Lectures on the sympathetic innervation of striated muscle by the late John Irvine Hunter : delivered at University College, London by G. Elliot Smith.

Contributors

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LECTURES

ON THE

SYMPATHETIC INNERVATION OF STRIATED MUSCLE.

BY

The late JOHN IRVINE HUNTER, M.D., Ch.M.,

CHALLIS PROFESSOR OF ANATOMY IN THE UNIVERSITY OF SYDNEY.

DELIVERED AT UNIVERSITY COLLEGE, LONDON.

BY

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Edwin Clarke
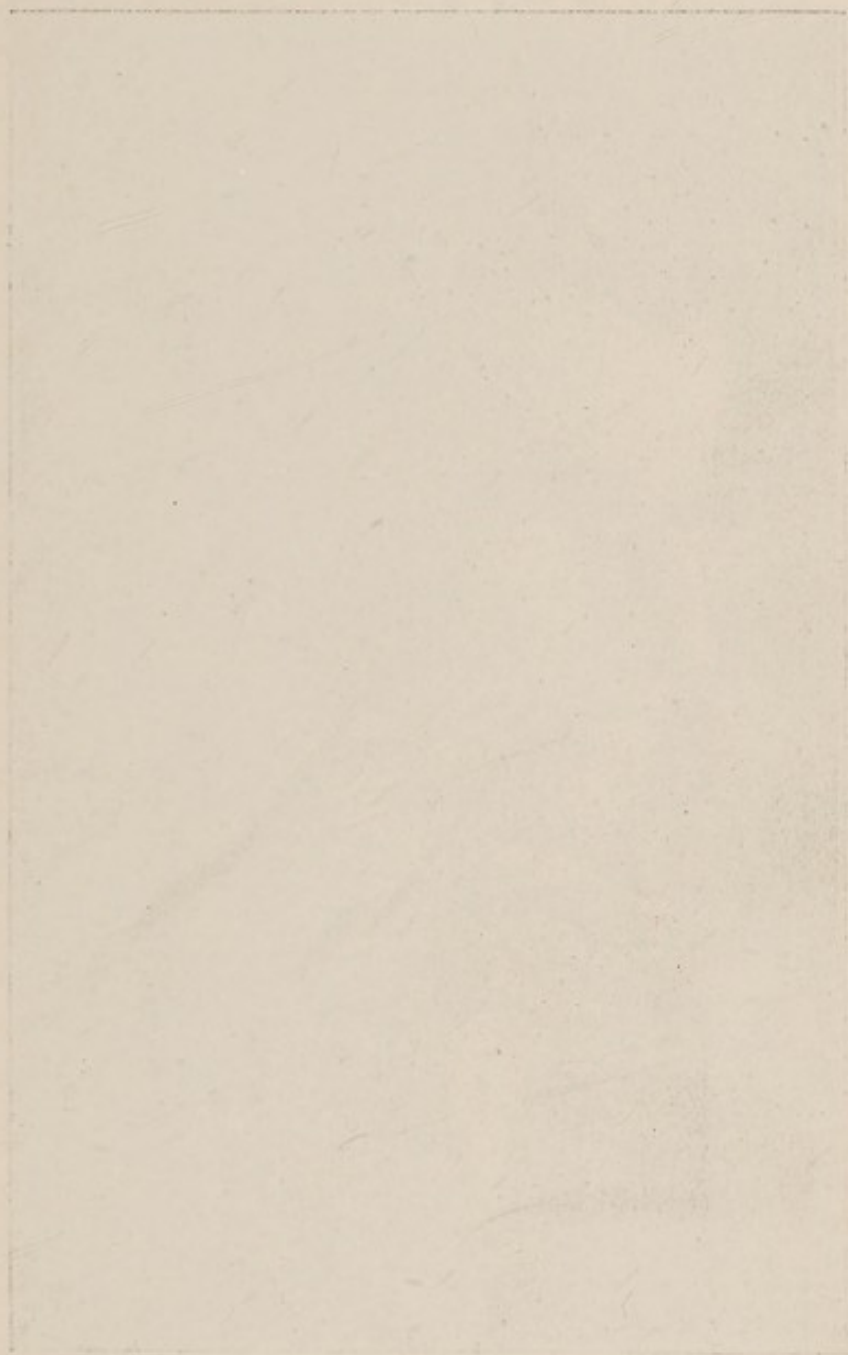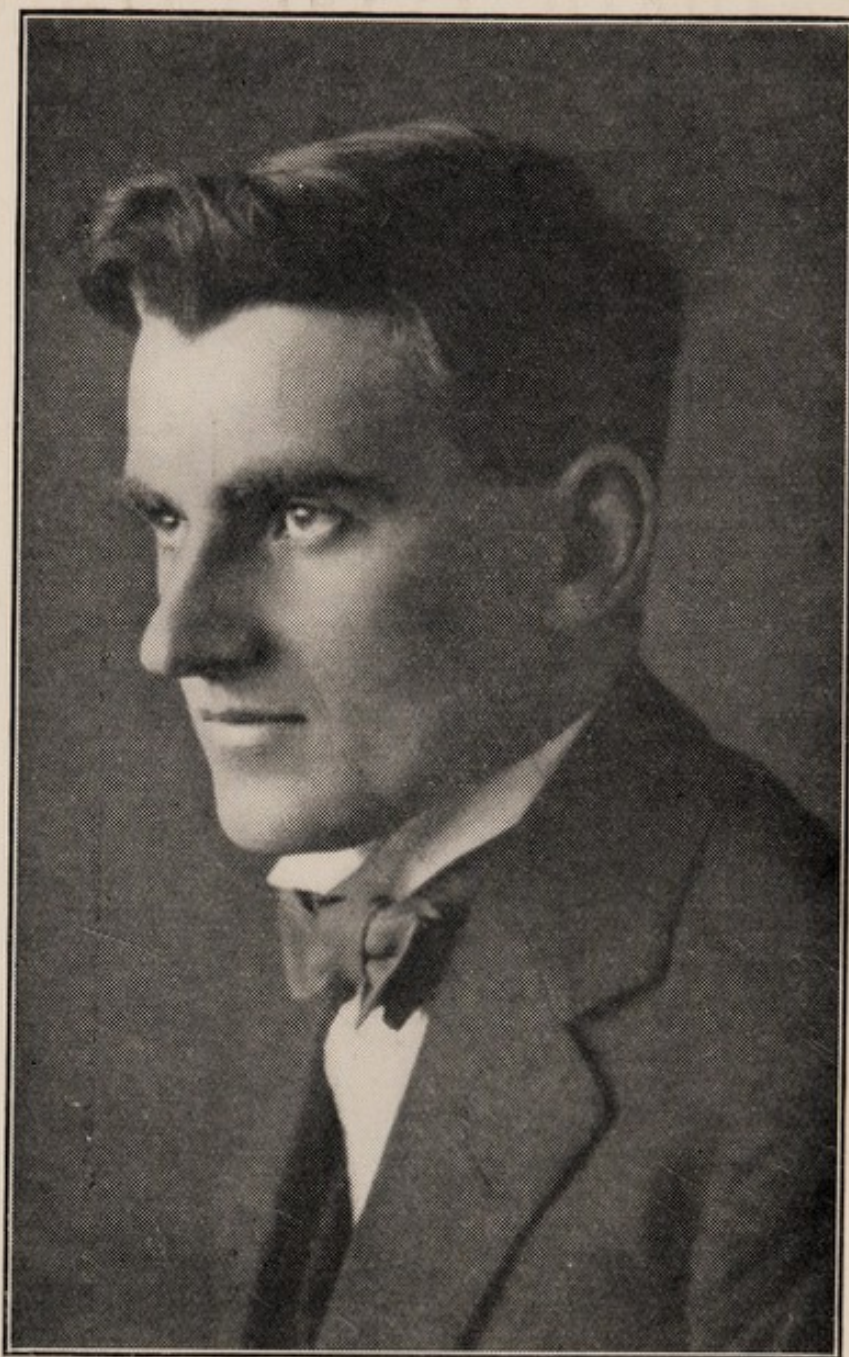28 September 1971

JOHN IRVINE HUNTER.

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INTRODUCTORY NOTE.

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 investi-

gations 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 (*Nederl. Tijdschr. v. Geneesk.*, September, 1913) 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."

Hunter was in the midst of his experimental work when he received the invitation from the American College of Surgeons to deliver the Murphy Oration in New York. He and the team of collaborators who were inspired by his enthusiasm were preparing to investigate a host of problems—anatomical, physiological, pharmacological, and

clinical—suggested by this work; and it was with the utmost reluctance that he left his laboratory last September. But he realized the value of a personal exposition of his results, and felt it his duty to accept the invitation from America. He fully realized how profound a revolution his work was destined to create in anatomy and physiology; and it is unspeakably tragic that he was not permitted to develop these investigations himself.

I refer to these matters to call attention to the fact that circumstances forced Hunter to make the two announcements of his results at times when he realized their incompleteness. One of these I have just mentioned —the call to New York just at the moment when he had got a clear vision of the host of fascinating problems, the solution of which seemed to be made feasible by his working hypotheses. The first announcement of his work on the sympathetic was made in 1923, during the visit of Sir William Macewen to the British Medical Association in Australia. The work was then still in the early experimental stage; but as the results were being applied to surgery it became necessary to explain the purpose and the principles underlying it for the guidance of those surgeons who felt it their duty to make use of a procedure that seemed to afford a certain hope of alleviating the chief troubles of the spastic paralytic patient.

Hunter had become keenly interested in the problems of the influence of the sympathetic upon visceral functions (which have not been discussed in these lectures); and if he had lived he had intended to embark upon a far-reaching inquiry as to the similarities and differences between the non-striated, cardiac, and striated muscles, and to correlate the actions of the sympathetic system on all three kinds of muscle.

In preparing these lectures for publication I have made free use of the work of Dr. T. K. Potts, published in the *Journal of Anatomy* (January, 1925), and the reports of the Murphy Oration in *Surgery, Gynecology and Obstetrics* (December, 1924); and I have to express my thanks to the editors of these journals (Sir Arthur Keith and Dr. Franklin H. Martin) for their generosity in allowing me to quote freely and copy illustrations. The drawings illustrating these lectures were made by Mr. T. Poulton, mostly from illustrations selected by Hunter himself. Dr. John Beattie and Miss Audrey Russell made special dissections for me to check some of the anatomical

points in the relations of the sympathetic rami in man and the fowl. Professor Hunter is in no sense responsible for Figures 2 and 10, which I constructed to give pictorial expression to the implications suggested in his argument.

G. ELLIOT SMITH.

University College.

LECTURE I.

THE DUAL INNERVATION OF STRIATED MUSCLE.

In his classical memoir on postural activity of muscle and nerve Sir Charles Sherrington 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* 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 differ-
ences 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* 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 ener-
getically 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. . . .

" 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 (sarco-
plasm), 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 and

Dr. Ffrangcon Roberts 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.

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

It was Kulchitsky's demonstration 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 col-

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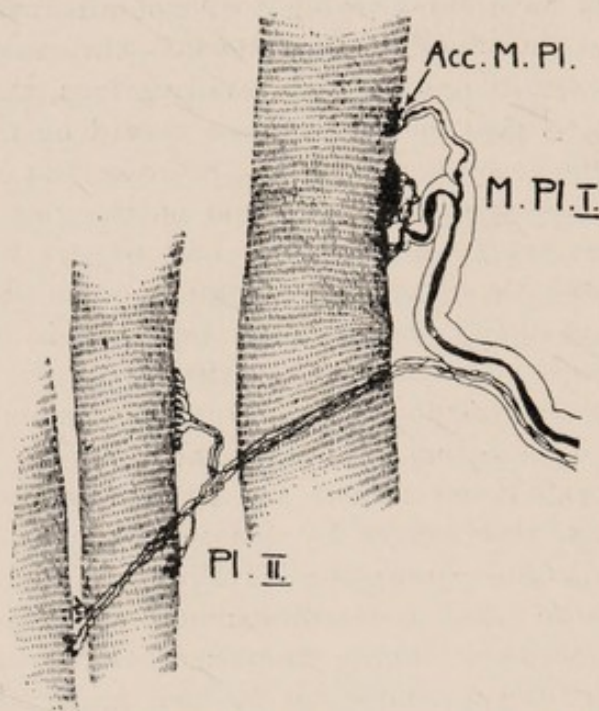
FIG. 1.—To illustrate Kulchitsky's demonstration of the dual constitution of striated muscle—large fibres innervated by medullated nerves ending in muscle plates (M. Pl. I and Acc. M. Pl.) and slender fibres innervated by non-medullated (sympathetic) nerves with so-called " grape-like " terminations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

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 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.

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 show-
ing atrophy of from three to sixty-three days' duration.
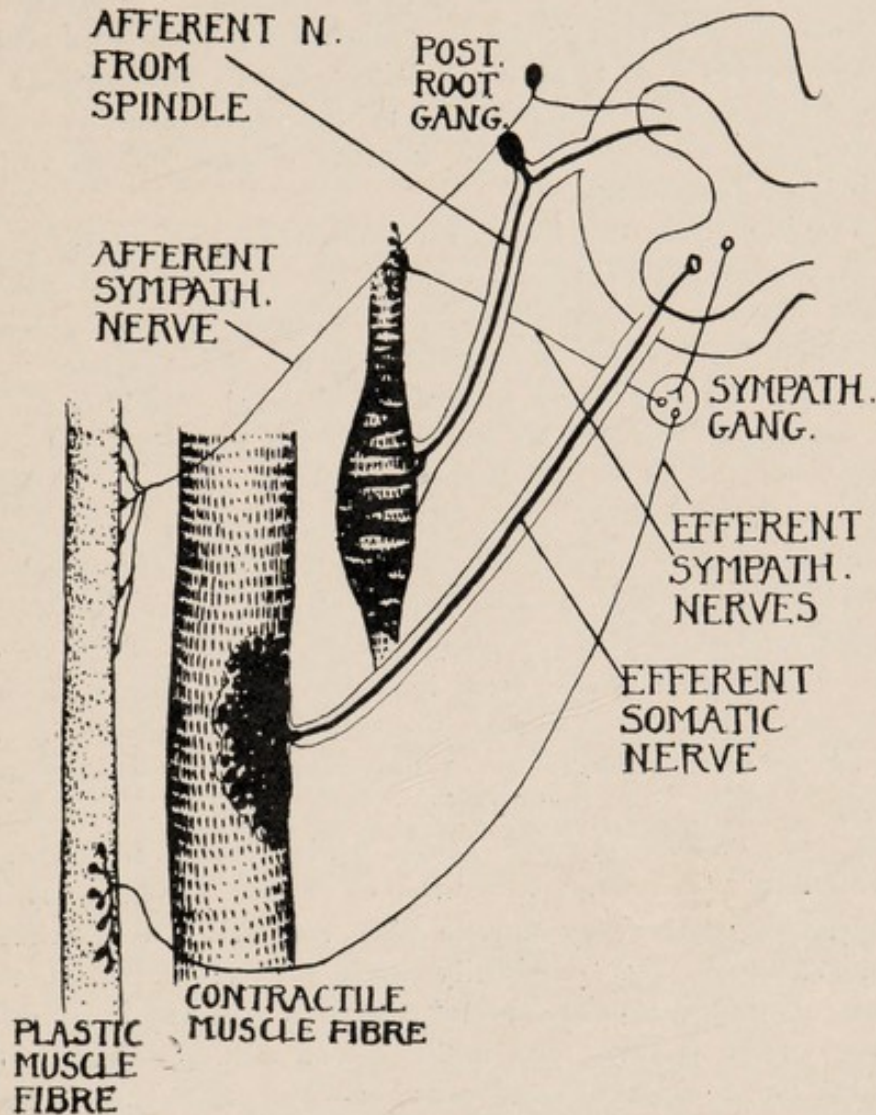These authors found a progressive decrease in fibre

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 sym-
pathetic 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.

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 prolifera-
tion 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 main-
taining a position imposed by active movement or by selec-
tive 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 pre-
parations 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 appear-
ance 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 con-
firmed. 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 calls " con- tractile 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 com- parable 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 sympatheti 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.

THE FUNCTIONS OF THE TWO GROUPS OF MUSCLE FIBRES:

EXPERIMENTAL EVIDENCE.

In the first lecture I submitted the evidence that has accumulated during the last half-century in demonstration of the fact that the striated muscles of vertebrates consist of two kinds of fibres (in addition to the muscle spindles) and that the difference in their innervation is as distinct as the contrast in their anatomical features, one group being controlled by the spinal cord through medullated somatic nerves, the other by the central nervous system through the intermediation of the sympathetic system, the post-ganglionic non-medullated grey rami communicantes.

In the present lecture I propose to discuss the evidence obtained by cutting the sympathetic and the somatic nerves respectively in proof of the fact that the functions of the two groups of muscle fibres are as sharply distinguished as their structure and mode of innervation. Our preliminary experiments were made upon goats, not only because they are large animals with the simplest type of "standing reflexes," but also because Royle and I had acquired some experience of these animals under experimental conditions in the course of our investigations on spinal shock in 1920 and 1921.

The details of the experiments upon the goat have been given in the earlier accounts of our work in the *Medical Journal of Australia*. I can more usefully employ the time at my disposal in these lectures to explain the principles that guided us in our work and to discuss the results and certain technical points that throw light upon the issues in the present controversies.

In Fig. 3 the essential connexions of the sympathetic system are represented in a purely diagrammatic way. The

white rami communicantes that issue from the spinal cord
in the thoracic and upper lumbar region end in the ganglia
of the sympathetic cord (or in one of the peripheral ganglia
not shown in the diagram). From the sympathetic ganglion
two series of non-medullated nerves emerge—one proceeding
directly to the viscera of the thorax and abdomen, the
other, forming the grey rami communicantes, passing to the
mixed nerve, to reach the striated muscles (*inter alia*)
along with the somatic motor nerves.

By cutting the grey rami communicantes at *A* (as it
should be the surgeon's aim to do in all human operations
on the sympathetic) sympathetic innervation of the muscles
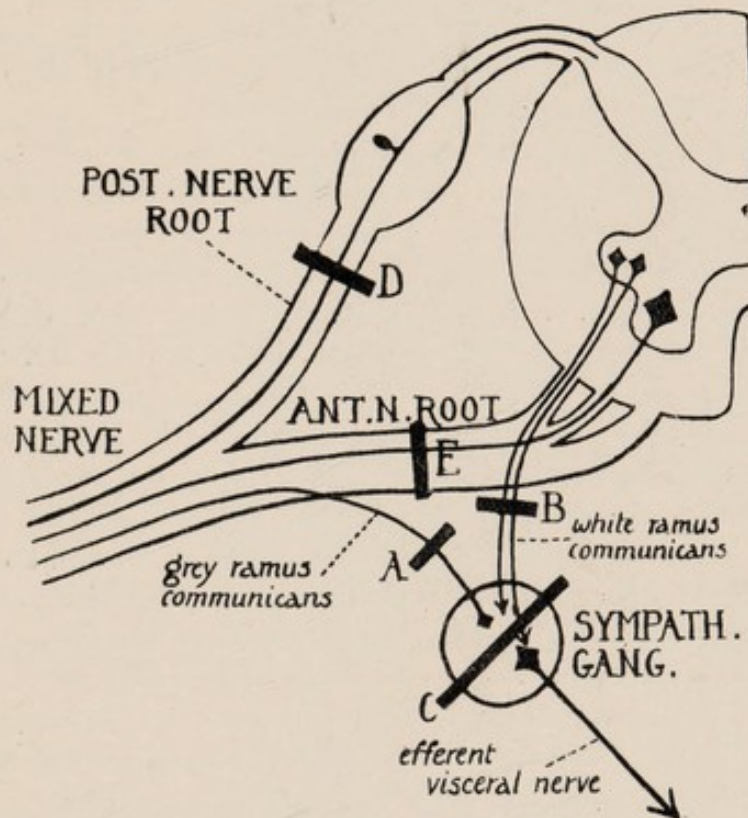in the area of distribution (as well as of the blood vessels

Fig. 3.—Diagram of the essential sympathetic connexions.

and sweat glands) is destroyed, but the sympathetic ganglia
and the visceral nerves are left undisturbed, and the patient
is spared the unfortunate effects of loss of proper control
of visceral function, to which he is rendered liable when
the sympathetic ganglia are needlessly removed. But for
experimental purposes it is often necessary to cut the white
ramus at *B*, and this is also done occasionally (for reasons
to be explained later) in human patients. In this case the
efferent channels from the spinal cord to the sympathetic
cord are severed, not necessarily, nor even usually, to the

ganglion (as Fig. 3 might suggest) that the ramus enters immediately, but to some part of the gangliated cord or one of the peripheral ganglia. In this case, as also in those cases where the sympathetic ganglion itself (at *C*) is cut or excised, the activity of both the visceral branches and the grey ramus is eliminated. The somatic efferent nerve may in some cases be cut at *E* without interference with the sympathetic rami. Another type of experiment—the section of the posterior root at *D*—cuts off all afferent impulses, both somatic and splanchnic. As the tone of muscle depends upon reflex activity, cutting off the afferent limb of the reflex arc destroys tone equally with damage to the efferent fibres (somatic at *E*, or sympathetic at *A*, *B*, or *C*;

In the human patient the grey and the white fibres may be so intermingled in the lumbar region as to make it impracticable wholly to spare the white fibres in the operation that Royle has called "ramisection."

With reference to the procedure for removing the influence of the sympathetic system on the hind limb of a mammal or the human leg, I cannot put the essential points more clearly than Royle has already done in his part of the Murphy Oration, illustrating the account with drawings (Fig. 4) made from the excellent dissection by Dr. T. K. Potts of Sydney (see *Journal of Anatomy*, January, 1925).

In experimental animals the sympathetic influence was removed from the left lower limb simply by avulsing the left abdominal sympathetic trunk. This operation could not be considered in the human subject on account of the changes that would follow removal of the sympathetic nerves to the abdominal viscera. The sympathetic nerves supplying the muscles of the lower limb arise from the lumbar ganglia and pass through the rami communicantes to the mixed nerves of the lumbo-sacral plexus. The human sympathetic ganglia receive white (preganglionic) fibres in some cases as low as the third lumbar nerve. Usually the contribution of white nerves to the sympathetic system ceases at the level of the second lumbar nerve. The distinction of white and grey rami in this situation is impossible, as it has been shown by N. Bishop Harman that the rami of the second and third nerves may contain both white and grey fibres. The sympathetic supply to the abdominal viscera is given off from the ganglionated trunk in a medial direction, and, provided the operation of ramisection were confined to lateral branches directed from the sympathetic trunk to the second, third, and fourth lumbar nerves, the effect upon the abdominal organs would be

negligible. The division of the sympathetic supply to the
fifth lumbar and to the sacral nerves presented a more
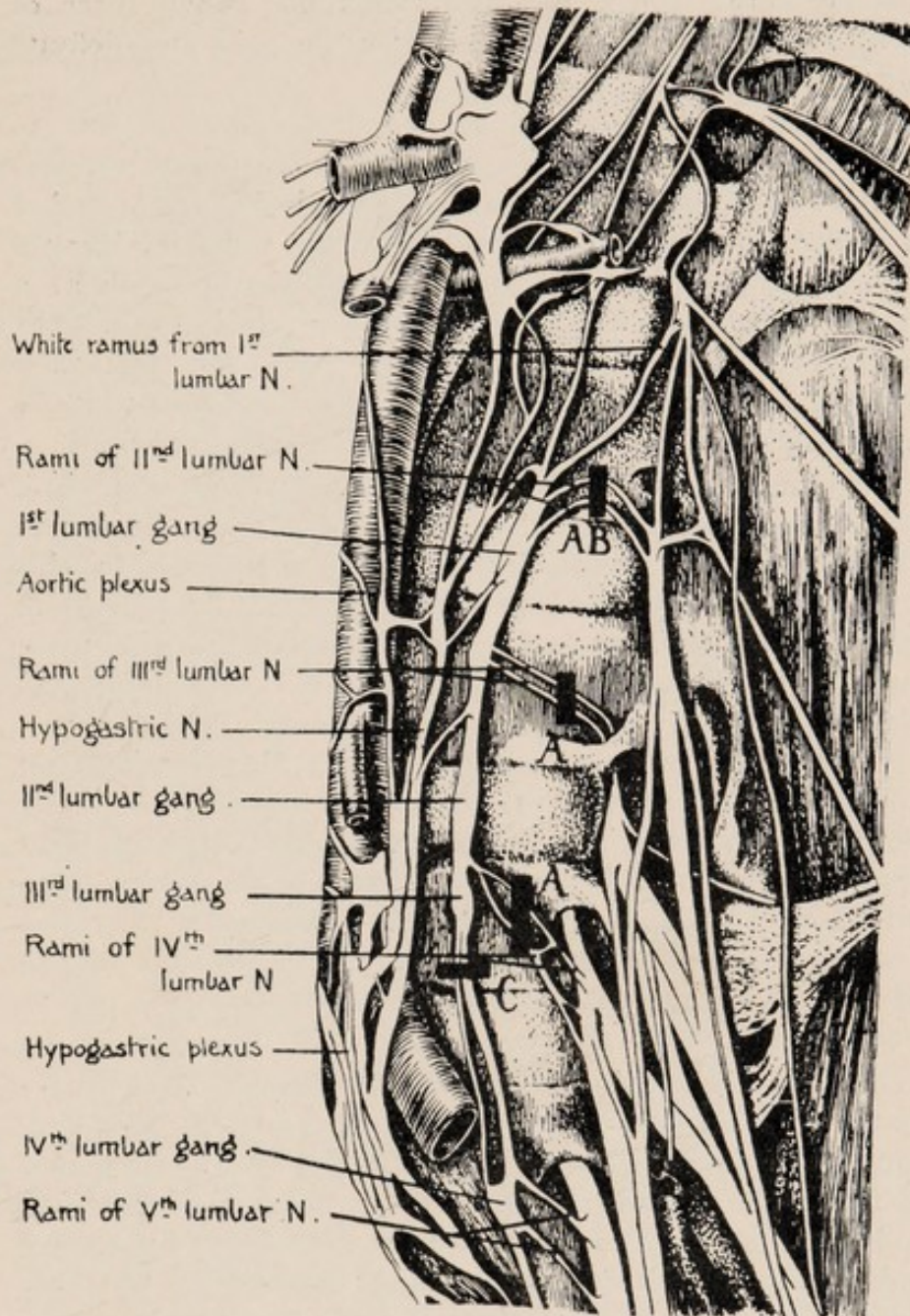difficult surgical problem, but this solved itself easily,

White ramus from Iˢᵗ lumbar N.

Rami of IIⁿᵈ lumbar N.

Iˢᵗ lumbar gang

Aortic plexus

Rami of IIIʳᵈ lumbar N

Hypogastric N.

IIⁿᵈ lumbar gang.

IIIʳᵈ lumbar gang

Rami of IVᵗʰ lumbar N

Hypogastric plexus

IVᵗʰ lumbar gang.

Rami of Vᵗʰ lumbar N.

FIG. 4.—Drawing to represent the arrangement of the rami com-
municantes passing to the left lumbar nerves in man. After Dr T. K.
Potts. The black bars represent the places where avulsion is effected
in the operation of " lumbar ramisection." The letters will facilitate
the interpretation (with the help of Fig. 3), *A* being a grey ramus,
A B a mixed ramus, and *C* the sympathetic cord.

because the sympathetic supply of the viscera is usually
given off above the level of the fifth lumbar nerve and com-
plete division of the sympathetic trunk at any point below
the level of the fourth lumbar nerve would not affect the

viscera. The sympathetic ganglia are not regular structures and do not always correspond in position to the lumbar nerves. The first ganglion usually lies in relationship to the second lumbar vertebra or the intervertebral disc below this vertebra. Below this the trunk may have three or more ganglia. There may, however, be only two definite ganglia.

The plan Royle adopted in the first operation was to divide the rami communicantes of the second, third, and fourth lumbar nerves (at the points marked *A B*, *A*, and *A* in Fig. 4, the letters being used with the same significance as in Fig. 3), and to divide the sympathetic trunk at a level corresponding to the fourth lumbar vertebra (*C*). The exact level of section must depend, however, upon the presence of a ganglion in this situation, and also whether that ganglion is supplying any medially directed fibres.

The ganglionated trunk itself is a very variable structure, and this particularly applies to the region of the fourth lumbar vertebra. On many occasions the trunk in this situation has been found to divide, and it was difficult to decide which division continued downward as the main trunk. The plan subsequently adopted was to define the ganglion which gives grey rami to the fourth lumbar nerve, lift it from its bed, and remove its lateral, posterior, and inferior connexions. Any medial fibres should be carefully preserved. When this ganglion is not present the ganglion supplying the third lumbar nerve may be unusually large and supply rami to the third and fourth nerves. The size of the ganglionated trunk may vary on each side of the body, and the rami may or may not come from the region of the ganglia.

The size of the rami varies with the number. A single ramus supplying a single nerve may be 2 mm. in diameter, though the usual size of a ramus varies between 0.5 and 1.5 mm. The accompanying diagram (Fig. 4) shows that the lumbar ganglion corresponding in position to the second lumbar nerve receives a large white ramus from the first lumbar nerve. In Royle's series of forty-two lumbar operations this arrangement was almost invariable; in only one instance was this large branch absent. In the first operation this ramus was mistaken for the white ramus of the second lumbar nerve and was divided, but subsequently the ramus has been avoided unless a special therapeutic effect was sought. In every operation both the white and grey rami of the second lumbar nerve have been divided. The position of the ganglia may cause considerable variation in

the position and direction of the rami, but, with the exception mentioned above, the rami tend to travel laterally or laterally and downward.

The operation of cutting these three rami and the sympathetic cord at a lower level Royle has called " lumbar ramisection." The procedure for severing the sympathetic supply to the arm he calls " cervical ramisection." In this
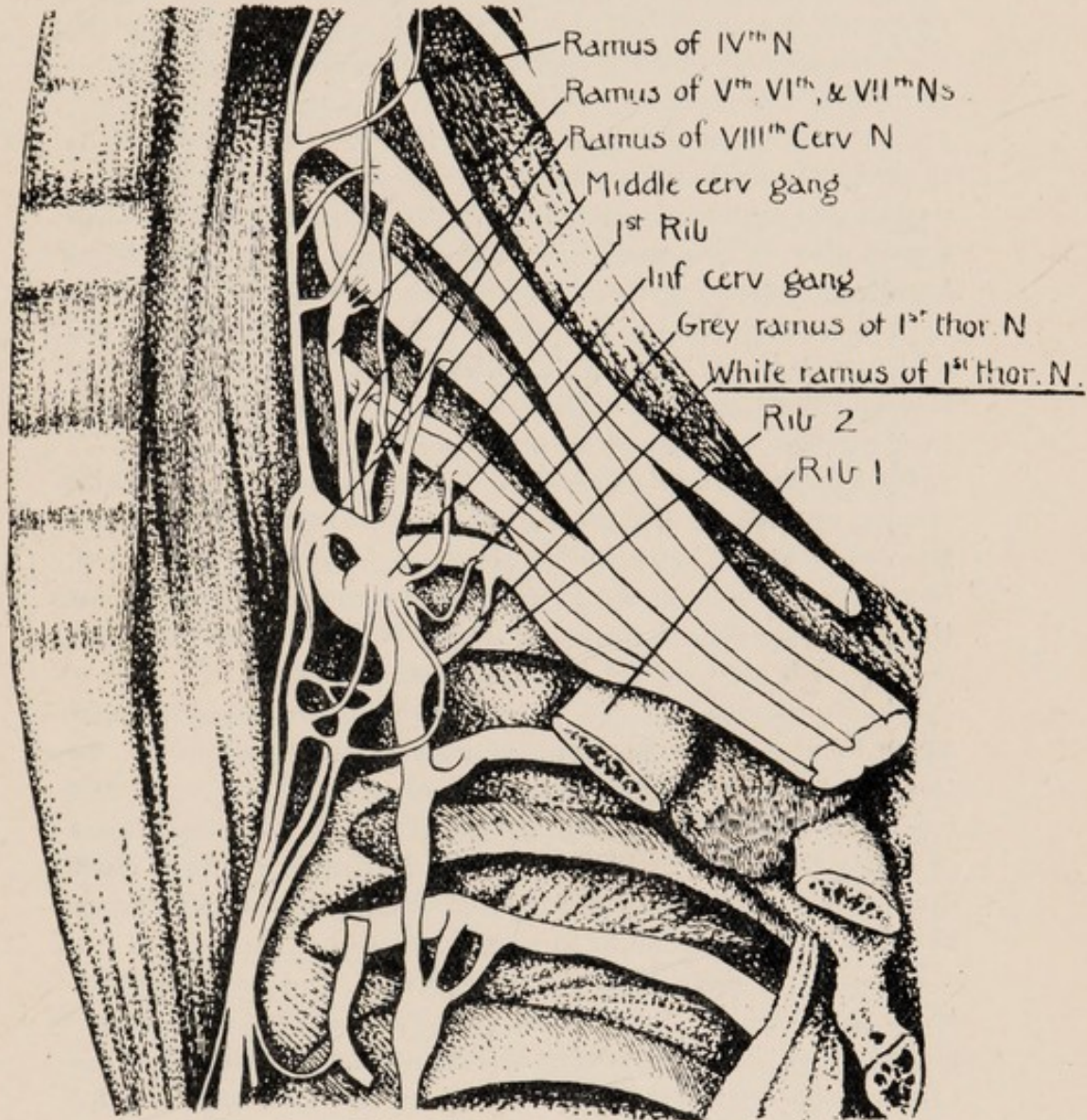

FIG. 5.—Drawing of the left brachial plexus in man to show the position of the grey rami communicantes which are avulsed in the operation of " cervical ramisection." After Dr. T. K. Potts.

case the operation can be strictly restricted to the grey rami communicantes without cutting any white fibres or the ganglionated cord of the sympathetic. In Fig. 5 a drawing of Potts's dissection is shown.

The sympathetic trunk does not come into the field of operation excepting in the approach to the first thoracic

nerve. The rami above the first thoracic nerve are composed wholly of grey (post-ganglionic) fibres, but the first thoracic nerve itself usually has both a white and a grey ramus. The sympathetic rami as a rule enter the nerve roots of the brachial plexus after they emerge from the intervertebral foramina, though occasionally rami will be found joining the nerve roots within the foramina.

According to the description of normal anatomy the nerve roots of the brachial plexus should emerge between the scalenus anticus and the scalenus medius muscles. In operations Royle says it is exceptional to find this arrangement. It is much more common to find the fifth and sixth roots piercing the scalenus anticus, and in several instances these roots have appeared anteriorly to the muscle. The seventh nerve also is commonly separated from the eighth by a bundle of muscle fibres. The eighth and the first thoracic nerves usually emerge together in a plane posterior to the scalenus anticus. A regular plexus considerably simplifies the operation, while the difficulty is increased if each nerve root emerges separately through the scalenus anticus.

All the grey rami proceeding to the roots of the brachial plexus are easily broken with a small strabismus hook in the operation of cervical ramisection. The grey ramus to the first thoracic nerve is found on the upper surface of the latter on the medial side of the white ramus (Fig. 5), cutting of which should be avoided if possible.

I have referred to the nature of the operations at this stage to give a precise idea of what actually is done. In the third lecture I shall return to the consideration of the indications for operation and the significance of the choice of these rami for avulsion. But before doing this I must discuss the experimental investigation of the functions of the two kinds of striated muscle.

Instead of describing the details of the experimental technique, which have been published in the memoirs already mentioned, I prefer to discuss the reasons for such extreme diversities of opinion as to the influence of the sympathetic nerves on striated muscle. This may be most profitably done by discussing certain points in experimental technique—such as (*a*) the reasons for allowing a considerable interval to elapse after removing the sympathetic before performing the operation of decerebration; (*b*) the method of examination of the animal so as to eliminate the disturbing effects of fear upon muscular tone, or the labyrinthine and cervical influences investigated by Magnus and de Kleijn; (*c*) avoidance of the effects of asphyxia and

of anaemia of the brain-stem in decerebrate animals; and
(*d*) the important matter of the choice of animals for
experimentation. The latter two points—(*c*) and (*d*)—will
be discussed in the third lecture. In this lecture I want to
direct attention to the important information obtained
from my experiments on birds, most of which has not
hitherto been published, although passing references have
been made to the preliminary results in the *Medical Journal
of Australia* (June 14th, 1924, p. 581), and in *Surgery,
Gynecology and Obstetrics* (December, 1924, p. 724).

THE FUNCTION OF THE SYMPATHETIC INNERVATION OF STRIATED MUSCLE.

In 1913 de Boer, as the result of experiments upon frogs,
claimed to have shown that the sympathetic nerve supply
of skeletal muscle was concerned with tone. He believed
that the tone of striated muscle was governed exclusively
by its sympathetic nerve supply. All subsequent workers
have shown that this contention is untenable; and many
of them have gone to the other extreme and denied any
influence of the sympathetic on muscle tone. The truth
certainly lies between these conflicting claims. De Boer's
view is being replaced by the conception that only a certain
element of muscle tone owes its origin to the sympathetic
nervous system. In 1915 Langelaan advanced the view that
the tone of skeletal muscles consists of two elements, one
component being governed by the somatic supply and the
other by the sympathetic innervation of the muscle. This
conception was independently arrived at by Revon. Later,
Langelaan (1922), as the result of experiments on frogs,
added further evidence in corroboration of this opinion.
He failed, however, to clear away the fundamental objec-
tion to the acceptance of his theory—namely, that no
investigator had shown tone to be altered consistently in
decerebrate preparations as a result of sympathetic denerva-
tion; or, conversely, that decerebrate rigidity could develop
if the sympathetic innervation were left intact while the
somatic nerves were severed.

The importance of decerebrate preparations consists in
the fact that, from their study in the hands of Sir Charles
Sherrington and others, most of the prevailing ideas of
muscle tone have been derived. Sherrington proved that
the tone of skeletal muscle was postural in function. He
found that the typical position of the decerebrate animal
was that of " reflex standing," with all four limbs rigidly
extended, and the neck retracted to a greater or lesser

C

degree. Between the phases of rigidity there were periods in which the limbs were no longer maintained in extension. During these periods, or when the extension of the limbs was overcome by passive movement, the musculature was found to exhibit a condition of what Sherrington has called " plasticity." If the leg were flexed at the knee, so lengthening the extensor muscle of the thigh, this position was retained (" lengthening reaction "). If the knee were now extended, so shortening the extensor muscle, the new position was again maintained (" shortening reaction "). Sherrington called the property of skeletal muscle which enabled it to exhibit these reactions " plastic tone." He emphasized that the degree to which this property was exhibited was independent of the length of the muscle fibres exhibiting it. It is important to remember that Sherrington was not using the word " plastic " in the popular sense of being adaptable or easily moulded; what he meant by it was the retention of any position in which a limb was placed. Following the suggestion of Gruetzner and others, he compared this property of skeletal muscle to that of involuntary muscle, such as that which surrounds the bladder wall, which enables it to adjust itself to enclose an increasing volume under practically the same wall tension. Speaking of this comparison Sherrington says: " Both are instances of the postural contraction of muscle; though the relation of the central nervous system to the postural activity is very different in the two cases." For Sherrington believed that the tone of striated muscle was entirely dependent on the intactness of the somatic motor nerve supply, while involuntary muscle can exhibit tone in the absence of its innervation.

The objection to the view that the tone of skeletal muscle is partially governed by the sympathetic nervous system, which has been put forward because experimenters employing the decerebrate preparation have obtained negative or apparently inconsistent results, disappears with the publication of our experiments (the memoirs of Royle and myself). In this work evidence of the connexion of the sympathetic innervation with the tone of skeletal muscle is forthcoming, not only from experiments upon the decerebrate goat, but from the effect of sympathetic ramisection in patients suffering from forms of spastic paralysis, which prior to operation revealed all the essential qualities of decerebrate rigidity. *In normal, " spinal," and " decerebrate " animals, and in human patients, sympathetic de-*

nervation of the limb musculature led to a consistent qualitative alteration in muscle tone. The defect was found to be a lessening of the efficiency of the muscle in maintaining a position once it had been assumed. This was the case whether the position had been imposed passively, reflexly, or by voluntary contraction; and, as I have previously argued, is due to the same fundamental change —namely, the loss of plastic tone. In the decerebrate preparation, after passive movement, the limb deprived of its sympathetic innervation failed to maintain the new position imposed upon it, when the extensor muscles were either lengthened or shortened. Instead, the limb would fall back to a posture determined by the action of gravity and the length of the fibrous tissues entering into its composition. This illustrates the effect of sympathetic denervation to remove plastic tone, as evidence of which is the absence of the " lengthening and shortening reactions " of Sherrington. The skeletal muscles of human patients show a similar qualitative alteration. This is clearly shown, for instance, in one of Dr. Royle's patients with spastic paraplegia supervening upon a gunshot wound of the cerebral cortex. Prior to operation this patient clearly exhibited " lengthening and shortening reactions " of the extensor muscle of the knee. Before operation, if the left thigh were lifted from the bed the unsupported leg would remain extended for a long period of time. If the extended leg were passively flexed at the knee-joint it would remain flexed in its new position. If it were now passively extended the extended position would be maintained. After left lumbar sympathetic ramisection these reactions, which are identical with the " lengthening and shortening reactions " of the decerebrate preparation described by Sherrington, were no longer exhibited—that is, plastic tone was removed by the operation.

But it is important to notice that tone does not entirely disappear after sympathetic denervation. Only one efferent pathway to the skeletal muscle has been removed (compare Fig. 3). The remaining somatic innervation is responsible for another component of muscle tone. In the acute decerebrate preparation, for instance, notwithstanding the removal of its sympathetic nerve supply, the typical extensor attitude of the limb is assumed. The neuromuscular mechanism concerned in imposing the extended position is obviously intact—that is, the medullated somatic nerves are responsible for this function. It will readily be seen that the extensor muscles must be shortened in order

that the extensor attitude of the limb may be attained.
The antagonistic muscle groups, on the other hand, are
reflexly inhibited, as Sherrington's studies of the acute
decerebrate preparation have shown. Their component of
tone, which is somatic in origin, and is exhibited as a
degree of contraction of selected muscle groups, may,
following Langelaan, be called " contractile tone."

Contractile and plastic tone are both postural in function.
Contractile tone imposes posture as a result of shortening
of appropriate muscle groups; plastic tone takes part in
maintaining this posture, once it has been attained, by
fixing the length of the muscles exhibiting contractile tone.
On account of the responsibility of these two components of
tone in the production and maintenance of posture they
may together be regarded as constituting postural tone.

As Sherrington has shown (by cutting the appropriate
afferent nerves) the production of postural tone depends
upon the existence of proprioceptive impulses. Posterior
nerve root section in all the spinal segments connected with
a given muscle removes both contractile and plastic tone.
Impulses arising in the muscles, therefore, discharge (via
the central nervous system) through both the somatic motor
nerve roots and the white rami of the sympathetic nervous
system. In other words, contractile tone is subserved by a
somatic proprioceptive reflex arc; plastic tone is governed
by a sympathetic reflex arc. As the result of the limited
connexions of the sympathetic nervous system with the
spinal cord, these reflex arcs for a given muscle group are
usually situated at different levels of the central nervous
axis. Purely spinal reflexes are, however, inadequate in
higher vertebrates for the exhibition of the postural tone
responsible for the natural attitudes of the body. The
reflexes responsible for the extensor attitude of the lower
extremities depend, for instance, upon reflex arcs that pass
as high as the pons in the brain stem. It appears that the
vestibulo-spinal tract is the descending limb of the reflex
arc subserving the contractile tone to the extensor muscles
of the limb; while plastic tone depends upon a reflex arc the
descending limb of which is constituted by the ponto-spinal
tracts. I have recently argued that these reflex arcs are
governed by the tectum, substantia nigra, and red nucleus
of the mid-brain, and the corpus striatum and the cerebral
cortex by way of the cerebellum. The influence of all these
structures upon postural tone is produced ultimately through
both the somatic and sympathetic efferent connexions to
skeletal muscle. In other words, there are two final common

pathways to each muscle. The excitatory impulses emerging through the somatic motor pathway all give rise to a contraction of the muscle or to contractile tone. The effect of the excitatory impulses emerging through the sympathetic rami communicantes is to fix the existing length of the muscle (plastic tone). It is obvious that this is a primary subdivision of postural tone according to the properties subserved by the two efferent connexions of skeletal muscle. The sources of the impulses emerging through each pathway are numerous in each case, as already mentioned. Both connexions are in fact final common pathways in the sense of the term employed by Sherrington.

Technique of Experiments in which the Decerebrate Animal was Employed to Determine the Effect of Removing the Sympathetic Innervation of Skeletal Muscle.

The negative and inconsistent results obtained by previous investigators employing the decerebrate preparation to determine the function of the sympathetic innervation of skeletal muscle call for comment. The following points appear to have been of importance in leading to the success of the experiments of this kind in the hands of Dr. Royle.

The Interval between the Removal of the Sympathetic Cord and the Operation of Decerebration.

In our experiments on goats the lumbar portion of the sympathetic trunk was removed from one hind limb. This was done as a preliminary procedure. Then, at a variable period after this operation decerebration was performed. In our first series the interval between the two operations varied from seven to seventy-three days. The best contrast between the hind limbs on the operated (left) and unoperated (right) side was seen in the animal in which the interval between the operations had been longest. In this animal extension of the left limb was easily overcome in contrast to the opposite limb. When not handled with the animal lying in the supine position, so fixed as to eliminate the disturbing influences, vestibular and cervical (such as Magnus and de Kleijn have described), the left limb rapidly fell from its temporary position of extension to a passive posture of semiflexion. In this stage of relaxation the " lengthening and shortening reactions " were absent.

These effects depend upon the loss of plastic tone. The comparative ease in performing passive flexion of the extended limb is due to the fact that contractile tone, which is responsible for thus imposing this position, alone has to

be overcome to alter the position. On the intact side, while
contractile tone is responsible for the position of extension,
it is assisted by plastic tone, which tends to fix the length
of the muscles necessary to maintain this position. When
contractile tone is overcome on the partially denervated
(that is, deprived of sympathetic nerves) side no further
resistance to movement is offered. On the opposite side,
though resistance suddenly gives way when reflex shortening
of the extensor muscles (that is, contractile tone) is over-
come, some degree of resistance to passive flexion is still
maintained, because plastic tone still persists. As Walshe
has pointed out, this phenomenon has its counterpart in the
clasp-knife effect of decerebrate rigidity.

Decerebrate rigidity is due to the presence of an exag-
gerated degree of both contractile and plastic tone. The
extended position imposed by contractile tone (as the result
of the selective reflex shortening of the extensor muscles)
is rigidly maintained by the fixation of the extensor

FIG. 6.—Decerebrate goat with both fore limbs and the right hind
limb rigidly extended. The left hind limb (deprived of its sym-
pathetic innervation) is relaxed. Head and neck fixed to prevent
Magnus and de Kleijn phenomena. Note the force necessary to bend
the right hind limb.

muscles in their shortened state by plastic tone. In the
absence of plastic tone this rigid fixation is no longer
apparent, and the limb fails to maintain the extended
posture (Fig. 6) once the reflex shortening of the extensors
dependent upon impulses emerging through the intact
medullated somatic nerves ceases. The active posture of
extension is now no longer maintained.

When the limb was passively extended or relaxed spon-
taneously it would fall into a semiflexed position deter-
mined by gravity and the length of the fibrous tissues
contained within the limb. If the knee-joint were now
passively flexed or extended the leg would resume its
original posture. In other words, a passive posture charac-

terized the limb instead of the ability to occupy active postures, which is the property of the normal musculature in the decerebrate preparation. For the " shortening and lengthening reactions " are no longer exhibited—that is, plastic tone is absent.

Unquestionably these three manifestations of the loss of plastic tone are not so clearly exhibited when the interval between lumbar sympathectomy and decerebration is short —for example, when decerebration is performed on the same day as that on which the lumbar sympathetic trunk is removed. I have records of three decerebrate preparations that exhibited the " lengthening and shortening reactions " in this way when both procedures were carried out on the same day. In each of these, however, the resistance to passive flexion and the tendency for the maintenance of the extended position were definitely less than on the control side.

The explanation of the progressive loss of plastic tone may be that this property of skeletal muscle is less dependent upon impulses emerging from the central nervous system than is contractile tone. In this respect skeletal muscle would resemble, to a certain degree, smooth muscle, the tone of which is not absolutely dependent upon its nerve supply. However, there are difficulties in accepting this analogy as an adequate explanation, because recovery in the tone of involuntary muscle occurs as time advances following denervation. But in view of the fact that only some muscle fibres receive sympathetic nerve fibres and are therefore alone responsible for the property of plastic tone (see the first lecture), it is feasible that these denervated " fixing " fibres slowly lose this property following sympathetic denervation, so differing from the neighbouring " movement fibres," which are absolutely dependent for their property of contractile tone upon the intactness of the central connexions of the somatic nerve fibres that supply them. Moreover, in the lumbar operation so far employed, it is necessary to bear in mind that all the sympathetic ganglia from which the grey rami to the lower limb arise are not removed, though efferent impulses from the spinal cord to them are eliminated. This fact may perhaps in some measure account for the progressive loss of plastic tone. However, the whole problem of the determination of the time necessary to produce the complete effect after sympathetic denervation is now being investigated. It can best be solved by studying the effects of the operation in the chronic decerebrate animal described by

Bazett and Penfield. Delaying the operation of decerebration until a long interval after the removal of the sympathetic cord disposes of certain claims that have been made in the attempt to explain the changes revealed after sympathetic denervation. In the first instance diminution in tone cannot be ascribed to sensory inhibition due to the wound inflicted in performing the operation of sympathectomy, for ample time is provided to allow healing of the wound to occur. Nor are the changes due to vaso-dilatation, because the diminution in tone persists, or even increases in degree, although the vasomotor changes are a maximum immediately after the operation.

Sympathetic ramisection in human patients affords similar results in this direction; for the loss of plastic tone has persisted for twelve months in the case of Royle's first patient subjected to the operation, although obvious vasomotor changes were present only in the first few weeks. In other patients the circulatory disturbance has been of greater duration; but it had a general tendency to be reduced in degree, while the loss of plastic tone was still apparent. Some of the effects of sympathetic ramisection upon tone may, however, be due to the attendant increase of blood supply to the limb. I refer to its effect upon contractile tone. Dr. Royle has noticed, for instance, that cold has less effect in increasing contractile tone in the limb of a spastic paraplegic which has been subjected to operation than in the limb of the opposite side. As a result of vaso-constriction the limbs of the spastic paraplegic are invariably colder than normal. The advent of vaso-dilatation (with an attendant increase in temperature of the limb) lessens the degree of contractile tone. This reduction is greater immediately after the operation than it is subsequently, for the vasomotor changes become less marked as time proceeds. But the reduction in plastic tone progresses in the opposite direction.

The Method of Examination of the Animal.

After removal of the sympathetic innervation of one limb the otherwise intact goat can walk, and run, in the normal manner. The characteristic change produced by the operation is revealed, however, if the animal is placed in the supine position with its head held rigidly in the mid-line. All limbs take up an extended posture under these conditions, but, as Dr. Royle has shown, when the cause for alarm is removed by gentle handling of the animal—for fear excites the defensive reaction of extension—the lower

limb of the operated side falls from the extended position into a passive posture determined by mechanical factors. This method of examination for changes in the postural tone of the limb was adopted with advantage for the decerebrate preparation. The goat is placed in the supine position in a cradle and the head is held firmly in the median line, or the animal is first encased in a leather jacket which fits round the trunk and neck, and then placed in the cradle. In this way the effects of the tonic labyrinthine and neck reflexes of Magnus and de Kleijn are excluded. Under these conditions the typical extensor posture, as already explained, is assumed by all four limbs. But after a short period the limb which has been deprived of its sympathetic innervation falls under the action of gravity to a passive posture of abduction and semiflexion.

By this method of examination any defect in the maintenance of posture is readily indicated by failure of the skeletal musculature to support the weight of the limb. This is a matter of importance, for efforts to test for diminution of tone by passive movement set up a reflex spasm of the musculature of the limb which is evidence of the excitability of the nervous connexions responsible for contractile tonus. Clinicians are familiar with this observation. For spastic muscles may before palpation show no evidence of an increased degree of contraction : but a reflex tonic contraction is set up immediately passive movement is attempted. In the first phase the posture is maintained predominantly by plastic tone. After examination of the limb is commenced increased contractile tone is superadded. Obviously the effect of passive movement will be to obscure any diminution in the degree of plastic tone. Nevertheless, passive movement overcomes contractile tone alone more easily than contractile and plastic tone combined.

The results of my experiments on the wings of birds are so important and illuminating that, at the risk of making this account unduly long, I must make some reference to them.

EXPERIMENTS ON BIRDS.

The folded attitude of the wings of birds when standing or walking affords an excellent example of what Sherrington has called an " active posture "—namely, the maintenance of position against the action of gravity by means of the activity of contractile tissues. I thought a study of the mechanism concerned in the production and maintenance of this posture would throw light on the postural activity of voluntary muscle generally, and provide a means of deter-

mining the exact part played by the dual nerve supply—somatic and sympathetic—of such muscle in the production and maintenance of posture.

The effect of gravity, which would be freely acting under normal conditions in some birds, would tend to cause drooping and falling outwards of one wing, if the mechanism for the maintenance of its posture were interfered with, and by comparison with the position of the normal wing of the opposite side the degree of interference is readily measurable. The wing offers advantages for study over the limbs of the cat, dog, and goat, in which the normal attitude is extension, for compensatory efforts are necessary in order to retain this position in the interests of maintaining the erect attitude. This tends to mask the effects of injury reducing the efficiency of the postural mechanism. Variations in the position of the wing may also be studied more easily than alterations in the degrees of flexion of the hind limbs of the frog after sympathetic ramisection, as suspension of the frog (which is necessary to allow the normal side and the injured side to be compared) introduces rotatory reflexes. This circumstance renders a careful analysis necessary in order to dissociate the effects of labyrinthine impulses from the proprioceptive effects produced in the musculature of the limb itself (cf. Langelaan, *Brain*, 1915 and 1922).

In his memoir, " The Postural Activity of Muscle and Nerve," Sherrington says:

" Section of the afferent roots of the wing affects little, if at all, the folded posture maintained by the wing when not in flight, i.e., during standing or walking. Nor has the source of the postural contraction of the flexors of the wing been found. Here, as in the case of the iris, the postural contraction, if, as is presumable, reflex, lies in receptors not those of the contracting muscle themselves—is, in short, allogenous not autogenous."

In view of our experiments on goats it appeared to me that a possible explanation for the failure to alter materially the folded position of the wing, by severing the posterior nerve roots corresponding to the origin of the brachial plexus, was due to the fact that in such an experiment the sympathetic innervation of the voluntary muscle of the wing was left intact. In previous papers (see, for example, *Surgery, Gynecology and Obstetrics*, December, 1924) I have argued that the function of the sympathetic nerve supply of skeletal muscle is the maintenance of posture once the position is attained—in other words, that it is responsible for the property of plastic tone. It appeared desirable, therefore, to ascertain the effect of removal of the influence

of the sympathetic nerve supply of the muscle of the wing by section of the cervical sympathetic. The result of the first experiment of this kind has already been recorded. The wing was markedly drooped compared with the normal side when the body of the fowl was supported in the hand during recovery from the anaesthetic. Later the droop of this wing was definitely noticeable but not so marked, its tip being 1.5 cm. lower than the tip of the intact wing. The wing also was less firmly folded to the side of the body. This condition was still noticeable when the fowl was kept at rest for some minutes up to the time of being killed seventy-four days later. A *post-mortem* examination revealed that the vertebral sympathetic cord had been cut below (or behind) the upper two roots of the brachial plexus only, so that the effect was incomplete. Subsequent operations of a more complete character, in which the sympathetic was approached by dissection of the intertransverse spaces from behind, instead of from the front as in the first experiment, gave similar results.

Anatomical Features of the Cervical Sympathetic Trunk of Birds.

The vertebral sympathetic plexus or cord, which contains the fibres that interest us in these experiments, passes through the foramina of the transverse processes along the vertebral vessels on a plane ventral to the roots of the brachial plexus. On approaching the ribs the cord usually splits into dorsal and ventral trunks, which pass respectively dorsal and ventral to the neck of the rib. The operation usually performed on the fowls was to divide these trunks above the first true rib (at *C* in Fig. 7)—that is, caudal to the last large nerve (the last cervical) which contributes towards the formation of the brachial plexus. In sea-gulls I invariably cut the dorsal and ventral trunks immediately behind (or below) the penultimate cervical nerve as well. This section produced a more marked effect on the eyelids than the more caudal section. Langley has shown that the last cervical nerve is the first nerve through which pre-ganglionic fibres of the sympathetic nervous system emerge from the spinal cord. He records that the criterion of movement of the feathers following stimulation shows that these fibres are distributed to the upper part of the neck and the head. It may be distributed to the anterior part of the wing, but the effect is only slight when it occurs there. Therefore the more caudal section of the sympathetic chain satisfies the purpose of the present investigation. But

the changes in the position of the eyelid are useful as indications that the chain has been successfully identified and cut. In the fowl the effect of section of the cervical sympathetic above the last cervical nerve (at C in Fig. 7) produces a raising of the lower eyelid and a more marked drooping and overhanging of the upper lid, so that the pupil is partially obscured. Normally the upper lid is retracted to such an extent that only its free edge is visible. After the operation, especially when viewed from above, it may be seen for an extent of several millimetres. When the effect is not so apparent as in the lower section alone a useful test is to draw the upper lid down over the eye on
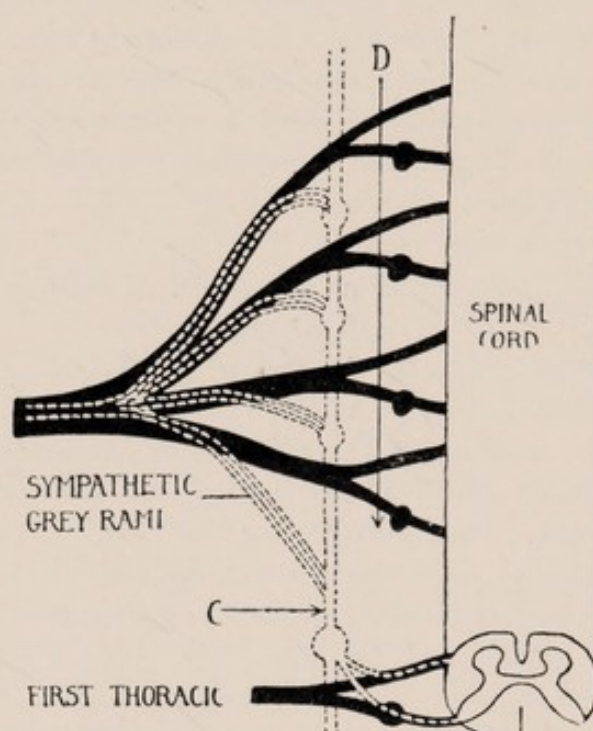

Fig. 7.—Diagram of the fowl's brachial plexus. C, The spot where the whole sympathetic connexions of the wing can be severed. D, The line along which either the posterior or the anterior somatic roots or both can be cut.

each side and compare the rate of its return on the two sides. It returns perceptibly more slowly on the operated side, and the return is, of course, not complete. The effects on the eyelid of the sea-gull are not so noticeable as in the fowl because they are smaller and less mobile. But the circular palpebral tissue becomes oval in shape following the operation.

The removal of the cervical sympathetic cord has an effect upon the pupil in the bird, as Langley has shown. The test of ruffling the feathers described by Langley is useful to determine whether the operation has been success-

ful. On the normal side the feathers rapidly return to their normal depressed condition, whereas on the side from which the sympathetic innervation has been removed the return is slow.

In this series of experiments the effect upon the blood vessels was not used as a criterion to indicate whether the sympathetic had been severed or not. In one case a marked increase of temperature of the comb occurred on the side of the operation. In another marked pallor was observed in the vascular appendages of the head following the operation. This was probably due to a state of strong contraction of the capillaries following sympathetic denervation described by Krogh. On examination on the following day in the above instance it was again present.

The Effect of Section of the Cervical Sympathetic upon the Posture of the Wing.

The immediate effects upon the position of the wing of section of the cervical sympathetic cord have already been briefly noted. In the fowl the wing is somewhat drooped on the affected side. This persists after healing has completely occurred. For instance, in one of the fowls the distance of the tip of the wing from the mid-line, as measured by the callipers on the eleventh day following the operation on the left side, was 4.2 cm. on this side, compared with the corresponding measurement of 3 cm. on the normal side. When the wings were stretched outwards and then simultaneously released, an average of three measurements on the left and right sides were 4.2 cm. and 2.2 cm. respectively. These differences are in part due to the falling away of the limb from the side (abduction) in addition to dropping downwards. An estimate of the difference due to these causes is also obtainable by measuring the distance of the outer surface of the wing at the level of the elbow-joint from the mid-line on each side. On the day in question the left and right measurements were 10.1 cm. and 8 cm. respectively.

Another change due to the operation is the slowness in the return of the partially denervated limb to its final position when released after stretching outward or downward or after elevation. This effect is perceptible to the eye and is constant over numerous trials. Cinematographic records confirmed this observation. The greater part of the return movement takes place relatively rapidly, though not so rapidly as on the normal side. The limb remains somewhat abducted and elevated, and then slowly settles

down to its final position, which is closer to the trunk and in a somewhat more depressed position. This latter element in the return movement may occupy several seconds. If the wing is passively placed in its normal position it rapidly falls to the depressed level. Sometimes the bird itself voluntarily lifts the wing to its normal position, but it quickly falls to its original position. This effect becomes more marked in fatigue—for example, after repeated examination.

In sea-gulls abduction and dropping of the elbow is apparent, but the effect is not so marked as in the fowl, because the tail is normally used to support the large wings, which in some of the specimens operated upon attain a span of a metre from tip to tip. In the normal position of the wings they lie crossed over one another resting on the tail. Subsequent to cervical sympathetic section the affected wing takes a position nearly parallel with the direction of the tail, and, following a two-sided operation, an interval may exist between the two wings which is not normally to be seen. When an affected wing is removed from the support of the tail it droops below the tail level approximately to the extent of 2.5 cm. The drooping of the wing is very marked during the process of recovery of the limb from the anaesthetic. Open ether was the anaesthetic employed in each experiment.

For purposes of control the vertebro-scapular muscles were severed on both sides, and both right and left sympathetic cords were exposed, but only the left was cut. The only difference between the two sides, therefore, is that section of the sympathetic cord was performed on the left side and not on the right side.

It is apparent from these remarks that the tone of the affected wing is reduced so that the normal posture is not perfectly maintained. But considerable tone remains, and it tends to impose a folded posture upon the wing. This influence must be due to the presence of the somatic proprioceptive reflex arcs which remain intact, but in the absence of the influence of the sympathetic innervation of the wing the maximum position of abduction and flexion can no longer be maintained against the action of gravity. This force leads to some degree of drooping and abduction of the wing. During light anaesthesia the effect is rendered more evident as the result of the partial removal of the influence of the somatic proprioceptive connexions. The influence of the somatic arc is also markedly reduced by fatigue, as already noticed following repeated stretching

of the wing in the fowl. The natural effort of sustaining
flight shows the result of fatigue to greater advantage.
These observations were carried out with the bird attached
to a light line mounted on a smoothly running reel. In
the unilateral operation the position of the normal wing
may be used as a control, as in sea-gull 3. Before flight
only slight abduction and droop of the elbow region of the
wing were apparent. After a flight of one hundred metres,
in which the wings were maintained in constant movement
so that no gliding occurred, the abduction and drooping
became very marked. The wing no longer rested on the
tail, and the bird made ineffectual attempts to place it in
its usual position. On supporting the body of the bird in
the hand and allowing the wings to drop freely a con-
dition resembling that seen in similar circumstances during
recovery from the anaesthetic resulted. Fatigue of the
somatically innervated muscles has apparently produced
this effect, so that the condition of the wing in such
circumstances is not far removed from that seen in flaccid
paralysis.

These observations are in accord with the results of our
operations on goats—namely, that the sympathetic innerva-
tion of voluntary muscles is responsible for the maintenance
of plastic tone. The defect following removal of the sym-
pathetic influence consists in inability of the voluntary
muscle to remain fixed at a given length—such, for instance,
as the length required to maintain the extended position of
the limbs in a quadruped when placed on its back, the
flexed position of the frog's hind limbs, or the folded posi-
tion of the wing normally assumed when a bird is walking
or standing. The flexed posture of the wing, to take the
latter instance, is conferred upon the wing by the intact
somatic proprioceptive reflex arc; and this tendency dis-
appears when this arc is interrupted. Therefore this arc,
when intact, subserves contractile tone (Langelaan, 1922).
The position of flexion of the wing imposed by the con-
tractile fibres fails to be maintained to the full degree in
the absence of plastic tone, which is subserved by the sym-
pathetically innervated fibres of the striated muscle of the
wing. Normally, therefore, plastic tone is the property of
muscle enabling the flexed position to be maintained. The
" catch " or " ratchet " mechanism of involuntary muscle
described by Uexküll is beautifully illustrated. The fixed
position of flexion of the wing can no longer be maintained
for an indefinite period with a minimum of fatigue in the
absence of the sympathetic arc. Furthermore, after volun-

tary activity of such partially denervated muscle, of which
flight provides the best example, exhaustion of the somatic
reflex mechanism manifests itself to a striking degree. It
is evident, therefore, that the sympathetic innervation plays
a part in movement as well as at rest. To retain the
analogy already mentioned, it would appear that an
" infinitely fine ratchet " assists in voluntary movement.
This helps to maintain the intermediate postures through
which the muscle passes during the execution of an active
movement.

In the absence of the sympathetic nerve supply it is
apparent that greater work is imposed upon the somatic
nervous system during voluntary activity, for it not only
performs the voluntary movement, but alone supports the
weight of the limb. When both wings have been partially
denervated by removal of the sympathetic nerve supply (as
in sea-gull 8) after several short flights both wings were
drooped and the bird was apparently exhausted, the mouth
was widely open, and respiration very rapid. On being
approached the bird only attempted short low flights to
avoid recapture.

The effect of the section of the cervical sympathetic trunk
in narrowing the palpebral fissure is to be ascribed to loss of
plastic tone of the striated muscle of the eyelid to a greater
degree than to the denervation of involuntary muscle. Dr.
Oliver Latham of Sydney has made gold chloride prepara-
tions which show the sympathetic non-medullated fibres
terminating in characteristic grape-like endings on con-
siderable bundles of the eyelids. Removal of the influence
of these fibres affects the capability of the muscle to remain
fixed at the length required to maintain the eyelids widely
separated.

Section of the Afferent Limb of the Sympathetic Proprioceptive Reflex Arc.

By cutting the posterior nerve roots (see the line D in
Fig. 7) Sherrington conclusively proved that tone is sub-
served by a proprioceptive reflex mechanism. The ques-
tion arises, then, as to whether a sympathetic proprio-
ceptive reflex arc is responsible for the production and
maintenance of plastic tone. Langley showed that the
feathers of the wing are influenced by stimulation of
the last cervical nerve and the upper two thoracic nerves.
Of these the first thoracic nerve has a strong effect on
the wing. The anterior part of the wing may be
affected by the last cervical nerve, but this effect when

present is only slight. The second thoracic nerve has a moderate or slight effect, usually on the posterior part of the wing only. Acting on the supposition that the sympathetic innervation of the voluntary muscle of the wing would have the same origin as that of the feathers, an operation was performed on the first thoracic posterior nerve root. This may be done by enlarging the first foramen seen on the dorsal view of the fused thoracic vertebrae. *Post-mortem* examination showed that this root was completely severed without injury to the anterior nerve root. In this case the brachial plexus received no somatic contributions from the first thoracic nerve. The large size of this root in all the specimens operated on is a striking feature in view of the slight part, if any, this segment takes in the formation of the brachial plexus. This confirms the suggestion that this nerve contributes the principal sympathetic connexions to the wing, so accounting for its large size. The effect of removal of the posterior root of this nerve upon the posture of the wing is in all respects the same as that following section of the cervical sympathetic cord caudal to the brachial plexus. Drooping and abduction of the wing are apparent; and, on releasing the wings after stretching, the affected side was perceptibly slower in returning to its final position. On the fifth day the measurements were as follows: The tip of the wing was 2.5 cm. from the mid-line on the left side, and 0 cm. on the right side; or, measured by the callipers, the elbows were 80 cm. and 6.8 cm. from the mid-line respectively. When the wings were stretched outward and then released the tips were 2.7 cm. and 2 cm. from the mid-line on the left and right sides respectively. It is evident, therefore, that if a sympathetic proprioceptive arc subserves plastic tonus afferent fibres must descend along the ganglionated (vertebral) chain to the first thoracic level and there pass to the nerve trunk at this level by way of one or other or both rami communicantes. In the experiment of section of the cervical sympathetic posterior to the brachial plexus both afferent and efferent fibres are therefore severed. The same effect follows section of the afferent limb of the arc only when the first thoracic posterior nerve root is cut through. Sherrington's preparations, in which the afferent nerves were cut, owe some of their features to removal of the influence of the sympathetic proprioceptive reflex arc subserving plastic tone, for in " deafferenting " the fore limb of the cat he removed *inter alia* the posterior nerve root of the first thoracic nerve, and in the case of the hind

D

limb of that animal the fourth lumbar posterior nerve root was one of the two roots resected. In the cat the thoracico-lumbar outflow extends from the first thoracic to the fourth lumbar segment: hence Sherrington's operations included the region of the sympathetic innervation of the limbs.

Persistence of Plastic Tonus after Removal of all the Posterior Nerve Roots Connected with the Brachial Plexus.

The anatomical connexions of the somatic and sympathetic nervous systems and the wing musculature make it possible to remove the influence of the former without materially affecting the innervation derived from the latter source: for the most important sympathetic connexion consists of a reflex arc at the first thoracic level. On one side the posterior nerve roots of four segments above this level were removed with a view to removing the influence of the somatic reflex arcs. In addition to the absence of voluntary movement the result of this operation is to remove the tendency of the wing to take up a flexed position—that is, contractile tone is absent. When the wing is stretched outwards, therefore, and released, it drops to the side of the bird, and instead of taking up the flexed attitude characteristic of the normal wing it remains dependent. If the wing is passively flexed it will remain in this new position. In this way the wing may be moulded into the position normally occupied by it, and it will remain there indefinitely.

The wing may now be drawn down to a dependent position, where it will remain. It has, therefore, the properties of a plastic body, enabling it to retain any position in which it may be placed. In other words, the flexors of the wing exhibit the " shortening and lengthening reactions." These reactions indicate the presence of plastic tone.

It may be inferred, therefore, that contractile tone, which normally tends to impose the typical posture upon the wing, is absent in such a preparation, and is therefore a function of the somatic proprioceptive reflex arc that has been destroyed. Plastic tone, which fixes the length of the muscle fibres to maintain a posture once assumed, is a function of the sympathetic proprioceptive reflex arc that remains intact. Together these components of tone are responsible for posture, so that the combination of the two may be called " postural tone,"

In one fowl in which the posterior roots of the brachial plexus had been severed, the relationship between plastic tone and the sympathetic innervation of the wing musculature was shown by a further experiment. The cervical sympathetic was severed immediately below (or behind) the last cervical nerve, directly after an examination that revealed the presence of plastic tone in the wing. After the operation the plastic tone had disappeared. The wing was heavy and dependent as in flaccid paralysis. It would not remain in any position of flexion in which it was placed. When folded over the back of the bird it dropped heavily to the ground. This experiment proves conclusively that the plastic tone exhibited after the first operation was
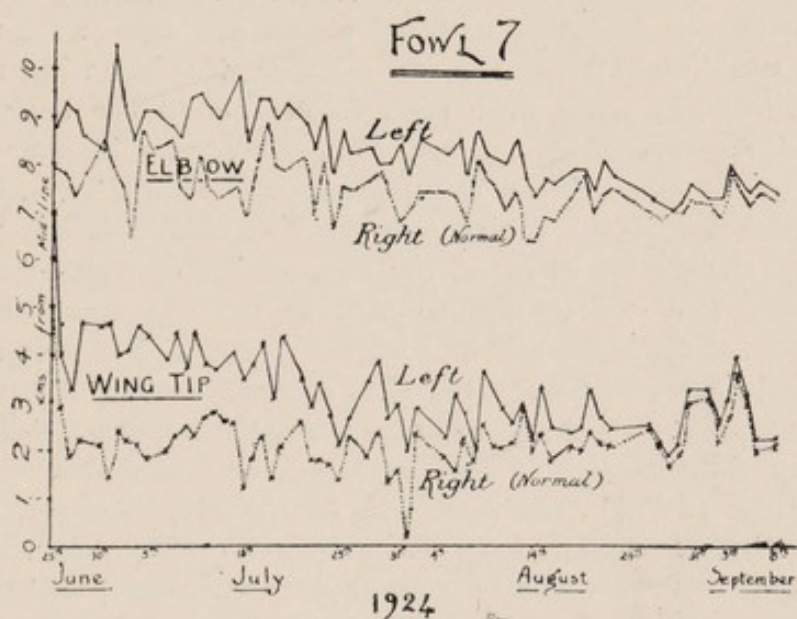
FIG. 8.—One of Mr. R. E. Murray's graphic records to express the compensatory increase in contractile tone in a fowl's wing after sympathetic denervation.

maintained by the sympathetic proprioceptive reflex connexions of the wing musculature. As other experiments have shown, this is at the level of the first thoracic segment in the fowl.

Compensatory Increase in Contractile Tone after Sympathetic Denervation of the Skeletal Muscle of the Wing.

To test the duration of the effect upon the wing of severing the cervical sympathetic trunk caudal to the brachial plexus, the position of the normal and affected wings of some preparations were daily measured. I am indebted to Mr. R. E. Murray, who carried out these daily observations. Fig. 8 is a graphic record of these observations. One observation was made each day on the position

D 2

of the elbow. An average of three readings of the position of the tips of the wings from the median line was recorded daily. Both graphs show the same features. The contractile tone increases in the affected wing until both wings are approximately equidistant from the median line. This condition is gradually attained and the distances become equal in about sixty days. A similar result is found after removal of the afferent limb of the sympathetic proprioceptive reflex arc.

When this compensation has taken place the effect of cutting the cervical sympathetic is manifested under two conditions; when the bird is kept at rest for a period of approximately fifteen minutes or longer, the droop and abduction of the operated side reappear. Fatigue has a similar effect. Starting with the elbows and tips of the two wings equidistant from the median line, the left wing and then the right wing were each folded across the back by passive movement fifty times. The difference in the distance of the elbows from the mid-line was then 2.2 cm. and the difference in the distance of the tips from this line was 2.9 cm., due to the droop of the wing on the operated side.

Plastic tone was therefore still absent. It remains to account for the increase in contractile tone. Magnus and de Kleijn have demonstrated that pathways other than the afferent nerves from the muscles themselves affect the tone of skeletal muscle. These accessory influences are the labyrinths and the proprioceptors of the neck muscles. In the resting conditions both these sources of impulses would no longer be effective, and consequently the contractile tone would be lessened, as in the experiment recorded above. It is noteworthy that Langelaan has shown that in frogs removal of plastic tone from the hind limb leads to domination of the labyrinth of the opposite side. This leads to extension of the normal limb and increased flexion of the limb upon the operated side.

LECTURE III.

THE PRACTICAL APPLICATIONS.

The Inconsistent Results obtained by Other Investigators.

In the second lecture attention was called to the evidence in support of the view that the two kinds of striated muscle fibres perform different functions. Only those innervated by the somatic medullated nerves are actively contractile and under the direct control of the will. The slender fibres innervated by the sympathetic non-medullated nerves are not contractile (although their length is passively altered by the activity of the contractile fibres alongside them): their function is to establish plastic tone, to support and maintain the more active and easily exhausted contractile fibres and relieve them of much of the work that would otherwise induce the rapid onset of fatigue.

When the grey rami of the sympathetic distributed to skeletal muscle are stimulated the muscles supplied show no sign of shortening (Bayliss). But, of course, this is to be expected if the sympathetic innervation is reponsible for plastic tone of skeletal muscle. The result of appropriate stimulation would be to fix the muscle fibres governed by the sympathetic system at their existing length. Obviously, therefore, athetoid movements or intermittent spasms of muscle, which depend upon the process of shortening of muscle fibres, are not dependent upon the sympathetic innervation of the muscle groups affected. No appreciable improvement of these conditions follows sympathetic ramisection, and their presence is, in general, a contra-indication to the performance of the operation. However, if marked improvement or loss of these features takes place, any remaining rigidity, which may be dependent upon the existence of plastic tone, may then be examined with a view to subjecting the patient to operation so as to enable further progress in education to proceed.

During recent years several writers have strenuously denied that any function of the sympathetic innervation of muscles had been demonstrated by experiment. It is hardly necessary, in view of the consistent results obtained by Langelaan and ourselves, to discuss in detail the reasons for the negative or inconsistent results obtained by other investigators. In some cases the negative results are due to imperfect denervation; in others to the fact that the observers were looking for an effect upon contractility, which, of course, they did not find. Our observations have been confirmed in the case of the dog by Foix, an investigator who was clearly free from any bias in favour of the results that he obtained, apparently unexpectedly.

Moreover, there is the very positive evidence obtained by Orbeli and his collaborators, which was summarized in the BRITISH MEDICAL JOURNAL (September 20th, 1924, p. 534). Orbeli stated in 1923* that the direct influence of the sympathetic nerves on skeletal muscle is fixed beyond doubt; the ability of the autonomic fibres to alter the condition and constitution of muscle becomes transferred from a small organ, the heart, to the whole skeletal muscle, thus fulfilling the prophecy of the " chemical tonus " of Pflüger and the " trophic innervation " of Pavlov. The sympathetic system, which controls all the vital properties of muscles and secures for them the greatest use of their reserve strength, must also affect their tone and metabolism. In 1922 Orbeli's collaborator Ginetsinsky found that stimulation of the sympathetic while fatigue was beginning to develop or had developed (as the result of stimulating the motor nerve) gradually restored the function of the fatigued and contracted muscle. The effect begins after a long period of latency, increases gradually, and reaches a maximum soon after the cessation of the stimulation of the sympathetic. Moreover, it lasts a long time.

These results are complementary to and consistent with those obtained in our experiments, and by others, as to the effects of adrenaline on fatigued muscle. The only criticism I would suggest of the work done in the Leningrad Medical Institute is that attention has been concentrated too exclusively on the phenomena of fatigue; and no adequate recognition has been given of the fact that the supporting and fatigue-sparing function of the sympathetically innervated muscle fibres is constantly being performed in every action of any muscle.

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* [As the result of a conversation with Professor Orbeli last November I have made certain verbal modifications of his expressions as translated by Dr. Horsley Gantt in the BRITISH MEDICAL JOURNAL.—G. E. S.]

I want now to consider two factors that have been responsible for much of the discrepancy in the results obtained by various experimenters.

Avoidance of the Effects of Asphyxia and of Anaemia of the Brain Stem.

It is clear from the argument of the second lecture that the results of loss of plastic tone would be more difficult to observe if any condition existed that would unduly increase the degree of contractile tone. As Dr. Royle has pointed out, asphyxia of the animal would produce this effect. To avoid this complication he employed intratracheal anaesthesia and then oxygenated the animal freely as soon as decerebration was performed. If asphyxia tended to develop later—for example, when the tube in the trachea was too small—the rigidity of all four limbs in extension would become extremely marked, and differences in the tone of the hind limbs due to the loss of plastic tone on one side would be completely obscured. Removal of the cause of asphyxia would invariably remove the tendency for the display of such an exaggerated degree of contractile tone. In several recent papers Walshe has argued that minimal degrees of oxygen in like manner may lead to hyperexcitability of reflex arcs. Evidence is accumulating that this factor may account for " irritative " symptoms following central nervous lesions, as Royle and I have shown. But the effects of asphyxia and anaemia that are manifested as reflex hyperexcitability are foreign to the condition of tone exhibited in decerebrate rigidity. Like the state of spastic paralysis, this condition is to be regarded as being due to a release of function in the nervous system, following the removal of higher levels of nervous activity. The term " release " is employed in the sense advocated by Hughlings Jackson, and developed in the present century by the work of Head and his collaborators. It appears to me that Sherrington's method of decerebration, which should be done in the goat by section of the mid-brain under direct vision, is preferable, for the purpose of observing the presence or absence of plastic tone, to the method of decerebration by anaemia induced by tying the carotid and basilar arteries, which has been introduced by Pollock and Davis. While a preparation made by the method of these Chicago neurologists is unquestionably useful for observing the reflex activities of such an animal, it gives misleading results so far as tone is concerned. It is impossible to be certain in how great an area of the brain stem the cell

stations are rendered hyperexcitable by a degree of anaemia that is insufficient to abolish function altogether.

The Choice of Laboratory Animal.

The animal selected for our experiments, in the first instance, was the rabbit. Dr. Royle procured an excellent result in the diminution in tone of the hind limb of a spinal rabbit on the side from which the lumbar sympathetic trunk had been removed. This effect was not reproduced in subsequent experiments; and the failure was attributed to the difficulty in this animal of completely excising the sympathetic trunk on the selected side without injury or removal of the trunk of the opposite side. Therefore the goat was used for all our subsequent mammalian experiments. In the second lecture I have already explained why the goat is peculiarly adapted for this type of experiment. In contrast to the goat a carnivorous animal such as the cat shows a capacity for great and numerous variations in the degree of postural tone. The cat does not take up the extensor posture when placed in the supine position. Variation in the degree of contraction in its four limbs imposes varied attitudes upon it; and no doubt in the well oxygenated decerebrate cat the variations in the degree of rigidity of the limbs are to be accounted for in a like manner. Such variations in the degree and selective activity of contractile tone possibly render the effects of loss of plastic tone less apparent than would otherwise be the case and render an analysis of the exact defect in tone more difficult at the outset. For it must be borne in mind, in this connexion, that in the experiments recorded in the literature, practically all of which were performed on cats, differences were found in the degree of tone upon the two sides following unilateral sympathectomy, which was performed in some cases before, and in others after, decerebration. For instance, Dusser de Barenne observed a diminution in tone in five cases out of nine, after removal of the lumbar sympathetic chain. Uyeno found differences in the tone of the fore limb after removal of the ganglion stellatum on one side, but attributed the diminution in tone to sensory inhibition due to the wound on this side; but in Royle's experiments this explanation is not admissible. Consequently the problem presenting itself is not to explain negative results, but the inconsistency of the effects. I believe that the factors to which attention has been called in the foregoing discussion explain the failures encountered. This is especially the case when in the past investigators have been seeking to observe quantitative diminution of

tone. I have attempted to show that contractile tone is well displayed after sympathetic denervation, and under certain experimental conditions may be present in an enormously exaggerated degree. It is only when qualitative changes due to the selective removal of plastic tone are looked for that the interpretation of effects in any such instance becomes clear.

The thesis maintained in these lectures (that plastic tone is a property of the sympathetically innervated fibres of skeletal muscle) no longer rests solely upon the evidence provided by experimental decerebrate rigidity. For the same effect as that which follows sympathetic denervation in the decerebrate animal is produced by sympathetic rami-section in human patients in those conditions of spastic paralysis which exhibit all the essential qualities of decere-brate rigidity. The excessive plastic tone characterizing these conditions is removed by the operation of ramisection. The evidence that may be obtained by studying the character of the knee-jerk is of special interest. For in both decerebrate rigidity and in the types of spastic paralysis to which reference has been made, the execution of the knee-jerks, slow before the operation, became brisk in character. This is due to the rapid rate of relaxation of the extensor muscle after completion of the jerk con-traction, which replaces the former tendency of the muscle to remain shortened ("shortening reaction") when con-traction ceases.

THE CONTROL OF TONE BY THE BRAIN.
THE SELECTION OF PATIENTS FOR RAMISECTION.

I shall now consider the reflex arcs concerned in main-taining the two elements of tone, and the scientific prin-ciples for the selection of patients for ramisection.

Plastic tone is enhanced in degree in the decerebrate animal. It may appear as a component of postural con-traction immediately after the mid-brain is cut across, so that, normally, prespinal pathways are employed by the impulses maintaining it. When decerebration is performed, plastic tone is increased in degree as a result of the release of this prespinal sympathetic reflex arc from higher levels of control. In addition to this, contractile tone is enhanced in value because of the release of a somatic prespinal reflex arc. In animals recently decerebrated this increase of contractile tone selects the antigravity muscles, and their antagonists are reflexly inhibited. The increase in plastic tone rigidly maintains the extended posture, which is endowed by contractile tone upon all four limbs of the

quadruped, and maintains the condition of " reflex stand-ing " for long periods of time. When the relaxation from the posture of extension occurs, plastic tone still remains, as is proved by the presence of " lengthening and shortening reactions."

The prespinal reflex arcs subserve the two components of tone of the normal skeletal muscle, and overactivity of
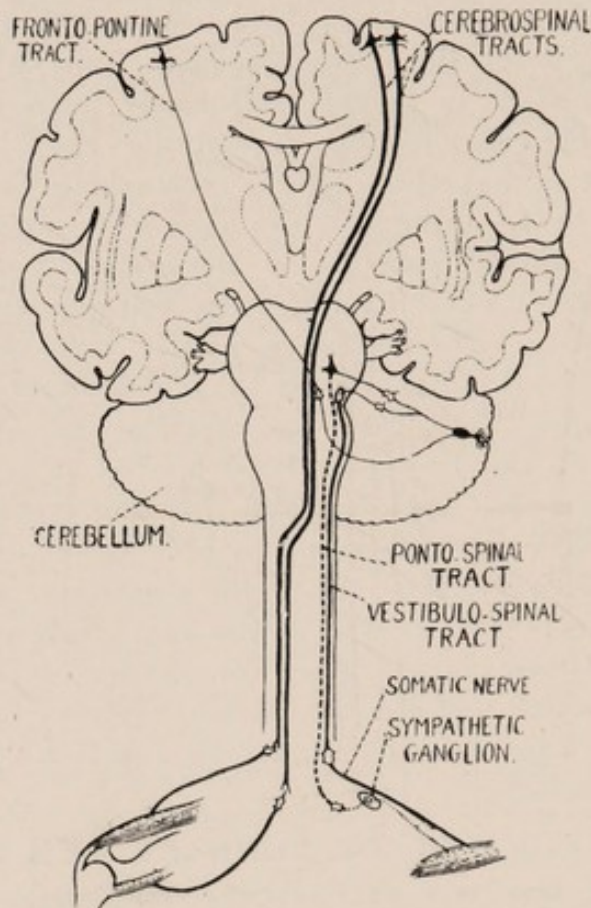

Fig. 9.—Diagram to indicate the part played by the vestibulo spinal tract (arising from Deiters's nucleus) and the ponto-spinal tract (arising from the reticular nucleus of the pons) in the two reflex arcs concerned respectively with contractile and plastic tone.

these arcs accounts for the phenomena exhibited by the muscle in decerebrate rigidity. It was shown by Sherrington that cutting across the medulla oblongata led to flaccid paralysis of the limbs. More precisely, as Magnus has shown, the limits within which section of the brain stem produces decerebrate rigidity are as follows: The cranial limit is a plane passing dorsally at the level of the caudal limit of the superior colliculus and ventrally in the region immediately caudal to the mammillary bodies. The decere-brate rigidity persists until the level of entrance of the eighth nerve is passed. Obviously, therefore, the nuclei that constitute the cell stations of the prespinal reflexes respon-sible for decerebrate rigidity lie within these limits.

The work of Thiele in 1905, which is supported by the recent results of Bazett and Penfield, indicates that the integrity of the lateral vestibular nucleus of Deiters is essential for the development of decerebrate rigidity. It may be concluded that this nucleus takes part in the completion of one of the reflex arcs, the hyperactivity of which is responsible for decerebrate rigidity. The vestibulo-spinal
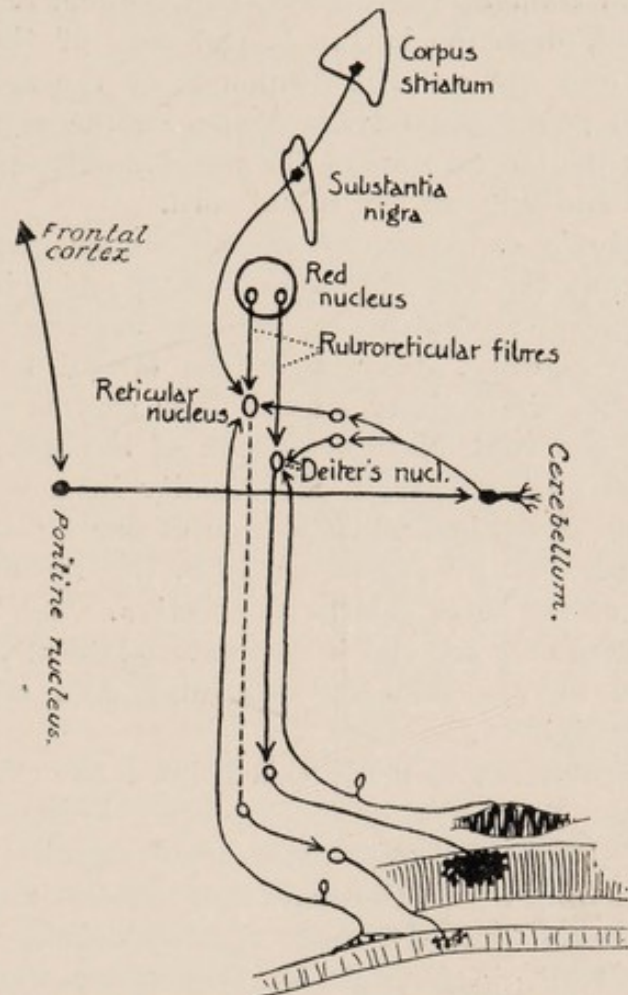

Fig. 10.—Diagram to represent in an entirely tentative way the influence of the cerebral cortex (acting via the cerebellum), corpus striatum, substantia nigra, and red nucleus upon the activity of Deiters's and the reticular nuclei. Only those tracts which are mentioned in the text have been represented. The relays in the ascending spinal tracts have not been indicated.

tract (Fig. 9), which lies in the region of the emerging motor root fibres of the spinal cord mainly on the same side as the nucleus from which it originates, constitutes the descending limb of the reflex arc.

The nucleus of Deiters is a special afferent somatic nucleus, and the reflex arc in which it is incorporated constitutes, therefore, the somatic prespinal reflex pathway. It subserves contractile tone, which has a selective incidence upon antigravity muscles maintaining the body erect.

The question arises whether the nerve cells incorporated in the sympathetic prespinal reflex arc can also be identified. The levels between which section of the brain stem produces decerebrate rigidity suggest that the formatio reticularis of the pons supplies the cell station of this arc. The reticulo-spinal tracts of the pons are anatomically of special importance. Collier and Buzzard have termed them the ponto-spinal tracts. The anterior ponto-spinal tract, which is uncrossed, descends in the lateral zone of the medulla oblongata and the anterior funiculus of the spinal cord. The lateral ponto-spinal tract crosses to the opposite side and lies in the lateral zone of the medulla oblongata and in the lateral funiculus of the spinal cord.

Sherrington's experimental results are compatible with the view that the vestibulo-spinal and ponto-spinal tracts convey impulses to the spinal cord that are responsible for decerebrate rigidity. Section of the lateral half of the bulb abolishes the rigidity on the same side as the lesion. Section of one ventro-lateral column of the spinal cord in the cervical region destroys the rigidity in fore and hind limbs of the same side, while section of one lateral column in the upper lumbar region abolishes the rigidity in the hind limb of the same side as the section. The ascending limbs of these arcs are also in the antero-lateral funiculus: for section of the posterior funiculus does not abolish decerebrate rigidity.

In an experiment to study this point I have found that plastic tone does not disappear after removal of the nucleus of Deiters. First, decerebrate rigidity was produced by cutting across the mid-brain between the superior and inferior colliculi. Extensor rigidity developed rapidly and well. Now, in a phase of relaxation, when plastic tone was well shown in the right hind limb, I isolated the region of the lateral angle of the fourth ventricle on the right side by a crescentic incision, removing Deiters's nucleus and severing the vestibulo-spinal tract by this procedure. But the " lengthening and shortening re-actions " were still exhibited. A second section at the junction of the pons and medulla was then made. The limbs became flaccid immediately. The " lengthening and shortening reactions " were no longer to be elicited. Obviously plastic tone depends upon a reflex arc that attains a level between the mesencephalon cranially and the medulla oblongata caudally. This is compatible with the view that the ponto-spinal tracts subserve the function of plastic tone.

It is possible for an incomplete lesion of the spinal cord to affect the pyramidal and concomitant descending tracts, so releasing the primary spinal arc from control, without affecting in any considerable measure the vestibulo-spinal and ponto-spinal tracts. Riddoch and Buzzard have recently described cases of quadriplegia from high cervical lesions of the spinal cord, in which the distinctive qualities of decerebrate rigidity were reproduced. Riddoch reports that *post-mortem* examination of one of these patients revealed a tumour in the region of the posterior and lateral columns of the fourth and fifth cervical segments of the spinal cord. The ventral portion of the cord was relatively little affected.

It is clearly to be borne in mind that the extensor posture is a relatively unimportant character in establishing an analogy between the condition of spastic paralysis in man and decerebrate rigidity experimentally produced. The posture assumed is due to the selective incidence of contractile tone upon the skeletal musculature. Riddoch and Buzzard recorded that, in their patients, the position of flexion was sometimes encountered. On these occasions the flexors were more spastic than the extensors. This condition could sometimes be induced by holding the limbs in the flexed position for a short time. Further, McAlpine reported a case in which rigidity was not confined to extensor muscles, and flexor rigidity of the knee-joint was sometimes obtained.

Graham Brown has demonstrated beyond all doubt that plastic flexor tone may be exhibited in the limbs of the monkey. These observations are of added significance in the light of Bazett and Penfield's work on chronic decerebrate rigidity. These authors describe two kinds of decerebrate rigidity—extensor and flexor. Their observations prove that the somatic reflex arcs producing contractile tone may selectively act upon either the extensor or flexor muscles. In extensor rigidity the reflex, of which the vestibulo-spinal tract is the descending limb, is involved. In flexor decerebrate rigidity the primary spinal reflex is, no doubt, responsible for the activity, for severe injury to the spinal medulla produces paraplegia in flexion. In both types of decerebrate rigidity plastic tone, which is enhanced in degree, and coexists with contractile tone, is maintained by the sympathetic prespinal reflex arc. In each case it is inhibited in the antagonists of the muscles exhibiting the rigidity.

Inhibition in the antagonists is not so complete in man as it is in the condition of acute decerebrate rigidity in animals. Dr. Royle has called attention to this point. Riddoch mentions the fact that though the antagonistic muscles are relatively relaxed " they are certainly in stronger contraction than the corresponding muscles of a healthy individual."

I believe the explanation of this is that in an animal that has recently been decerebrated the extensor reflex arcs, chiefly through the nucleus of Deiters, immediately manifest increased activity. The isolated flexor spinal arcs regain activity only after a period of inactivity. When this occurs the selective action of contractile tone on the extensors is not so complete, for the spinal arc endows this aspect of tone upon the flexors also. Reflex inhibition is now not complete. Bazett and Penfield's experiences with the chronic decerebrate animal support this view. Moreover, in patients suffering from spastic paralysis, plastic tone is not inhibited in antagonistic muscle groups; which accounts, in some measure, for resistance to active, reflex, or passive movement of the limb.

I have commented on the work of Bazett and Penfield to emphasize the fact that the posture of the patient is not the all-important criterion of rigidity. Even the flexed position may be due to a combination of both contractile and plastic tone which together cause rigidity in the sense in which this term is employed in this lecture. Conversely, the extensor position may be wholly due to contractile tone. Sympathetic ramisection in such a case would be of no avail. Extensor fits usually fall into this category. This is beautifully illustrated in a case recently reported by Walshe, in which two stages of the illness were observed. In the first stage the patient exhibited a condition of decerebrate rigidity. The limbs were extremely " plastic " and tended to remain for a considerable time in any position passively imposed upon them. The lower extremities were extended and adducted and the feet plantar-flexed. As is usual in man the upper extremities were semiflexed at the elbows, with the forearms pronated and the wrists and digits flexed. This attitude often replaces that of extension of the fore limbs of quadrupeds because the upper extremities are no longer " simple locomotor props." Passive movement revealed the presence of the " clasp-knife " character of the spasticity. The tendon-jerks exhibited tonic prolongation, and in some instances in response to repeated taps " step-ladder "

shortening of the muscle was observed. In recording these features, Walshe established beyond doubt the identity of this condition with decerebrate rigidity experimentally produced.

In the second phase of the illness this condition was replaced by the progressive failure of reflex activity and deepening coma. In this stage tonic fits appeared as a concomitant of cardiac and respiratory irregularities. In these fits the respiratory muscles were fixed and the limbs became so rigid in their customary posture that no tendon reflexes could be elicited. In severe fits of this kind the head retracted forcibly. At this stage none of the essential qualities of decerebrate rigidity, enumerated as characterizing the first phase of the illness, were exhibited, for plastic tone was not apparently enhanced in degree. The second phase was in all probability due to hyperexcitability of the somatic reflex pathways due to asphyxia or anaemia (cf. Walshe, Stewart and Pike, Warner and Olmsted, Hunter and Royle). The fits are not comparable to decerebrate rigidity in which the enhanced tone is due to release in function of two prespinal reflex arcs—somatic and sympathetic. Yet the posture displayed in each condition is the same. Taking into account the results of tests for the presence of plastic tone in addition to posture Walshe and Riddoch have been able to establish the essential identity of decerebrate rigidity and the condition of spastic paralysis, such as that which occurs in hemiplegia, quadriplegia, and the extended form of spastic paraplegia.

The only patients who can be expected to benefit from the operation of ramisection are those whose voluntary control of their muscles is intact, but whose movement is hampered by excessive plastic tone. By cutting the sympathetic nerves plastic tone is eliminated and the limbs freed from the spasticity. *The presence of " lengthening and shortening reactions " is an indication for the operation of sympathetic ramisection for the relief of spastic paraplegia. Slowness in execution of the tendon reflexes is an important indication for the operation.*

Conversely, rapidly executed reflex movements usually constitute a definite contraindication. The greater number of spinal injuries are accompanied by this type of reflex and plastic tone is at a minimum. This is due to the fact that a prespinal reflex is essential in higher forms for the maintenance of this property of muscle, and usually, though not always, as will be proved subsequently,

this reflex is rendered inactive when the spinal cord is injured.

HIGHER LEVELS OF THE BRAIN CONTROLLING THE TONIC REFLEX ARCS.

Magnus has shown that in animals, such as the rabbit, cat, dog, and monkey, the whole of the cerebral hemispheres, including the corpora striata, may be removed and the tone of skeletal muscle remain of normal intensity. Nor is the tone altered when the brain stem is cut across behind the thalamus. Such a " mid-brain " animal, unlike the decerebrate preparation, is capable of a great variety of reflex activities—as walking, running, and jumping. It can right itself if overturned, the head at once resuming its normal posture. These are the " postural reflexes " of Magnus. Obviously, therefore, in these animals, the mid-brain provides an important part of the nervous mechanism utilized in the regulation of posture. It is when this region is taken away that release of the prespinal reflex arcs takes place to produce decerebrate rigidity. For instance, in higher forms, at least, as Magnus's observations upon the monkey reveal, the connexions of the visual pathway with the mid-brain play an important part in the nervous regulation of posture. Tecto-bulbar connexions therefore control the prespinal reflex arcs in these forms. Moreover, decerebrate rigidity develops after the removal of the red nuclei, and, as Walshe mentions, " it seems as though removal of the greater part of the red nucleus is an essential preliminary to the development of rigidity." In this process rubro-reticular fibres, which in man have attained special importance, are severed. The cells of the substantia nigra are also known to send axones to the tegmental region of the brain stem.

In view of prevailing conceptions it is noteworthy that in the animals described by Magnus the postural reactions are carried out by the mid-brain in the absence of the corpus striatum. It would, however, be unwise to argue that in man the mid-brain structures exhibit this independence of the corpus striatum, for the principle of the shifting forward of function in the nervous system must not be lost to sight in this connexion. Moreover, it may well be that the physiological value of the corpus striatum is only adequately expressed in the presence of voluntary activity. In such a case the symptomatology of lesions of the corpus striatum, with the cerebral cortex intact, will be different from the experimental results of

complete removal of both the cerebral cortex and corpus striatum.

For these reasons the observations of Magnus that " thalamus " and " mid-brain animals " exhibit tone of normal intensity and distribution cannot unreservedly be applied to man. It is possible that the corpus striatum in man, with the cortex intact, controls through the intermediation of subpallidal nuclei, as the substantia nigra, the sympathetic prespinal arc subserving plastic tone. To study this point I have removed the corpus striatum on one side in birds, employing the domestic fowl and the sea-gull for this purpose. Birds represent a group widely divergent from mammals. In birds the corpus striatum has attained a relatively enormous importance, both structurally and functionally, and in certain respects its influence may present a closer analogy to that of man than is the case in most mammals. The operation is easily performed on birds because the corpus striatum constitutes, except for the septum and a small superficial area of cortex, the entire cerebral hemisphere. Further, in removing the corpus striatum, which is readily accessible because it forms the greater part of the surface of the hemisphere, the cerebral cortex may be lifted up and left in communication with the septum. In this way the tractus cortico-septo-mesencephalicus is left intact.

This operation produces rigidity of all the limbs. Standing is not evenly maintained owing to rigidity of the hind limbs. On this account in sea-gulls a tendency to rise on the toes is constantly exhibited and the bird does not maintain any given position for long. Birds in this condition often squat down, presumably to avoid balancing on the rigid limbs. The wings are also rigid, and here the nature of the rigidity may readily be studied. The wings are sometimes maintained in a position somewhat higher than usual, so that the adjacent borders are almost in contact with one another. The rigidity maintains its intensity during passive movement, and on account of its rigidity the wing remains fixed in the new position assumed. This occurs even though the position be so abnormal, as when the wing is folded over the mid-line of the back, that the fibrous structures contained within are put upon the stretch. Dependent positions are maintained equally well. Both wings exhibit this phenomenon after the unilateral operation, but the rigidity is greater on the same side as the injury. The rigidity is responsible for slowness of movement, especially on the same side. This is readily seen on

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watching the movements of the wing during attempted flight while the bird is held captive in the hand. A greater effort is necessary to carry the wing through a smaller range of upward movement than on the less affected side; increased effort marks downward movement also, and the wing seems to overshoot the position at which it normally ends. These alterations in the nature of the movement of the wings are greater on the side of the injury, so that the flight of such a bird, when released, is always in a circle, the bird tending to fly toward the more affected side.

This diffuse muscular rigidity is strongly reminiscent in an exaggerated form of the condition of the wing already described, in which, after the removal of contractile tone, plastic tone is accessible for independent study. I cannot avoid the deduction that increased plastic tone in both flexor and extensor muscles of the wing is responsible for the diffuse muscular rigidity which follows the removal of the corpus striatum in birds. This element of tone is so enormously increased that manifestations of the presence of the contractile component are in the background.

The condition of rigidity of the wing of birds above described is remarkably similar to Parkinsonian rigidity in man. Its diffuseness, resistance to stretching, and the tendency for fixation of the muscle at any length passively imposed upon it, are common to the two conditions; and in both conditions poverty and slowness of voluntary movement, which are probably due in part to the underlying phenomenon of rigidity, are notable concomitants.

Removal of the influence of the sympathetic innervation by section of the cervical sympathetic trunk caudal to the brachial plexus abolishes the rigidity of the wing. This property, like normal plastic tone, is subserved therefore by the sympathetic system. It is difficult to escape the conclusion that the basis of the rigidity following lesions of the corpus striatum is increased plastic tone, which is exhibited in all muscle groups, and that this is due to removal of control from the sympathetic prespinal reflex arc which maintains the plastic tone of normal skeletal muscle.

The different manifestations of excess of plastic tone in those cases of spastic paralysis which resemble experimental decerebrate rigidity, and in the condition of Parkinsonian rigidity, are capable of reconciliation. The fundamental difference between the two conditions is that, while plastic tone is increased in both, an excess of contractile tone is also exhibited in spastic paralysis, while it

is not greatly in evidence in Parkinsonian rigidity. Contractile tone is selective in its incidence, and the plastic tone of the antagonists of the muscles selected by it is, to a very varying degree, reciprocally inhibited. In Parkinsonian rigidity this selective incidence upon muscles, and consequently the selective inhibition of plastic tone in the antagonists, are absent. In spastic paralysis resistance to passive movement is considerable till the position imposed upon the limb by contractile tone is overcome, when the resistance becomes less. A combination of contractile and plastic tone is responsible for the initial position in spastic paralysis. The posture assumed in Parkinsonian rigidity is due to plastic tone only exhibited in agonists and antagonists, and therefore resistance to passive movement is the same throughout the whole range of movement. The fact that postural reactions and intercurrent reflex movements are not exhibited in Parkinsonian rigidity as in spastic paralysis is a further indication that somatic activities, which include contractile tone, are in abeyance in this condition. The mechanism which inhibits plastic tone in order that a movement may be performed or to allow a new posture to be assumed is no longer active. This effect is probably the cause and not the result of the rigidity—that is to say, a predominant function of the corpus striatum is to regulate plastic tone. From a consideration of the other effects of corpus striatum lesions it seems that this regulation is especially in the interests of automatic and associated movements, and of emotional expression. These functions are no doubt impaired by the lesion; the rigidity itself may limit these activities still further.

It remains to be proved that the rigidity of paralysis agitans and allied conditions is subserved by a proprioceptive mechanism in order to establish completely the identity of the tendency in this condition to fixation of the muscle at any length imposed upon it, with the " lengthening and shortening reactions."

In the first place it must be borne in mind that the sympathetic reflex arc subserving plastic tone is not necessarily at the same level as the somatic connexions. Therefore, in posterior root section, contractile tone may be affected without removing plastic tone.

Surgical operations upon the posterior nerve roots have necessarily been less complete than is possible under experimental conditions.

Leriche's cases, in which posterior root section was performed for the relief of paralysis agitans, are evidence of

this. In one case the fifth, sixth, and eighth cervical posterior nerve roots were divided. In this case the rigidity was undiminished. Obviously, however. the sympathetic afferent connexions of the skeletal muscle of the limb were left intact by this operation because the posterior root of the first thoracic nerve was not attacked. Therefore this case does not disprove that rigidity is maintained by a proprioceptive mechanism. The first principle of posterior root section in man should be to include the posterior root of the first thoracic nerve in the case of the upper limbs, and of the first or second lumbar nerve in the operation for the lower extremities.

However, Walshe has recently brought forward strong evidence that the rigidity of paralysis agitans is due to the activity of a proprioceptive reflex mechanism. He has shown that injection of 1 per cent. novocain into the muscle at its motor point causes rigidity to disappear. While admitting the possibility that this effect may be due to direct action upon the muscle, he shows convincingly that the balance of evidence is in favour of the view that the afferent nerve terminations are affected.

Walshe's investigations upon the rigidity of paralysis agitans beautifully illustrate the fact that the tremor exhibited in this condition and the rigidity are subserved by two different nervous mechanisms. For although novocain abolishes rigidity the tremor is totally unaffected. The indications are that impulses through the cerebro-spinal tracts are involved in the production of spontaneous tremor, for it disappears after hemiplegia. This is in accord with the results of sympathetic ramisection in this condition. The rigidity is markedly diminished, voluntary power is increased, and movements are more ample and rapid, but the tremor is not appreciably affected when well established. But a patient with Parkinsonian rigidity without tremor, as for instance as a sequela of encephalitis lethargica, may derive sufficient benefit to justify the operation.

In a recent paper McAlpine has described a patient who, as a sequela of epidemic encephalitis, developed Parkinsonian rigidity on the right side and a condition strongly resembling decerebrate rigidity on the left side. According to views advanced here, the diffuse muscular rigidity on one side was due to a generalized increase of plastic tone, lack of selective incidence being due to the absence of increase in contractile tone. The rigidity on the other side, however, was sometimes flexor and sometimes

extensor. Therefore contractile tone was present and acted
selectively on different groups of muscle at different times.
Plastic tone was also enhanced in the upper and lower
limbs of this side. It was exhibited by the presence of the
" lengthening and shortening reactions." It was shown
to the greater extent in the flexor and extensor muscles
at any particular time according to the selective incidence
of the contractile tone at the time. In the erect posture
tone predominated in the extensor muscles of these limbs.
Since the tone responsible for this decerebrate attitude
consists of the two normal components of tone, the term
" plastic tone " alone is clearly inadequate to describe the
condition. Sherrington's term " postural tone " may be
used for this purpose. Contractile tone reflexly imposes the
position upon the body and plastic tone maintains this
position once it is assumed. On passive movement the
characteristic " lengthening and shortening reactions "
indicating the presence of plastic tone are elicited.

In a natural attitude such as standing contractile tone
is responsible for selective action upon the antigravity
muscles and plastic tone fixes the length of the muscle
fibres necessary to maintain this position. To accomplish
voluntary movement from this position the prespinal reflex
arcs responsible for postural tone must be controlled by
the cerebral cortex. Evidence is accumulating that the
cerebral cortex not only causes contraction of the appro-
priate muscle groups by way of the cerebro-spinal tracts,
but inhibits the reflexes responsible for postural contrac-
tion. It effects this purpose through the intermediation
of the cerebellum (Figs. 9 and 10).

An inhibitory pathway leads from the cerebral cortex
to the anterior part of the superior vermis of the cere-
bellum through the medial part of the crus cerebri and the
pontine fibres. Stimulation of the crus in a decerebrate
cat leads to complete rigidity in the limbs of the same
side and diminution of rigidity in those of the other side.
Warner and Olmsted have traced the origin of this in-
hibitory tract to the frontal region of the cerebral cortex.
When the motor area was cut away no increase of extensor
tone was observed on either side of the body. Definite
rigidity developed at once in the opposite fore and hind
limbs when the frontal area was removed. This observation
is of great significance in view of the fact that, in man, pure
cortical lesions of the pyramidal tracts do not produce
spasticity. On the other hand, lesions of the area of the
frontal lobe from which the fronto-pontine tracts originate

(Campbell) are associated with a condition of " tonic innervation " expressed as inability to relax a contracted muscle group.

Warner and Olmsted have elucidated the course of this tract arising in the frontal region by studying the inhibition of rigidity obtained by electrical stimulation of the cut surface of the brain in various situations. They found that the inhibitory effect of the tract is bilateral, but predominantly on the crossed side. The tract passes from the frontal lobe through the medial part of the internal capsule. Below the level of the superior colliculi it crosses, in greater part at least, to the other side of the brain stem. It continues to the cerebellum by way of the middle cerebellar peduncle. The inhibitory tract is therefore fronto-ponto-cerebellar in its connexions. (See Figs. 9 and 10.)

Warner and Olmsted state that when this tract is stimulated a limb exhibiting extensor rigidity goes " limp and flaccid." Miller and Banting describe the effect of stimulation of the anterior surface of the cerebellar vermis as being " immediate and general relaxation of the rigidity." Obviously the inhibition affects both contractile and plastic components of tone which are enhanced in degree to produce decerebrate rigidity. The fronto-ponto-cerebellar tract, therefore, inhibits the effect produced by the somatic vestibulo-spinal and sympathetic ponto-spinal tracts. When this tract is ineffective the power to relax the muscles after being employed in muscular effort is defective. In the absence of a case purely of this nature in Dr. Royle's series it is interesting to note that the effect of sympathetic ramisection improves the power of relaxation of contracted muscles in spastic paralysis. It is to this fact that the increased control and rapidity of effecting voluntary movement are due. The patient need no longer inhibit plastic tone. His cortical control is mainly concentrated on executing movement.

It is worthy of note that tumours of the middle lobe of the cerebellum give rise to fits of a tonic character in which the extensor attitude of decerebrate rigidity is assumed (cf. Hughlings Jackson). Sherrington found that a rigidity somewhat similar to that ensuing on removal of the cerebral hemisphere set in after median section or ablation of the cerebellum. He was not convinced that the two conditions were identical. Thiele, however, regarded the bilateral rigidity which followed removal or bisection of the vermis as being like decerebrate rigidity. He explained it as being

due to loss of the inhibitory control of the vermis over the nucleus of Deiters. No doubt also the ponto-spinal tracts are released from control. It will readily be seen that the only effect of sympathetic ramisection upon tonic extensor fits following interference with the fronto-ponto-cerebellar pathway is to diminish the degree of rigidity during the extensor spasms. Since contractile tone remains practically unaffected after this operation the extensor attitude will still be assumed. This is another instance of posture alone not being an indication for ramisection.

The fact that the cerebral cortex employs the cerebellum as an intermediate organ through which it exerts an inhibitory influence over the postural reflex arcs of the brain stem is of great general significance. It confirms the suggestion of Walshe that " the cerebellum is the organ through which the cerebral motor cortex influences postural activities and regulates posture in the interests of co-ordinated purposive movement." " It may be," he proceeds, " the subordinate mechanism employed by the cerebral cortex in the refined correlation of posture and movement." This view indicates that the cerebellum is employed by the cortex in the performance of active movements also. It reinforces postural tone in order to maintain the attitude of the body assumed during the performance of the movement initiated and executed by motor impulses which have their origin in the cerebral cortex.

In 1900, discussing the significance of the cerebro-cerebellar pathway which passes through the brachium pontis, Sherrington said: " Thus one and the same cerebral discharge may perhaps pour upon the motor root nerve cells a combination of cerebral and cerebellar impulses." It is on account of the influence of the cerebral cortex in the regulation of posture through the intermediation of the cerebellum that lesions of the cerebellar hemisphere cause inco-ordination of voluntary movements.

When a voluntary movement is completed cortical impulses reinforce contractile tone to determine the attitude assumed by the body. Plastic tone aids in maintaining this position because the muscle fibres exhibiting it are fixed at their new length. After sympathetic ramisection this accessory contribution is lost, but the influence of the cerebral cortex on contractile tone remains. In this connexion it is well known that tone is increased by attention. Dr. Royle has noticed that during the first period of re-education after sympathetic ramisection when the patient's attention is focused on the performance of a

voluntary movement, under orders, the cortex greatly increases the amount of contractile tone exhibited in the limb. This increases the difficulty of the patient in performing the movement. On this account gently executed movements are far more effective than considerable effort in this stage of the re-education process.

Evidence is not wanting that plastic tone is of use also during the performance of voluntary movement. In ordinary circumstances a patient who has been subjected to the operation of sympathetic ramisection cannot detect any disability in consequence of the loss of the sympathetic nerve supply of his voluntary muscles. However, to test this matter closely I have observed the effect of sympathetic denervation after the exercise involved in the flight of a bird. During the flight of a sea-gull in which the unilateral operation has been performed, no obvious difference is to be detected in the movement of the two wings. After completing a flight of one hundred metres, however, the position of the wing on the operated side is in marked contrast to that on the normal side (see second lecture). It is drooped and abducted to a remarkable degree, although hardly any deviation from the normal position may have been visible prior to undertaking the flight. The explanation of this observation seems to be that plastic tone enables the fixing muscle fibres to follow up the contraction of the active fibres and assist in maintaining the intermediate positions assumed at all stages of the movement. When plastic tone is removed, voluntary effort is increased in order to maintain these intermediate positions against the action of gravity as well as to perform the movement.

It appears, therefore, that in voluntary movement postural tone, made up of a contractile and a plastic component, is first inhibited; the "movement" muscle fibres then contract and are assisted in maintaining the advantage gained by the plastic tone of neighbouring " fixing " fibres which are passively shortened; and finally cortical impulses determine that contractile tone is exhibited in the muscles whose contraction is necessary to confer the required position upon the body; the length of the muscle when this position is attained is maintained by plastic tone exhibited by " fixing " muscle fibres.

In certain cases of spastic paralysis plastic tone is in excess. This interferes with voluntary activity, because it is imperfectly inhibited at the outset of voluntary effort. When excessive voluntary effort initiates movement the exaggerated degree of plastic tone, which is present in both

agonists and antagonists, as Dr. Royle has shown, tends to provide resistance to the execution of the movement by fixing, to an abnormal degree, the length of the muscles of the limb at all the intermediate positions through which the moving part passes. In this way the effects of diminished voluntary power are enhanced in degree on account of excess of plastic tone, which is no longer adequately controlled by the cerebral cortex. In fact this defective control is not infrequently the greater disability, and on account of it the voluntary motor pathway may be unable to function to the full extent of which it is capable. This desideratum is attained by removing the plastic tone entirely, when the rigidity of the muscles disappears. The result is that the initiation and the execution of voluntary movement are both improved.

Dr. Royle found that one patient, with a gunshot wound of the cerebral cortex, who illustrated the presence of excess of plastic tone to a striking degree before the operation, was able to inhibit the tone of the extensor muscles of the knee following ramisection. He was unable to flex the knee voluntarily, but he could inhibit the tone of the muscles sufficiently to let the leg fall into the flexed position. This was impossible prior to the operation. In other words, this patient was unable to inhibit plastic tone. After ramisection he was able to inhibit the contractile component of tone which alone remained. This patient illustrates that the cerebral cortex normally inhibits both components of postural tone, and that injury may affect the control over the plastic component to a greater extent than that of the contractile element. This accounts for the marked improvement in control which follows sympathetic ramisection.

Consideration of these facts reveals the far-reaching influence in the interpretation of the functions of the cerebrum and cerebellum the further investigation of the central control of muscular tone is likely to exert.

THE SURGICAL OPERATIONS.

From the reports that have reached us Dr. Royle and I have been convinced that most of the failures have been due to two main causes: (*a*) the neglect to determine whether voluntary control and excess of plastic tone were present, and (*b*) faults in the technique of the operation, more especially the failure to cut the appropriate rami communicantes. The long discussion in this lecture should

make clear how to choose cases that are likely to benefit from ramisection.

The basic principle of the operation of sympathetic ramisection is that it removes plastic tone. It is only indicated when plastic tone is in excess and hampers the voluntary activities which have persisted in spite of the central lesion. A study of the nature of the spasticity of the spastic limbs, and an estimate of the anatomical defect of the central mechanism responsible for the condition, must go hand-in-hand, and only when the physiological indications are discoverable is the operation to be undertaken.

With reference to the operation it is a matter of great importance not to remove the sympathetic ganglia, because the unnecessary removal of their control of visceral function is wholly unwarrantable. Dr. Royle attaches great importance to the adoption of the lumbar route for the operation of lumbar ramisection, not simply because it is for the patient a less formidable procedure than the abdominal route involves, but especially because it permits a clearer view of the rami and a more certain identification of the right ones to avulse.

In the second lecture I indicated which rami should be cut, and why.

The Operation of Lumbar Ramisection.

Royle has given the following account of the surgical technique.

The patient should be made to lie on the side opposite to that of operation and should be inclined slightly toward the surgeon, who faces the patient's back. The space between the ribs and the crest of ilium should be made as wide as possible by placing a sandbag beneath the patient, or, better still, by using the adjustable support devised for operations on the kidney.

Step 1.—The incision is made from the last rib to the crest of the ilium and thence forward to the anterior superior spine of the ilium. If the quadratus lumborum muscle can be palpated, the downwardly directed part of the incision should follow its lateral margin, but if not, the lateral margin of the sacro-spinalis should serve as a guide. The forwardly directed part of the incision should lie about 1 cm. below the actual crest of the ilium. This enables the attachment of the external oblique muscle to be exposed. The flap of skin and fascia outlined by this incision is reflected forward to expose the attachments of the latissimus dorsi to the lumbo-dorsal fascia and of the external oblique muscle to the crest of the ilium.

Step 2.—The trigonum lumbale Petiti is next defined and from this point forward the oblique muscles are freed from the crest of the ilium to within 6 or 8 cm. of the antero-superior spine of the ilium. In doing this it is possible in most subjects to divide the external oblique through definite tendinous tissue close to its insertion and to avoid cutting the actual muscle fibres. This gives a decided advantage in closing the wound. The internal oblique and the transversus abdominis muscles are divided through the muscle
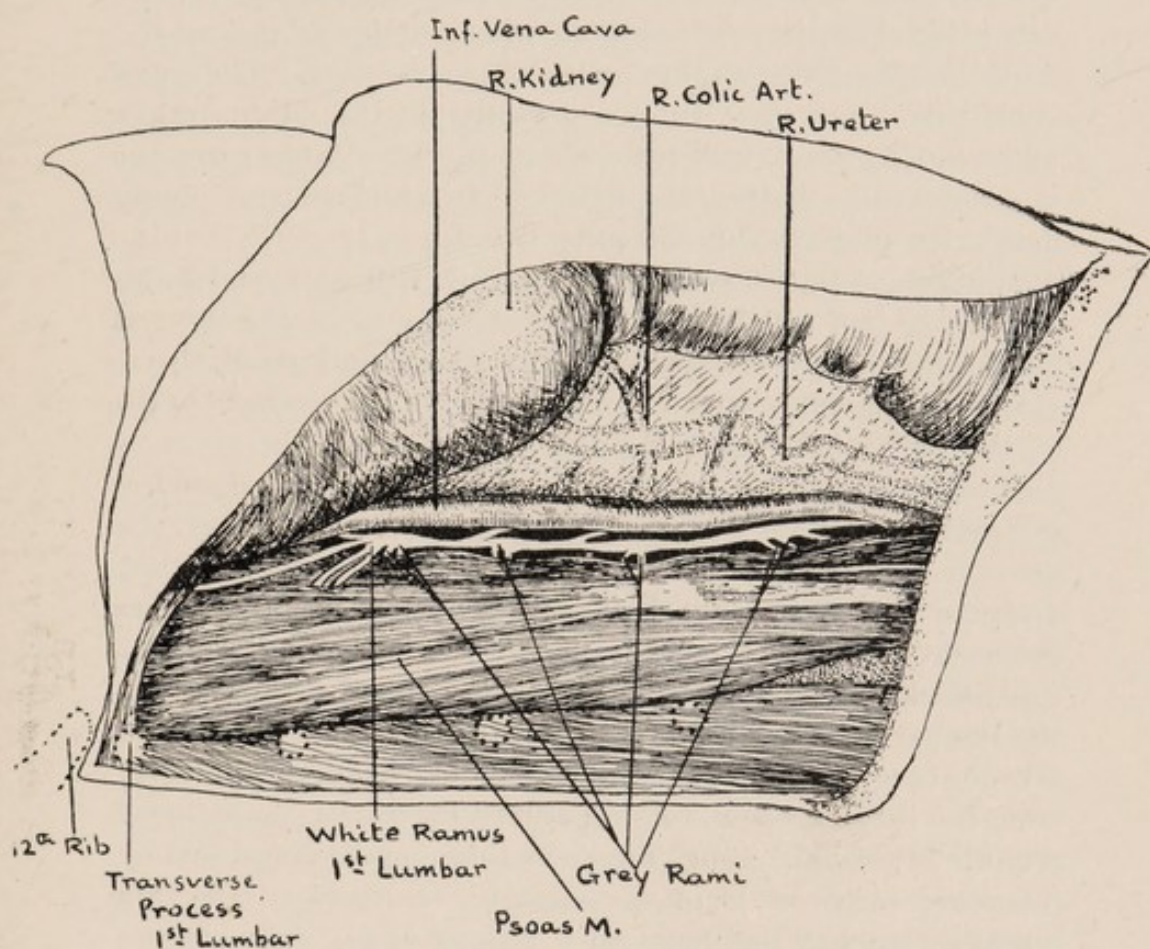
Fig. 11.—Dissection to show right lumbar rami communicantes as seen in the operation of lumbar ramisection. The incision runs from the twelfth rib along the border of the erector spinae muscle and is continued for three inches along the crest of the ilium. The tips of the transverse processes are seen in relation to the quadratus lumborum muscle, and the genito-femoral nerve is seen on the anterior aspect of the psoas.

fibres close to their attachment. The dissection is then carried upward and the lumbo-dorsal fascia is divided at the lateral border of the quadratus lumborum. In doing this it may be necessary to cut through the fibres of the latissimus dorsi.

Step 3.—The abdominal wall is now free to be thrown forward and after dividing the fascia transversalis the hand can be passed in front of the quadratus lumborum and the

psoas muscles until the medial border of the psoas is pal-
pated. Suitable retractors are then placed in position.
Care should be taken not to disturb the fascia covering the
quadratus lumborum and the fascia covering the psoas
muscle.

In a very fat subject, however, the approach to the sym-
pathetic trunk may be rendered more easy by leaving the
fascia transversalis intact except at the medial border of
the psoas muscle, where it must be pierced to reach the
sympathetic trunk. The ganglionated sympathetic trunk
can often definitely be palpated where it lies at the medial
border of the psoas muscle before it can be seen. The psoas
itself sometimes constitutes a difficulty in the adult subject
by obscuring the trunk from view, and a suitable retractor
is necessary to flatten the muscle. In children and poorly
developed subjects this difficulty is not great.

The ganglionated sympathetic trunk will be found lying
on the bodies of the lumbar vertebrae near the medial
border of the psoas muscle. The abdominal sympathetic
trunk on the left side is easy to define, if the medial border
of the psoas is sought. In this situation a thin layer of
connective tissue passes from the psoas muscles across the
sympathetic trunk and great vessels to the region of the
psoas on the opposite side. This is easily slit with a blunt
dissector and the sympathetic trunk comes into view. On
the right side the trunk lies under the lateral margin of
the inferior vena cava and is usually placed anteriorly to
the lumbar vessels. This, however, is by no means constant,
for on several occasions Royle has experienced difficulty
from the lumbar veins crossing anteriorly to the sympathetic
trunk. When this occurs the operation may be simplified by
removing one or more of these veins. On the left side this
complication has not been met, but in young subjects the
lumbar arteries can be mistaken for rami communicantes,
which they sometimes resemble in size and direction. In
a few instances the lumbar lymphatic vessels and an
unusually low formation of the receptaculum chyli has made
the definition of the sympathetic trunk more difficult. In
one instance the lymphatic vessels lay between the sym-
pathetic trunk and the attachments of the psoas muscle.
On lifting the lymphatic vessels the rami appeared from
under their posterior surfaces, and patient dissection was
required to define each structure.

In defining the sympathetic trunk long blunt dissectors
are necessary. Royle's dissectors are 25 cm. long and have
rounded ends. A long probe with a flat handle and curved

on its end like a strabismus hook is useful for lifting the sympathetic trunk when defining its branches. Long straight, or slightly curved, artery forceps, 20 cm. long, are also essential, and four should be provided. The structures of the abdominal wall and abdominal viscera demand a large, broad, and deep retractor. Royle's retractor for use in operations on the average adult is 8.75 cm. wide and 12.5 cm. deep. It is constructed to act as a light-reflecting surface and has a shelf extending forward from its lower edge so as to depress structures medial to the ganglionated cord. The sympathetic trunk and the rami communicantes should be clearly defined before section. The method of dividing the rami communicantes is usually by avulsion. Each ramus may be seized by a pair of artery forceps and drawn away from its lateral connexions, though in many instances it is necessary to divide a big ramus with a long pair of blunt-pointed scissors. In young subjects the rami may be easily and effectively broken with the blunt dissector. When ramisection of the second, third, and fourth lumbar nerves has been effected, the ganglionated cord is then divided at a level corresponding in position to the fourth lumbar nerve. The operation is then completed. The edges of the lumbo-dorsal fascia are first sutured in the region of the trigonum lumbale. The oblique muscles are then sutured to the crest of the ilium and a special point is made of suturing the tendinous portion of the external oblique to its original attachment and to the adjacent fascia lata. When this is done carefully the raw area on the crest of the ilium comes in contact with a raw area of considerable width on the under surface of the external oblique tendon, and this facilitates adhesion. The lumbo-dorsal fascia and the latissimus dorsi muscles are then sutured. The skin is closed without drainage.

The whole operation should be performed with very little loss of blood except from small vessels occasionally encountered in freeing the oblique muscles. There is no bleeding in the depth of the wound if the approach is confined to the plane between the peritoneum and the fascia covering the quadratus lumborum and the psoas muscles. Sharp instruments should not be introduced into this wound. The essential dissection can be done with blunt dissectors and long artery forceps.

The ilio-hypogastric and ilio-inguinal nerves are both drawn forward with the abdominal wall and the ureter with the parietal peritoneum. The incision has been

designed so far as possible to divide only fibrous structures in approaching the sympathetic trunk. The internal oblique and the transversus abdominis muscles have, usually, to be divided through their muscle fibres at their insertion to the crest of the ilium. The incision also avoids all important nerves and blood vessels, and, if carefully sutured, should leave the abdominal wall as strong as before the operation.

The Operation of Cervical Ramisection.

The rami communicantes only are divided in the cervical operation. The sympathetic trunk does not come into the field of operation excepting in the approach to the first thoracic nerve. The rami above the first thoracic nerve are
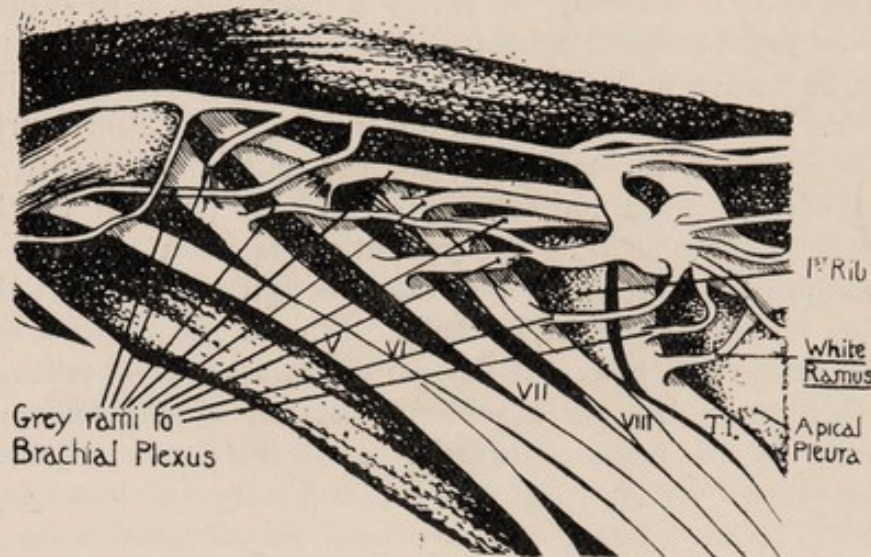
Fig. 12.—Diagram to illustrate the arrangement of the cervical rami communicantes on the right side. After Dr. T. K. Potts.

post-ganglionic fibres, but the first thoracic nerve itself usually has both a white and a grey ramus. The sympathetic rami usually enter the nerve roots of the brachial plexus after they emerge from the intervertebral foramina, though occasionally rami join the nerve roots within the foramina.

Step 1.—The patient lies with the chin turned away from the side of operation and with a small pillow placed beneath the shoulders. The field of operation is reached through an incision extending from the clavicular insertion of the sterno-mastoid backward and slightly upward across the posterior triangle. In young subjects and in those patients in whom the nerve roots all emerge from behind the scalenus anterior this incision suffices, but occasionally it is necessary to make a second small incision upward

along the posterior border of the sterno-mastoid to be sure of reaching the connexions to the fifth and sixth nerves.

Step 2.—The platysma is divided and the external jugular vein is secured in the line of the original incision. The anterior layer of the cervical fascia is divided and blunt dissection is then carried out to expose the deeper layer of fascia covering the brachial plexus and the scalenus muscles. Between these two layers of fascia the superficial cervical artery will be found occasionally. The transversus colli
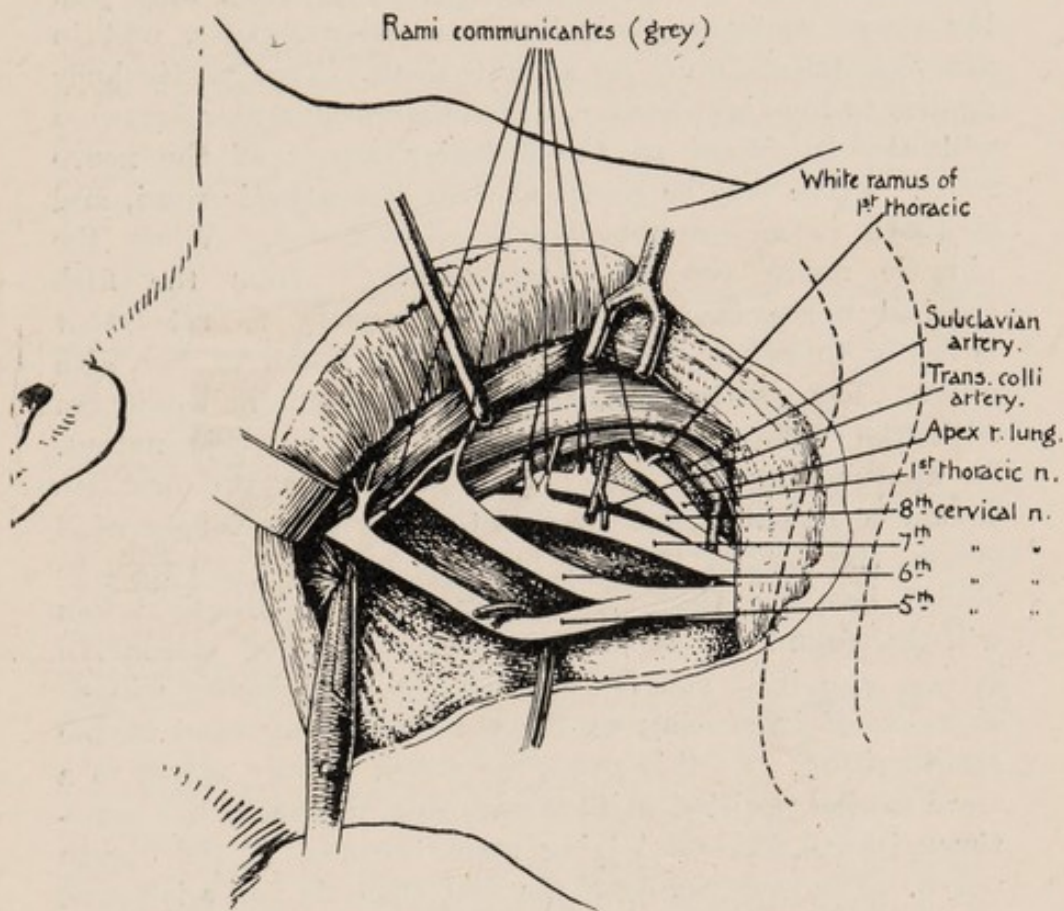
FIG. 13.—Royle's figure of the rami communicantes, as exposed in his operation of cervical ramisection, modified by Dr. John Beattie and Miss Audrey Russell. Note the three slips of the anterior scalene muscle between which the grey rami to the upper three nerves emerge. Position of clavicle indicated by broken lines.

artery appears in a deeper plane crossing the nerve roots, and in Royle's experience most frequently between the seventh and eighth nerve roots. To obtain a clearer view of the plexus this artery should be tied and divided. The omo-hyoid muscle, appearing in this space, can be retracted downward.

Step 3.—In the upper part of the plexus it is necessary to look for and define the phrenic nerve as it lies on the anterior aspect of the scalenus muscle. The nerve

roots are then exposed and traced to the intervertebral foramina. The subclavian artery is identified and pulled forward to expose the eighth cervical and the first thoracic nerve. The rami communicantes are not easy to define. Those to the fifth and sixth nerves may come across the anterior surface of the scalenus anterior to join the nerve trunks or they may come through the muscle itself (Fig. 13). In addition there may be two or more branches; and it is necessary in dealing with each of the nerve roots to be sure that all anterior connexions are divided right up to the intervertebral foramina. Grey rami may join the nerve roots on their antero-inferior aspects, and in many instances must be sought there. This particularly applies to the eighth nerve. Medullated muscular branches will also be found on the anterior aspect of the nerve roots. These may be confused with sympathetic rami, and if there is any doubt should be removed. When the phrenic nerve receives communications from the fifth cervical nerve it will be found necessary to retract it laterally to get a clearer view of the trunk of the fifth nerve. The greatest difficulty will be found in connexion with the eighth cervical and the first thoracic nerves. In approaching this part of the dissection the first rib should be palpated and the first thoracic nerve sought as it crosses the neck of the rib. This nerve trunk can then be traced into the thorax. The cervical sympathetic trunk will be found on a plane posterior to the subclavian artery, and if it can be well defined no difficulty will be experienced in picking up the communicating rami to the eighth nerve. At this point the trunk usually moves to a more medial position as it travels into the neck, but sometimes it will be found lying upon the root of the eighth nerve. The grey ramus of the first thoracic nerve is found on its superior surface medial to the white ramus, which should be avoided if possible. The rami in this operation may usually be easily broken with a small strabismus hook. After ramisection has been completed the wound is closed by drawing together the edges of the platysma and by suturing the skin without drainage.

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