motor and postural sensations arise. Perceptions of posture and of movement, if faulty, are faulty to more or less the same degree. But in spite of this faulty perception, habitual movement may not be obviously disturbed.

The associations between a postural and a motor image, and between a motor image and its externalization, being fixed by the mordant action of frequent repetition from early infancy, are primitive, engraved associations, and enable the motor externalization of such associations to occur more or less faultlessly in absence of conscious supervision. Indeed, it is well known that gross movements until they can be performed without conscious control tend to be clumsy, and, in spite of cortical lesions affecting the impulses which underlie the appreciation of posture and movement, may still be performed coördinately and correctly.

When a cortical lesion affects the Rolandic area, the appreciation of posture and of movement may be little interfered with, but the voluntary performance of movement is then greatly restricted or rendered wholly impossible. The awaking of postural or motor concepts and the association of these concepts proceeds uninterrupted, but the link between the motor image and the reflex mechanism necessary to perform the externalization of that image is broken. Under these conditions, not only does immobility arise, but a great increase of tone occurs in the immobilized muscle. This increased tone is evidenced in rigidity affecting mainly the flexor groups, and as this rigidity persists in

spite of the destruction of the cortex, it must be of subcortical origin. Hughlings Jackson, Sherrington, and others have shown that the rigidity is dependent upon the loss of cerebral control over the proprioceptive impulses. The cerebrum exerts an inhibitory influence on muscle tone, and thus permits of phasic alterations in that tone, such as are necessary for conscious action; whereas, the cerebellum exerts a tonic influence upon muscle tone, such as is necessary for automatic action.

Consciously we can move and inhibit movement; we can control the gross rate and force of a movement; we can control the gross spatial qualities of a movement: consciously, we do no more. The force, the rhythm, the rate, and the synergic quality of muscular contraction in the course of movement are as a rule unconsciously controlled.

But we have consciously acquired movement; we have consciously learned to subjugate to our will the various qualities of the muscular apparatus displayed in movement. So long as the connection between our will sphere and the lower motor neuron, the final common path of the afferent impulses from the muscular apparatus, remains intact, there is no reason why purposeful movement should not be acquired.

In the ataxia of tabes, it is mainly reflex integration which is faulty. The peripheral, spinal and cerebellar components of coördinate movement may all be affected. False postural and motor images arise, "interfere" with those engraved in memory by practice, and hence derange the psychic component and produce chaotic effects in the externalization of movement: but the psychic common path,—the Rolandic area, and the tract from it—remains unaffected. There is no reason why we should move only at the dictates of the habitual postural images which have been engraved upon the brain by practice. There is no reason why ataxics cannot acquire new perceptions of posture from the sensations which actually persist, why they should not learn to associate these sensations with appropriate motor images and why these motor images should not be properly externalized in coördinate movements. This process of acquiring coördinate movement is aptly termed reëducation. Obviously, it is a conscious process. Sensations from the muscular apparatus must be consciously perceived, and consciously identified with the posture and movement which underlie them. The coördinate movement must be per-

formed for the ataxic, so that he may realize the sentient elements in it, and learn to identify it from them. From this identification, a reproduction follows, for the motor images are still linked by their usual channels with the exterior. The success of the whole process of reëducation of the ataxic therefore rests upon his ability, first, consciously to attend to the sensations which underlie movement; second, properly to interpret these sensations; and third, to link these perceptions with their appropriate motor images. Experience teaches us that if this art be consciously acquired and assiduously practised, it will gradually be relegated from a wholly conscious to a largely unconscious performance.

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