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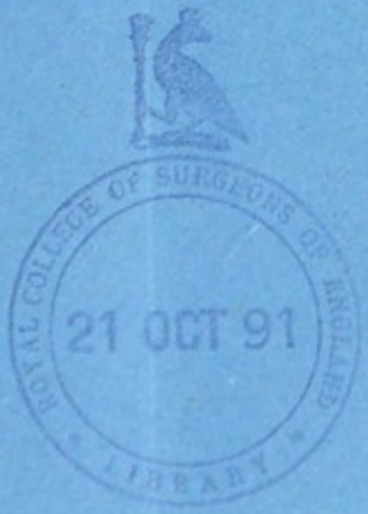
FROM THE

JOURNAL OF ANATOMY & PHYSIOLOGY

VOL. XXV.



THE VALUE OF NERVE-SUPPLY IN THE DETERMINATION OF MUSCULAR HOMOLOGIES AND ANOMALIES.[1]

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The Heidelberg School of Anatomy is responsible for the theory that a muscle is to be regarded as the end-organ of a nerve, and that if we succeed in recognising the latter, we have in our hands a sure and infallible means of determining the homology of the former. This view, which was first advanced by Gegenbaur, and which has been maintained and elaborated with so much ability by his pupils Fürbringer and Ruge, has exercised for some ten years or more a marked influence upon morphological work.

Prior to its enunciation, investigations into the comparative anatomy of the muscular system were conducted in a very unsatisfactory manner, and the great majority of the papers which were written on the subject contained little more than dreary catalogues of origins and insertions with haphazard hints as to homologies.

One writer, indeed, in this country—the late Professor Rolleston—in his well-known observations upon the serial homologies of the muscles in connection with the shoulder and pelvic girdles, had employed the nerve-test with marked success, but in the determination of ordinary homologies it was customary to rely solely upon a consideration of the position and attachments of a muscle.

But whilst there cannot be a doubt that the nerve of supply is the best and safest guide to follow in our endeavours to trace the history of any muscle or group of muscles, and that it will, in the vast majority of cases, lead us to right conclusions, there is grave reason for the belief that it is not an absolutely infallible guide.

Nine years ago, at the meeting of the International Medical

[1] This communication was the opening statement in the discussion on this subject in the Section of Anatomy and Physiology, British Medical Association, Birmingham, July 1890.

Congress in London, I discussed this matter, and brought forward some facts in support of the opinion which I have just expressed. Since then much has been written on the subject, and the present appears to be a convenient time for reviewing the evidence which has been advanced on both sides.

A proper solution of the problem can only be obtained by approaching the question from two points of view:—(1) by studying the early connections which exist between the nervous and muscular systems in the embryo; (2) by examining one or more groups of muscles, the homologies of which are undoubted, in a large series of different animals, or in a large number of individuals of the same species, and observing whether in every case the nerves of supply are the same.

Fürbringer, in his great work upon the "Morphology of the Bird," has reviewed at considerable length, and, it must be admitted, in a very impartial spirit, the embryological aspect of the question. He puts before us three possibilities in regard to the neuro-muscular connection.

1. Do the ganglion cells, nerve-fibres, and muscle-fibres, which constitute the neuro-motor apparatus, present a loose and changeable combination of originally independent elements?

2. Does the apparatus present in its fully formed state a real and unchangeable unity—a unity, however, which is only brought into existence by the *secondary* union of originally separate nerve and muscle elements?

3. Does it represent an apparatus which is formed out of the same elements, so that ganglion cells, nerve-fibres, and muscle-fibres not only present a community of origin, but also an original and indissoluble union?

The epiblastic origin of the nerves and the mesoblastic origin of the muscles would appear to be absolutely established by the writings of Balfour, Marshall, His, and Kölliker, and if this be the case the last of these views is altogether untenable. And there is little use in taking shelter behind the statement made by Hensen, viz., that no one in ontogeny has ever seen the free growing end of a nerve-fibre, because here the observations of Professor Paterson may be appropriately cited. In his important investigations into the "Fate of the Muscle Plate," Mr Paterson has traced the formation of the nerves as

they spread out from the spinal nerve-trunk into the limb, and he has shown that they are built up of epiblastic elements foreign to the limb and distinct from the mesoblast which forms the muscles.

With regard to the precise manner in which the neuro-muscular connection takes place, we have few observations to go upon. Two observers, Calberla and Bremer, have dealt with the question. Both maintain that it is a secondary union of originally separate elements, but they are at variance with each other as to the actual manner in which the union is brought about. Calberla holds that the extra-muscular nerve-fibre becomes united to an intra-muscular end-organ. Bremer, on the other hand, asserts that the connection is brought about by a growth of the whole nerve-fibre, including its end-organ and sheath, to the muscle-fibre.

But it is needless to pursue this aspect of the question further. The theory that nerve and muscle present a community of origin appears to be contrary to what we are in the habit of regarding as well-established fact.

It now remains for us to discuss the two other possibilities put forward by Fürbringer regarding the neuro-muscular connection. Is the secondary connection which is established of a loose and changeable kind, or is it fixed and unalterable? To say that the relation is a loose one would be to infer that variations in nerve-supply are of frequent occurrence, which is certainly not the case; whereas, on the other hand, to affirm that the relationship is unalterable, and not only holds good for the past and the present, but will also hold good for the future, lands us in this difficulty, that variations in nerve-supply are undoubtedly met with, not only in the homologous muscles of different animals, but also in the case of the same muscle in different individuals of the same species.

Of course it may be held that what appears to be a variation in nerve-supply may not in reality be so; that in fact we are merely dealing with a case where certain nerve-fibres have adopted a different path to reach their destination, and although the connection be a secondary one, yet *the same ganglion cells* are invariably connected with the *same muscle-fibres*. A great deal may be said for this view, and, considering the constancy of

the relation between muscle and nerve, it must be regarded as a perfectly legitimate opinion to hold. At the same time in many cases it is incapable of proof, because when once nerve-fibres forsake the path they are accustomed to follow, their identity is extremely difficult to establish. Outside the spinal cord it may be done, and no doubt is frequently done, but when the transference takes place inside the cord, as, for example, by a group of fibres coming out at a higher or lower level, it is almost impossible to recognise them with any degree of certainty. The nerve to the subclavius may perhaps be quoted as an example of nerve-deviation within the spinal cord. As a rule this little twig comes out with the 5th spinal nerve, but, as Dr Brooks has pointed out, it may emerge a stage higher up with the 4th spinal nerve.

Every anatomist has observed examples of transference of nerve-fibres, during their course outside the spinal cord, from a familiar to an unfamiliar route. Several years ago I called attention to the connection which exists between the varying magnitude of the communicating loop which usually passes from the 2nd to the 1st dorsal nerve, and the varying size and range of distribution of the intercosto-humeral and lesser internal cutaneous nerves, and in the light of this Professor Wilson, of Sydney, has been able to explain what at first sight appears to be a discrepancy in the nerve of supply of the "achselbogen" muscle, and indeed to localise it in the 2nd dorsal metameric segment. In some instances the "achselbogen" muscle receives its nerve of supply from the intercosto-humeral, but in other cases it comes from the internal anterior thoracic or the lesser internal cutaneous nerve of Wrisberg. In all cases the source from which the fibres are derived is the same. They come from the 2nd dorsal nerve. In the one case they pass directly to the muscle through the intercosto-humeral nerve; in the other cases they follow the tendency exhibited by all limb nerves, viz., they enter the plexus before they finally pass to their destination.

The accessory phrenic and the accessory obturator are other examples of nerve transference, and Sir William Turner has recorded two very striking cases in which the long buccal nerve proceeded from the superior instead of the inferior maxillary

division of the 5th nerve.[1] Many other instances might be given, but those that I have quoted are sufficient to show, what indeed is a matter of common knowledge to every teacher of anatomy, viz., that nerve-fibres outside the spinal cord do not in every case follow the same paths as they travel towards their different destinations.

Both muscles and the nerves which are associated with them are arranged in groups, and it is where these come into contact with each other that there is a tendency exhibited for one or other of the nerves to overstep the boundary line and extend its territory at the expense of its neighbour.

In dealing with this question on a former occasion, I chose the intrinsic muscles of the foot and the two plantar nerves for the purpose of testing the value of nerve-supply in the determination of muscle homologies. No better ground could be found, because here we have a series of muscles which are easily and readily identified. We may fairly assume that the muscles attached to any particular digit are homologous with the muscles connected with the corresponding digit in all animals.

Amongst the large number of different mammals which I examined, I only encountered four in which there was a decided deviation from the ordinary typical distribution of the plantar nerves. In three of these, viz., the Elephant, Hyrax, and Beaver, the internal plantar nerve invades the territory of the external plantar and seizes upon muscles which usually do not belong to it. The Fox-bat affords an example of the opposite kind; the external plantar lays hold upon a muscle which in the typical condition is under the sway of the internal plantar. I need not enter further into particulars, but I may be allowed to mention that, by the appearances presented, I was led to consider that the muscular distribution of the internal plantar nerve has in all probability been more extensive at one time than it is now. It is possible that at one time the two plantar nerves took an equal share in the intrinsic muscle supply of the foot. The hand and foot of the Hyrax present a condition which approaches very nearly to this. Judging from the arrangement in the Fox-bat, there appears to be a tendency for the external plantar nerve to drive the internal plantar nerve out of the field altogether.

[1] *Proc. Roy. Soc. London*, 1868, p. 456, and *Jour. Anat. and Phys.*, Nov. 1866.

This struggle for supremacy, as it were, between two contiguous nerves supplying contiguous groups of muscles, opens up an interesting field for work, and Dr Brooks has recently pointed out that the same contest may be observed in the hand, between the corresponding nerves, viz., the ulnar and median. In some cases the ulnar, and in other cases the median, may be observed to gain ground.

But in these cases of variation in the nerve supply of the intrinsic muscles of the hand and the foot we are dealing with nerves which come off from the same plexus, viz., the plantar nerves from the sacral plexus, and the median and ulnar nerves from the brachial plexus. Further, Mr Herringham has shown that the fibres which enter into the formation of the inner head of the median and the ulnar nerve, are derived as a rule from the same spinal nerves. Certainly, therefore, these cases of nerve-deviation in the supply of the hand and foot muscles cannot be held as furnishing us with absolute proof against the hypothesis of an unchanging and unalterable connection between the ganglion cells and muscle-fibres, because they can satisfactorily be explained by supposing a slight deviation from the path followed by certain of the nerve-fibres.

One circumstance, however, militates somewhat against this view. Mr Herringham, in his elaborate dissections of the brachial plexus, has satisfied himself that the intrinsic muscle nerve-fibres of the median come from the 6th, or the 6th and 7th spinal nerves, and travel downwards through the outer head of the median, whilst the corresponding nerve-fibres of the ulnar come from the 8th or the 8th and 9th spinal nerves. The nerve-transference then, if there be any, is thrown back into the spinal cord.

But examples are not wanting in which there is a substitution of the ordinary nerve of supply, by one which comes from a different nerve-plexus. Ruge, the distinguished Professor of Anatomy in the University of Amsterdam, furnishes us with a striking instance of this. Thus, in the Ornithorhynchus, the tibialis anticus and the inner part of the extensor longus hallucis are supplied by a branch from the anterior crural nerve, which is prolonged downwards to its destination over the external condyle of the femur. Ruge is a firm believer in the immuta-

bility of nerve-supply, and this is an awkward case for him to bring into reconciliation with his views. He assumes that the muscles concerned are not homologous with the similarly named muscles in other mammals, but belong rather to the extensor muscles of the thigh. He further believes that the fibres, which in the leg are supplied by the anterior crural, are gradually abolished, and that their place is taken by others derived from the external muscles of the leg, which drag their nerve of supply along with them.

With one part of this hypothesis I entirely agree, viz., that the innervation of these muscles points to their original derivation from the extensor muscles of the thigh; but I cannot accept the other part of the theory, viz., that the muscles thus derived are afterwards replaced by others similarly situated and similarly attached. It is much more reasonable to suppose that the distribution of the peroneal nerve is extended so as to include all the extensor muscles of the leg; that, in other words, the peroneal nerve invades the territory of the anterior crural in the same manner that the external plantar nerve encroaches upon the domain of the internal plantar nerve.

This supply of leg muscles by the anterior crural nerve, in a case where the leg muscles at the knee-joint are almost completely segmented off from the extensor muscles of the thigh, must be regarded as the persistence of a very archaic condition. Professor Humphry and Dr Brooks have shown that in cryptobranchus, and menobranchus there is a continuity over the knee-joint of the extensor muscles of the thigh and leg, by means of flattened tendons, and yet all the extensors of the leg are supplied by the peroneal nerve. In these two forms, therefore, we have a continuous muscle sheet, and a discontinuous nerve-supply; whilst in the Ornithorhynchus we have a break in the continuity of the muscles, but a continuous nerve-supply.

Dr Gadow furnishes us with several examples of the same muscle being supplied by a nerve from a different plexus in different animals. Thus, he has pointed out, that in the Iguana the ischio-femoral muscle is supplied by the ischiadic plexus; in the Crocodile it is supplied by the obturator nerve; while in Varanus it is supplied by both. And he very justly remarks that if we did not know the condition in the Monitor, the nerve

of supply in the other two cases would be more likely to lead us astray than to help us in our endeavours to determine the homology of the muscle in question.

He endeavours to explain this deviation by supposing that the muscle is composed of different factors in each case.

I presume that the ischio-femoral muscle to which Dr Gadow refers is the adductor magnus of mammalian anatomy. If this be so it is interesting to note that we meet with somewhat corresponding variations in its nerve-supply amongst mammals, and seeing that it lies as it were in the interval between the extensor and flexor groups of muscles, this need not be a matter for surprise. The typical supply of the adductor magnus in Mammalia is, as in the Monitor, a double one from the obturator nerve and the sacral plexus. In marsupials, however, as in the Iguana, the nerves of supply are derived solely from the sacral plexus. That the condition is not a stable one, is shown by the interesting case recently recorded by Prof. Wilson, in which he noticed in a human subject a tendency for the ischiadic nerve-filaments to extend beyond their confines, and usurp a portion of the muscle which is usually held by the obturator.

Other examples of homologous muscles being supplied by nerves which come from different parts of the spinal cord in different animals might be given, but those which I have cited are sufficient for our purpose. The question, therefore, now comes to be: How can these decided nerve-deviations be accounted for? Three very different explanations may be offered, viz., by supposing—

1. A complete obliteration, and then a reconstruction of both muscle and nerve elements—the muscles assuming the position and attachments of their predecessors. It is in this way that Ruge accounts for the disappearance of the archaic form of nerve-supply to which we have referred in the leg of the Ornithorhynchus.

2. A retention of both nerve and muscle elements, but by the adoption of a new and more convenient path by certain of the nerve-fibres. This view receives considerable support from the fact, that the great majority of apparent deviations from the typical nerve-supply, can be more or less satisfactorily shown to be due to nerve-transference.

3. A retention of the muscle elements, but a substitution of new nerve-elements.

The first of these hypotheses I reject *in toto*. It would indeed be a curious caprice of development if muscles once formed, and in every respect competent, were abolished to give place to others similar in position and attachments. But again, in the cryptobranchus and menobranchus, we have the clearest proof that the primitive extensors of the leg are not abolished, although they have got rid of their archaic nerve-supply. Extensors of the leg and extensors of the thigh are in direct anatomical union with each other.

With regard to the two last hypotheses I am not prepared to advocate either of them very strongly to the disadvantage of the other. Those who have worked chiefly at the lower vertebrates, will probably incline most to the view that the same ganglion cells are invariably connected with the same muscle-fibres, and that deviations in nerve-supply are merely to be regarded as deviations in the path chosen by the nerve-fibres. At the same time, I hardly think that this explanation is capable of accounting for every case of deviation in nerve-supply. I am inclined to believe that in some cases we may have a real substitution of new for old nerve-elements. Mr Paterson's researches would seem to indicate not only the possibility, but even the probability, of such a change occasionally taking place.

But notwithstanding all this I agree with Fürbringer, when he says that the nerve of supply is "the most important and indispensable guide for the determination of muscle homologies." It is not an absolutely infallible guide, however, and in rare cases it might lead the observer astray.

And if the nerve of supply be valuable as a means of determining muscular homologies, it must be equally so in deciding upon the true nature of a muscular anomaly. It is upon this ground that I hold so strongly that the musculus sternalis is to be regarded *in all cases* as a portion of the pectoralis major. Its nerve of supply from the thoracic nerves has now been traced by seven independent observers in no less than forty-six cases. Twenty-nine of these cases occurred in my own department, and I maintain that this is the invariable and constant supply

of the sternalis. That, along with its true thoracic nerve of supply, there may in rare cases be associated a minute twig from one or other of the intercostal twigs is proved by Professor Shepherd, but that this should ever constitute its sole nerve of supply, as Professor Bardeleben asserts (more especially as he states in eleven consecutive cases), I simply cannot believe.