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(*Extracted from the Edinburgh Monthly Journal of Medical Science—May* 1841.)

ON THE

RELATION BETWEEN MUSCULAR CONTRACTILITY AND THE NERVOUS SYSTEM.[1]

Numerous physiologists have devoted much labor to ascertain the exact relation of the nervous system to the contractile tissues, and more especially to the muscular. From the universal distribution of the nervous filaments in the contractile tissues of man and of the higher animals,—from the facility with which contractions can be induced in the muscular bundles of the limbs and trunk, by causes acting through the nervous system—and from the circumstance that sensation is, in the normal state of the body, linked with many muscular movements:—conjoined perhaps with certain theoretical notions regarding the supremacy of the nervous system in the vital actions of the body, many physiologists still maintain that the property of contractility is derived from the nervous system.

An opposite doctrine was advocated by Haller and his followers. From numerous experiments, in which Haller found the contractility of the muscles remain after their nerves had been cut through, and even after they had been removed from the body; strengthened by the arguments suggested by the structure and endowments of the lower organised bodies, and by an examination of the order in which the different parts of the fœtus are developed, conjoined with various other facts and considerations, he arrived at the conclusion that the property of contractility is independent of the nervous system, and is inherent in the muscular fibre itself.[2]

This doctrine, directly opposed to that of the "animists," who had become an influential sect at that period, could not possibly be allowed to pass without animadversion; and accordingly a controversy arose among the learned physiologists of Europe, which

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[1] An epitome of this paper was read at the last meeting of the British Scientific Association.

[2] Memoires sur les Parties Sensibles et Irritables. Lausanne, 1760. Elementa Physiologiæ, tom. iv.

for several years was carried on with great keenness and acrimony, and has since that time ranged physiologists into two classes—the Hallerians, or those who believe in the inherent contractility or irritability of the muscular fibre—and the Neurologists, or those who maintain that the muscles derive this property from the nervous system. Some of the followers of both sects, but more particularly the Neurologists, have admitted considerable modifications in the tenets so dogmatically espoused by the original supporters of these doctrines. On the other hand, many of the Hallerians have extended the term contractility, and in our opinion justly, to certain contractile movements which may be induced in the arteries, in various secretory ducts, in the cellular tissue, and in the skin. They have also freely admitted certain effects of the nervous system upon the muscular contractility, such as the influence of mental emotions, &c., upon the contraction of the heart, a conclusion which Haller would have willingly avoided. On the other hand, very many Neurologists have given up the original opinion, that muscles derive their contractility from the central organs of the nervous system, the brain, and spinal marrow, and maintain that the nerves distributed in the different muscles have themselves the faculty of furnishing the conditions upon which contractility depends, believing that in the muscles of involuntary motion this is effected by the ganglionic or sympathetic system of nerves, and in the muscles of voluntary motion by the cerebro-spinal nerves. Some, again, exclude the cerebro-spinal nerves from all participation in this faculty, and confer it entirely upon the ganglionic system.

It is not our intention to enter into any lengthened examination of the various arguments which have been adduced by the supporters of these different views, but shall confine ourselves to one point only, on which the opponents of the Hallerian doctrine have more lately assailed it by new facts, against which its author has left no adequate defence. The point to which we refer is the effect of the injury of a nerve upon the contractility of the muscular bundles in which it is distributed; and on this, the arguments of those Neurologists who maintain that the property of contractility is dependent upon some influence transmitted along the nerves to the muscles, from the central organs of the nervous system, may be thus stated in general terms,—that functional and structural derangements of the brain and spinal chord usually produce paralysis of some part of the body, which, if continued for any length of time, is followed by diminished contractility, size, and strength of the muscles paralyzed; and that the section of a nerve, or even the tight application of a ligature around it, most certainly induces those effects in the muscles in which it is distributed. To these arguments it may also be replied, in general terms, that all that can be meant by the term paralysis, in the

cases referred to, is, that the muscles have ceased to act in obedience to the mental act of volition; for, if mechanical excitation be applied to the nerve, below the point where it has been cut across or included in the ligature, within a certain period of time after the muscles have been thus rendered quiescent, equally active and durable contractions can be produced in the muscles which are said to be paralyzed, as in other muscles whose nervous connection with the central organs of the nervous system has been left untouched; and that the subsequent disappearance of the contractility in muscles thus insulated from the central organs of the nervous system, is due to the imperfect nutrition which follows a state of inaction, in whatever organ of the body this may be induced. We shall now examine the specific facts upon which these arguments are based, and attempt to ascertain their relative value. Valli[1] observed that the muscles of the limb of a frog frequently ceased sooner to respond to the excitation of galvanism, when the large nerve passing to them had been left uninjured, than when it had previously been divided. Dr Fowler[2] found that when one sciatic nerve was cut in a frog nine days before decapitation, no apparent difference could be detected in the vigor and persistence of the contractility of the two posterior extremities. Nysten[3] satisfied himself upon the bodies of two apoplectic patients, who died several days after being attacked with the disease,—the one from the first and the other from the second attack,—that the application of galvanism excited as violent contractions in the muscles of the paralyzed, as of the sound side. Dr Wilson Philip performed and repeated the following experiment:—The large nerve of the posterior extremity of a frog was divided, and the limb wholly deprived of sensation and voluntary movements. The skin was then removed, and a stimulant (a solution of salt) was kept constantly applied to the muscles till no further contraction could be excited in them, which happened in about twelve minutes. The skin was then removed from the opposite limb, and the muscles subjected to a similar treatment, without injuring the trunk of the nerve, and all signs of contractility ceased in a somewhat shorter period than in the limb in which the communication between the muscles and the central organs of the nervous system had been cut off.[4] This difference may be accounted for by the circumstance, that in the limb in which the nerve had been left entire, the animal would continue to exercise voluntary movements, so that its muscles were exposed both to the effects of the artificial stimulants and of the ner-

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[1] Experiments on Animal Electricity, &c., p. 21. London, 1793.
[2] Experiments and Observations on Animal Electricity, p. 109. Edinburgh, 1793.
[3] Recherches de Physiologie et de Chimie Pathologique, p. 269. Paris, 1811.
[4] On the Vital Functions. Exper. 35.

vous agency. Mr J. W. Earle,[1] after testing the facts advanced by Dr W. Philip, admits their accuracy, but objects to the conclusions deduced from them, and maintains that they can only enable us to judge of the amount of contractility in the muscles at the time the experiment was commenced, and cannot give us any information as to the source from which it was derived; and has further maintained, that before we can agree in the inference drawn from such experiments, it would be necessary to ascertain if the contractility would return with equal rapidity in the limbs, after being treated in the manner described. These objections, it is obvious, apply equally to the experiments of Nysten, Valli, and Fowler, as to those of Dr Wilson Philip. Mr Earle instituted a few experiments on this point, and states that he has satisfied himself, that while the contractility returned in the limb in which the nerves had been left entire, it remained extinguished in that in which the nerves had been divided. The mode of experimenting followed by Mr Earle, is, however, liable to an obvious source of fallacy, for it must necessarily have produced great inflammation and all its consequences in the limbs thus treated; and from Mr Earle's own description, it would appear that the limb in which the nerve had been cut was more disorganized than that in which it had been left entire. If such an experiment could be relied upon, it would most decidedly prove that, after the muscles of a limb had been cut off from all nervous communication with the central organs of the nervous system, and then exhausted of their contractility, they never regain this property. With the view of deciding this point, we made, at the suggestion of Dr Alison, an extensive series of experiments, the results of which were laid before the British Scientific Association.[2] These were made also upon frogs, and in such a manner as to exhaust the muscles of their contractility without disorganizing the textures of the limb. The large nerve of one limb was exposed, cut across, and part of it removed, while in the opposite limb it was simply exposed. The skin was allowed to cover the muscles in both limbs. The muscles of both limbs were then strongly galvanized until they had ceased to contract—one wire being applied to the nerve, the other being placed on different parts of the surface of the limb, and a solution of salt used to moisten the part of the surface of the limb upon which the wire was applied. It was ascertained that the contractility returned as quickly and strongly in the one limb as in the other, though in one of these the muscles had been insulated from all nervous connection with the brain and spinal chord, as evinced by the circumstance

[1] A New Exposition of the Functions of the Nerves. 1833.
[2] Transactions of British Scientific Association, vol. iv.

that they remained quiescent when the chord was crushed and a stilet pushed down the spinal canal, while the muscles of the other limbs were thrown into violent contractions. We have, in the result of these experiments, sufficient evidence that the contractility will reappear in the muscles of a limb in which it had been previously exhausted, and when the nervous connection between them and the central organs of the nervous system had been broken through; and are, consequently, forced to conclude that this property of contractility cannot be derived from the central organs of the nervous system. We have also several times performed the experiment by using pure water to moisten the limb, instead of the solution of salt, and with the same result. No one can even perform the experiment of exhausting the muscular contractility in the limb of a frog, after the sciatic nerve has been divided, without feeling fully satisfied that the property of contractility cannot be derived from the central organs of the nervous system; for he finds that if he again applies the wire a very few minutes after the contractility of the muscles has ceased to respond to the excitation of the galvanism, pretty strong contractions may again be produced, and this rapid re-appearance of the contractility will occur many times in quick succession. In performing such experiments, it is found to be a tedious process to exhaust the contractility; and even when we have succeeded most perfectly in our endeavours to exhaust it, feeble muscular contractions may be excited after a quiescence of a few minutes. Dr Marshall Hall has suggested, that in these experiments the division of the nerve may have acted in the manner of a shock upon the muscles in which it is distributed; and the re-appearance of vigorous muscular contractions after from two to four days, may be due to the passing off of the effects of the shock, and not to the muscular bundles having regained that contractility which was lost.[1] With the view of testing that suggestion, I exhausted the muscles of the posterior extremity of a frog, having removed a portion of the sciatic nerve, as in the former experiments. After waiting four days, the muscles of the limb were again exhausted, but the contractility, two days after this, had returned as vigorous as before. The experiment was continued further, and these muscles were exhausted four different times, and each time the contractility returned, though the trunk of the nerve had not been disturbed after the first part of the experiment, when a portion of it was removed. This experiment was repeated, and with the same results when the animal was healthy. These facts are sufficient to prove, apart from other considerations, that the re-appearance of the muscular contractility in these experi-

[1] Cyclopædia of Anatomy and Physiology—Article Irritability, vol. iii.

ments, cannot be attributed to any supposed temporary diminution of it, in consequence of the injury done in dividing the nerve supplying the muscles. Müller has detailed some experiments which he believes to be subversive of the Hallerian doctrine, and to which he appears to attach much importance. He divided the ischiatic nerve in the middle of the thigh in a rabbit; and though, after the expiration of a period of one month and twenty days, the muscles of the limb still contracted when irritated, yet if a longer period was allowed to elapse, they were found to have lost their contractility. In an experiment upon a rabbit, five weeks after the division of the nerve, contraction of the muscles could not be excited by irritating the nerve either mechanically, by a chemical stimulus, caustic potash, by galvanism, or by irritating the muscle itself. The muscles in the limb of a dog contracted slightly ten weeks after the division of the nerve leading to them.[1] Similar results had been observed by Fowler in experiments upon frogs.[2] But before we can admit that these experiments afford any evidence in favour of the opinion that muscular contractility is dependent upon some influence transmitted along the nerves to the muscles by the central organs of the nervous system, it would be necessary to prove that a state of complete inaction for so long a time, would not of itself be sufficient to produce such effects, since we know that muscles rapidly lose in bulk and in the vigour of their contractions, when thrown into a state of perfect quiescence. And this inquiry becomes the more necessary, when we are informed by Valentin, that on miscroscopic examination of the muscular fibre after such experiments, the diminution in the vigour of the muscular contraction was proportionate to the physical changes which had taken place in the structure of the muscular fibre, as observed through the microscope;[3] and we also learn from Mr Skey that he has observed similar changes in the muscles of the human species, thrown for a long time together into a state of inaction, and where the nervous communication between the muscles and spinal chord had not been interrupted.[4] With the view of obtaining satisfactory evidence on this point, the following experiments were performed:

Exper. 1.—The sciatic nerve was divided in a rabbit, and a portion of it removed. One wire from two galvanic batteries of thirty pairs of plates, was applied over the course of the nerve, and the other wire was applied over the foot, which was kept moist until the muscles had ceased to contract. Three days af-

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[1] Elements of Physiology, by Baly, p. 460 and 680. 2d edition.

[2] Opus cit.

[3] De Functionibus Nervorum Cerebralium et Nervi Sympatheci, p. 126–7. Berne, 1839.

[4] Philosophical Transactions (1837) p. 371.

ter this a weaker battery was used, and the muscles of the limb had recovered their contractility, and contracted powerfully. The more powerful battery was used as before, until the muscles had ceased to respond to the excitement, and three days after this they had again recovered their contractility.

Exper. 2.—The sciatic nerve was divided in a rabbit, and a portion of it removed. Seven weeks after the operation, the animal was killed by a dose of prussic acid, and the muscles of both posterior extremities were exposed and irritated by the direct application of the wires of a galvanic battery to the muscles. The muscles of the leg of the paralysed limb contracted very feebly, while those of the other leg were thrown into powerful contraction. The muscles of the leg of the paralysed limb were evidently much smaller, paler, and softer than the corresponding muscles of the opposite leg. The muscles of the two legs were then carefully removed, and weighed in a delicate balance, and their respective weights were as follows :—

Weight of the muscles of the leg of the sound limb, .	327 grains.
——— paralysed, . .	170
Weight of the tibia and fibula of sound limb, . .	89
——— paralysed, . . .	81

On examining portions of the muscles of both legs under the microscope, a very obvious difference in the physical appearance in the muscles of the two limbs at once presented itself. The muscular fibres of the paralysed leg were considerably smaller, had a somewhat shrivelled appearance, and the longitudinal and transverse striæ were much less distinct than in the muscles of the sound leg. From these experiments, we believe we are justified in concluding,—First, That in the warm, equally as in the cold-blooded animals, the contractility will return as vigorously as before in muscles which have been insulated from the central organs of the nervous system, and their contractility exhausted, or at least much enfeebled. Secondly, That the loss of contractility which subsequently occurs in muscles insulated from the central organs of the nervous system, may be satisfactorily explained by their imperfect nutrition, consequent upon the state of inaction into which they are thrown.

To decide whether or not this imperfect nutrition was dependant upon inaction, or upon any supposed nervous influence flowing along the nerves to the muscles, another series of experiments was performed.

Exper. 3.—The spinal nerves were cut across, as they lie in the lower part of the spinal canal, in four frogs, and both posterior extremities were thus insulated from their nervous connections with the spinal chord. The muscles of one of the paralysed limbs were daily exercised by a weak galvanic battery, while the muscles of the other limb were allowed to remain quiescent.

This was continued for two months, and at the end of that time, the muscles of the exercised limb retained their original size and firmness, and contracted vigorously, while those of the quiescent limb had shrunk to at least one-half of their former bulk, and presented a marked contrast with those of the exercised limb. The muscles of the quiescent limb still retained their contractility, even at the end of two months; but there can be little doubt that, from the imperfect nutrition of the muscles, and the progressing changes in their physical structure, this would in no long time have disappeared, had circumstances permitted me to prolong the experiment.[1]

We believe, then, that we have adduced sufficient evidence to shew, that though the facts detailed by Müller are perfectly correct, yet the inferences which he has drawn from them, regarding the dependence of the property of muscular contractility upon the central organs of the nervous system, are untenable. Dr Marshall Hall has lately published some experiments bearing upon this question.[2] He divided the spinal chord immediately below the brachial plexus, in six frogs, and then cut across the sciatic nerve in one of the posterior extremities of each animal. In these animals, then, both the volitional and excito-motory movements were paralysed in one extremity, while, in the other extremity, the excito-motory movements were retained, as the nervous communication between the muscles of that limb and the spinal chord was left uninjured. He found, after the lapse of a few weeks, that when galvanism was transmitted through the water in which the animals were kept, while the muscles of the limb which still retained their connection with the spinal chord were thrown into contraction, the muscles of the opposite limb remained quiescent. "This difference in the degree of irritability in the muscular fibre of the two limbs, was observable when these were entirely separated from the rest of the animal." We have no intention of calling in question the facts contained in the memoir of this distinguished physiologist, nor the very interesting practical deductions which he has based upon them; we only object to the correctness of his inference, that the source of muscular contractility is seated in the spinal chord. Before we can lay down a law in any of the sciences, or, in other words, arrive at a true generalization, it must include all the facts of the case; and consequently, if the facts which we have detailed in the above experiments be correct, the generalization at which Dr M. Hall has arrived, cannot be the true one, for it does not include these facts. To prevent this argument from being retorted upon

[1] The application of the results of these experiments to the treatment of certain cases of paralysis, is so obvious as to require no illustration.

[2] London Medico-Chirurgical Transactions, vol. xxii.

ourselves, it is incumbent upon us to endeavour to point out how the facts observed by Dr M. Hall can be included in the generalization for which we are contending, viz. that the property of contractility is inherent in the muscular fibre. Two circumstances likely to aid us in doing this, have suggested themselves: 1. As the muscles of the limb in which the sciatic nerve had been cut, could only be called into contraction by direct excitation of the muscular fibre, while the muscles of the limb in which the excito-motory movements were retained, could be called into contraction both by direct excitation of the muscular fibre, and also by excitation of the skin, it is obvious that the more vigorous contractions observed in the limb in which the nerve had been left entire, may have been partly dependent upon the galvanism acting as an excitant upon the skin in the one limb, and not in the other. That galvanism can act as an excitant upon the skin, and produce vigorous excito-motory movements, we have satisfied ourselves by experiment. 2. Though the muscles of the posterior extremity of a frog no longer respond to the motive influence of volition, after the spinal chord has been cut across, yet if the excito-motory movements remain, these muscles, as we have satisfied ourselves by experiment, may be occasionally thrown into contraction by various causes, such as the rubbing of the skin against the surface of the vessel in which the animal is placed, when it crawls onwards by the action of its anterior extremities, while those of the limb in which the nerve has been cut, remain perfectly quiescent. And if this be the case, it is obvious that these occasional muscular contractions in the one limb, may retard, or perhaps arrest, in the muscular bundles of that limb, those physical changes which are incompatible with the manifestation of the property of muscular contractility.

We believe that the facts and experiments we have here detailed, are sufficient to prove, that the property of muscular contractility is not derived from the central organs of the nervous system. We are also satisfied, that a careful consideration of all the facts and arguments adduced in support of the opinion, that the property of contractility is derived from the nervous filaments distributed in the muscular fibres, would prove that they have totally failed in effecting this purpose, and that here the evidence likewise preponderates considerably in favour of the Hallerian doctrine. Upon the examination of this part of the question, however, we do not intend, nor do we think it necessary, to make any remarks.