XIV. *Electro-Physiological Researches.—Eighth Series.* *By Signor* Carlo Matteucci. *Communicated by* W. R. Grove, *Esq., F.R.S.*

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I PROPOSED to myself in my former memoirs* to embrace under some general views the phenomena of muscular contraction, of the production of electricity in fishes, and of the relation between the electric current and nervous force. I shall now endeavour to redeem my pledge, thankful to Providence in being permitted to resume my studies, and to seek in them some alleviation of the profound grief occasioned by the recent disasters of my country.

Previously to giving an account of my recent researches, it will be advisable to recall, in a few words, the leading results which may be said to form the summary of my former studies on electro-physiology, and which have been the starting-point of my later investigations.

1. A constant development of electricity takes place in all animal tissues, and principally in the muscles. All the laws of the muscular current, which have been established by a great number of experiments, lead to the conclusion that this development of electricity is owing to the chemical actions of nutrition, and particularly to that of muscular fibre on arterial blood. This electro-physiological phenomenon is therefore simply dependent on a general physical law: we may compare a muscle in which arterial blood circulates, conveying thither the elements of nutrition, to a collection of particles of zinc surrounded by acidulated water. The two electricities separate, and are reunited instantaneously between the molecules of metal and of liquid. If we establish a circuit between muscular tissues and the parts which communicate with them, which do not suffer the same chemical action on the part of the blood, we obtain signs of an electric current the direction of which is already determined by the physical conditions of this source of electricity.

2. In each prism of the electrical organ of fishes, the two electricities are separated under the influence of nervous action propagated from the brain towards the extremities of the nerves: a relation exists between the direction and the intensity of the nervous current, and also between the position and the quantity of the two electricities developed in the prism: according to this relation, verified by experiment, if we represent (as Ampère did for electro-magnetic action) the nervous current by the figure of a man extended on the nerve and looking towards the tail of the torpedo, or the dorsal surface of the gymnotus, the positive electricity of the prism

* Phil. Trans. 1847.

is found invariably to the left of the man. We may account for the position of the poles at the extremities of each prism, and the intensity of the discharge being proportionate with the length of the prisms, by the fact that each prism of the organ is a temporary electrical apparatus, as has been proved by numerous experiments.

3. It is proved by experiments that the strictest analogy exists between the discharge of electrical fishes and muscular contraction; there is not a circumstance which modifies one of these phenomena without acting equally on the other.

4. The contraction of a muscle developes in the nerve with which it is in contact, the cause by means of which the nerve excites contractions in the muscle through which it is ramified. Although it has not been possible as yet to decide by experiment whether this phenomenon ought to be considered as a case of nervous induction, or as the proof of an electric discharge produced by muscular contraction, we are compelled by analogy to adopt the latter hypothesis.

5. The electric current modifies the excitability of the nerve which it traverses, in a manner which differs greatly according to its direction: the electric current which is propagated in the same direction as the ramification of the nerve, destroys its excitability: the current which is propagated in a direction contrary to that of the ramification of the nerve, increases its sensibility: the phenomena excited by the cessation of the electric current which traverses the nerves of the animal, are produced by the modification which the excitability of the nerve has undergone by the passage of the current according to its direction: the voltaic alternatives are explained by the same cause, which is as follows:—the muscular contractions are excited by a current which is made to pass in a contrary direction to that in which its action is nullified.

After having thus briefly recapitulated the fundamental conclusions which I have scrupulously drawn from my lengthened researches in electro-physiology, I shall begin the exposition of my recent studies on this subject by describing some experiments the application of which I shall give in the sequel. I wished to satisfy myself whether the nervous filaments which conduct an electric current into a liquid, are capable, like metallic wires, of acting as electrodes and giving rise to the production of electro-chemical decomposition. In order to ascertain this point, I plunged in a solution of iodide of potassium two large nervous filaments taken from living animals, each of which was separately attached to the metallic extremities of a pile of fifteen couples. I did not obtain the slightest trace of electro-chemical decomposition. I concluded from this experiment that terminals formed of nervous filaments cannot serve to obtain electro-chemical decomposition, which appears to me to demonstrate that the conductibility of nervous matter is due to the liquid part of the matter itself.

I studied again the relative conductibility of the muscles to that of the nerves: I had already discovered that one might estimate the conductibility of the muscle as four times greater than that of the nervous substance. I had also found that a hempen thread soaked in water, and a very fresh nervous filament, both being as nearly as possible of equal dimensions, presented resistances to the electric current in the proportion of 12 to 15. But the main object which I had in view in studying the relative conducting power of muscles and nerves, was to ascertain whether, when a current was impelled through a mass of muscle, any part of the current might have passed through the nervous filaments spread throughout that muscle. For this purpose I took a piece of muscle from the thigh of a rabbit, a dog, or a fowl which had been dead for sufficient time for muscular irritability to have ceased; I cut this mass of muscle with a knife, and introduced into the opening thus made the nerve of a highly sensitive galvanoscopic frog; I covered over the nerve and a part of the leg, endeavouring to envelope them perfectly in the piece of muscle. When the contractions, which often occur in the galvanoscopic frog itself immediately after it has been prepared, had ceased, I passed an electric current of from 25 to 30 elements of FARADAY through the mass of muscle, applying the poles to different parts of its surface. In whatever way I varied this experiment, provided I did not touch very close to the nerves of the galvanoscopic frog, this frog never entered into contraction, although a very powerful electrical current traverses in all directions the mass of muscle in which the nerve of the frog was contained. I have remarked already that in this experiment a mass of muscle must be employed in which all irritability is extinct, because if muscles are made use of which contract on the passage of the electric current, the galvanoscopic frog exhibits phenomena of *induced* contraction; we are convinced of this by observing that they cease when the muscular irritability has disappeared. We may therefore conclude from this experiment, that when the poles of a pile of 25 or 30 elements are applied to the surface of the muscles of a living animal, the phenomena produced by the passage of the current must depend either on the *direct* action of the current on the muscular fibre, or on the *indirect* action or *influence* of the electric current transmitted by the muscular fibre on its own nervous filaments, or, to express it more clearly, on the nervous force existing in these filaments.

Convinced of the great importance of this conclusion, I have varied these experiments in order to confirm them in different ways. I have already, in the commencement of this memoir, spoken of the difference of excitability produced in a nerve by an electric current according to its direction. This electro-physiological law is easily demonstrated by an experiment which I have detailed at some length in my memoirs*, and which is made by preparing the frog in the ordinary manner,—cutting it at the junction of the two thigh-bones, and then placing it astride between two glasses of water with one foot in one glass and one in another. When the two poles of the pile are plunged into the liquid (pure water) contained in the two glasses, it is obvious that one of the limbs is traversed by the electric current in the same direction as the ramification of the nerve, and the other in a contrary direction.

* Philosophical Transactions, 1846.

The experiment consists in this: that after fifteen or twenty minutes of the passage of the current, that limb only which is traversed by the inverse current, that is to say, in a direction contrary to the ramification of the nerve, contracts at the opening of the circuit.

When the frog is reduced to this state, if the nerve traversed by the inverse current is touched by a small portion of muscle, we see the limb instantly contract as if the circuit had been interrupted; and in fact the current ceases to pass through the nerve and enters the muscle on account of the greater conductibility of the latter substance.

I shall cite another experiment of the same kind. Having succeeded in modifying the excitability of the nerve by the passage of the current, as in the experiment just described, we can easily convince ourselves that this modification is confined to the exposed or isolated portion of the nerves. For if those portions of the nerves in both thighs, which had been previously buried in the muscles, be now laid bare, no alteration in their excitability is found to have occurred; but the altered excitability is limited to the pelvic portions of the nerves previously exposed and traversed by the current. It is evident that if the nerve, buried among the muscles of the thigh, were traversed by the current as its exposed portion above is, the modification of the excitability would extend through the whole length of the nerve. I repeat, therefore, once again, that when a muscular mass is traversed by an electric current, we are compelled to admit that no sensible quantity of that current is conducted by the nervous filament belonging to such muscle.

Another subject of research which has greatly interested me, and the exposition of which will precede that of the experiments which form the principal subject of this memoir, relates to the influence which the integrity of the nervous system exercises on the excitability of the nerves. In other words, supposing that a certain contraction is produced in the limb of a frog by the passage of a constant electric current through its lumbar nerves, would that contraction remain the same, or would it be increased or diminished were the spinal marrow to be cut? I had read in the 'Comptes Rendus' of the Academy of Paris an experiment by M. Bois Seguard, from which one would be led to conclude that the section of the spinal marrow increased the excitability of the lumbar nerve, at least during a certain period of time.

In order completely to satisfy myself on this point, which I consider as very important with regard to the theory of nervous functions, I was obliged to operate with the greatest possible exactitude, and to measure in every instance the contractions excited. In order to this I employed an apparatus invented by M. Breguet, the description of which I have given in my fourth memoir*. The results to be obtained from this apparatus are as exact as can be desired, provided the operation is carried on with sufficient patience, and that the necessary degree of practice has been acquired in the use of the machine. As it is necessary, in the first instance, that the current

* Philosophical Transactions, 1846.

should be constant, a WHEATSTONE's pile is the best adapted for the experiment. As the nervous filament by which the current is transmitted must be perfectly free from all trace of blood or other animal substance, it must be carefully cleaned, using a pair of forceps and lightly wiped with a piece of blotting-paper. It is also requisite that the gilded steel needle, which is introduced into the muscle of the thigh as nearly as possible to the insertion of the nerve, and which serves to complete the circuit, should, so far as is practicable, be always inserted in the same position in all the experiments. Lastly, care must be taken in choosing suitably the weight attached to the limb of the frog: if the weight be too small, the limb is not brought back to its position after contraction; on the other hand, if the weight be too great, the nerve is stretched, and the indications given by the apparatus are too small. I found that a weight of 0·600 gr. is the best adapted for the purpose.

I here give one of a series of experiments, undertaken with the view of resolving the question which I had proposed to myself.

I fasten a living frog to the clamp of the apparatus by passing a thread of silk round the thorax under the front claws: I then remove all the viscera of the abdomen, one of the limbs, and the muscles, as well as the bones of the pelvis: the frog, thus prepared, retains its natural liveliness for at least twenty or thirty minutes. I proceed to pass the *direct* current through the lumbar nerve, and I obtain contractions measured by the apparatus at 14°, 12°, 10°, 9°, 8°. I continue the passage of the current as short a time as possible, and close the circuits instantly after having opened them. The contractions first of all diminish rapidly, and then for a certain time they remain the same, if we are careful to leave the circuits closed as short a time as possible. When the deviation of the needle points constantly at 8°, I cut the spinal marrow of the frog, and pass the current again immediately: I have again the contraction 8° as before. I have frequently repeated this same experiment, and invariably with the same result. I also found that the duration of the contractions which persist the longest does not vary, in consequence of the section of the spinal marrow. It is therefore certain that the excitability of the nerve undergoes no immediate change after its separation from the nervous centre.

I then continued my investigations of this subject, conducting my experiments in a different manner from that already described, that is, by comparing the contraction of the muscular fibre excited by the passage of the electric current in a nerve which had been separated for several hours from the nervous centre, to that of another similar muscle the nerve of which had not undergone this operation.

It is hardly necessary to repeat, that, in order to the success of these experiments, BREGUET's apparatus must be used, employing the precautions already mentioned; the most indispensable of which is the careful removal of all traces of blood, &c. from the lumbar nerves of frogs submitted to these comparative experiments; they should also, as far as possible, be prepared in the same manner, so that their conditions should be similar.

I took the frogs as they came to hand, from among a considerable number, and divided the spinal marrow at about the middle. Twelve hours after this operation I began an experiment, preparing at the same time the frogs whose spinal marrow had been divided, and others which were intact.

In order that the comparison should be as perfect as possible, I employed successively in BREGUET'S apparatus for measuring contractions, two frogs, one of which had the spine divided, the other entire. In each experiment I operated on four frogs in the former, and four in the latter state. I made my experiments with a direct current, keeping the circuit closed as short a time as possible, and marking the variations of the needle of the dynamometer after ten or twelve passages of the current, because it is then only that the variations become constant; if the passage of the current in the same frog is prolonged, the variations gradually diminish; operating with a certain degree of dexterity, experiments on eight frogs may be completed in less than a quarter of an hour.

The following are the results of two experiments:—

Exp. 1.

Contraction of a frog the spinal marrow of which had been divided 12 hours.		Contraction of a frog with the spinal marrow entire.
16°	to 14°	14°
18	20	18
18	16	12
20		12
20		12

Exp. 2.

After 18 hours.		
24°	to 22°	8°
22	24	10
22	16	12
17	16	12

According to these results, and others of the same kind, which it is unnecessary to give here, it is clearly proved by experiment that the contraction excited in the muscles of a frog, of which the spinal marrow has been divided from twelve to eighteen hours, is stronger than that which is obtained under the same circumstances from the muscle of a frog immediately after it is killed, without having been previously subjected to any alteration in its nervous system.

An observation which I had occasion to make in all my experiments, gave me some insight into the cause of this singular phenomenon. If a vigorous frog is rapidly prepared and subjected to experiment in the dynamometer, the first contractions which are obtained are very feeble, particularly if the weight attached to the limb, to bring it back to its position after the contractions have ceased, be extremely small. If we continue to operate on this same frog, we see the contractions become stronger and increase during a certain time. In all cases the muscles of frogs killed and prepared rapidly, are stiff, and seized with a kind of tetanic contraction; while the muscles are in this state, the contractions which are obtained by the passage of the electric current are necessarily less strong than those which are developed when these same muscles have ceased to be contracted naturally.

After having repeated some experiments of this kind with the dynamometer, I soon came to the conviction that this was the real cause of the phenomenon under observation. I shall only give one of these experiments, which proves the truth of this explanation.

I operated on very vigorous frogs, four of which had had the spinal marrow divided twenty-four hours before experiment, and four other similar frogs which were intact.

The following are the numbers found immediately after the preparation:—

Contraction of the frog of which the spinal marrow had been divided for 24 hours.	Contraction of the frog in the natural state.
30°	26°
28	24
26	24
24	20

I left the frogs untouched for forty minutes, and then repeated the experiment: the following are the results:—

10°	22°
8	20
8	16
8	16

The difference of contraction obtained in the two experiments is therefore evidently due to the state of the muscles differing in the two cases, according to whether the frog was submitted to experiment immediately after death, or whether it had had the spinal marrow divided for a long time, and consequently the muscle relaxed for a considerable period. The contractions excited by the electric current in a frog immediately after death, are feeble at first, on account of the nearly tetanic condition of the muscles; whereas, if left in repose, so as to give time for the muscles to become relaxed, the contractions then excited by the current are stronger. The contrary to this occurs if the experiment be made on a frog the muscles of which have been for some time without contraction, in consequence of the spinal marrow having been divided ; the contractions are very strong at first, but they soon diminish in strength, and that rapidly.

It would therefore be a mistake to conclude that muscular contraction increases because the nerve traversed by the electric current has been separated from the nervous centre: we have seen what is the true explanation of the phenomenon, and that this conclusion is only apparent.

On the other hand, these experiments prove, as did also those of the preceding section, that the excitability of a nerve is not altered by its separation from the nervous centres, or, rather, that the only alteration which it undergoes consists in the increased rapidity with which the excitability diminishes under the action of stimulants. Thus, the contraction produced by the passage of an electric current through a nerve is sensibly the same, whether this nerve be in communication with the nervous centres, or separated from them for several hours, or an instant after the separation has been effected: when the action of the current is repeated, its effects diminish the more rapidly exactly in proportion to the length of time which has elapsed since the separation of the nerve from the nervous centre.

I think it is scarcely necessary for me to remark, that these conclusions are not contrary to those of MÜLLER and LONGET; according to which it was shown that when the nerves had been separated from the central mass, for weeks and months, the sensibility of these nerves and the irritability of the muscular fibre were diminished. M. LONGET has given the interpretation of this phenomenon, grounded on experiment.

In order to complete the first part of this memoir, I now proceed to relate the experiments and considerations by which the strict analogy existing between electricity and nervous force, together with the nature of that analogy, are demonstrated in a most satisfactory manner.

At the beginning of this memoir, referring to my preceding researches in electro-physiology, I mentioned the law according to which, by the influence of the nervous current, a development of electricity takes place in the organ of electrical fishes. We shall now consider what may be called the converse of this phenomenon, that is to say, the development of nervous force under the influence of the electric current, which development is produced exactly according to the same law as that of electricity by nervous force. This influence of electricity on nervous force is manifested in the muscular fibre: we have already observed at the beginning of this memoir that the phenomena presented by the organ of electrical fishes, as well as those of the muscular fibre, together with the modifications of these phenomena under various circumstances, invariably followed the same course, and preserved the strictest analogy with each other, so that what was true with regard to the electrical discharge of the torpedo, was equally so with regard to muscular contraction.

This fact admitted, we proceed to the experiments.

Expose in a living dog, rabbit or frog, the muscles of the thighs, removing entirely the skin and membranes, then transmit through the muscles the electric current from an ordinary pile of from 30 to 40 elements, applying one of the poles to the upper, and the other to the lower part of the thigh. If the positive pole is placed above and the negative below, the current traverses the muscle in the same direction as the ramification of the nerves; the contrary is the case if the position of the poles be reversed.

Experiments of this kind date from the earliest times of galvanism; but the difficulty in these researches of separating truth from error, that which is constant and invariable from that which is merely accidental, and, above all, the still imperfect state of electro-physiological science, have hitherto prevented the attainment of any positive conclusions.

In experiments on this subject, great precaution is necessary in order to be certain that the electric current does not traverse the nervous filaments of the muscle; this certainty is obtained, as we have already seen, by keeping the poles of the electrical pile in contact with the surface of the muscle, at the greatest possible distance from the nervous filaments which spread through its interior. We must carefully remove from the surface of the muscle all traces of blood or other liquids; and I have generally been in the habit of applying one pole to the upper and the other to the under surface of the muscle.

When the electric current traverses the muscular mass of the thigh of a living animal in the same direction as the ramification of the nerves, a very strong contraction always takes place, which contraction is excited not only in the muscle directly traversed by the current, but also in the inferior muscles of the leg and in the foot.

When the electric current traverses the muscular mass in the contrary direction to that of the ramification of the nerves, the animal utters loud cries, and gives other indications of suffering severe pain, accompanied by contractions much less violent than in the preceding case, and which never extend beyond the muscles traversed by the current.

If we were to satisfy ourselves with seeing these experiments once only, or were to confine ourselves to a few trials only, we might easily be led to form an erroneous conclusion; in fact, at the beginning of the experiment, particularly if a somewhat powerful current be employed, there are both cries of pain and contractions at the same time; but this soon ceases, particularly if we know how to regulate duly the strength of the current. The constant effects which distinguish the action of the electric current, according to its direction, in the muscles of living animals, are those which I have indicated, namely, pain, when the electric current is what is commonly called inverse,—contraction, when the current is direct.

Now, setting aside all hypothesis, there can be but one way of explaining these phenomena: when there is a contraction, there must necessarily be a current of nervous force propagated from the brain towards the extremities of the nerves: when there is a sensation of pain, this current must be impelled in a contrary direction, that is, from the nervous extremities towards the brain. We must bear in mind that it has been demonstrated by direct experiments, that when an electric current is propagated in a muscle, this current never quits the muscular fibre in order to pass into the nervous filaments. It is therefore perfectly evident that the phenomena of which we have spoken, excited by the passage of the electrical current through a mass of living muscle, are exclusively owing to the *influence* of electrical states propagated in the muscles upon the nervous force contained in the nerves. To speak with more precision, we should say thus: it is demonstrated by experiment that an electric current transmitted through a living mass of muscle in the same direction as its nervous ramification, developes a nervous current which is propagated in the direction of the ramification of the nerve, and which reaches to its extremities; if the electric current pass in a contrary direction to that of the ramification of the nerve, the nervous current which it developes follows the same direction, that is, from the extremity of the nerve towards the brain.

The great importance of the conclusions drawn from these experiments consists in this, that they lead to the same law which establishes the analogy between nervous force and the electrical discharge of fishes.

We obtain an electrical discharge in fishes, when we produce a nervous current by stimulating the nerve which communicates with the organ. In experimenting on living animals, we produce a nervous current by the electric discharge which we transmit through the muscles. When this discharge is directed through the muscle in such a way as that the positive and negative states of electricity are disposed relatively to the ramification of the nerves, as in the discharge of electrical fishes, a nervous current is produced by the influence of the electric current having the same direction in both cases; in the torpedo, the nervous current produces the electrical states; in the muscular fibre, the nervous current is produced by the influence of the electric current.

Following up the analogy, we are led to expect that when the electric current traverses a muscular mass in a contrary direction to that of the ramification of the nerve, it would produce a nervous current in an opposite direction to that which is developed by the electric current passing along the muscle in the same direction as the ramification of the nerves. This is a conclusion the truth of which is clearly demonstrated by the phenomena of sensation or of pain, which are produced by the passage of the electric current in a contrary direction to that of the ramification of the nerves.

Satisfied to go forward with a slow but sure step in the vast and very obscure field of electro-physiological science, I cannot but regard as highly important the discovery set forth at the close of this memoir, of the strict correlation existing between the electric current and nervous force.

Pisa, June 1849.