IX. *Electro-Physiological Researches. Physical and Chemical Phenomena of Muscular Contraction.—Tenth Series.* Part I. *By* Carlo Matteucci, *Professor in the University of Pisa. Communicated by* Michael Faraday, *Esq., D.C.L., F.R.S. &c.*

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The present Series of these Researches is divided into two parts: in the first I propose to treat of the development of heat, electricity, and *vis viva*, by the muscle in a state of contraction; in the second, of the chemical changes produced by the muscle in contraction on the air.

PART THE FIRST.

§ 1. That the temperature of an animal is raised by muscular exercise, is a fact generally admitted and proved by common experience. M. Becquerel having introduced the point of a thermo-electric pile into a muscle of the human body, found an increase of temperature during contraction which amounted to a degree Centigrade: Mr. Newport also discovered a remarkable increase in the temperature of insects while in movement. M. Becquerel attributed this increase of temperature in muscles during contraction to the greater activity of sanguineous circulation which apparently takes place in a muscle in that state. In support of this interpretation, M. Becquerel showed, that, by compressing one of the large arteries distributed in a muscle under experiment, an immediate decrease of temperature takes place in that muscle. M. Bernard discovered an increase of heat in one of the ears of a rabbit or dog after having cut the cervical ganglion connected with the nervous filament of that ear: this remarkable fact is also associated in some unknown manner, depending on the peculiar action of the ganglionic system, with a more rapid capillary circulation of blood in the ear in which the temperature is highest. It remained therefore still to be proved by experiment whether an increase of temperature is produced by the act of contraction in a muscle which is separated from the body, and as far as possible is devoid of blood, in which consequently sanguineous circulation is extinct. The experiment was easily made and the result not doubtful.

I employed for this purpose two thermometers such as those used in M. Regnault's hygrometer, and constructed by M. Fastrè. The cylindrical bulb of these thermometers is very small, and by means of a telescope I could read distinctly variations of $\frac{1}{20}$th of a degree Centigrade. I had two cylindrical wide-mouthed glass bottles of about 100 cub. cent., provided with good cork stoppers. One of these corks was traversed by two thick copper wires, pointed at the extremities, and bent round horizontally parallel with each other, so as to leave an interval of 10 to 12 millimetres between them: the other cork was furnished with five hooks. A hole was bored through the middle of these corks, through

which the thermometers might be introduced into the bottle. Five frogs were then got ready in the usual manner, that is, by cutting off the heads, and removing the skin and viscera; when thus prepared and wiped dry, they were fixed on the two copper wires by passing these through the pelvis, and the cork with the frogs thus attached, was applied to the mouth of one of the bottles. In the bottom of the other bottle I put five other frogs similarly prepared, or suspended them on the hooks fixed in the cork; in some experiments instead of frogs I put a little water in the second bottle: the two bottles thus prepared with their thermometers, were placed in a room free from currents of air. I then observed the two thermometers: after the lapse of some minutes the column of mercury inserted in the midst of the frogs remained at the same division, or at least it was only after the lapse of many minutes that a diminution of $\frac{1}{20}$th of a degree was visible. In one of the experiments I found the temperature of the bottle in which there were no frogs to be $+12^{\circ}\cdot60$, while that of the bottle containing the frogs remained fixed at $+13^{\circ}\cdot10$. Then by means of two or three small elements of DANIELL, I set in activity a little electro-magnetic machine constructed by FROMENT, remarkable for the uniform sound which it produces when the circuit is closed. On connecting this machine with the two copper wires which issue from the cork of the bottle containing the frogs, the frogs contracted violently from the action of the interrupted current on the lumbar nerves; almost at the same instant the column of the thermometer began to rise, and after a lapse of five or six minutes stood at $+13^{\circ}\cdot50$. If the experiment is prolonged, this temperature is maintained for many minutes. The copper wires used in this experiment must be thick, in order to prevent their being sensibly heated by the passage of the current: I assured myself of this by direct means, which I shall shortly describe.

In another experiment, in which the temperature of the bottle without frogs was $+12^{\circ}\cdot80$, and that of the five frogs $+13^{\circ}\cdot50$, the temperature of the latter rose to $+13^{\circ}\cdot95$. After an hour's repose I recommenced the experiment on the same frogs; the temperature, which was now $+13^{\circ}\cdot40$, rose only to $+13^{\circ}\cdot60$ after the renewal of the contractions, which were naturally weaker than at first.

Finally, in another experiment in which there was no sensible difference between the temperature of the frogs and that of the air, the temperature of the frogs after four or five minutes' contraction rose from $+13^{\circ}\cdot55$ to 14°, where, as usual, it remained constant for a certain time. This experiment was repeated after an interval of fourteen hours; the passage of the current which had no longer any physiological action produced no sensible increase of temperature.

It is therefore proved *that living muscular tissue developes heat by the sole act of its contraction* *.

* This result may be easily shown by employing, instead of thermometers, two thermo-electric pincers of bismuth and antimony, terminating in points. The point of each pair of pincers is introduced into each of the severed thighs of a prepared frog. The strips of the same metal of each pincer are brought into communication, and the other two strips are united to the end of a delicate short-wired galvanometer. On producing contractions, by any means, in one of the thighs, the needle is deflected, indicating heat in the convulsed thigh.

Perhaps it may not be devoid of interest to note the result of a comparative experiment made on the same number of frogs similarly prepared, and suspended in the same way in two separate bottles, with this difference only, that the frogs in one of the bottles had been firmly bound together with a ribbon wound many times round them: the passage of the interrupted current through the lumbar nerves could not awaken in the latter any general movement of the limbs, but produced a palpitation in the muscles which appeared to diminish rapidly. The frogs thus confined showed an increase of temperature during the passage of the current, but to a much less degree, being in each of the two experiments about one-third less than that of the frogs which were suspended freely.

§ 2. I now proceed to treat of the development of electricity in muscles during contraction.

Before entering more fully on this subject, I think it advisable to describe some new researches on muscular electricity. Two methods have been hitherto followed in order to arrive at a rigorous demonstration of the principal facts and laws of muscular electricity. In one of these methods the muscular elements are united in form of a pile, and the intensity of the muscular current increases with the number of muscular elements of the pile: this fact suffices to exclude any doubt of the existence of electromotive power which might be generated by the platinum plates of the galvanometer, or by the liquid, in which the pieces of muscle forming the outer elements of the pile are plunged. This doubt is also excluded by employing the nerve of the galvanoscopic frog instead of a galvanometer.

The other method, which is that employed by NOBILI and myself in my earlier researches on the electrical current of the frog, has been greatly improved by M. DU BOIS REYMOND, who has rendered it sure and of easy application. The apparatus of M. DU BOIS REYMOND consists, as is well known, of two small glasses, in each of which is laid a thick strip or cushion formed by numerous layers of blotting-paper or flannel; one extremity of this cushion touches the bottom of the glass, while the other rests on its edge so as to form a short horizontal stratum. By means of two little wooden columns, the platinum plates of the galvanometer are held vertically in the liquid, which is a solution of common salt, and remain in constant contact with the paper or flannel cushions above described. At first the two cushions are held in contact until all heterogeneity between the platinum plates has ceased; the two glasses are then drawn asunder, so as to leave a small interval between them. A gastrocnemius or a half-thigh of a frog laid on a narrow strip of gutta-percha held in the hand, is placed in contact with the conducting cushions so that the circuit is closed with the extremity of the muscle. The initial or impulsive deflection of the needle, which is of 40° or 50°, when the galvanometer is very delicate, ceases almost immediately if one element only is employed instead of a pile: if the muscle is removed and the conducting cushions are brought into contact, there is a great deflection in the opposite direction, owing, as is already known, to polarization. I had learnt from many experiments made long since on the electrolytic action of induced currents, that the best way of avoiding polarization is the substitution of care-

fully amalgamated plates of zinc for those of platinum, and the use of a saturated solution of chloride of lime or sulphate of zinc, as liquid. The merit, however, of this great improvement in the apparatus for electro-physiological researches is due to M. J. REGNAULD, as this young physicist was the first who published it, he having employed plates of distilled zinc instead of platinum. Now that the existence of muscular electricity, and that of its principal laws, is proved beyond all doubt, we may freely employ this method, the advantages of which will shortly be seen, without fearing, as formerly we justly did, errors which might be introduced into the experiment by the use of zinc electrodes and highly conducting liquids. I need only cite the following instance to show the great difference which results from this mode of making the experiment. With plates of platinum and diluted solution of common salt which I am in the habit of employing, either a gastrocnemius or a half-thigh of a frog of ordinary vigour produces, with a galvanometer of 24,000 coils, a deflection of 30° or 40°, which in a few seconds decreases to 2°, then 1°, and soon ceases almost entirely. With plates of amalgamated zinc immersed in sulphate of zinc, all heterogeneity between the plates having ceased, a gastrocnemius or half-thigh gives at the first impulse a deflection of the entire quadrant, the needle then rests at 70° or 80°, and descends extremely slowly; when the muscle is taken away and the needle fixes at 0°, no sign of polarization is obtained by bringing the two conducting cushions into contact.

I shall now state the results of my recent researches on the muscular current in some general propositions: the experiments of which I shall have occasion to speak have been so often verified that they may be easily repeated without uncertainty.

Prop. I. *The electromotive power of a cut muscle is independent of the size of its transverse section.*

Several half-thighs of frogs of equal vivacity are prepared of the same length, taking care to leave no portion of muscle beyond the articulation of the leg. These half-thighs are ranged opposite to each other in pairs, in order to ascertain the equality of their electromotive power; any elements which are unequal are rejected. Five or six of these half-thighs, laid closely one upon the other in the same direction, are then piled upon the usual gutta-percha holder; a single half-thigh is opposed to this heap. The circuit is closed, and the differential current is either null or very small, sometimes in the direction of the single thigh, sometimes in that of the heap. I repeated this experiment with two elements only, *i. e.* with two half-thighs taken from frogs of different size and weight; the difference of weight between these elements was as between 1 and 5 or 1 and 6. It is easy to perceive that this method is less exact than the former, since the larger frogs are more robust in the same conditions. The differential current was always extremely weak, but in the greater number of cases the direction was determined by the largest, and consequently most robust element.

Prop. II. *The electromotive force of the muscle increases with its length.*

This proposition may also be established by the differential method. Take two half-thighs of equal length, and which have the same electromotive power. Reduce by a

fresh section one of these half-thighs to a third or fourth of its length, and recompose the double pile. A differential current arises due to the longest half-thigh. The same experiment may be made on two gastrocnemi, which, however, are rarely to be obtained of equal electromotive power. Two gastrocnemi, as equal as possible, are opposed, after having previously made in each a transverse section towards the tendo Achillis: if the two muscles thus prepared are of equal length and taken from the same frog, it is almost certain that there will be no differential current. One of these gastrocnemi is then reduced to one-half or one-third of its length, the double pile is again formed, and the differential current is immediately produced by the longest muscle. I ought to remark here that these experiments should be made with the usual platinum plates in diluted saline solution: in employing amalgamated zinc plates and solution of sulphate of zinc, the smallest differences of the electromotive power produce strong and durable currents, and hence it is difficult to have the two muscular elements sufficiently equal to admit of comparison.

When, by a fresh section, the length of one of the elements is diminished, as a further precaution, an exceedingly thin section should be made in the other element. If a small difference exists between the electromotive power of two elements of equal length, the strongest ought to be shortened.

This experiment is still more striking when made on a strip of the long muscle of the spine of a living rabbit; the surface and transverse section of this muscle may be touched with the plates of the galvanometer so as to have a muscular stratum interposed of either 8 to 10 or 70 to 80 millimetres. The current in the second case is eight or ten times greater than in the former. This experiment recalls that made on the electric organ of the Gymnotus or the Torpedo, by employing strata of various lengths of this organ. I think, that, notwithstanding our ignorance as to the form of the electromotive element of muscles, this proposition leads us to believe that muscular fibre acts as a reunion or series of electromotive elements.

This proposition furnishes a clear explanation of several important facts of muscular electricity. The first of these facts is, that a differential current takes place constantly on closing the circuit with the gastrocnemius of a frog united with its half-thigh, the current being determined by the gastrocnemius. The experiment succeeds equally, if, instead of leaving the tendon attached to the gastrocnemius, the latter is cut transversely: in all cases it is essential that one of the muscles be longer than the other, so that either the gastrocnemius or the half-thigh may predominate. The same result may be obtained by employing a prepared frog reduced to two half-thighs of unequal length attached to a piece of the spine.

This same proposition leads us to explain the fact discovered by M. Du Bois Reymond, namely, that a current is obtained by touching with the plates of the galvanometer the central points and the edge of the same transverse section of a large muscle. In fact, the central points belong to the longest muscular fibres, and therefore play the same part towards the points near the edge of this section belonging to the shortest fibres, as the interior of a muscle towards its surface.

I take this opportunity of calling attention to a fundamental difference existing between a muscular electromotor and a voltaic pile. Let us take an entire muscle, such as the thigh of a frog, and cut it in half: it is known that the two sections thus formed have the same electrical state, and that a pile can be formed by placing in contact the internal section of one of the half-thighs with the superficies of the other. This result cannot be obtained with a voltaic pile: on the other hand, the proposition which we are now considering, leads us to admit a certain analogy between a muscular electromotor, and the organ of electric fish or the voltaic pile.

The relation existing between muscular electricity and the physiological conditions of muscle, forms the subject of the next proposition.

Prop. III. *The electromotive force of muscles, in living or recently killed animals, is greater in mammifers and in birds than in fish and in amphibia: the duration of this force, which in all cases decreases most rapidly in the first moments after death, is greater in fish and amphibia than in the muscles of the higher orders of animals. The nerves have no direct influence on the electromotive force of muscles. In general, all the causes which exert an influence on the physical structure and chemical composition of muscle, to modify in ways unknown its irritability or contractility, act equally on its electromotive power.*

This proposition is founded on experiments which I have already published, and particularly on those described in the Memoirs contained in the Philosophical Transactions. Since their publication I have frequently repeated and varied these experiments, employing the new method above described, and have succeeded in fully confirming them. I shall here only add a very brief description of some of these experiments, which place the existence and nature of muscular electricity in the clearest light. The object of the first of these experiments is to compare the electromotive power of the muscles of pigeons, rabbits and frogs.

For this purpose, I form, with muscles of these animals rapidly prepared, the usual elements which I oppose to each other. I form thus several double piles of muscular elements of frog and pigeon, of frog and rabbit, of pigeon and rabbit, and I measure successively the differential currents of these piles, closing the circuit of the galvanometer with the usual platinum plates. At first, the electromotive power of the muscles of the pigeon and of the rabbit greatly predominate over that of the muscles of the frog. After twenty or thirty minutes the differential current is null, or already inverted, and after the lapse of an hour or more, this inverted current, due to the muscles of the frog, is remarkably increased: this takes place in the pile of pigeon and frog sooner than in that of rabbit and frog.

Another very conclusive experiment is made on muscles exposed to great cold. Several gastrocnemi and half-thighs of frogs are left in a glass tube, surrounded by a mixture of salt and ice: after twenty or thirty minutes it is found that these muscles have entirely lost their electromotive power. By forming the usual piles with frozen and unfrozen muscles opposed, we acquire the certainty that the frozen muscles have lost their electromotive power, but not their conductivity. If we operate on muscles of frogs which have perished in nitrous or hydrosulphuric acid, we obtain the same results as from frozen muscles.

Before quitting this subject, I gladly avail myself of this opportunity of mentioning an important fact discovered by M. Du Bois Reymond. From the period of my earliest researches in electro-physiology, I had vainly endeavoured to obtain electrical phenomena from the nerves of a living animal, or of one recently killed; and even now it is demonstrated, that, notwithstanding the use of the most delicate modern galvanometers, no sign of electrical current is to be obtained from a nerve laid bare in a living animal and left in its natural state. M. Du Bois Reymond has, nevertheless, demonstrated, and the fact is easily verified with a very delicate galvanometer, that a piece of nerve detached from a living animal prepared and disposed in the same way as a half-thigh, in the circuit of the galvanometer, produces constantly an electric current, which, like that of the muscle, is directed from the surface of the nerve to the interior in the galvanometer. I have proved, by experiments made on pieces cut from the lumbar nerves of a frog, that the intensity of the current of the nerves increases with the number of elements united to form a pile, and that a pile of five or six of these elements acts on the nerve of a galvanoscopic frog and excites contractions. I have compared the electromotive power of a muscle with that of a nerve, both belonging to the same frog. It is hardly necessary to say that this was done by opposing to a half-thigh as many nervous elements as were required in order to there being no differential current. In two experiments I found that one half-thigh predominated over seven nervous elements, and that nine of the latter predominated over one half-thigh; in a third experiment eleven or twelve nervous elements were required to predominate over the muscle. I left these piles under a glass bell, the air of which was saturated with moisture; I could not perceive any marked difference in the relative duration of the electromotive power of muscles and nerves.

§ 3. Let us now pass on to the development of electricity in the act of contraction. The first fact of this kind, which, for the sake of brevity, I shall continue to call *induced contraction*, was discovered by myself in 1842. I shall give here a very concise summary of the chief characteristics of induced contraction, although already known, having recently been led to repeat my former experiments, and to determine these characteristics with greater precision.

In order to succeed in these experiments, it is necessary to operate on frogs in a vigorous condition, and prepared very rapidly. The fundamental experiment is made by laying the nerve of a galvanoscopic frog upon any muscle of a living animal. In order to simplify the experiment, I employ a single thigh of a frog, to which remain united the lumbar nerve and a portion of the spine. On provoking contractions in the thigh, either with an intermittent current sent through the nerve, or by stimulating it in any other way, simultaneous contractions take place in the galvanoscopic frog. The disposition of the nerve stretched over the thigh is immaterial, as is also to a certain degree the length of the nerve put in contact with the muscle, as long as the muscle and the galvanoscopic frog are vigorous. I have frequently seen the strongest effects of induced contraction when the nerve of the galvanoscopic frog, isolated from the operator, was in contact with any portion of the surface of the thigh for 2 or 3 millimetres only; it is therefore by no means essen-

tial for induced contraction that the nerve of the galvanoscopic frog should give signs of muscular current at the moment in which it is laid on the thigh. The internal part of a muscle may also be used for obtaining this phenomenon; this is done by immerging the nerve of the galvanoscopic frog in a longitudinal wound made in a muscle. From this we may infer that a phenomenon of the same kind as that of induced contraction takes place on a whole living animal, when an electrical current makes one of the muscular masses of the upper part of a limb contract: although it may be admitted that the nervous filaments concealed in that mass, and which pass through it as they branch towards the inferior muscles, are not traversed by the current on account of their low conducting power, yet at the moment in which the superior muscles contract, the lower ones contract also. This fact, of which I treated in the Eighth Series of my Researches*, appears to be thus traced up to its true cause, namely, that it is a natural and perhaps physiological case of *induced contraction.*

I shall add, finally, that when a stratum, however thin, of a good conducting body, or a like stratum of a solid isolating body, is interposed between the muscles in contraction and the nerve of the galvanoscopic frog, no *induced contraction* is obtained, as may be verified with gold-leaf or an extremely thin lamina of mica; on the contrary, with a piece of wet paper, and also with an excessively thin stratum of liquid turpentine, the phenomenon continues to manifest itself.

The many fruitless efforts which I made, and even the contradictory results at which I arrived, in endeavouring to determine the cause of *induced contraction* by means of the galvanometer, are well known. Although, as far back as 1838, in verifying the observations of GALVANI, I had assured myself that when a frog enters into violent contractions, or into a state of tetanus, its muscular current is much weakened, yet I had never succeeded in discovering by the galvanometer in a distinct and certain manner, what took place in this current during contraction. I am now convinced, as I shall shortly show, that my want of success was due to defective instruments and method. In the Ninth Series of these Researches†, having given up the use of the galvanometer, and substituted that of the galvanoscopic frog, I succeeded in establishing the true nature of that phenomenon on which the present researches will throw a new light, proving beyond all doubt *the production of an instantaneous electrical discharge in the muscle during the act of contraction.*

But before proceeding to the exposition of my new researches, it is just that I should say to what point M. DU BOIS REYMOND has brought this subject. The use which this philosopher had made of a highly sensitive galvanometer, and of an electro-magnetic machine for exciting sustained contractions, accounts for his having succeeded in obtaining from muscles in contraction a distinct electrical effect on the galvanometer. The well-known fundamental experiment of M. DU BOIS REYMOND is made by closing the circuit of the galvanometer with the gastrocnemius of a frog which remained united to its nerve; when the needle comes to rest, M. DU BOIS REYMOND provokes contractions in the gastrocnemius by sending interrupted currents through the nerve:—"At the moment in which the

* Philosophical Transactions, 1850.

† Philosophical Transactions, 1850.

muscle begins to be convulsed, the needle is deflected through the zero-point, and is seen to oscillate on the negative side of the zero, until the contracting power of the muscle is exhausted, which always happens before the needle has had time to come to rest*." This fact, which M. Du Bois Reymond has analysed with much care, is interpreted by him in the following manner, which, for the sake of greater exactitude, we give in the words of the above-cited *abstract*, which are in accordance with the opinion repeatedly expressed by the author himself in his original work†:—"At first it might be supposed that this showed a current during the tetanus in a direction contrary to that during rest; but this is not the case. Before the tetanus begins, the secondary polarity is evolved on the platinum plates in the conducting vessel. This polarity tends to produce a current in the opposite direction to the muscular current. As soon, then, as the muscular current, in consequence of the tetanus, diminishes to a certain degree, the current of the secondary polarity becomes the more powerful, and the needle is instantly deflected to the negative side‡." M. Du Bois Reymond evidently admits that the electromotive power of a muscle decreases in the act of contraction, which is equivalent to saying that in all cases of *induced contraction*, considered as owing to a negative variation of the muscular current, as well as in all his experiments of this kind made with the galvanometer, the muscular current ought necessarily to circulate previously either in the nerve of the galvanoscopic frog, or in the wire of the galvanometer.

I can only refer here to the descriptions of experiments contained in the Ninth Series of my Researches on Electro-physiology §, several of which prove very clearly that induced contraction is obtained in conditions in which the previous circulation of the muscular current cannot be verified.

On the other hand, I was thus impelled to redouble my efforts to arrive at a clear idea of the phenomena of *induced contraction*, and I feel satisfied in being now enabled to say that I have at length succeeded in attaining my object. I shall be as concise as possible in describing the three principal experiments on which my last conclusions are founded.

It is not necessary that the galvanometer employed in these experiments should be the most delicate, that is, of 24,000 coils, an ordinary one of 1500 or 2000 coils being sufficient for the purpose. The metallic plates with which the circuit is closed should be of zinc, perfectly well amalgamated, that is, recently immersed in diluted sulphuric acid, then in pure mercury, and afterwards washed repeatedly in water. The two plates thus prepared, plunge in a saturated and neutralized solution of sulphate of zinc contained, as before described, in two small glasses, provided with strips or cushions of paper or flannel which imbibe the liquid in the manner adopted by M. Du Bois Reymond. If

* "On Animal Electricity," Abstract of the Discoveries of Émil Du Bois Reymond; edited by Dr. Bence Jones, p. 132.

† Untersuchungen über thierische Electricität.

‡ "On Animal Electricity," Abstract of the Discoveries of Émil Du Bois Reymond; edited by Dr. Bence Jones, p. 134.

§ Philosophical Transactions, 1850.

these cushions are left for a certain time in contact, the needle rests at 0°, and no sign of current is visible on reopening and closing the circuit again.

Exp. 1. I lay on the quadrant of the galvanometer, exactly in contact with the end of the needle in its state of equilibrium, a solid body, which may be either a piece of marble or glass, provided it is dry and polished: the needle resting against this support is prevented from deflecting in one direction, and is free to move only in the opposite. I then lay on the usual strip of gutta-percha either one gastrocnemius, or five or six of these muscles so as to form a pile; I close the circuit in such a way that the deflection cannot take place in the direction in which the needle is prevented from moving, and I leave it closed for some seconds. I then withdraw the pile rapidly, and close the circuit between the two glasses immediately. The needle remains motionless; there is therefore no sign of secondary polarity; and it was foreseen that, in employing this method, there could be none, although the electromotive power brought into action was much stronger than that with which we were to operate subsequently.

Exp. 2. I prepare a vigorous frog which I reduce to two thighs, one of which only is left with its lumbar nerve intact; this nerve is supported on a piece of gutta-percha destined for the purpose. I close the circuit by touching indifferently any two points of the thigh, which are not necessarily the extreme points; it is enough if there be a distance between them of about 12 or 15 millimetres. With a common galvanometer the deflection is small; with the most delicate one it varies from 50° to 60° and upwards, in the direction of the usual current of the thigh, that is, in the direction of the current of the gastrocnemius. I had left the other thigh, though it ought not to form part of the circuit, in order to avoid the possibility of the interior of the muscle in the upper part of the thigh submitted to experiment becoming part of the circuit. Having allowed the needle to fix, keeping the thigh in its place by pressing slightly on it with a piece of gutta-percha (which occasions little or no variation in the deflection), I begin to excite the nerve with an extremely weak interrupted current; for this purpose I prefer a small pile of zinc and platinum wires which I hold in hand, to an electro-magnetic machine, although I do not believe it probable that the use of that machine can cause any error in the experiment. At the very moment in which the thigh begins to contract, the needle descends towards 0°, and the contraction continuing, the needle passes beyond it and comes to rest on the opposite side. When we cease to excite contraction, or when the contractions are weakened from natural lassitude of the muscle, the needle descends again slowly and deflects in the same direction as at first, but rarely attains the point reached at the beginning. This experiment, repeated with the gastrocnemius, gives the same result, as also with the entire muscles of other animals. I prefer, however, as will be readily understood, the use of a single entire thigh of a frog, in order that the muscular current which circulates at the beginning of the experiment may be as small as possible. Among the numerous experiments which I have made, the muscular current has often been excessively weak, sometimes so weak as to leave the needle at 0°. During the contractions the deflection was in the same direction as that found when the needle

was deflected first in the opposite direction, and that deflection was certainly not inferior to the one in the second case.

Since no secondary polarity can interfere in these experiments (Exp. 1), they prove, that in the act of the contraction of these muscles, an electrical current, which, from its instantaneousness, I shall call electrical discharge, takes place, which circulates in the external conducting arc in a direction contrary to that of the muscular current.

Exp. 3. I make a small incision in the upper part of the thigh of a frog, in order to lay open the inside of the muscle: it is easy to understand, that, on closing the circuit with the two extremities of this thigh, the current, which in this case is differential, is null, or is in an opposite direction to that of the usual current of the thigh. The needle having been allowed to come to rest, and the usual contractions excited, the deflection which is obtained is always in the same direction, that is, opposed in the external arc to the usual current of the thigh when it has not been cut. Hence, if the needle is deflected at the beginning by the predominant current due to the transverse section of the upper part of the thigh, the deflection increases rapidly during the contractions.

Finally, the experiment may be made by putting the two thighs of a frog into the circuit, touching the under extremities of the thighs, but leaving, nevertheless, only one of the lumbar nerves. The current which is obtained on closing the circuit is in no fixed direction, being either null, or now in the direction of one of the thighs, now in that of the other. In all cases during contraction of the thigh provided with its nerve, the usual deflection occurs, that is owing to the current circulating in the external arc of the muscle from the inferior towards the superior extremity of that muscle.

I shall now add a few brief observations, which may throw further light on the interpretation of these experiments. I need not stay to prove that the effects observed by means of the galvanometer, produced by a muscle in contraction, cannot depend either on a portion of the current employed to irritate the nerve, or on changes of contact between the muscle and the extremities of the galvanometer, or finally, on the variable resistance of a muscle in contraction; these doubts have already been completely removed by the experiments of M. Du Bois Reymond. In endeavouring to understand the nature of the electrical phenomena which occur in a muscle during contraction, the fact which merits our chief attention is, that the needle of the galvanometer, which deflects at first in the direction of the muscular current of the gastrocnemius, or of the entire thigh, descends rapidly to zero at the moment of contraction and remains deflected in an opposite direction to that of the muscular current, during the whole time that the contractions are frequent and powerful. M. Pouillet, in his remarkable report*, gives a lucid *résumé* of the conclusions at which M. Du Bois Reymond arrived, in the following terms: —"D'après les principes de M. Du Bois Reymond l'effet d'une contraction soutenue n'est pas de faire naître un courant, mais d'affaiblir et de suspendre par intermittance un courant qui pré-existait; il faut donc un courant pré-existant, ou il en faut deux qui soient égaux et opposés et qui se neutralisent," &c. &c. The slightest reflection on the three

* Comptes Rendus, t. xxxi. p. 28.

experiments to which I have just referred, can leave no doubt as to the necessity of giving another explanation of the effects produced on the galvanometer by a muscle in contraction: when a gastrocnemius or a single entire thigh is in the circuit, M. Du Bois Reymond attributes these effects to the secondary polarity of the plates of platinum; but I have clearly proved that the effect is the same when there is no trace of secondary polarity. In operating on a thigh, the upper part of which has been cut transversely, in which case the current is either null from the neutralization of the two electromotive forces, or in an opposite direction to the usual current of the entire thigh, we have seen the needle deflect, during the contractions, as in all other cases, indicating that a current is directed in the galvanometer from the inferior to the superior extremity of the muscle. According to the principles cited in M. Pouillet's report, we should have to admit that the two currents of this muscle, which are identical and have the same origin, are differently modified in the act of contraction, and this would be contrary to all analogy.

We are therefore led by the experiments referred to, that is, by studying the electrical phenomena of muscles in contraction with the galvanometer and by the method we have described, to the same conclusion as that to which we were led by the researches made with the galvanoscopic frog; namely, that "a conducting homogeneous arc, the extremities of which are applied to any two points whatever, at a certain distance from each other, of a muscle of a frog, is at the moment of contraction traversed by an electric current, or rather discharge, directed from the inferior towards the superior extremity of that muscle." In confirmation of this conclusion, I have only to add the principal results obtained with the galvanoscopic frog.

Whoever has once seen a piece of living muscle, however small, on which is laid the nerve of a galvanoscopic frog, produce the phenomena of *induced contraction* each time that contractions are excited in that muscle by cutting it with a fine pair of scissors, cannot but be struck with the analogy which exists between this phenomenon and that which occurs, under like circumstances, in a piece of the electric organ of the torpedo. In order to study *induced contraction* with the galvanoscopic frog, I proceed as follows: —I prepare several galvanoscopic frogs, which are immediately submitted to the passage of a weak electrical current in the direction of the ramification of the nerve; in a few seconds these frogs cease to contract, except at the closing of the circuit, and are therefore fitted to show the existence of a current or electrical discharge only in case that current is *directed* from the nerve to the leg. An assistant has in the meanwhile prepared from a vigorous frog a thigh, to which is united the lumbar nerve and part of the spine. Nerves of several of the galvanoscopic frogs are now stretched in various directions over this thigh; two strips or rolls of paper, 4 or 5 millimetres long, imbibed with slightly salt water, are put in contact at one end with the extremities of the thigh, and the other ends of these strips of paper are united by two nerves of galvanoscopic frogs, turned in an opposite direction. The thigh is then made to contract: at first several of the galvanoscopic frogs enter into contraction; but if the experiment is continued, it will be seen that contractions take place only in those of the galvanoscopic frogs in contact

with the muscle, or with the two rolls of wet paper, which have their nerves stretched from the lower towards the upper extremity of the thigh. I have repeated this experiment on the muscles of living pigeons and rabbits, and although the difficulties are much greater in these cases, the results were generally the same.

In order to obtain a still clearer insight into the signification of this experiment, I have operated under the same conditions on the organ of a torpedo, in which the direction of the discharge is always clearly indicated by the galvanometer. I suspend a living torpedo by the tail, and rapidly lay bare the brain, and with a pair of scissors cut one of the electric organs in half, parallel to the length of the fish. Having thus obtained a section of the organ, I lay on it (as before on the thigh of a frog) several nerves of galvanoscopic frogs, and also the two extremities of a galvanometer. I then stimulate slightly the electrical lobe of the brain, and at the same instant the needle of the galvanometer deflects, and those frogs only contract whose nerve is extended from the back towards the belly of the torpedo, whether that nerve be in contact with the prisms of the organ, or complete the circuit of the two already mentioned strips of wet paper in contact with the extremities of those prisms.

From the whole of the experiments referred to, it appears to me that the truth of the conclusion which we have deduced is placed beyond all doubt; namely, that "A conducting homogeneous arc laid longitudinally over the surface of a muscle, or applied to that muscle at its extremities only, is, at the moment of contraction, traversed by an electric discharge directed from the inferior to the superior extremity of the muscle, considered in its natural position."

Here the experiments finish, and with them the rigorous results which can be deduced from them. The difficulties encountered in experimentizing on superior animals have deprived these conclusions of the character of generality. Admitting the experiment of M. Du Bois Reymond made on the arms of a man, one of which he contracts voluntarily, the direction of the current obtained at the instant of contraction would be contrary to that of the frog. In the obscurity, not to say entire ignorance, in which we are of the structure of the electromotive element of muscle, we are unfortunately obliged to satisfy ourselves with analogous and equally obscure cases; as for instance that of the direction of the electrical discharge of fishes, without a known relation with the structure of the organ or the form of the fish. Because an exterior arc applied over an entire muscle in repose is traversed by a current in a direction opposite to that which occurs at the moment of contraction, ought we to conclude that the two phenomena have a totally different origin? Or ought we rather to say that, should the form of the electromotor element become known to us, we may probably come to explain the opposite direction of the current as being due to variations of form produced by contraction? Were we not unwilling to diverge into hypothesis or undemonstrated analogies, we might gather many arguments tending to show the greater probability of the latter of these two ideas: according to the analogous case of the organ of the torpedo, we might also suppose that the electrical current is directed in the same sense in muscles in repose as it is in those in action. Since there does not exist, as we know, any analogy between the form of the

voltaic electromotor and that of the muscular electromotor, it is not impossible to conceive that the change of form which takes place in the muscle in contraction may be momentarily followed by the inversion of the current in the exterior arc. Neither would examples be wanting, taken from certain cases of electro-dynamic induction and also of voltaic circuits, in which this inversion of the current can be obtained by change in the form or in the relative distance of different parts of the circuit. But this is a new field of inquiry which cannot be given up to simply hypothetical views; let us be satisfied with having proved that muscular contraction is accompanied by an electric discharge.

In the second part of these Researches we shall show that an augmentation in the chemical phenomena of muscular respiration takes place in the act of contraction. Notwithstanding our present ignorance of the form of the electromotive element of muscle, we may therefore admit that the development of muscular electricity is most probably due to the chemical actions belonging to living muscles.

§ 4. We shall now speak, in the last place, of the mechanical effects of muscular contraction, limiting ourselves to experiments on the frog, because in this case only it is possible to make the research with a certain degree of exactitude, and because after having determined the mechanical effect for a frog, we shall be able to compare the *effective work* of a muscular contraction with the *work* which we shall call *theoretical*, according to the principles of the dynamic theory of heat.

This research should be made on a single muscle, and not on the whole system of muscles, as in an entire frog, because in the latter case the opposite effects of these muscles neutralize themselves almost completely. I therefore employed the gastrocnemius of a frog to which a small weight was attached, and which was made to contract by the passage of an electric current. The object of the experiment is to determine the height to which this weight is raised in the act of contraction; this I did by means of the dynamometer described in the Fourth Series of my Electro-physiological Researches *.

Among the experiments published by M. HELMHOLTZ in his very important memoir on the velocity of the propagation of nervous power, there are several which might have served our purpose, if the weights attached to the muscles had not been too great; for the comparison we propose requires the determination of the mechanical work of the contraction of a muscle in raising its own weight only. Neither could we deduce from the numbers found by M. HELMHOLTZ, the muscular work in the case of muscles to which a small weight is fixed, because it is known and admitted, according to the experiments of SCHWANN, that the quantity of work produced by a muscular contraction increases, to a certain limit, with the weight which stretches the muscle and which that muscle raises: this singular property of the muscular engine has necessarily the effect of weakening more rapidly the contractile power of the muscle.

The medium result of a great number of my experiments has been, that the contraction of a gastrocnemius which weighs 0·300 gr., stretched by a weight of 10 grs., raises that weight to the height of 1·412 mm. The mechanical work of a contraction of a gastrocnemius is therefore expressed by 0·00001457 kilogramme metres. This number being

* Philosophical Transactions, Part IV. 1846.

found, it was of some interest to determine the quantity of electricity necessary, in acting on the nerves or muscles of a frog, to produce that contraction; the results obtained in this last research led me to the experiments on muscular respiration which form the subject of the second part of this memoir. After having measured the quantity of zinc oxidized in a given time in a pile, the current of which is employed to excite contractions in a gastrocnemius, we have still to find the duration of the passage of that current necessary for obtaining a contraction. For this purpose a current of a couple, amalgamated zinc and platinum, in water slightly salt, is sent for upwards of twenty-four hours into a neutral solution of nitrate of silver. The silver collected on the negative electrode, exactly weighed, gives the quantity of zinc oxidized in the pile. In order to determine the time of the passage of the current in a gastrocnemius required to produce normal contraction, *i. e.* the work already determined, I employed a method differing little from that imagined by M. POUILLET for measuring very short intervals of time. I fix on the radius of a wheel, *six* or *seven* metres in circumference, a strip of amalgamated copper 1 millimetre wide. The wheel being set in motion with a uniform velocity of about four turns in a second, the time employed by the circumference of the wheel in passing an arc of 1 millimetre is necessarily very short, but can nevertheless be measured accurately. While the wheel is in movement, two amalgamated brass springs are brought in contact with its periphery: these springs form part of the circuit of the pile, in which are comprised a gastrocnemius recently prepared and fixed in the dynamometer and a galvanometer. I have thus obtained *normal contraction* by the passage of a current, which produced no sensible deflection of the needle of the galvanometer, and of which the duration was about $\frac{1}{10,000}$th of a second. If we admit, which we may do without error, that the conducting power of the gastrocnemius does not exceed that of the solution of nitrate of silver, the quantity of zinc oxidated in the pile during that time is measured by the 7 *billionth* of a milligramme of zinc*.

Taking the mechanical equivalent of heat determined by the experiments of JOULE, and reasoning according to the principles of the dynamical theory of heat, and finally supposing that all the zinc oxidated in the above experiments is converted into electrical current, and hence into muscular energy, one arrives at a conclusion which is far from being in conformity with the theory: the quantity of *vis viva* of a muscle corresponding to the above-mentioned quantity of zinc, would be enormously greater than that deduced from the principles of that theory. This discordance will cease, when it shall be proved that nervous irritation excites new chemical actions in the muscle, and that these are associated with its state of contraction: in this way the electrical current acting on a nerve should be considered in its mechanical effects as the spark which ignites gunpowder or a mixture of hydrogen and oxygen.

* These numbers represent only a limit; but if one reflects that the contraction of a frog is excited by the discharge of a Leyden jar of the smallest possible dimensions and which has been previously discharged by a metallic arc, it becomes evident that this limit greatly exceeds the reality.