creases at higher pressures probably as a result of recombination. With mercury vapor, the values of β are about 50 per cent. greater.

These results indicate that 60 or even 70 per cent. of the primary electrons lose nearly all of their energy on their first collisions with atoms and the remaining atoms lose energy less than that needed to produce ionization. Since 2 or 3 ions may be formed by each electron it appears that the primary process involved in ionization by 30 to 200 volt electrons is the production of an *excited* atom or ion which takes up nearly the whole energy of the incident electron. Then, by collisions with other atoms, or more probably by radiation, this excited atom causes the ionization of several other atoms.

This mechanism seems essentially different from that postulated in a recent paper by R. H. Fowler (Phil. Mag. *47*, 257 (1924)).

The foregoing results confirm nearly all the conclusions drawn by Eldridge in his study of the ionization of mercury vapor.

Experiments are in progress using hydrogen, helium, nitrogen, neon and carbon monoxide.

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PLURISEGMENTAL INNERVATION OF SKELETAL MUSCLE FIBERS AND IMPLICATIONS CONCERNING FATIGUE

THE traditional picture of the fiber of skeletal muscle represents it as receiving one motor nerve-fiber which is assumed to be connected with it near its middle point. Text-books of histology[1] sometimes refer to the possible innervation of a single muscle-fiber by two or more nerve-fibers, but the impression is usually conveyed that this is an atypical condition. Physiologists have pointed out that the complete involvement of a muscle-fiber in the process of contraction must be secured more promptly when stimulation is made to take effect at two places than when it is restricted to one. But a simple calculation shows that any such gain in speed of developing contraction can be only slight even if the spacing of the myoneural junctions is ideal. Other aspects of reduplicated innervation brought out some years ago by Agduhr[2] have been too little regarded.

This observer discovered that in cases where a muscle in the leg of a mammal can be made to contract by stimulating either of two motor nerve-roots it may develop nearly as much tension in response to the excitation of one root as when both are stimulated at the same time. This would not be the case if each fiber in the muscle could be reached by one and only one nerve-path. The alternative, Agduhr considered, must be an organization of the motor system such that the same muscle-fibers can be called into action by distinct efferent elements. The arrangement indicated he has denominated plurisegmental innervation.

Agduhr sought and found histological evidence of such a relation. Making use of cats and rabbits he performed experiments in which the principle applied was one of differential degeneration. After sectioning a certain motor nerve-root, he kept the animals alive for from 58 to 144 hours. Postmortem preparations of particular muscles then showed normal and partially degenerated nerve-fibers in the same fields. Again and again pairs of myoneural junctions were seen upon single muscle-fibers. These were not widely separated as though adapted to insure more speedy responses, but usually close together. Most significant was the fact that where two nerve-fibers were traced to endings in one muscle-fiber the criterion of degeneration showed that they were derived from separate spinal nerves.

In this communication we desire to make a preliminary report on some experiments which were originally undertaken to see whether such a type of organization is to be found in the frog as well as in the mammal. They have been fruitful of suggestions which we did not at all anticipate. The gastrocnemius lends itself conveniently to such a study. The sciatic nerve of the frog, as observed near the spinal cord, is found to be represented by three strands. Two of these generally contribute to the motor innervation of the gastrocnemius. There is considerable variation in the relative size of these two bundles of fibers, but in many cases they are nearly equal. When this is true, it has been our experience that the contractions of the selected muscle evoked by stimulating the two components alternately are also of about the same magnitude. This holds for simple or tetanic, isotonic or isometric responses.

When we compare the tension developed by the gastrocnemius when one of the nerve divisions is stimulated with the tension recorded when both are excited at the same time it becomes apparent that but little is gained by calling in the second system to assist the first. In other words, Agduhr's experiment succeeds with the frog as well as with the mammal. Examples of this may be cited. Calling the two divisions of the nerve A and B, we note in

[1] Piersol, "Normal Histology," 1916, 86. Lewis and Stöhr's "Text-book of Histology," 1913, 163.

[2] Agduhr, *Anat. Anzeiger*, 1916, XLIX, 1–13; 1919, LII, 273. Also Wilson, *Brain*, 1921, XLIV, 234.

one case that the tension of the muscle during tetanic stimulation of A is 45 grams, with B it is 40 grams, and with both together only 48 grams. Again: A alone gives 30 grams, B alone 45 grams, and both together 50 grams. Our inference is necessarily the same as Agduhr's, namely, that the majority of the muscle-fibers have a plurisegmental innervation.

Fatigue Phenomena.—Since we can call most of the working units of the gastrocnemius into action by stimulating about half its motor nerve-fibers, it is possible to make fatigue records with this procedure and then to shift our excitation to the second motor component. The result is singularly clean cut. When we stimulate one division of the motor nerve with single shocks or with a tetanizing current until the muscle has practically ceased to respond, we can rouse it to renewed activity by transferring our stimulation to the other division. A second series of contractions of the same order and duration as the first can generally be secured.

What are we to conclude from the facts at hand? If we had only the data of fatigue we should explain the result very simply: we should say that the motor fibers of the first component brought one set of muscle-fibers into action and that those of the second component presided over a distinct set which had remained at rest during the contractions of their fellows. But we know from our measurements of tension that nearly all the muscle-fibers have been active from the outset. It seems impossible to escape the conclusion that what we have fatigued is not the mechanism of contraction, but something which serves to transmit the stimulus. Such fatigue has been commonly held to occur at the myoneural junction or end-plate and the present finding is consistent with the prevalent impression. But it is probably premature to single out a specific anatomical structure as the precise seat of the change. All that we know is that a stage of fatigue exists at which certain avenues of approach to the work-part of the muscle are blocked while others remain open.

Sherrington[3] and Forbes[4] showed some years ago that a similar state of fatigue is often demonstrable in the central nervous system. Certain afferent paths may become ineffective, while others remain available for the production of reflexes. The inference has been that such fatigue is synaptic. Physiologists have accordingly recognized the possibility of renewing reflex activity when it is flagging by the employment of new channels of access to the centers, but they have not hitherto considered that muscle-fibers also may have alternative approaches.

[3] "Integrative Action of the Nervous System," 1906, 218.

[4] *American Journal of Physiology,* 1912, XXXI, 102.

It must be borne in mind that when we excite muscle through its nerve we can not truly increase the strength of the stimulation which is brought to bear upon the contractile units by increasing our electric current. We can not force the nerve-impulse above a fixed intensity. If the threshold of the muscle rises to such a level that nerve-impulses fail of effect, we can not surmount it by any modification of indirect stimulation. We can, however, lead our stimulating current through the muscle itself and compel it to resume activity. There are two ways in which this result may conceivably be secured: the current may break over the elevated threshold at the original sites or it may find its way to other places where there has been no previous metabolism to induce fatigue. When we are making use of direct stimulation we can repeatedly force the contractions of a declining muscle nearly to their initial height by intensifying the shocks. The most probable explanation of this possibility would seem to be the following: To intensify the current sent through a tissue is equivalent to shifting and multiplying its points of effective application (physiological kathodes). It is more difficult than is generally assumed to be sure that all the resources of a muscle have been exhausted. We are convinced that fatigue in laboratory preparations usually consists in a resistance to the transmission of the excitatory process and that fatigue of this type can be quite sharply localized.

This conception has an odd corollary. If we are right in our belief that muscular activity is most prolonged when different points of attack are utilized successively, it is to be anticipated that supramaximal stimulation will exhaust a large part of the excitatory apparatus prematurely and thus limit the possibility of later shifting. We have obtained some evidence that this is the case. According to the same reasoning, we shall get more work out of a gastrocnemius when we stimulate adequately first one and then the other of its two nerve-components than when we play upon the whole nerve at once. When we excite nerve-fibers which end in muscle elements whose innervation is already provided for by other motor connection, we must be using up the equipment to no useful purpose.

The facts have an interesting bearing on human fatigue, endurance and training. On the clinical side they must affect the prevailing judgment as to the extent of degeneration and probable recovery in such diseases as poliomyelitis.

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