Here it was impossible that the heat which raised the temperature of the body could be obtained from the bath, itself never hotter than the bodies of the boys before undergoing the experiment. If the formation of heat was lessened so as exactly to meet the diminished loss by conduction and radiation, the heat of the body would have continued at the same point; but this was not the case, and thus it appears that the formation of heat cannot be suddenly lessened to such an amount.

Thus the increased heat of the body ensuing from a vapour-bath is certainly in part due to accumulation of heat, which under other circumstances is lost by evaporation and radiation. Is all the heat imparted to the body by the vapour-bath to be accounted for in this way? Some part must, in the nature of things, be absorbed from the bath, and is evidenced in our experiments, the elevation being too rapid to be caused solely by an accumulation of heat in the body.

May 3, 1877.

Dr. J. DALTON HOOKER, C.B., President, in the Chair.

The Presents received were laid on the table, and thanks ordered for them.

The Right Hon. Lord Coleridge and the Right Hon. Sir Henry Bartle Edward Frere, K.C.B., whose certificates had been suspended as required by the Statutes, were balloted for and elected Fellows of the Society.

In pursuance of the Statutes, the names of the Candidates recommended for election into the Society were read from the Chair as follows:—

Prof. James Dewar, M.A.
Sir Joseph Fayrer, M.D., K.C.S.I.
Rev. Norman Macleod Ferrers, M.A.
Thomas Richard Fraser, M.D.
Brian Haughton Hodgson, F.L.S.
John W. Judd, F.G.S.
William Carmichael M'Intosh, M.D.
Robert M'Lachlan, F.L.S.
Prof. John William Mallet, Ph.D.
Henry B. Medlicott, M.A.
Henry Nottidge Moseley, M.A.
Prof. Osborne Reynolds, M.A.
William Roberts, M.D.
Prof. James Thomson, LL.D.
Prof. William Turner, M.B.

The following Papers were read:—

I. "Further Observations on the Modification of the Excitability of Motor Nerves produced by Injury." By GEORGE J. ROMANES, M.A., F.L.S. Communicated by Prof. BURDON SANDERSON, M.D., LL.D., F.R.S. Received April 11, 1877.

In my former paper on this subject* I showed, among other things, that injury of a motor nerve is attended with a very marked and peculiar alteration in its relative excitability towards the stimuli which are respectively supplied by closing and opening a voltaic circuit. In the present paper I propose to detail the results which have been obtained by continuing this line of research; and, in order to render them more easily intelligible, I shall begin by briefly restating such of the previous results as form the basis of the present ones.

It will be remembered, then, that my method of experimenting was as follows. Having pithed a frog and laid it on a frog-board in such a position that one of the hind legs should hang over the edge of the board, I divided the tendo Achillis, dissected out the gastrocnemius as far as its point of origin, and removed the tibia just below the knee. The exposed though uninjured gastrocnemius was then laid with its flat surface on non-polarizable electrodes, in such a way that while one electrode supported the extreme tarsal end of the muscle, the other supported its extreme femoral end. By means of a rheochord it was then ascertained what strength of voltaic stimulus the muscle required to give its earliest response, (*a*) to the anodic† make, (*b*) to the kathodic make, (*c*) to the anodic break, and (*d*) to the kathodic break. It will be remembered that, under these circumstances, "the muscle is usually more sensitive to minimal stimulation supplied by *closure* of the constant current when the femoral end rests on the kathode [case (*b*)], than when this end rests on the anode [case (*a*)]. Conversely, under similar circumstances, the gastrocnemius is more sensitive to minimal stimulation supplied by *opening* of the constant current when the femoral end rests on the anode [case (*c*)], than when this end rests on the kathode [case (*d*)]. In view of the other facts of electrotonus the present ones are of interest, because, as the sciatic nerve enters the gastrocnemius near the femoral end of the latter and then spreads out its peripheral ramifications as it advances, in the experiments just mentioned one electrode is in almost immediate contact with the nerve-trunk where it enters the muscle, while the other electrode supports the part of the muscle that contains only peripheral

* Proc. Roy. Soc., May 4, 1876.

† Throughout this paper I shall designate the direction of the voltaic current through the gastrocnemius by employing the terms "anodic" and "kathodic" with reference to the *femoral* end of the muscle, *i. e.* where the nerve-trunk first enters the latter. Thus, for instance, "anodic make" means closure of the current in a direction descending from the femoral to the tarsal end of the gastrocnemius.

nervous elements. It is therefore to be expected, upon the theory of electrotonus, that the muscle under these conditions should prove itself most sensitive to the closing excitation when the nerve-trunk rests on the kathode, and most sensitive to the opening excitation when the nerve-trunk rests on the anode. . . . .

"If the gastrocnemius of a frog be placed on non-polarizable electrodes in the position just described, and if care has been taken not to injure the attached sciatic nerve, I find that upon now dividing this nerve, either near or just within the muscle, remarkable alterations ensue, not only, as is already known, in the *general* sensitiveness of the muscle, but also, and more particularly, in its *relative* sensitiveness to make and to break of the current. . . . For just as before cutting the *normal* sensitiveness of the muscle is greatest to the closing excitation when its femoral end (or uninjured nerve-trunk) rests on the kathode, and most sensitive to the opening excitation when this end rests on the anode, so, after the general sensitiveness has been exalted by cutting, the *exaltation* shows itself in a far higher degree to the closing excitation when the femoral end (or severed nerve-trunk) rests on the kathode, and to the opening excitation when this end rests on the anode."

Having thus described the qualitative effects of nerve-injury in relation to electrotonus, my former paper went on to describe also the quantitative effects; but for my present purpose it is unnecessary to quote the latter. For having observed that the particular effects of nerve-injury which I was investigating decreased with great rapidity after the first infliction of the injury, I deemed it desirable to confirm the quantitative results already published by employing a more rapid method of varying the intensity of the voltaic current. Accordingly, instead of using the rheochord, I introduced into the exciting circuit a rheostat consisting of a long U-tube charged with dilute solution of zinc sulphate. Into each leg of the U-tube there dipped a zinc rod of the same length as the tube. These two rods formed part of the circuit, and as, by means of an appropriate mechanical arrangement which need not be described, they could be slid up and down the legs of the tube with great facility, the resistance offered by the tube could thus be varied with great rapidity.

In some other respects, also, I changed the method. Instead of non-polarizable electrodes I used platinum plates measuring 4 millims. across. Also, in order to estimate the *maximum* effect produced by nerve-injury in each of the four cases (*a*), (*b*), (*c*), and (*d*), I only made one comparative observation on every muscle I employed. That is to say, if I wished to ascertain the *maximum* degree in which the excitability of a nerve is increased by section in any one of these four cases, I began by observing, in the uninjured nerve, the *maximum* number of Ohm's units of resistance which I could afford to throw into the U-tube, so as only just to procure a response to the make or break stimulus as the case might be. Having noted this, I raised the sliding rods to the top of the U-tube, so as to

throw in the entire resistance of which the tube was capable, *i. e.* a greater resistance than could possibly be required to cause minimal stimulation in the next stage of the experiment. I now cut the gastrocnemius through at its extreme femoral end; and the same instant that I did so I began rapidly to pass the sliding rods down the U-tube with one hand, while with the other hand I closed and opened the current a number of times in as rapid succession as possible. Having observed the point at which the responsive contraction was first given, and throwing away that particular muscle, I repeated the experiment with another muscle, and so on —never using the same muscle for more than one such observation, and so always obtaining a record of the *maximum* increase of excitability *immediately* after infliction of the injury.

The results of a number of experiments conducted on this improved method confirm, in the main, those previously obtained. As before, however, I encountered immense individual variations in different muscles, and therefore, as before, I here select mean cases for quotation. It is only necessary further to explain that in the appended Table the figures represent the number of Ohm's units of resistance which, with two Grove's cells, I required to introduce in each of the eight cases before I procured minimal stimulation.

	Anodic make.	Kathodic make.	Anodic break.	Kathodic break.
Before cutting	90,000	100,000	14,000	6,000
After cutting......	140,000	300,000	195,000	14,000

These proportions, as already observed, agree pretty closely with those which I obtained by the method previously employed. Such differences as exist are to be explained, partly by the superiority of the later method, and partly by the fact that in the one series of experiments I employed *Rana temporaria*, while in the other series I employed *R. esculenta*—the muscles of the latter species being less excitable than those of the former. It is interesting to note that the chief difference in the two series of results has reference to the kathodic make, and that the difference is of such a kind as to render the degree in which the excitability is increased by section in this case more proportional to the degree in which it is increased in the case of the anodic break. The two cases, however, are still very far from being *numerically* proportional, the degree of increase in the two cases being respectively represented by the numbers 1 : 3 and 1 : 14 (nearly). To explain this numerical discrepancy, therefore, we must still resort to the considerations set forth in my previous paper (see vol. xxv. pp. 12, 13). I may here add that in some instances of *maximum* increase of excitability, due to nerve-injury, I have observed the kathodic make to

rise from 80,000 to 600,000 Ohms, and the anodic break from 15,000 to 400,000 Ohms.

§ 2. The rapidity with which this abnormal excitability declines after the injury is, as already stated, considerable. The following instances, which refer to the anodic break, will serve to show this:—

Time.	Degree of Excitability in Ohms.
Before cutting	13,000
2 seconds after cutting	280,000
30 " "	244,000
1 minute "	210,000
2 minutes "	170,000
3 " "	150,000
4 " "	134,000
5 " "	100,000

Another instance:—

Before cutting	22,000
2 seconds after cutting	300,000
30 " "	230,000
1 minute "	180,000
2 minutes "	150,000
3 " "	130,000
4 " "	110,000
5 " "	95,000
6 " "	80,000
7 " "	73,000
8 " "	67,000
9 " "	60,000
10 " "	54,000
15 " "	25,000
20 " "	13,000

I may here state that if the excised gastrocnemius be inserted under the skin of a freshly killed frog, and the latter be kept in a moist cool place, the nerve will sometimes retain its irritability for 48 hours or more—the muscle, when placed on the electrodes at the end of that time, still continuing to respond to the kathodic make and to the anodic break. But of course a very much stronger current is now required to produce these responses than was required to do so when the nerve and muscle were in a fresh state.

§ 3. A strong voltaic current, or a strong induction-shock, allowed to break into an uninjured nerve-trunk, causes in the latter an increase of excitability analogous to that which is caused by mechanical injury. Thus, for example, a momentary exposure of an uninjured sciatic to the full

strength of a single Grove's cell caused the excitability of the nerve towards the breaking excitation, supplied through the same electrodes by a small Daniell's cell, to rise from 5000 to 100,000 Ohms. Similarly a strong induction-shock supplied by a single Grove's cell with the secondary coil at zero, and thrown in between the electrodes from a small Daniell's cell, caused the excitability of the nerve towards a closing stimulus supplied by the latter to rise from 40,000 to 185,000 Ohms. In conducting these experiments, I was not able to perceive that the *direction* of the strong or injuring current made any difference in the nature of the results.

§ 4. This concludes my observations so far as stimuli of minimal intensity are concerned; and, at the suggestion of Dr. Burdon-Sanderson, I terminated this inquiry regarding the electrotonic condition of injured nerves by substituting for voltaic stimuli of minimal intensity, voltaic stimuli of minimal duration. The method which I employed in this part of the research was as follows:—The frog (*R. temporaria*) having been prepared as already described in § 1, the duration of the voltaic stimulus was graduated by means of a heavy pendulum, which constituted one pole of the battery, and which, while swinging, made contact at the lowest point in its arc with the other pole. The latter consisted of a fixed platinum wire placed vertically, and the contact was made with it by means of a pointed piece of metal attached to the moving pole and placed horizontally. Thus by increasing or diminishing the distance through which the pendulum, or moving pole, was allowed to swing, a stimulus of any required duration could be supplied to the muscle interposed in the circuit. As a battery I employed a single Daniell's cell; and, lastly, I interposed a rheochord, a commutator, and a key. Such being the apparatus, the course of any one experiment was very simple. By means of the swinging pendulum, the uncut muscle was supplied with a stimulus of measured duration, which was then graduated down to the point at which the break of the current succeeded the make with a rapidity just sufficiently great to prevent the muscle from responding to either stimulus, (*a*) when the femoral end rested on the anode, and (*b*) when this end rested on the kathode. These two durations having been noted, the nerve was cut through at the usual place, and the observations (*a*) and (*b*) repeated as rapidly as possible. It was invariably found that in both cases a much shorter duration of the voltaic stimulus was required to produce minimal stimulation than had been required to do so before the nerve was cut, the *intensity* of the voltaic current, of course, being kept uniform throughout.

An apparent objection to this method of experimenting is apt to suggest itself, viz. that the make and the break must follow one another much too rapidly to admit of the observer being able to eliminate the effects of the former from those of the latter stimulus. But, as a matter

of fact, the desired elimination is performed by the nervo-muscular tissue itself. For it usually happens that a gastrocnemius presents some perceptible difference in the character of its contraction, according as the latter is given in response to make or to break of the current. Therefore, by first ascertaining, with an ordinary key, the optical appearance which the responses to make and break respectively present, it is not difficult afterwards to recognize which of these appearances is presented by the response to rapidly succeeding make and break stimuli, and so to determine which of these rapidly succeeding stimuli is the one to which the response is given. Now I found in this way that, by making the duration of contact sufficiently brief, the nerve, whether or not injured and in whichever direction the current was allowed to pass, only responded to the closing stimulus. Therefore, by choosing a strength of current which, in each of the cases (*a*) and (*b*) before nerve-injury, was just sufficiently strong to elicit a response when the voltaic stimulus was of t duration in the one case and t' duration in the other, I was sure that in each of the two cases the response which I obtained was given to the closing, and not to the opening, excitation. Having noted the values of t and t', I divided the sciatic just where it enters the gastrocnemius, and then shortened the duration of contact down to the point at which, in each of the two cases (*a*) and (*b*), the muscle again only just responded to the stimulus. Let these durations be respectively represented by T and T′. As before, I ascertained that the responses had exclusive reference to the closing excitation; so that, by recording the values of t, t', T, T′, I was able to obtain for responses to stimuli of minimal duration representative numbers, such as those in the former Table, which have reference to stimuli of minimal intensity. It is only necessary further to state that, as different gastrocnemius muscles exhibit considerable variations in the degree of their natural irritability towards voltaic stimuli of short duration, and as for my purposes it was desirable to obtain a physiological, as distinguished from a physical, basis whereon to institute my comparisons, in the case of each muscle I began by graduating the *intensity* of the current down to that point at which the duration of contact required to produce minimal stimulation before nerve-injury was the same as it had been in my previous experiments. Or, in other words, by appropriately varying the intensity of the current to suit the degree of excitability manifested by each particular muscle before injury, I was able, notwithstanding the differences in excitability presented by different muscles, to render t a constant. When this was done, however, t', T, and T′ were all found more or less variable in different muscles—as, of course, we should expect from the analogous case of responses to stimuli of minimal intensity. I therefore tabulated the results yielded by twenty gastrocnemius muscles, and then calculated the average duration of contact which in each of the cases (*a*) and (*b*) before cutting, and (*a*) and (*b*) after cutting, was required to cause minimal

stimulation. It is the averages so obtained which are rendered in the following tabular statement of results:—

	Anodic make.	Kathodic make.
Before cutting	·00533 sec.	·00439 sec.
After cutting............	·00311 sec.	·00117 sec.

Concerning these results it is only necessary to observe that there is a tolerably close parallel between them and those which were previously obtained by employing stimuli of minimal intensity. That is to say, in the case of the anodic make the increase of excitability due to injury is, roughly estimated, in the proportion of about 3 : 5, and *this whether such increase is estimated by employing stimuli of graduated intensity, or stimuli of graduated duration*; and similarly in the case of kathodic make, though the proportions here yielded by the two methods are not quite so equal as in the other case. But this general parallelism between the quantitative results yielded by the two methods in the case of both the closing excitations serves but to render more conspicuous the difference in the results yielded by the two methods in the case of the anodic opening excitation; for while in the first of the two methods, viz. that in which stimuli of minimal intensity were employed, it was found that after injury the excitability of a nerve towards the anodic-break stimulus is greater than it is towards the anodic-make stimulus, such is not found to be the case when, as in the second of the two methods, these two stimuli are made to follow one another in very rapid succession. I can only explain this fact by supposing that, for the breaking excitation to be fully effectual, a certain interval of time is required for the nerve to become polarized by the passage of the voltaic current; and, therefore, that, in my experiments with currents of minimal duration, a response to the anodic make was always given when a shorter duration of the current was employed than that which was required to produce a response to the anodic break*.

§ 4. In conclusion, I may state that the period of latent stimulation does not appear to be perceptibly affected by nerve-injury.

* *How much* shorter I was not able to ascertain, from the fact that the contraction due to the make and that due to the break, when they both occur together, become so blended that the eye is not able to analyze them with sufficient precision to decide at what point the anodic-break contraction first asserts itself. Hence we must rest satisfied with the general statement, that the minimal anodic-break stimulus is in some unknown degree of longer duration than the minimal anodic-make stimulus; and this even after the susceptibility of the nerve to the former stimulus is so enormously augmented by injury as, from the other method of experimentation, we know it to be.