

ON THE PROPRIO-CEPTIVE SYSTEM, ESPECIALLY IN ITS REFLEX ASPECT.

BY C. S. SHERRINGTON, F.R.S.

Professor of Physiology in the University of Liverpool.

REFLEXES, as judged by various criteria, are variously classified. Each arrangement, in so far as based on distinctions truly broad, may be of service to neurology. For reflexes have, besides intrinsic practical importance, a value for theory. Among them may be expected prototypes which, in simple form, represent generic divisions of nervous reaction in general. Any natural classification of them may therefore assist recognition of groups of nervous reactions embracing those even of high complexity.

In every reflex a decisive stage is that initial one wherein are started the centripetal impulses, which, in due course, excite the central reaction. In natural reflexes these initiatory impulses are excited by the reaction of peripheral apparatus, itself excited by some adequate stimulus. In so far as sensation accrues to the central reaction, the peripheral receptive apparatus may be termed sensory. But sensation may not accrue, although a central reaction is set up. In many cases it is hazardous, and for many purposes it is immaterial, to state whether sensation does or does not attend the central reaction; in such cases the peripheral apparatus is preferably so designated as neither to predicate nor to preclude sensation as being one of the features of the central reaction. Adopting the term *receptor* as a neutral one to apply to the peripheral apparatus for this purpose, it is obvious that, in trying to analyse the functions of the central nervous system, recourse may be had to the qualities of the receptors as furnishing a criterion. On that basis various parts of the central nervous system may have, and have

already had, their functions distinguished. Certain inferences as to the general scope and relationships of reflexes may be drawn from the broad scheme of distribution and situation of the receptors in the body.

The receptor organs, if one regards their distribution from a broad point of view, fall naturally into two great groups, as judged by their locus in the body. They are distributed in two great separate fields, each field circumstanced fundamentally differently from the other. Multicellular animals, regarded broadly throughout a vast range of animal forms, are cellular masses which present to the environment a surface sheet of cells and, underneath that surface sheet, a bulk made up of cells more or less screened from the environment by the surface sheet overlying them. The surface sheet is directly exposed to the environment, and is adapted to react to many of the factors composing that environment, these factors constituting stimuli. Bedded in the surface sheet are numbers of receptor cells, developed in adaptation to the stimuli delivered by environmental agencies. Many of the agencies by which the environment acts on the organism do not, however, penetrate to the mass of cells forming the organism's deeper parts. Thus various stimuli in the forms of light and heat, and localised pressures, and chemical substances expend themselves as stimuli at the surface sheet, and do not penetrate into the depth of the organism. But the deep tissues, although devoid of receptors adapted to these surface-reaching stimuli, are, nevertheless, not unprovided with receptors. They have receptors of other kinds apparently specific to them. Some agencies act not only at the surface of the organism, but also through its mass. For some of these agencies no receptors appear to be adapted; for instance, there seem to be none adapted for the Röntgen rays. For others of more common occurrence, receptors in the deep tissues seem to have been evolved. The deep receptors appear to be very usually adapted to mechanical stimuli of certain kinds. Thus, they seem adapted to react to the compressions and strains produced by muscles, and an important adequate agent for them seems to be mass acting in the

modes of weight and inertia, involving mechanical pressures and mechanical stresses.

The main fields of distribution of the receptor organs fundamentally distinguishable seem, therefore, to be two, namely, a *surface* field constituted by the surface layer of the organism, and a *deep* field constituted by the tissues of the organism beneath the surface sheet.

But the surface field is further broadly subdivisible. Its subdivisions are two. Of these one lies freely open to the numberless vicissitudes and agencies of the environment; it is co-extensive with the so-called external surface of the animal. It is cutaneous in the widest sense of that term. It possesses as receptive organs not only those of touch, &c., in the skin proper, but also the eye, nose, and organ of hearing. This subdivision of the surface field contrasts with a second subdivision of it, constituted by what is commonly termed the internal surface of the animal, the alimentary or intestinal surface. This latter surface is, it is true, in contact with the environment; but the environment with which it is in contact is a portion of the environment greatly modified from the general environment outside by lying almost completely surrounded by the animal itself. This part of the receptive field of the animal's surface, which is turned inward upon the alimentary contents, may be termed the *intero-ceptive*, in contradistinction to that larger part of the surface field which looks outward upon the free environment in general, and the latter may from that circumstance be termed the animal's *extero-ceptive* surface.

It is this latter, the *extero-ceptive* field, which is most rich in receptive organs, both as regards number and variety. For this to be the case, is in accord with what might be expected. It is this *extero-ceptive* field which, facing outward on the general environment, receives and has received for countless ages the full stream of all the varied agencies for ever pouring on it freely from the outside world. Mere enumeration of the different species of receptor organs recognisable in it, suffices to illustrate the importance of this great field in regard to "reception." It contains receptors specifically adapted to react to mechanical contact, to cold,

to warmth, to light and sound, and agents, whether mechanical, chemical, or radiant, which inflict injury (*noxa*). A number of these species of receptors are distributed to the extero-ceptive field exclusively; receptors adapted as these are not known to exist either in the deep field or in that part of the surface field termed *intero-ceptive*.

Less, however, is known concerning the receptors of the intero-ceptive field. Of certain points regarding them we may feel fairly assured. The portion of body surface—the so-called “internal”—which forms their field of distribution, is alimentary and digestive in function. For purposes of retaining food, digesting and absorbing it, an arrangement of common occurrence in animal forms is the deep recessment of a part of the free surface. In this recess a fraction of the environment is more or less surrounded by the organism itself. Into the sequestered nook so formed the organism by appropriate reactions gathers morsels of environmental material, whence by chemical action and by absorption it draws nutriment. Hence that surface of the organism which lines this recess is in contact with a part of the environment largely separated from, and profoundly modified from, the environment in general. This specialised part of the environment is specially rich in digestive stimuli, and by the screening and selective action of the organism itself is practically free from many of those stimuli which abound in the general environment at work on the creature's outer surface.

The receptive field lining this digestive chamber, this kitchen, appears especially adapted to chemical stimuli. At the ingress to the chamber, namely, in the mouth, species of receptor organs occur, whose adequate stimuli are chemical. The sensations induced through them are gustatory. Their reflex actions include reflex secretion of saliva. But further inward, along the digestive surface, we know as yet comparatively little about the receptor organs and the reactions they evoke. The fine work by Bayliss and Starling has shown that the pancreas can be excited to secrete by chemical agency without direct intervention of the nervous system at all. From a number of facts it seems clear that

the internal digestive surface of the body is relatively sparsely endowed with receptor organs, as compared with the free extero-ceptive surface outside. The number of afferent nerve fibres in the sympathetic system, which is mainly a visceral system, is small in comparison with the number of afferent fibres in the cerebro-spinal nerves from the skin and receptive structures of the external surface. Recent observations by Warrington show that the number of cells of the spinal ganglia which exhibit regressive changes after severance of the white rami—containing the afferent fibres from viscera—forms but a small fraction of the total number of the cells in those ganglia. Similarly no *wholly* afferent nerve-trunk appears to exist in the sympathetic system, but such are common in the nervous system belonging to the extero-ceptive surface. Conversely, in the latter system, no *wholly* efferent nerve-trunk is known, though in the sympathetic such trunks exist.

Returning to the receptor organs bedded in the deep tissues, and to the study of the reactions which they subserve, two characters attract attention as differentiating them from those of the surface field, whether extero-ceptive or intero-ceptive. Of these features, one is that the *stimuli* effective on the receptors of the deep field differ fundamentally from those operative on the receptors of either subdivision of the surface field. Most of the stimuli by which the external world commonly acts on the surface of the animal are excluded from the deep field. But the organism itself, like the external world surrounding it, is a field of ceaseless change where internal energy is continually being liberated, whence chemical, thermal, mechanical, and electrical effects appear. It is a microcosm in which forces which can act as stimuli are at work, as in the macrocosm around. The receptors which lie in the deep tissues appear adapted for excitation by changes going forward in the organism itself. These changes work, it appears, largely through the agency of mass with its mechanical consequences of weight and inertia, and also largely through mechanical strains and alterations of pressure resulting from contractions and relaxations of muscles. *There-*

fore, a character of the stimulations occurring in this deep field is that the stimuli are traceable to actions of the organism itself, and are so in much greater measure than are the stimulations of the surface field of the organism. Since in the deep field the stimuli to the receptors are delivered by the organism itself, the deep receptors may be termed proprio-ceptors, and the deep field a field of proprioception.

But the bodily reactions which act as stimuli to the deep receptors are often themselves directly excited by external stimuli delivered at the animal's free surface by the outside world. Thus, the mechanical strain or compression which stimulates some deep receptor arises, as the result of some antecedent reflex movement provoked through some surface receptor, usually of the extero-ceptive field. The immediate stimulus for the reflex started at the deep receptor is supplied by some part of the organism itself acting as agent; but that part became an agent of stimulation in the majority of cases because of a reaction induced in the deep organs of the animal by some environmental agent acting on receptors of the animal's surface. *Hence the reactions produced by the receptor organs of the deep field are results primarily due to the stimulation of the organism by itself, but secondarily due to the stimulation of the organism by the environment.* This secondary relation to surface stimuli is habitual. Reflexes arising from proprio-ceptive organs come, therefore, to be habitually attached and appended to certain reflexes excited by surface receptors. In a muscular movement induced by a stimulus to the skin of the spinal dog, the change in form and tension of the muscles, the movements of the joints, &c., excite receptors in these tissues and their accessory structures, and these proprio-ceptors in their turn excite a reflex in their own arcs. A character of the reflexes of the proprio-ceptive field is therefore that in contradistinction from those of the surface fields, they are related not primarily, but only secondarily to the agencies of the environment.

It would appear that in many cases the proprio-ceptive reflex which thus ensues as a secondary reaction, *allies itself*

in its effect to the primary reflex excited from the extero-ceptive surface, and reinforces it. The flexion reflex of the hind limb of the dog can be excited by a stimulus applied to the skin of the foot. A similar flexion reflex of the limb can be excited by stimulation of the afferent nerve-fibres of the flexor muscles themselves. A subliminal stimulation of the skin of the foot becomes effective when a subliminal stimulation of the afferent nerve of one of the flexor muscles is delivered synchronously. These stimuli mutually reinforce each other. The reflex due to the extero-ceptive surface is reinforced by the appropriately chosen proprio-ceptive reflex. On the other hand, a flexion reflex of the limb provoked from the skin can be cut short by reflex inhibition on stimulating the afferent nerve of a flexor muscle of the opposite limb. In this case the second or proprio-ceptive reflex restores the posture of the limb which the extero-ceptive reflex had disturbed. In this case the proprio-ceptors evoke a *compensatory reflex* in the opposite direction to the reflex excited from the skin, the extero-ceptive surface

A third character of the receptors of the deep or proprio-ceptive field seems their tendency to induce and maintain *tonic* reactions in the skeletal musculature. The steady, long-continued, untiring, and, for the most part, mild contraction, which is observable so frequently in skeletal muscles, and is known as their tone, where traceable to spinal reaction, has been traceable reflexly not to the receptors of the surface, but to the proprio-ceptors of the muscles and their accessory structures. Thus, the proprio-ceptors of the limbs appear to be a main source of the reflex tonus of the muscles of the limb. In the decerebrate dog, the tonic extensor rigidity of the leg seems reflexly maintained by afferent neurones reaching the cord from the deep structures of the leg itself; for after severance of the afferent roots of the nerves of the limb the tonic rigidity hardly appears, although it does appear unimpaired when the main skin nerves have been severed. Similarly, if in the spinal animal the knee-jerk be accepted as evidence of a spinal tonus in the extensor muscle of the knee, this tonus seems maintained by afferent fibres coming from the exten-

sor muscle itself, since the knee-jerk is extinguished by severance of those fibres. Again, the rapidity of onset of *rigor mortis* in a muscle is high in proportion as its tonus, prior to death, has been high. Section of the afferent roots of the nerves of the limb, prior to death, not only lowers the normal tenseness of the muscles of the limb, but also delays in them the onset of *rigor mortis* as judged by the onset of *post-mortem* stiffness at the knee; and this delay is not observable when the skin nerves only have been severed.

It is often asked, What may be the utility of the tonus of skeletal muscles? A suggestion may be hazarded, which is germane to the present argument. One function this tonus may serve is that of an adjuvant to so-called muscular sense. The steady, mild tension which the muscles exert in virtue of their reflex tonus may, by acting on joint surfaces, tendons, and muscles, &c., assist the functioning of the sense organs belonging to those structures, much as the reflex tonus of the constrictor pupillæ is adjuvant to the visual receptive surface, and affords the eyeball a favourable condition for its function. But the reflex tonus of skeletal muscle still persists, after destruction of the higher centres to which we have to relegate the operations of sense, and *inter alia* those of the so-called "muscular sense." And it is clear that the receptors of muscles, joints, &c., are concerned with much outside the production of sensations. The reflex tonus of skeletal muscles must therefore have, it would seem, a purpose outside that of directly subserving muscular sense. I would suggest that this reflex tonus is the expression of a *neural discharge concerned with the maintenance of attitude*. Though of many reflex reactions the outcome is movement and the muscles reacting are thus used as organs of motion, much of the reflex reaction expressed by the skeletal musculature is not motile, but postural, and has as its result not a movement, but the steady maintenance of an attitude. The bony and other levers of the body are thus held in certain positions, both in relation to the horizon and to one another. The frog, after removal of its cerebral hemispheres, rests squatting in its tank preserving an attitude very different from that which gravi-

tation would give it were its musculature not in action. Evidently a great part of its skeletal musculature is steadily active all the while, antagonising gravity in maintaining the trunk semi-erect, the fore limbs semi-extended, and the hind limbs tautly flexed. Innervation and co-ordination are as fully demanded for the maintenance of a posture as for the execution of a movement.

A posture of the animal as a whole, a *total* posture, is a complex built up of postures of portions of the animal; segmental postures, just as movement executed by the animal as a whole, *total* movement, *e.g.*, locomotion, is compounded of segmental movements. With only the hinder portion of its spinal cord intact, the hind limbs of the frog still maintain a posture. Owing to spinal reflex action, the hind limbs are then kept flexed at hip, knee, and ankle. When displaced from that posture they return to it. The deep receptors of the limbs, the proprio-ceptors, give to their segments, namely, those of the hind limbs, by local spinal reflex action a definite *attitude*.

The vertebrate animal, as regards the scheme of arrangement of its spinal and cranial reflex arcs and the musculature which they innervate, may be regarded as a fore and aft series of segments. In each segment there tend to recur reflex arcs of similar functional kind to those occurring in the other segments. For instance, to each segment there belong reflex arcs arising at the skin surface (extero-ceptive) and arcs arising in joints, muscles, tendons, &c. (proprio-ceptive). The arcs of analogous function belonging to successive segments unite to a homogeneous reflex system extending more or less continuously through the length of the animal. Thus it is that the *proprio-ceptors and their reflex arcs have, in their sum total, to be treated as a proprio-ceptive SYSTEM*.

As the segments, *e.g.*, of a vertebrate, are followed toward the head end of the animal, that is, toward the end which leads in habitual locomotion, the receptor organs are found to exhibit in the head or leading segments a greater development and general importance than in the other segments. This is strikingly obvious in the receptors of the external

surface. It is at the leading end of the animal that the great extero-receptors constituting the eye and the organs of hearing and of smell are met. This leading end it is which, when the creature moves in the direction of its habitual locomotion, explores that portion of the environment into which the body is about to pass. And when the creature is not itself in active locomotion, but, as often happens, allows a moving environment, *e.g.*, a stream of water or a current of air to drift by, the posture assumed by it is usually such as makes the moving environment impinge upon the head segments first. It is not surprising, therefore, that the reflex arcs and centres of the head or leading segments are found to dominate the arcs of analogous function in all the segments behind their own. A segmental series of reflex arcs of analogous function in its integration to a unified system tends to exhibit a functional hierarchy, in which the reflex arcs belonging to the head are supreme. As regards the system of the proprio-receptive arcs, it remains to enquire whether there also the head segments are of higher general importance than the rest, and exert a special predominance in their system.

Taking the case of the vertebrate, in it there lies in one of the leading segments (head segments) a receptor organ, the *labyrinth*, recessed off from the surface as a sort of cyst. This receptive organ is adapted to mechanical stimuli. It consists of two parts, both endowed with low receptive threshold, and with refined selective ability to differentiate stimuli. One part, the otolith organ, is adapted to react to changes in the incidence and degree of pressure exerted on its nerve-endings, by contents of higher specific gravity than the fluid otherwise filling the organ. The second part, the semi-circular canals, appear to react to minute mass movements of fluid contained within it. These two parts may be taken as typically constituting the labyrinth. The incidence and degree of pressure of the otoliths upon their receptive bed alter with changes in the position of the segment, in which the labyrinth lies, relatively to the horizon line. Similarly, movements of the segment stimulate the labyrinthine receptors through the inertia of the

labyrinthine fluid as well as of the otoliths. There are some obvious resemblances between these labyrinthine functions and the functioning of the proprio-ceptors, *e.g.*, of a limb. In the stimulation of the labyrinth, the active agent which directly excites the receptor is a portion of the organism itself, and is not an item of the environment. Moreover, the stimulation is provoked commonly by a reactive movement of the organism itself, and that reactive movement is commonly in its turn a response to an environmental stimulus acting on some receptor of the extero-ceptive surface. Both these are points of resemblance to the conditions above shown to obtain in regard to the stimulation of the proprio-ceptors, *e.g.*, of a limb. The segment to which the labyrinth belongs is commonly rigidly conjoined with the other segments composing the head. Postures and movements of the head are thus the immediate causes which stimulate the labyrinth. Thus, the labyrinthine receptors, like the proprio-ceptors in other segments, are stimulated by the animal itself as agent, though secondarily to action of the environment at work upon the animal.

There is another functional likeness between the labyrinth and proprio-ceptors elsewhere. The latter, as was mentioned, are the source of a reflex tonus in the skeletal muscles. J. R. Ewald and others have shown that to the labyrinth is traceable a share of the neural tonus of many muscles. Ewald concludes his work on the labyrinth by designating it the tonus labyrinth. And these tonic actions of the proprio-ceptors and of the labyrinth appear to reinforce mutually. Thus the tonus of the extensor muscle of the knee, in the cat and dog, appears to have, under many circumstances, a combined source in the proprio-ceptors of the limb and in the receptors of the labyrinth.

A further functional resemblance between the labyrinth and other proprio-ceptive organs, lies in both of them initiating compensatory reflexes. It was mentioned that to the proprio-ceptors of the hind limb seems traceable in the spinal animal, the active reflex resumption of a posture temporarily disturbed by an intercurrent movement. The

limb is returned to its original attitude by help of a movement which is reflex and traceable to afferent nerves from the articulo-muscular mechanisms of the disturbed part. Similarly, the reflex posture and the compensatory reflexes of the head are largely traceable to the receptors of the labyrinth. From the labyrinth are excited reflexes which adjust its segment—and with that segment the others of the head are rigidly conjoined—to the horizon line. That the adjustment is to the horizon line seems particularly shown by the eyeballs. The retinæ, those refined photo-receptive patches of the head surface, conduct reflexes delicately differential in regard to space. The due reaction of the animal to stimuli, acting above or below, or to right or to left, in the photo-receptive patches, depends on a fairly constant relation being kept between the normals of the patches and true horizontality. This is the meaning of the laws of Donders and Listing regulating eye-ball movements. The photo-receptive patches are set movably in the head. By the action of muscles they can retain their bearing to the horizon, although the head itself shifts its bearing to the horizon. The reflex control of these muscles lies largely in the power of impulses from the labyrinth. When temporary causes disturb the usual relation of the normal of the head to the normals of the retinæ, compensatory reflexes bring back the parts to their previous habitual relation both to each other and to the horizon line. These compensatory reflexes, as well as the habitual maintenance of that primary harmonious attitude, are largely traceable to the operation of the reflex arcs which arise in the receptors of the labyrinth. Thus, *as the proprioceptors of a limb are in large measure responsible for the reflex posture and the compensatory reflexes of the limb, so the labyrinthine proprioceptors are largely responsible for the reflex posture and the compensatory reflexes of the head.*

It seems therefore legitimate to include the labyrinth within a great and distinctive system, reflex and sensual, which from the special conditions attaching to the stimulation of its receptors, may be termed a system of proprioception. This *proprioceptive* system possesses, in virtue of

the labyrinth, an important component placed in the head segments. With other receptive systems composed from segments in series, the receptors of the head segments tend functionally to dominate the rest. It is so, likewise, in the proprio-ceptive system. The influence of the proprio-ceptors of a limb on the reflex maintenance of posture is confined practically to the limb; the influence of the proprio-ceptive organ of the head upon posture is exhibited not only by the posture of the head itself, including the eyeballs, but extends to the limbs and trunk as well. Thus, destruction of the labyrinth in fish, frog, pigeon, dog, produces not only malposture of the eyeball and head, but of the limbs and body as a whole. In man the "knock-out" blow, where the lower jaw conveys concussion to the labyrinth, reduces in a moment a vigorous athlete to an unstrung bulk of flesh, whose weight alone determines its attitude, if indeed a reactionless mass can be described as possessing attitude at all. The proprio-ceptor of the head, namely, the labyrinth, embraces within its field of reflex effect all of the segments of the body. The posture of the head, guided as that is by the labyrinth, is itself dependent on the action of muscles in a whole series of segments behind it, and conversely the posturing of the entire animal often has as its chief objective the bringing of the head into some requisite direction. Hence the cranial proprio-ceptive organ is in reflex touch with a whole train of the segments of the body, and these latter may be regarded as in a measure appended to the otic segment which contains the cranial proprio-ceptor.

As mentioned above, a posture of the animal as a whole, a total posture, is composite in the sense that it is built up of postures of portions of the animal, segmental postures. The postural flexion of the hind limbs of the spinal frog is maintained by spinal reflex action. It is maintained when the animal is inverted; and rolled over upon its back. A frog, after removal of its fore and mid-brain, when inverted, reverts at once by reflex action to the right-side-up posture. It corrects the malposition as does a normal frog. But when the labyrinths or their nerves are destroyed, this compensatory reflex is at once lost. The reflex evoked by

the cranial proprio-ceptor keeps the world right side up for the animal, by keeping the animal right side up to the world. The proprio-ceptors of the spinal region are unable to do this. The proprio-ceptors of the limbs give to the limbs a definite reflex attitude less in reference to the external world than in reference to *the other segments of the body, i.e.,* to the rest of the body. The proprio-ceptive organ of the head, on the other hand, gives the animal a definite reflex attitude in reference to *the external world*. Thus, it maintains not merely a limb in flexion or extension, but a posture of the whole animal in regard to gravitation.

Evidently the proprio-ceptive organs of the leading segments play in the proprio-ceptive system a rôle which is a dominant one. The reflex arcs of the proprio-ceptors of these segments embrace peculiarly large fields of the skeletal musculature. The reflex arcs of the proprio-ceptors of the other segments act only on more limited fields of musculature. In conformity with this, the proprio-ceptive organs of the leading segments possess long internuncial efferent paths; for instance, the vestibulo-spinal proceeding from Deiter's nucleus to the eye nuclei, and to all levels of the spinal cord.

It was seen that the proprio-ceptive system can be distinguished as a functional unity extending throughout the whole series of segments of the vertebrate organism. Other functional reflex systems are similarly distinguishable as segmentally composed. In all such systems a tendency is manifest for the nervous centres of the system to fall under the dominance of one of their own number, situate so as to receive the afferent paths from a pre-eminently important group of the receptors of the system. The whole reflex mechanism of the system tends to be, so to say, focused upon the centre belonging to that group. Thus, in the reflex system dealing with respiratory movement, the chief centre controlling the taxis of that movement lies in the bulb, where afferent paths from the lung itself enter and make central connections. In the proprio-ceptive reflex system, the most important group of receptors was seen above to be the labyrinthine. Concordantly with this the

central mechanism of the proprio-ceptive system is built preponderantly and developed chiefly in the hind brain, which receives the vestibular nerves. Johannes Müller, years ago, declared the tuberculum acusticum, with its fibres received from the labyrinth, to be in *Petromyzon* the representative of the cerebellum of higher fishes. Johnston recently insists on the close structural resemblance and connection between the tuberculum acusticum and the cerebellum in this same low aquatic vertebrate. To the region of the hind brain, which receives the vestibular nerves, internuncial paths from many proprio-ceptive centres in other segments of the nervous axis converge as to a focus. These, with those from the labyrinth, form there a sort of organ of confluence for them all. A central organ of high complexity is thus formed in this region. Its size, as traced from animal species to animal species, strikingly accords with the range and complexity of the habitual movements of the species; in other words, with the range and complexity of the reflex taxis of the skeletal musculature. This central organ is the *cerebellum*.

The symptoms produced by injury or destruction of the cerebellum, in whole or in part, resemble, therefore, in various respects the disturbances set up by injury of the labyrinth itself, and in some respects the defects produced by damage of the proprio-ceptors of the body regions. The cerebellum likewise influences the tonus of skeletal muscles as would be expected, seeing the influence on that tonus exerted by proprio-ceptive arcs in general. There is a close connection structurally and functionally between the cerebellum and the so-called motor region of the cerebral hemisphere, just as there exists an intimate association of the simpler proprio-ceptive arcs and reflexes to the mechanisms of extero-ceptive reactions. Knowledge on many points is not yet sufficient to warrant an attempt to offer an adequate definition of the function of the cerebellum. Many authorities have defined it as the centre for the maintenance of the mechanical equilibrium of the body. Others regard it as the organ for the co-ordination of volitional movement. Herbert Spencer suggested that it is the organ of co-ordina-

tion of bodily actions in regard to space; the cerebrum, he suggested, being the organ of co-ordination of bodily actions in respect of time. Hughlings Jackson, nearly thirty years ago, insisting on his co-operative antagonism between the cerebellum and the cerebrum, wrote with characteristic penetration of thought, "The cerebellum is the centre for continuous movements, and the cerebrum for changing movements." Lewandowski considers the cerebellum the central organ of the muscular sense. The function attributed to it by Munk is the finer taxis of the maintenance of bodily equilibrium. And Munk well points out that its influence upon certain muscles and their actions is much greater than it is upon others. Luciani, the most widely-recognised physiological authority on the cerebellum, describes it as the organ which, by unconscious processes, exerts a continual reinforcing action on the activity of all other cerebro-spinal nerve centres.

All these separate pronouncements appear to me to harmonise with the supposition that this organ is the chief co-ordinative centre, or rather group of centres, of the reflex system of the proprioceptors. *The cerebellum*, it would thus be permissible to describe as *the head-ganglion of the proprioceptive system*; and in the proprioceptive system, as in other systems of receptors and their arcs, the head-ganglion is the *main* ganglion.

The above brief sketch has allowed of no treatment of the proprioceptors as generators and modifiers of sensation. The system, whose basis they form, is, however, no less distinguishable, when regarded in its sensual aspect, than when exhibited, as in the present condensed statement, in the light only of its reflex action upon the musculature.