Problems of Muscular Receptivity.¹

By Sir CHARLES SHERRINGTON, O.M., G.B.E., P.R.S.

THE nervous system in its relation to skeletal muscles is commonly and permissibly likened to an electric installation with connected central exchanges whither run wires from receiving stations and whence issue wires to outlying motor machines. Through it a receiving station has touch with any of many of the motor machines outside. The central system is so contrived that a receiving station can put these or those machines into action and simultaneously throw out of action these or those others which would impede them.

The exchanges stand for nerve-centres in spinal cord and brain; the motor machines for muscles, and the receiving stations for the sense-organs, the wires the nerve-fibres connecting all these into a system. The receiving stations are commonly called sense-organs; the reaction which light, sound, or other external stimuli excite through them in the central exchanges is one which partly documents itself to mental experience in a specific way, a way related by the mind to a specific external agent. But that sensual result accrues only when the central reaction involves certain sets of the central exchanges. The central reaction taken as a whole consists of much that does not document itself to the mind. It is preferable, therefore, where the whole central reaction has to be borne in mind, to replace as an appellation for the receiving station the term sense-organ by the simpler term "receptor." This term is suitable in view of either of the two central results, the non-mental "reflex" and the sensual mental; whereas the term sense-organ becomes a misnomer where dealing with the purely reflex.

Of the two-fold central result the reflex moiety can, in experiment, be sundered from the mental, by taking advantage of the partial separateness of the central exchanges for the two; the nerve from the receptor does, however, lead to both. Disease similarly destroys sometimes the mental part without destroying the purely reflex, and indeed sometimes the converse occurs.

The receptors are points of the organism specialised for the surrounding world to act on. They lie at the surface of contact of the organism with its external world. They aim at the muscles with a trajectory through the nervous system. They enable requisite, for the most part speedy, adjustments of the organism reacting to events in its surroundings. They enable this by means of their attachment to the nervous system, which gives to these reactions sufficient speed for their purposive success. These speedy reactions employ machines speedy in their action, the striped muscles. Hence these muscles are, in the constructive plan of the animal, placed at the disposal of the receptors operating through the nervous system. These, the skeletal muscles, are the motor machinery for all that life of the animal which the older physiologists were wont to call the "life of external relation." Of the importance of that life of external relation the moralist has written that even in man the crown of life is an

action, not a thought. Should we demur to this distinction, we can still endorse the old adage that to move things is all mankind can do, and that for such the sole executant is muscle, whether in whispering a syllable or in felling a forest.

The receptors played upon by the events of the external world supply their "drive" to the muscles. In reflex action they do so far more simply and for far more simple purposes than when the trains of reaction they set going have to thread the mazes of the higher brain, and, so to say, obtaining mental sanction, issue in acts remoter from the original stimulus. Yet in both cases, the muscles lie at the behest of the receptors, as instruments of their hand.

We should go too far, however, did we infer that the muscles themselves are instruments entirely passive under drive of the receptors acting on them from without. That they are agents not purely passive is shown by their possession of receptors of their own. On their own behalf they send messages into the central exchanges. This must mean they have some voice in their own conditions of service, perhaps ring themselves up and ring themselves off. Let us attempt to penetrate into the significance of this their "receptivity."

It is a receptivity differing obviously from that of other receptors, rightly more commonly chosen to exemplify receptive function, such as retina, ear, tongue, tactile organs, and so on, for in the case of the receptors of muscle, instead of being stimulated directly by agents of the external world, they are stimulated by happenings in the microcosm of the body itself, namely, events in the muscles themselves. In muscular receptivity we see the body itself acting as stimulus to its own receptors. The receptors of muscle have therefore been termed "proprioceptors."

Following the functional scheme of all receptors, we may be sure that the central reactions provoked by the receptors of muscle will be divisible into, on one hand, the purely reflex, and on the other hand, those which subserve mental experience.

Let us turn to the simpler of these divisions, the purely reflex. For that purpose, appeal can be had to what may with justification be regarded as a partially surviving animal; an animal which, its cerebral hemispheres having been removed, is a wholly inconscient and purely reflex automaton. From it no sight or sound evokes evidence of perception. There is total inability to evoke from it any sign of mentality, of emotion, let alone intelligence. It remains motionless hour after hour; yet if planted upon its feet in the upright position it stands, and statuelike continues to stand.

Now, standing is a postural act, and one of course of high importance. In maintaining posture the muscles, though they perform no external work, are active with an activity often technically termed "tonus," a postural contraction. In this maintenance of the erect posture by the decerebrate animal, we meet a co-ordinated posture involving many separate muscles harmoniously co-ordinated reflexly. For this reflex postural act of standing some stimulus must be at work

¹ The Linacre Lecture of St. John's College, Cambridge, delivered at Cambridge on May 6.

evoking and maintaining it. We have to ask what that stimulus may be.

If the afferent nerves that pass from a limb to the spinal centres be severed, the standing posture in that limb is no longer executed or maintained. The stimulus exciting the posture in that limb must be something which is applied to the receptors of that limb itself. The skin surface of the limb is rich in receptors, one region especially rich being the sole of the foot. On the receptors of the skin of the sole of the foot the external world may evidently be acting as a stimulus in the form of pressure from the ground upon the skin. To test whether that is the source of the reflex posture, the skin of the foot can be deprived of all its receptors by severing their nerves. This is found to exert no obvious influence upon the posture. Nor does severance of all the receptive nerves from the skin of the whole limb, nor, indeed, of all of the four limbs. The stimulus producing and maintaining the posture is therefore not pressure of the skin against the ground, nor indeed any cutaneous stimulus whatsoever. On the other hand, if, even without interference with the skin nerves, the receptive nerves of the limb muscles—the motor nerves, of course, remaining intact—be severed, the reflex posture disappears at once from the limb. The stimulus which produces and maintains the posture is something which is acting on and exciting the receptive nerves of the muscles of the limb.

What are the muscles which, by their contraction, execute this postural act? The posture keeps the head and neck from sinking, the trunk straightened and the spine supported, the tail from drooping, the limbs from yielding and folding under the superincumbent weight of the body. In a word, the reflex posture counteracts in the various parts of the body the effect of gravity on them in the erect attitude. Experimental analysis shows that throughout the muscular frame of the animal all those muscles, and only those, are in action, the activity of which counteracts gravity in the erect attitude; for example, in the hind-limb the muscles which extend hip, knee, and ankle. The muscles which execute the reflex we may, in short, term "antigravity" muscles. Even the jaw is included; the lower jaw, which, but for its postural tonus would drop, is held lifted against the upper.

If in the limb the receptive nerve of one of these antigravity muscles be cut, that muscle no longer contributes to the reflex posture. On the other hand, severance of the receptive nerves of all the other muscles does not destroy the postural reflex of the muscle the receptive nerve of which remains intact. The stimulus which is the source of this reflex standing is therefore one acting on the receptors of those limb-muscles which are themselves executants of the posture.

The excitability of a receptor is selective. That is, construction fits the receptor to respond to stimuli of one particular kind only, the so-called "adequate" stimulus; thus, the retina to light, a taste papilla to "sweet," and so on. Hence Pavloff's term "analyser" for the receptors, because by them the various complex events which play upon the body and cause reactions of it through the nervous system are to some extent analysed. A wave breaking on the shore excites the retina by its reflected lights, the

ear by sound vibrations, and, maybe, the skin by the spray dashed up. The wave as "object" and stimulus from the external world is thus partially analysed by the receptors.

Seeing that the receptors of muscle are an appanage of an organ mechanical in function, a near supposition is that their adequate stimulus is of mechanical kind. What is the adequate stimulus at work in these anti-gravity muscles in their posture of standing?

A muscle representative of the whole antigravity group is the extensor of the knee. Suppose it isolated from the rest and its freed tendon attached to a stiff spring, and to the spring a light lever so fixed that movement of the lever-point is photographically recorded. If then, by its bony attachments, the muscle be pulled against the spring, we can passively stretch the muscle and record the tensile strain developed in it by the stretch. Let us take the case of the muscle paralysed by severance of all nerves both afferent and efferent which connect it with the nerve-centres (Fig. 1). The tension developed in the muscle as it is stretched yields a curve resembling that given by various fibrous

FIG. 1.—Knee-extensor muscle. Effect of reflex inhibition, evoked between i and i' from afferent nerve, on the muscular reaction M to 6.5 mm. stretch T compared with reaction P of the "paralysed" muscle to similar table-stretch. Myograph multiplies tendon-movement 62 times. Time in seconds. (Liddell and Sherrington.)

and elastic tissues of the body, not unlike that given by a strip of indiarubber. Let us repeat the observation, but with the difference that the muscle retains unimpaired its purely efferent motor nerve. The stretching produces the same tensile curve as before, a curve practically indistinguishable from that of the wholly paralytic muscle. Then let us make the observation, with the further difference that the muscle this time retains not only its motor nerve but its receptive nerve as well. We find the muscle yields now a completely different curve of tensile strain. The tension developed by it is much greater, and its curve under equable progressive increase of the stretch runs, tensions being ordinates, convex instead of concave to the abscissa-line. The muscle in response to the stretch now replies not merely by passive strain but also by active contraction of its muscle fibres. In the muscle/with its reflex arc intact, the passive pull provokes a reflex contraction of the muscle. Evidently a mechanical stretching of the muscle supplies an adequate stimulus for receptors in the muscle.

The reflex is closely graded by the degree of stretch; and the degree of stretch required to excite reflex contraction is quite small. Mr. Liddell and I have seen a stretch, extending the muscle's resting length by less

than one per cent., produce a reflex contraction registering 2000 grams of tension. The reflex contraction provoked by the stretch tends to produce equilibrium between the extending force and the contractile resistance of the muscle and thus to prevent further elongation of the muscle. This is so whether the passive stretching is applied slowly or quickly. So soon as the stretch ceases to be increased, increase of the reflex contraction promptly ceases.

Reflex contractions produced in this muscle by other means than stretch have not such dead-beat character. Commonly, they long outlast the receptive stimulus which excites them. Stretch-reflexes, though with cessation of further increase of the stretch-stimulus further increase of the reflex contraction ceases, show persistence of the degree of contraction already reached after the progressive stretch has ceased. The question arises whether this persistence of the contraction is due, as in those other cases, to continuance of central reverberation after the exciting stimulus has ceased, or whether the residual passive stretch constitutes a persisting stimulus. Whether, in fact, under appropriate conditions the stretch-reflex can present itself in a purely static form. The question is not unimportant, because, if the residual stretch is a stimulus exciting and maintaining the reflex contraction, then a passive stretch-posture is exciting an active postural contraction.

This question can be examined in several ways. One is as follows. It is possible to subject the reflex arc of the muscle to inhibition; in other words, to throw it out of action temporarily. Such inhibition annuls a stretch-reflex already in progress and, if suitably timed, prevents contraction in response to a stretch however powerful. The muscle passively stretched when the inhibition is in operation exhibits the same curve of merely passive tension as does an entirely paralytic muscle. This being so, we can arrange for the inhibition to begin before and continue while the stretching movement, the "kinetic stretch," is being applied to the muscle and then, when the stretch-

ing movement is over and the residual, merely static, stretch remains, remove the inhibition. In this way the reflex arc of the muscle on which the stretch-reflex depends is, so to say, put to sleep during the kinetic stretch and until the stretching movement is finished, and then, when that is over, the reflex arc is, so to say, allowed to wake. On doing so it will find its muscle has assumed a state of stretch, of steady strain, a passively stretched posture. The result observed by

FIG. 2.—Successive reactions M of normal, I of reflexly inhibited, and P of paralyzed muscle to stretch T of 7 mm. The inhibition (by afferent nerve) was on first occasion from i to i' , on second occasion from i' to i'' and again from i'' to i''' , giving therefore on second occasion the fall from and reascent to the plateau line n of the first occasion. The inhibitory nerve gave slight concomitant contraction, so that full inhibitory effect is seen only close subsequent to cessation of the inhibitory stimulation. The less steep dotted line T gives the stretch for observation M; the other for observations I and P. Myograph multiplying tendon-movement 62 times. Time in seconds. (Liddell and Sherrington.)

this method is that the muscle on its nervous arc so waking immediately develops a reflex contraction, and then steadily maintains it (Fig. 2). The passive stretched posture acts *per se* as a stimulus. The proprioceptive nervous arc of the muscle reacts to the passive stretched posture imposed upon the muscle, and its reaction results in the production and maintenance in the muscle of an active contraction posture which opposes the passive stretch to which the muscle is subjected.

(To be continued.)

The British Empire Exhibition.¹

EXHIBITION OF PURE SCIENCE ARRANGED BY THE ROYAL SOCIETY.—II.

THE physics section of the Royal Society's exhibition comprises apparatus illustrating the most important modern work on the structure of matter and the nature of electricity and on the various parts of the electromagnetic spectrum, together with metrological and metallurgical exhibits and some apparatus of great historical interest. Demonstrations are given, and these will be changed from time to time. The exhibition has largely been arranged to show the historical development of existing knowledge and its applications, and brings out clearly the way in which important developments arise in the first instance out of researches undertaken from no other motive than curiosity. It is important for physics that the public should recognise this fact, which is the keynote of the exhibition. Knowledge is often valued less for itself than for the industrial developments which it makes possible, and the capitalist who finances inventions gets wealth

while the inventor who applies physical discoveries gets fame, but physics generally finds itself in the position of Cyrano de Bergerac when he wooed the fair Roxane in order that another might climb to her balcony:

"Pendant que je restais en bas, dans l'ombre noire,
D'autres montaient cueillir le baiser de la gloire!"

A foremost place must be given to some of the original apparatus by means of which the electron was discovered and its nature investigated. This includes various forms of Crookes's tube, Sir J. J. Thomson's apparatus for measuring e/m and v , and Prof. H. A. Wilson's apparatus for determining e , and though the proverbial sealing-wax and string is not greatly in evidence, the unobtrusive character of the apparatus contrasts with the importance of its results. A series of ten exhibits by Prof. O. W. Richardson comprises originals and models of the means by which he developed the theory of thermionic emission during the years

¹ Continued from p. 864.