Lectures

ON

THE SYMPATHETIC INNERVATION OF STRIATED MUSCLE.

BY

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EXPLANATORY INTRODUCTION

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[When Professor Hunter arrived in England last November he was invited by the University of London to give three advanced lectures in anatomy, which were to have been delivered in the second week of December: but the large audience that assembled to hear the first lecture were informed of the grave illness to which he succumbed two days later (see BRITISH MEDICAL JOURNAL, December 20th, 1924).

He had been looking forward with the keenest interest to the delivery of these lectures, because they would have provided him the opportunity for clearing away the misunderstanding of his work and for demonstrating the adequacy and reliability of his evidence and the inferences he had drawn from it. In particular he was anxious to explain the scientific principles that should guide the surgeon in the selection of patients for the operation that he had devised (in collaboration with Dr. Norman Royle) for the relief of certain patients subject to spastic paraplegia—namely, those whose voluntary control of muscular actions was unimpaired except for the interference resulting from an exaggeration of what Sherrington calls "plastic tone"; and it had been his intention to describe the surgical procedure in so far as the reasons for the choice of the rami to be cut were concerned.

In the third lecture he proposed to discuss the discordant conclusions that had been drawn by different physiologists and surgeons respectively from their experiments (especially in the cat) and operations on the sympathetic in human patients, and to give the explanation of this apparent lack of consistency.

Finally, he intended to deal with the wider scientific bearings of his anatomical and experimental researches, and the possibilities thus opened up for promising investigations in many directions—anatomical, physiological, pharmacological, and clinical.

This much the compiler of these reports gathered in conversation with Hunter, who, unfortunately, had not prepared any manuscript of the three lectures he had intended to give. It had been his intention, as was his usual custom, to speak without notes, and apart from these conversations and the large series of lantern slides and cinematographic films, he has left nothing in the form of lectures. Yet the subject is so important in its scientific bearings, and the need for some explicit guide to surgeons is so urgent, that the attempt has been made to do what Hunter had intended to do, and to publish the reports.

The compiler has done nothing more than select passages from Hunter's published and unpublished works and endeavour to give a connected and consistent account of his results. In addition to the three memoirs published in the *Medical Journal of Australia* (January 26th, June 14th, and September 27th, 1924), in *Brain* (August, 1924), and in *Surgery, Gynecology and Obstetrics* (December, 1924), the compiler has in his hands the manuscripts of three unpublished memoirs of Hunter's on this subject, as well as the shorthand reports of discussions in which he took part at Brooklyn and Philadelphia in October. Moreover, Hunter had intended to make use of the information provided by Orbeli and his collaborators, of which an account was given by Dr. W. Horsley Gantt in the BRITISH MEDICAL JOURNAL of September 20th, 1924 (p. 533).

While the statements made in the following pages are Hunter's, any faults of arrangement or of literary form are to be attributed to the compiler. Discussing the problem which Hunter sets out to solve in these lectures Pekelharing[1] twelve years ago wrote: "The most direct investigation of the mechanism of muscular contraction will be afforded by microscopic study: but, unfortunately, we must wait for a happy inspiration to reveal the road to follow." The compiler of these lectures is convinced that Hunter has got the "happy inspiration."]

LECTURE I.

THE DUAL INNERVATION OF STRIATED MUSCLE.

IN his classical memoir on postural activity of muscle and nerve Sir Charles Sherrington[2] makes the statement that: "The existence in various invertebrata of muscles separately differentiated for execution of movements and for maintenance of posture respectively seems without parallel in the skeletal musculature of vertebrates. In the latter, one and the same muscle is used for the two purposes, though some muscles are predominantly concerned with the one, some with the other function." Discussing the same subject, the late Sir William Bayliss was frankly sceptical. Thus, in his *Principles of General Physiology*[3] he says: "It is not easy to understand how two fibres of different function and different innervation could coalesce with retention by the combined cell of both kinds of innervation." The chief aim of these lectures is to justify Bayliss's attitude of scepticism by showing that no such coalescence does in fact occur, for the muscular tissues of vertebrates are at least as highly differentiated in structure and function as those of invertebrates.

In his discussion of the sympathetic innervation of striated muscle that led to this expression, Bayliss admits that "two kinds of function are performed by two separate kinds of muscle fibres, as in the auricle of the tortoise, or by separate muscles, as in the mollusc"; yet he goes on to express the commonly accepted view in these terms: "But in other cases, as in the vertebrate bladder or in that of voluntary muscles, the same fibres undertake both functions, so far as can be made out." I shall first give reasons for the conclusion that the same fibres do *not* undertake both functions.

The evidence in support of this conclusion is provided (*a*) by the appreciable structural differences in the two kinds of fibres in striated muscles; (*b*) by different modes of innervation of the thick and the thin fibres; (*c*) by the totally different effects produced by cutting the medullated (somatic) and the non-medullated (sympathetic) nerves passing respectively to the thick and the thin fibres; and (*d*) the interpretation of the effects of stimulation of the sympathetic or the influence of adrenaline, veratrine, etc., such as Oliver and Schafer (1895), Cannon and Nice (1913), Cannon and Cattell (1916), and Orbeli and his collaborators (1922-24), amongst others, have recorded.

THE ANATOMICAL EVIDENCE OF TWO DISTINCT KINDS OF STRIATED MUSCLE FIBRES.

Forty years ago Ranvier called attention to the differences in structure in red and white muscles, and since then he and many others have examined the evidence more fully and correlated the anatomical facts with differences in function of the two types of muscle. In his *Textbook of Microscopic Anatomy*[4] Sir Edward Sharpey-Schafer has summed up the evidence so clearly that I cannot do better than quote his statement:

> "In the rabbit, as pointed out by Ranvier (1887 and 1889) and Krause, certain of the voluntary muscles present differences in appearance and mode of action from the rest. Thus, while most of the voluntary muscles have a pale aspect and contract energetically when stimulated, some . . . are at once distinguished by their deep red colour, as well as by their slow and prolonged contraction when stimulated. When subjected to microscopical examination it is found that in the red muscles the fibres are more distinctly striated longitudinally and the transverse striae are more irregular than usual. The muscular fibres are generally finer (thinner) than those of the ordinary muscles, and have a larger amount of sarcoplasm. The nuclei are more numerous and are not confined to the inner surface of the sarcolemma, but occur scattered in the thickness of the fibre as well. There is also a difference in the blood supply of the two kinds of muscle. . . .

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"A similar difference between red and pale muscles may be also seen in the rays amongst fishes. In other animals the distinction is not found as regards whole muscles, although it may affect individual fibres of a muscle. This is the case, as shown by Klein, in the diaphragm, in which in many of the fibres there are numerous nuclei, and these are imbedded in protoplasm (sarcoplasm), which forms an almost continuous layer underneath the sarcolemma. The distribution of the two kinds of fibres in different muscles has been especially investigated by Gruetzner (1884)."

The contrast between the structure, mode of innervation, and functions of the two types of muscle, as well as the striking differences in their respective liability to fatigue, have been emphasized by many other investigators; and I might mention the memoirs of Dr. John Hay[5] and Dr. Ffrangcon Roberts[6] as important contributions to the evidence and interpretation of this interesting fact.

These records establish quite definitely the fact that there are two kinds of striated muscle, distinguished by contrasted morphological and physiological properties. But it is important not to confuse red and white muscles with the thin and the thick fibres respectively. While it is established that the sluggish red muscle is composed mainly of slender fibres innervated mainly by fine nerve fibres, and the briskly reacting and easily fatigued white muscle of thick fibres innervated by large medullated fibres, it yet remains to be decided whether or not all striated muscles are composed of both kinds of fibres—obviously, of course, in very different proportions in the various muscles.

It is right that some reference should be made here to Gruetzner's insight when, in 1887, he put forward his brilliant suggestion as to the real meaning of the work of Ranvier and his collaborators. Gruetzner attempted to correlate the physiological phenomena exhibited by skeletal muscle with the then recent developments in knowledge of the histology of muscle. He developed the idea of an "intrinsic support" within the muscle, enabling one contraction to be superposed upon another. He put forward the view that some muscle fibres were responsible for the contractions and others for the "intrinsic support." If some muscle fibres are supplied by somatic nerves and the remainder by sympathetic nerves only, the general principle of the functional duality theory of Gruetzner would, in the light of the experimental analysis undertaken by Royle and me, be established.

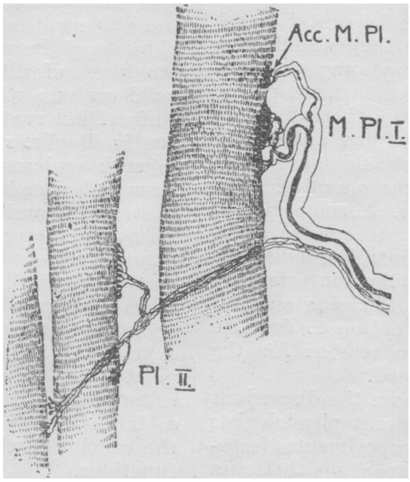

FIG. 1.—To illustrate Kulchitsky's demonstration of the dual constitution of striated muscle—large fibres innervated by medullated nerves ending in muscle plates (M. Pl. I and Acc. M. Pl.) and slender fibres innervated by non-medullated (sympathetic) nerves with so-called "grape-like" terminations (Pl. II).

DIFFERENCES IN THE INNERVATION OF THE TWO KINDS OF STRIATED MUSCLE FIBRE.

It was Kulchitsky's demonstration[7] of the fact that "the medullated and non-medullated fibres never terminate in the same muscle fibre" that impelled me to investigate by experiment the influence of the non-medullated nerves, which Boeke had clearly proved to be sympathetic, upon muscular function. During the year 1922 I was fortunate in being able to work with Professor Kulchitsky at University College, London, and to be permitted to take back to Sydney (early in 1923) some of his beautiful preparations of the endings of the medullated and non-medullated nerves in striated muscle, the description of which he did not publish until a year later. When I returned to Australia Dr. Norman Royle (with whom I had previously collaborated in an experimental investigation of the effects of transverse lesions of the goat's spinal cord) consulted me with reference to the inadequacy of the surgical operations to relieve spastic paraplegia. We studied Kulchitsky's preparations of nerve endings and the review of the present state of our knowledge by our former master, Professor J. T. Wilson,[8] and decided that, as certain of the muscle fibres were innervated solely by the sympathetic, some definite effect ought to be produced by cutting the sympathetic nerves going to limb muscles.

Hence we devised the series of experiments, and eventually the surgical operations which I shall discuss in the second and third lectures. But before doing this it is essential that I should consider the problem of the nerve endings, which is a matter of fundamental importance in this inquiry.

It has already been mentioned that as early as 1884 Ranvier called attention to the fact that there are two kinds of striated muscle fibres—one slender and rich in sarcoplasm with irregular transverse striae, the other thicker and much more energetic. Five years earlier (1879) Tchiriev had recorded that the thinner fibres are innervated by non-medullated nerves with grape-like endings, whereas the thick fibres are supplied by medullated nerves with end-plates such as Kuhne had described. This important discovery attracted little attention because Tchiriev supposed the fine muscle fibres with their non-medullated nerves were merely embryonic forms of the larger fibres with medullated nerves.

In 1902 Perroncito confirmed Tchiriev's observations that the different kinds of nerves (medullated and non-medullated respectively) were not supplied to the same muscle fibre. But since then Boeke has put forward the claim that both kinds of nerve may end in the same muscle fibre; and for more than ten years experimenters and morphologists have been trying to harmonize the facts of their fields of investigation with Boeke's statement.

Before giving the reasons for dissenting from these views, which are opposed to the observations recorded by Tchiriev, Perroncito, Kulchitsky, and others, reference must be made to Boeke's important demonstration of the fact that the non-medullated nerve fibres proceeding to striated muscle are really sympathetic. By the application of the experimental method to the elucidation of morphological problems he was able to show that the non-medullated nerves in question are the terminal portions of grey rami communicantes which arise in the thoracico-lumbar ganglia of the sympathetic cord. Boeke found in cats that three weeks after section of the nerves to certain of the eye muscles near their origin from the brain stem, many non-medullated fibres had resisted degeneration. He rightly concluded that these were sympathetic fibres from the cervical sympathetic chain which had been transferred to the eye muscle nerves distal to the point of experimental section of these nerves. Boeke performed the converse experiment of removing the superior cervical ganglion, but, beyond the fact that he was able to record the impression that the non-medullated fibres were fewer in number at the end of two weeks, this experiment was unsuccessful. Agduhr, on the other hand, after removal of the ganglion stellatum in a cat, was able to find, on killing the animal six days later, the remains of degenerated non-medullated nerves supplying skeletal muscles of the fore limb. It must be accepted, therefore, that some at least of the non-medullated fibres found supplying skeletal muscle take their origin from the vertebral ganglia of the ganglionated sympathetic chain. To employ the terminology of Langley, who confines the term "sympathetic" to the thoracico-lumbar outflow, the skeletal muscles receive post-ganglionic non-medullated fibres of the sympathetic nervous system by way of the grey rami communicantes. In addition, of course, this muscle receives the ordinary cerebro-spinal nerve fibres of somatic origin. In this sense skeletal muscle has a double innervation.

But if Boeke and Agduhr have rendered this great service of establishing the origin of the sympathetic fibres to striated muscle—a discovery which necessitates a new orientation of our ideas of the sympathetic and stultifies the definition of the sympathetic system still found in all our textbooks—they have also introduced an element of discord by their claim that both kinds of nerve end in the same muscle fibre.

Limitations of space make it impossible to give an adequate account of my reasons for rejecting the opinion of Boeke on this matter. In collaboration with my colleague, Dr. Oliver Latham, I have carefully examined the mode of ending of the nerves proceeding to the limb muscles of the goat and fowl, the animals used by Dr. Royle and myself in our experimental work. A full account of our results will soon be published; all I need say at present is that in no case were we able to discover a muscle fibre receiving both kinds of nerve fibres. In this respect our results confirm those previously obtained by Kulchitsky and the pioneers Tchiriev and Perroncito. Kulchitsky is not willing to admit that any of the grape-like endings of the non-medullated nerves are hypolemmal, whereas Tchiriev says they are definitely hypolemmal. Latham was able to show that there are two kinds of nerve endings on the slender muscle fibres—those of the efferent nerves, which are the grape-like hypolemmal terminations, and others, presumably afferent epilemmal endings. It is interesting to note, in confirmation of these claims, that Agduhr states that he has Bielschowsky preparations to demonstrate that, in addition to hypolemmal terminations, "there are also epilemmally situated sympathetic terminal plates in the limb musculature." It is evident, therefore, that efferent (hypolemmal) and afferent (epilemmal) sympathetic nerve endings are distinguishable from one another. In the next lecture I shall demonstrate the experimental proof of the existence of both afferent and efferent fibres from the sympathetically innerved muscle fibres.

In collaboration with Mr. R. E. Murray, B.Sc., of the University of Sydney, I have made a critical examination of the evidence cited by Boeke and Agduhr in support of their claim for the double innervation of individual muscle fibres. Our memoir on this important issue is ready for publication with a series of illustrations. At present I shall quote merely certain passages from the full statement.

Boeke established the existence of a plexus of non-medullated nerve fibres supplying skeletal muscle, which appeared to be quite independent of the ordinary medullated nerve fibres. He termed this system of fibres together with their terminations on striated muscle fibres "accessory," and in 1913 suggested that this system was sympathetic or autonomic in character. He supplemented his morphological researches by experimental investigations, which he summarized in 1917 in an extensive memoir. See also his London lecture published in *Brain* (1921). This work proves beyond doubt the validity of his contention that the extrinsic striated muscles of the eyeball are innervated by sympathetic as well as by the cerebral motor nerves. But at the same time his results raise a doubt whether he is right in describing all the fibres and endings which he originally termed "accessory" as being sympathetic in origin.

The most striking result which points to the improbability of Boeke's contention is provided by the fact that a marked difference in the histological picture of the nerve supply to the extrinsic muscles of the eye is to be seen after section of the cerebral motor nerves to these muscles, according to the time after the operation at which the examination of the muscle is made. In some cases he allowed a short period for degeneration (three to five days), and in others a longer period—for example, three weeks. After a short period specimens stained by the Bielschowsky method revealed that all the medullated fibres and their associated end-organs were undergoing degeneration. But the non-medullated "accessory" system was so well represented that apparently at least one "accessory" nerve ending was to be seen on each muscle fibre. In similar preparations of material in which degeneration had proceeded for the longer period, however, the greater number of these non-medullated fibres had disappeared. The conclusion justified by these observations is that the minority of the non-medullated nerve fibres which resist degeneration altogether are derived from sympathetic communications to the motor cerebral nerve which join the nerve distal to the site of section. On the other hand, the degenerated fibres and terminations of the "accessory" system of Boeke obviously belong to another category. Boeke's explanation of the failure of these fibres to resist degeneration is that they are cranial autonomic in origin; but, as Wilson[9] points out, he does not indicate in which ganglion the cells providing these non-medullated fibres are situated. Wilson also calls attention to the fact that, in any case, the section of the motor cerebral nerve is close to the brain stem, and the ganglion should remain uninjured, and therefore degeneration should not occur. Furthermore, Wilson raises the point whether Boeke has established beyond doubt that the tardily degenerating fibres are actually non-medullated rather than finely medullated fibres whose sheaths have already suffered degeneration. Nor does Boeke's converse operation of removing the superior cervical sympathetic ganglion establish that all the "accessory" fibres are sympathetic in origin. For the entire system did not disappear, though Boeke thought the fibres were fewer in number.

These anomalies in Boeke's interpretation of the origin of the "accessory" system undermine his contention that every individual muscle fibre receives both a sympathetic and somatic nerve ending, for any given case cited by Boeke may well be an example of two somatic endings, and not of double innervation in the sense in which that term is used in this lecture.

In later experiments by Boeke and Dusser de Barenne (upon the double innervation of the intercostal muscles of the cat) no mention whatsoever is made of the relation of the somatic and sympathetic endings to each individual muscle fibre. This work proves only that the intercostal muscles as a whole receive both sets of nerves.

In this respect the evidence of Agduhr is of great importance. This author investigated experimentally the result of partial denervation (somatic or sympathetic) of the muscles of the fore limb of the cat. After removal of the ganglion stellatum he succeeded in observing in Bielschowsky preparations of the brachial musculature, secured six days after the operation, the remains of degenerated non-medullated nerves. He also cut the last four cervical and the upper two thoracic nerves in the intervertebral foramina between the spinal ganglia and the point of divergence of the white ramus communicans. He killed the animal, the histological investigation of which is described in detail, five days after the operation; but he records finding similar appearances after a period of ten days. He observed that all the medullated fibres (motor and sensory) had undergone degeneration. On the other hand, many non-medullated fibres were seen to be intact; they were lying along blood vessels and were partly bound up with degenerated medullated fibres.

The point of interest in the present discussion is that Agduhr describes a single muscle fibre which shows two hypolemmal end-plates upon it. One of these is degenerated and therefore the termination of a somatic nerve fibre. The other receives a non-medullated nerve fibre. In consequence of this Agduhr describes this as an instance of a single muscle fibre receiving both a somatic motor and a sympathetic termination. He records, however, that the plate regarded by him as being sympathetic in origin had a large extension on the muscle fibre, and on account of this approached in character the somatic motor terminal plates. Further, he states that the distance of the two plates from one another is "such as one finds in a spinal plurisegmental innervation of the separate muscle fibres." If we add to these considerations the short period of degeneration allowed in the specimen figured by Agduhr (five days), in the light of the fact that Boeke found that non-medullated fibres may be seen for a considerable period when actually undergoing degeneration, no proof is provided that the muscle fibre described is actually innervated by both somatic and sympathetic nerve endings. It is possible that the second plate is the ending of a non-medullated collateral of a medullated fibre rather than an independent sympathetic termination.

Kulchitsky, whose careful work stimulated the present investigation, has described, for instance, such additional plates provided by collaterals. Dr. Oliver Latham of Sydney has found a beautiful example of a non-medullated collateral of a medullated nerve fibre ending hypolemmally in precisely the same way as the fibre which is figured by Agduhr. This collateral arises at a considerable distance from the site of termination of the medullated fibre, and the distance between the two plates is comparable to that which separates the endings in Agduhr's preparations.

Thus the contention of Boeke and of Agduhr that each muscle fibre receives a double innervation cannot be confirmed; nor does it agree with the evidence of other observers. Obviously the experimental method should afford evidence to settle the question whether individual muscle fibres are innervated by both somatic and sympathetic nerves. For this reason the muscles of the hind limbs of some of the goats employed by Dr. Royle for excision of the lumbar sympathetic chain on one side were histologically examined. The normal side was used for control. The preparations from the operated side showed in transverse section a number of small muscle fibres which were in marked contrast to the fibres of average size in the same preparation which were apparently normal. These diminutive fibres were too numerous to be accounted for as the conical or pointed terminations of normal muscle fibres. Further, the connective tissue (endomysium) between the individual muscle fibres has increased in amount. This was specially noticeable in a preparation secured by killing the animal six months after performing the operation.

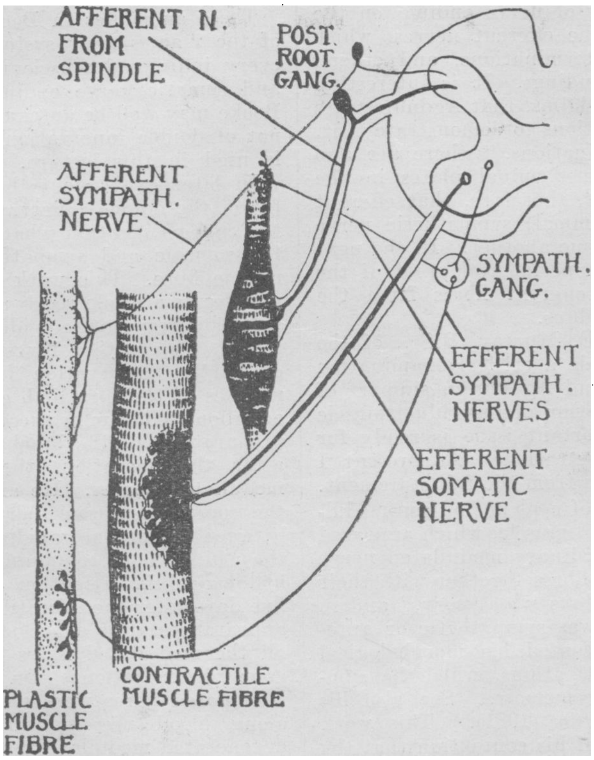

FIG. 2.—Diagram to indicate the three constituent elements of striated muscle, slender fibres, thick fibres, and muscle spindles, and their nervous connexions—efferent non-medullated fibre from sympathetic ganglion to slender fibre, afferent non-medullated fibre from slender fibre to the posterior root ganglion, medullated nerve from the spinal cord to the thick muscle fibre (whether or not it has an afferent fibre is not known), and muscle spindle, connected to posterior root ganglion by a medullated nerve and to the sympathetic ganglion by an efferent non-medullated nerve.

Conversely, the somatic innervation may be removed and the sympathetic nerve supply to the striated muscle left intact. The wing of the domestic fowl readily provides a preparation of this kind. Both the anterior and posterior nerve roots of the lowest three cervical nerves were severed without injury to the cervical sympathetic ganglia or the white ramus communicans which emerges at the level of the first thoracic segment. In this way the wing was deprived of the major part of the somatic nerve supply. Seventy days later the bird was killed. *Post-mortem* examination revealed that the operation had been successfully performed and the cervical sympathetic trunk was found intact. On microscopic examination large numbers of degenerated medullated nerve fibres were found in a preparation from the flexor muscles of the forearm. These muscles when stained in haematoxylin and cut in transverse section showed a marked contrast to the corresponding muscles from precisely the same point of the normal wing, which were treated in exactly the same manner. The individual muscle fibres of the normal muscle showed remarkably little variation in size throughout the preparations. The muscle of the wing from which the somatic innervation had been removed was in marked contrast to this. Many of the fibres were normal in size or slightly larger than the largest fibres of the normal muscle. These appeared in groups, and some fasciculi were entirely composed of them. Other fibres showed a marked diminution in diameter to approximately 33 per cent. of that of the muscle fibres of average size. These also occurred in groups, and in some cases they formed entire fasciculi. Other fasciculi were made up of groups of both normal and diminutive fibres lying in juxtaposition. The connective tissue of the muscle was increased in amount; a few masses of young connective tissue cells were in evidence between the bundles, and the endomysium was slightly more developed than in the control specimen.

It is firmly established that diminution in the size of all the muscle fibres follows complete denervation. The work of Willard and Grau on white mice may be cited as evidence of this. The leg muscles on one side were deprived of their innervation. The corresponding muscles of the other side were used as a control. Specimens were investigated showing atrophy of from three to sixty-three days' duration. These authors found a progressive decrease in fibre diameter, this change being unaccompanied by any change in the number of fibres. They describe the decrease in diameter as being "up to 68 per cent." During the period under observation there was no connective tissue proliferation between the muscle fibres. The difference in the findings of Willard and Grau and our observations in regard to the proliferation of connective tissue is no doubt accounted for by the fact that a partly denervated muscle is not entirely inactive. In the case of sympathetic denervation, which removes plastic tone, increase of fibrous tissue no doubt renders the muscle more efficient in maintaining a position imposed by active movement or by selective reflex activity. When contractile tone is removed by somatic denervation only a very slight increase of connective tissue occurs over a period of sixty days. The support of the wing during this period had therefore been provided practically entirely by the healthy muscle fibres which exhibited plastic tone.

The conclusion can be drawn from the experimental facts that partial denervation—somatic or sympathetic—affects some fibres and not others. This confirms the evidence obtained from a study of gold chloride preparations. On the basis of innervation, therefore, skeletal muscle is found to consist of two sets of fibres. In the experimental preparations the fibres of each set tend to occur in groups. This is in accordance with the findings of Latham in gold chloride preparations of the skeletal muscle of the domestic fowl and goat, that a considerable number of fibres, either receiving the endings of only non-medullated fibres or of only medullated fibres, tend to occur in proximity to one another. Even in teased preparations a group of as many as seven muscle fibres may receive non-medullated fibres, while no terminations of medullated endings may be visible in the same field. Such an appearance may have been a source of error in the past in suggesting that every muscle fibre receives a sympathetic innervation. The possibility arises, therefore, that the mode of innervation of skeletal muscle is that any individual muscle fibre receives one motor nerve ending—somatic or sympathetic as the case may be—and not both motor endings, and that each type of muscle fibre occurs in groups.

As an instance of the presence of a single type of motor innervation it may be recalled that the muscle fibres of muscle spindles receive sympathetic motor terminations. The existence of a double motor innervation to these muscle fibres, although suggested by Perroncito, has not been confirmed. Recently, on the other hand, Agduhr has found sympathetic terminations on these intrafusal fibres in the limb muscles of the cat. Kulchitsky and Dart have found these endings in relation to the fibres of the muscle spindles of the python. Dart is in error in regarding the fibres as being finely medullated, but he shows clearly that the endings are associated with diminutive sole plates. This type of ending has already been described in this lecture as being sympathetic efferent in character. The intrafusal fibres seem, therefore, to have a single efferent innervation which is sympathetic in origin. This is in itself a point of great importance, for it suggests that other fibres may be similarly innervated.

I suggest, therefore, that the skeletal muscle of vertebrates consists of two sets of muscle fibres disposed in groups each with its own specific innervation, and, consequently, its own specific function, the experimental investigation of which will be discussed in the next lecture. I shall then endeavour to establish the proof of the following claims. The fibres receiving somatic nerve endings are concerned in shortening as the result of voluntary and of reflex activity, and in isometric contraction during the continuation of the stimulation. These fibres are responsible, therefore, for voluntary movement and for what Langelaan[10] calls "contractile tone." They are comparable to what Sherrington calls the "movement muscles" of invertebrates. Other fibres, innervated by the sympathetic system, are first inhibited and then lengthened and shortened during these processes, and remain at the new length passively imposed upon them. In other words, these fibres exhibit what Sherrington has called "plastic tone." They are comparable to the "fixing muscles" of invertebrates. During movement these fibres aid in supporting the weight of the moving part. At the termination of movement they take part in maintaining the position attained as the result of the movement.

Further, some of the "fixing muscle" fibres appear to be included within a sheath to form the special sense organs (muscle spindles) which transmit afferent impulses to the central nervous system by means of somatic sensory fibres. The degree of lengthening and shortening imposed upon these intrafusal fibres is maintained by the influence of their sympathetic innervation. Epilemmal sympathetic endings found on other fibres that receive also a sympathetic motor innervation probably constitute in a similar way sympathetic proprioceptor organs.

All the evidence related above in regard to the exact mode and the function of the double innervation of skeletal muscle indicates that the differentiation of muscles into "movement" and "fixing muscles," which is so apparent in some invertebrates, is not lost in vertebrates. These two muscle systems of invertebrates are represented as small muscle groups which mingle together to constitute the skeletal muscles of vertebrates.

From the standpoint of physiology the existence of such an arrangement would readily account for the marked similarity in the behaviour of the "catch" mechanism of invertebrates and the activities of skeletal muscle in maintaining posture. In reviewing the points of comparison between the two processes, Bayliss recalls the suggestion of A. V. Hill that a more efficient mechanism of maintaining a weight must be exhibited under natural conditions than that displayed by the sartorius muscle of the frog when its nerve is stimulated by induction shocks. He compares also the process of inhibition of the "catch" mechanism (von Uexküll) with that of the tonic contraction of skeletal muscle during decerebrate rigidity (Sherrington); and he calls attention to the existence of an extremely low rate of metabolism during the activity of the "catch" mechanism (Parnas, Bethe) and of skeletal muscle in the state of decerebrate rigidity (Roaf, Lovatt Evans). If separate muscle fibres exist in vertebrate skeletal muscle for the fixation of posture and for active and reflex shortening and for isometric contractions of the muscle, the differences in metabolism and in the nature of inhibition during the manifestations of these activities of the two different muscle groups will be readily comprehended.

From the pathological standpoint this view introduces a line of attack to relate the symptomatology and pathology of such diseases as myotonia atrophica, the muscular dystrophies, and myasthenia gravis. In poliomyelitis it has long been known that sometimes the sympathetic ganglia partake of the degeneration found in the lower somatic motor neurone system. Such cases are, no doubt, those in which the tone of the muscle affected is completely lost. In other cases, in which there develop rapidly structural deformities due to the tendency for the limb to remain fixed in positions imposed upon it, the sympathetic innervation probably remains intact. Further, according to this conception, the operation of sympathetic ramisection for spastic paralysis consists in removing the nerve supply to the fixing muscle fibres only. All the movement fibres remain entirely unaffected. This, no doubt, accounts for the efficiency of the partly denervated muscles after long periods of time—for example, twelve months. On the other hand, according to the prevailing theory of the existence of the double innervation of each individual muscle fibre, the operation would entail partial loss of the nerve supply of each fibre of the muscle; or, more precisely, that the sarcoplasm of each muscle fibre is deprived of its nerve supply. This is unlikely in view of the unimpaired activities of reflex and of active shortening of the muscles which remain for long periods after the operation.

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PER-URETHRAL OPERATIONS FOR PROSTATIC OBSTRUCTION.

BY

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THE introduction of suprapubic prostatectomy in 1901 led almost immediately to the abandonment of the various palliative methods of treatment that had previously been tried with indifferent success. Since that time prostatectomy has grown in popularity, so that nowadays it is regarded by many surgeons as a routine method of treatment to be carried out in all cases of enlargement, except where some special contraindication exists. With improved technique the mortality of the operation has steadily diminished, so that patients who thirty years ago would certainly have been condemned to catheter life are now subjected to operation. But great as has been its success, prostatectomy must still be regarded as a serious operation and one that, even in the hands of the most competent, is attended by a comparatively high mortality rate. In view of this and of the fact that there must exist cases in which prostatectomy is unjustifiable, it may not be out of place to describe certain less drastic procedures which, in suitable cases, give excellent results.

Objections to Partial Removal of the Prostate.

Three criticisms are usually levelled against any operation that fails to effect a complete removal of an enlarged prostate: first, that the treatment is likely to fail in its object; second, that even when it succeeds the results are temporary; and third, that as an apparently innocent prostate may microscopically show malignant changes it is unwise not to remove it. The first two of these objections will be discussed more fully later. Suffice it for the moment to state that the whole success of partial operations on the prostate depends on a judicious selection of cases, and that failures are generally due to an ill advised attempt to tinker with a large prostate that is amenable only to total enucleation.

With regard to the third objection, as long ago as 1900 Albarran and Hallé called attention to the fact that a certain number of prostates which clinically appeared to be examples of innocent enlargement showed malignant changes when examined microscopically. This observation has since been confirmed and a figure approximating to 14 given as the percentage of cases in which these changes are found. From this it has been argued that as it is impossible to be sure that an enlarged prostate is pathologically innocent the wisest procedure in all cases is to carry out total prostatectomy. This argument for the wholesale removal of enlarged prostates would be unanswerable but for two facts—the first, that total prostatectomy itself has