

THE EFFECT OF FREQUENCY OF STIMULATION ON THE HEAT PRODUCTION OF NERVE.

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IN the experiments previously reported by Downing, Gerard and Hill⁽¹⁾ on the heat production of nerve the stimulating agent employed was a Harvard coil in which the ordinary spring had been replaced by one which gave 140 complete vibrations per second, so supplying 280 shocks per second, 140 make and 140 break. It was assumed that, up to the limit where a stimulus would fall within the absolute refractory phase of its predecessor, the heat production would increase with frequency of stimulation, and, since the measurement of the heat is by no means easy, it was desired to have as much heat as possible to measure. In occasional experiments the ordinary Harvard coil was employed, giving 100 stimuli per second, 50 make and 50 break, and we noticed always that the heat production did not fall off nearly as fast as the frequency: between 100 and 280 stimuli per second the total heat fell off only in the ratio of about 3 to 2. Since in dealing with the mechanism of nerve activity it is desirable to know the heat-production per impulse, it is necessary to divide the observed total heat by the frequency in order to obtain what one requires, and it became obvious that this would not be constant as the frequency changed, so that the heat per impulse required further definition. Nearly all work on the nervous impulse (apart from that of Erlanger and Gasser and their colleagues^(2, 3)) has been concerned either with single impulses, or with pairs of impulses, so that from this point of view it was obviously desirable to find the heat per impulse when unaffected by the presence of other impulses, and to study the rate at which the energy liberation in the impulse "recovered" after a previous stimulation. The heat production, however, in a stimulated nerve is so small that there is no hope at present of being able to determine it directly in a single impulse. It is necessary

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to work with a long succession of impulses, several hundred at least, in order to obtain any accuracy, and these must follow one another in fairly rapid succession, since the rate of heat loss of the thermopile is so great; thus it is essential to know the relation between frequency of stimulation and heat production in order to proceed further. Incidentally, the investigation of the relation has supplied some interesting information about the "recovery process" which is completed in nerve during a fraction of a second after stimulation¹.

Method. It was necessary to obtain some suitable means of applying stimuli to a nerve at a rate varying from (say) 20 per second up to (say) 500. We attempted at first to use a valve-generator, supplied by the Cambridge Instrument Company, which produces an alternating current approximating to a pure sine wave; the frequency of this can be varied as desired, by changing the capacity of a condenser. The higher frequencies were easily attainable with this arrangement, but the lower frequencies provided a difficulty. Moreover, the stimulating effect on nerve of a pure sine wave current is very poor when compared with the energy it contains. For many purposes there is no harm in using such a means of stimulation, because no polarisation results from an alternating current, and even though it contains an unnecessary amount of energy it does not injure the nerve; while in most types of experiments the heat liberated by the stimulating current is of no importance. In the present experiments, however, it was essential that the stimulating agent should liberate the minimum of energy in the nerve, because if the energy so liberated is excessive it conducts down from the stimulating electrodes, reaches the thermopile in spite of all precautions, and causes serious errors in the results. A more satisfactory agent is a series of extremely rapid induction shocks, as supplied by a coreless coil. With such a coil the stimulus is produced very suddenly by the rapid rise of the induction shock, and no energy is wasted in the interval between successive stimuli, as is the case when an alternating current is passing continuously between the stimulating electrodes.

The ordinary vibrating spring, with a pointer moving in and out of a bowl of mercury, we did not regard as a sufficiently accurate and reliable means of regulating the shocks, since it is difficult to ensure either that make and break shocks are equally spaced, or that they are

¹ The use of the word "recovery" in this sense is well established, as also is the term "recovery" in muscle in a completely different sense. The "initial recovery" of nerve, complete in a few hundredths of a second, has no relation to the "delayed recovery process" which occupies ten minutes or more.

equal in magnitude, and there is no easy way of eliminating the make shocks if desired. We arranged therefore for the construction of the contact-breaking device shown in Fig. 1, which has proved extremely

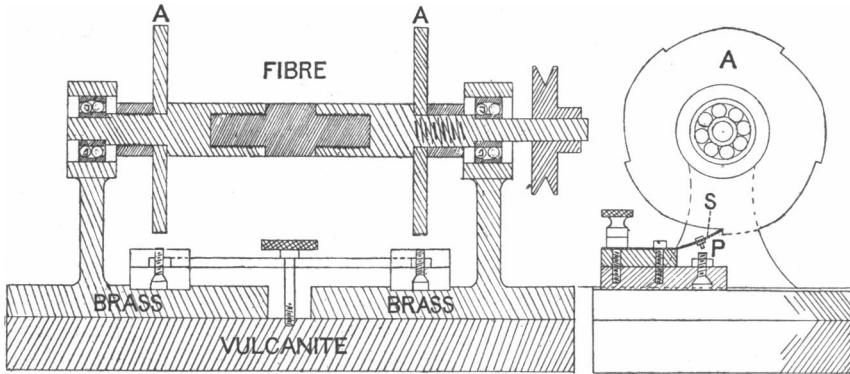


Fig. 1. Revolving contact-making and breaking device, carrying two steel discs *AA* insulated from one another on the same shaft, each supplied with five cams for making and breaking contact at the point *P* carried by the phosphor bronze spring *S*.

satisfactory. As designed, there are two circular discs running, insulated from one another, on the same shaft, each containing five cams which lower the tip of a phosphor bronze spring and then suddenly release it, so making and breaking contact at regular intervals¹. It was expected that it would be necessary to employ only break shocks in the investigation, so that one of the cam discs was designed to make and break the primary circuit of the coil, as it revolved, while the other cam disc was intended to short-circuit the make shocks (or, if desired, the break shocks) only. As a matter of fact, we found it unnecessary, except for a few special purposes, to employ both discs, and have used both make and break shocks, which, with the coreless coil employed, have proved to be practically equally effective; this has the advantage also of avoiding polarisation in the nerve.

The cams and springs were so arranged that the contact, which was between two platinum points, occurred almost exactly half-way between two breaks. This could be tested by eye, or better by putting a voltmeter across the contact and marking the points at which a deflection occurred when the wheel was slowly revolved by hand. The breaks were very sharp, being caused by the spring falling off the end of the cam.

¹ For the success of the instrument we are mainly indebted to the skill of Mr A. C. Downing.

It was obviously necessary to ensure that the shocks were approximately equal at all frequencies. For this purpose a very fine resistance wire, wound non-inductively round the junctions of a thermopile, was employed; the current from the induction coil ran through the resistance wire, so warming it and thereby the junctions of the thermopile, the E.M.F. from which gave on a moving-coil galvanometer a deflection proportional to the energy in the induction shocks. Setting in motion the contact-making and breaking device, connected in the ordinary way with a coil, and reading its speed (and so the frequency of the shocks) with an accurate tachometer, the energy per second in the induction currents from the secondary could be compared with the frequency. If the shocks were equal at all frequencies the total energy read on the galvanometer scale would be proportional to the frequency, and this was found actually to be the case up to frequencies of 400 shocks (200 make and 200 break) per second. Beyond that limit the total energy continued indeed to increase with the frequency, but at a diminishing rate, the energy per shock becoming somewhat less. The coil employed was coreless, so ensuring quickness of rise and fall in the primary current and rapidity in the induction shocks.

A similar method was employed in order to be sure that the make and break shocks were equally effective. For this purpose the energy of the make shocks alone was determined, by short-circuiting the break shocks by the second cam-disc and contact, or the energy of the break shocks alone was determined, short-circuiting the make shocks. These came out about the same and equal to about half the energy found when both make and break shocks were employed. Since the total amount of current passing in a make shock is necessarily the same as that in a break shock (for a given resistance, coil distance, and primary current), the equality of the energy in the two shocks shows that they were practically of the same form, and therefore would have the same stimulating efficacy.

The stimulus was varied by altering a resistance in the primary circuit, the secondary being fixed over the primary. Supermaximal shocks were employed, as large as it was practicable to use without producing "current heat" in amount sufficient to conduct from the stimulating electrodes down to the thermopile, and so cause an error in the result. It is necessary, at high frequencies, to use stimuli which are very considerably supermaximal, because the excitability of the nerve takes an appreciable time after a stimulus to attain its original value. In all previous experiments with the Harvard coil giving 280

shocks per second, the position for maximal stimulation at that frequency was known. Employing our contact-making device at the same frequency, we were able to show that it produced the same response as the coil for considerably weaker currents than we actually used in the following investigation. For frequencies, therefore, of 280 per second and below, our stimuli were certainly maximal, and probably also for a considerable range above that frequency.

The contact-making and breaking device was driven by a motor through a pair of countershafts carrying cone pulleys, so that any desired frequency of revolution could be obtained. The constancy of speed as read by the tachometer was amply sufficient for our purpose. All speeds were read as revolutions per minute of the cam arrangement, and multiplied by 10 (5 make and 5 break shocks per revolution) and divided by 60, that is altogether divided by 6, to obtain the number of shocks per second.

With the extreme sensitivity required for these experiments on the heat production of nerve, difficulty is often experienced from electric leaks, and it was found necessary to remove the whole of the stimulating arrangements to the next room and to bring only a flexible wire, carrying the make and break induction shocks, into the experimental room. Two observers therefore were needed, one to read the scale and to manipulate the apparatus for measuring the heat, the other in the next room for adjusting and measuring the speed and giving 10-second stimuli. The period of stimulation was always the same; the observer, employing a stopwatch, pressed a Morse key in the primary circuit and released it at the end of 10 seconds, giving appropriate warning to the observer at the scale in the next room.

The accuracy with which the heat can be read, especially at low frequencies where it is small, is relatively low, so that it is necessary to make a large number of observations. The relative infatigability of nerve enables large numbers of observations to be made, the most reliable condition being that stimuli should be spaced at regular time intervals, for example of one or two minutes; in that case hundreds of observations can be made on a single set of nerves, passing several times up and down the range of frequencies desired. It is not practicable to work at frequencies of less than about 20 stimuli per second, because below that limit the heat becomes so small that random errors due to extraneous disturbances render the results unreliable; and we have not considered frequencies above 400 to 500 per second, for at such frequencies we pass into the range where many of the stimuli must be

ineffective, for example, every alternate one falling in the completely refractory phase left by its predecessor. So far as our experiments go, the heat production still continues to increase slightly, however far the frequency is pushed. Owing, however, to the theoretical complication introduced by the nerve no longer following the stimuli at the higher frequencies, we limited our observations to the range, 20–420 per second. It is obvious, of course, that the origin of zero frequency must lie upon the curve.

Results. The individual observations are so numerous that they cannot well be recorded here. Their number, however, ensures that random errors due to extraneous causes do not appreciably affect the results, and we have taken a mean for the following frequencies from the smoothed curves of several experiments. In each case the curve was reduced to the same scale before reading off the value for calculating the mean. All experiments were made at about 18° C.

TABLE I. Mean values of heat (arbitrary units) at different frequencies (stimuli per second), from which Fig. 2 is constructed.

Frequency	0	20	40	60	80	100	140	180	220	280	360	420
Heat	0	23	40	52	61	67	77	82	87	93	97	99

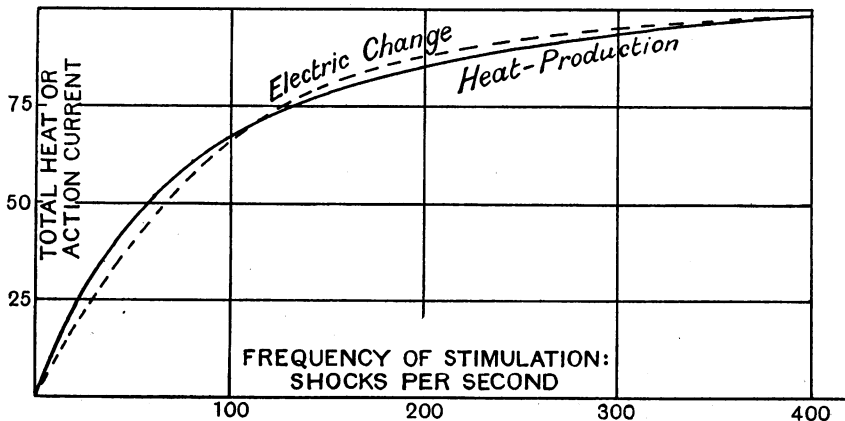


Fig. 2. Relation between total heat per second (full curve), or total action current per second (broken curve), and frequency of stimulation in shocks per second. The scale of each curve is arbitrary, but the two curves are made to coincide at a frequency of 400.

The result is shown in Fig. 2, where there is also given for comparison a curve of “total” action current obtained in the manner described below.

The curve in Fig. 2 is in arbitrary units of heat. We can interpret

it in absolute units, for maximal stimulation of a frog's nerve, by using the data of the paper by Downing, Gerard and Hill(1). There it was shown that one second of maximal stimulation at about 15° C., at a frequency of 280 per second, liberates, of initial heat, about 7.6×10^{-6} calorie per grm., of total heat, that is initial plus delayed, about 69×10^{-6} calorie per grm. Assuming these values at 280 stimuli per second, we may calculate those for any other frequency. The result is given in the following table expressed in terms of heat per impulse, the heat per second being obviously obtainable by multiplication by the frequency. For the purpose of the argument which follows we give also, in the second column, the interval between stimuli. The last entry, that at zero frequency, refers to the case of a single isolated impulse unaffected by any previous stimulation of the nerve. It is obtained by laying off the tangent at the origin to the curve of Fig. 2.

TABLE II. Absolute values of the heat per impulse at different frequencies, reckoned per gram of nerve.

Frequency (shocks per sec.)	Interval between shocks (σ)	Initial heat $\times 10^{-8}$ cal.	Total heat $\times 10^{-8}$ cal.
400	2.5	2.03	18.4
350	2.86	2.27	20.6
300	3.33	2.56	23.2
280	3.57	2.71	24.6
250	4.00	2.98	27.0
200	5.00	3.47	31.5
150	6.67	4.30	39.0
100	10.0	5.53	50.2
80	12.5	6.28	57.0
60	16.7	7.19	65.2
40	25	8.26	75.0
20	50	9.49	86.1
0	∞	10.32	93.7

The entries in the last two columns are smoothed values, and so are given to three significant figures

The most interesting entry in Table II is the last one, showing that in a single isolated impulse in a nerve there is a rise of temperature, corresponding to the initial heat, of almost exactly one ten-millionth of a degree Centigrade, while the total heat (initial plus delayed) in a single impulse is nearly one millionth of a calorie per grm. These may be compared with the case of a single muscle twitch, where there is an *initial* rise of temperature of about $3/1000$ of a degree, 30,000 times as much as for the nerve, and a *total* heat of about 7.5×10^{-3} calorie per grm., about 8000 times as much.

Similar experiments have been performed, measuring the total action current instead of the heat. The term "total action current" requires

some explanation. The nerve, mounted in a suitable chamber, and arranged to give a monophasic response, with two non-polarisable electrodes of the zinc-zinc-chloride gelatine-Ringer type, was stimulated at a point distant from these electrodes and, to use the classical term, the "negative variation of its injury current" was recorded on a sensitive high resistance galvanometer. The instrument employed was a Downing galvanometer⁽³⁾ of very high resistance (20,000 ohms), the extreme sensitivity of which allowed a deflection of 30 mm. or more to a single shock, in spite of the rapid movements (half a second deflection time). The injury current of the nerve was balanced and the galvanometer brought to zero, a stimulating current from the make and break arrangement described above being allowed, by means of a Lucas revolving contact-breaker, to pass for half a second through the nerve. The deflection obtained was read ballistically on the scale. The readings represent the total area of the action-current-time-curve, above a base line corresponding to the balanced injury current. In other words, the "total action current," as we have called it, measures $\int C dt$ where C is action current, and t is time and the limits of the integral are the beginning and end of activity in the nerve.

The process described above in reference to the measurement of heat was repeated in respect of electric change on a number of nerves. Twelve reliable experiments were performed on twelve different nerves, and each of the curves relating electric change to frequency of stimulation consisted of a sequence of observations with increasing frequency, followed by another sequence with decreasing frequency, so as to eliminate as far as possible any effect of fatigue, or of change in the nerve. These curves were then averaged and the resulting mean curve is shown by the broken line of Fig. 2. The scale adopted is arbitrary, the curve of electric change being made to coincide with that of heat production at a frequency of 400 per second. In nearly all respects, except that a different chamber was used, these experiments on the electric change are comparable with those on the heat, the stimulating arrangement and the temperature being the same, *Rana esculenta* being employed in either case. The only difference, and it is one which can scarcely affect the results, is that the curve of electric change corresponds to stimuli of only half a second duration, while that of heat corresponds to stimuli of 10 seconds' duration. No fatigue, however, occurs in a nerve in such a short interval of stimulation as 10 seconds, so we may regard the two curves of Fig. 2 as being strictly comparable with one another.

Discussion. One noticeable characteristic of the heat curve in Fig. 2

is the way it starts to bend round soon after leaving the origin. According to Lucas, Adrian, Kato and others, the relatively refractory period of the quickest fibres of a nerve, following an excitation, is over, or very nearly over, at 20σ . At the corresponding frequency of 50 per second the heat per impulse as here measured is obviously falling off. Clearly, as regards heat production, the "recovery process" (in the sense in which that term is employed by Lucas and Adrian) of all the fibres of a nerve considered in the aggregate, takes longer than does the "recovery process" of the quickest fibres in respect of excitability. It is useful, therefore, to express our results in another way, in which the recovery of the capacity for liberating energy can be studied.

If we take the data of Table II and plot the heat per impulse against the interval between successive impulses, regarding the heat at zero frequency as being 100 p.c., we obtain the curve marked "return of energy liberation" of Fig. 3. It is not possible to follow this curve

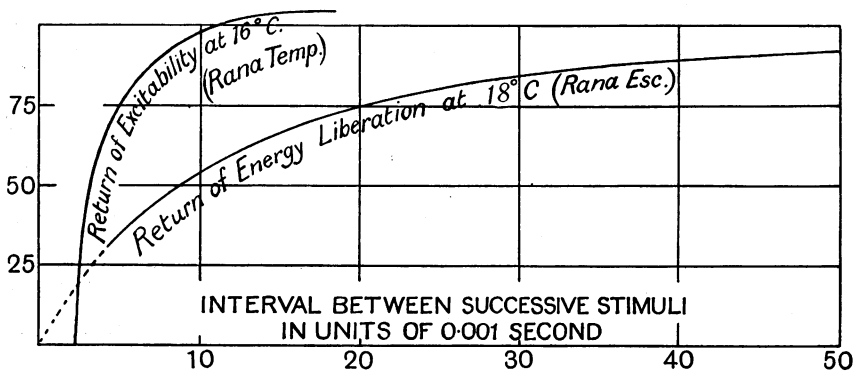


Fig. 3. Return of energy liberation and return of excitability. For the former the heat per impulse is given as a function of the interval between successive stimuli and is calculated from the curve of Fig. 2. The return of excitability is derived from data supplied by Dr Adrian which were obtained from measurements of the least interval for muscular summation for different strengths of second shock.

experimentally to the right with any accuracy, for the reason given above, namely that at very low frequencies the total heat per sec. is so small (however large it may be per impulse) that random errors affect the result. The curve is dotted in below 4σ , as with intervals less than this some, at any rate, of the stimuli must be falling in the absolutely refractory phase of their predecessors. Within the range, however, of 4σ to 50σ there is no doubt of the general form of the curve. The initial energy liberation of the nerve, judging from the duration of the rising

phase of the action current (as shown by Bishop, Erlanger and Gasser⁽²⁾), is very short, say of the order of 0.75σ . If we neglect it completely we may perhaps regard the origin as lying upon the curve, for at zero time after a previous stimulus the nerve has obviously not recovered at all its power of liberating energy. If we regard the initial breakdown process as lasting for 0.75σ , a point distant 0.75 along the horizontal axis should lie on the curve. Our present knowledge is not adequate to allow us to distinguish between such alternatives. If, however, the initial liberation of energy be complete within $x\sigma$, then the point $(x, 0)$ should lie upon our "recovery" curve. For the present we have drawn it as a broken line passing through the origin.

The recovery curve of energy liberation does not obey exactly any simple formula and it is probably composite in its nature. It represents presumably the average recovery of a number of fibres differing widely in their time relations. According to Bishop, Erlanger and Gasser⁽²⁾ some of the fibres in the frog's sciatic nerve take about four times as long to recover as do the most rapid fibres. As a rough approximation the curve might seem to be exponential in character, corresponding to the assumption that the rate of recovery at any moment is proportional to the amount of recovery still to be completed. The curve, however, rises initially more rapidly, and later more slowly, than it should on such an assumption: though this would be explained if it were compounded of a series of exponential curves of different time-relations. There would seem at present to be insufficient evidence to warrant any further discussion of its physico-chemical basis.

The recovery of excitability of a nerve after a stimulus follows the relation described by Lucas and Adrian and investigated by many observers since. The particular curve shown in Fig. 3 has been supplied by Dr Adrian as a typical recovery-of-excitability curve for English *Rana temporaria*. The nerves actually used in our investigation were those of Dutch *Rana esculenta*. It is obvious that the return of excitability under their conditions follows a very different relation from the return of energy liberation under ours. It should be noted, however, that the curve giving the return of excitability refers to those fibres of the nerve trunk which recover their excitability most rapidly—the observations on which it is based involve the measurement of the least interval required for minimal muscular summation, for given strength of second shock. The curve, on the other hand, of return of energy liberation refers to all the fibres of the nerve, since maximal stimuli were employed, at any rate for intervals greater than 4σ . It may well be

the case that, taking the difference between the conditions into account, the two curves of recovery are fundamentally the same: in other words, that if it were possible experimentally to observe the heat only of those fibres which recover most quickly, the curve of recovery of heat would nearly reach its asymptote also within 20σ or so.

In Fig. 2 it is seen that the total electric change follows very much the same course when the frequency alters as does the heat production. What the significance may be of this relatively close agreement it is not possible as yet to say. The similarity of the two curves of Fig. 2 ensures that if we calculate a curve of return of electric change, similar to that of the return of energy liberation of Fig. 3, we shall find the return of electric change to be similar in general to the return of energy liberation.

In view of the demonstration by G. Kato and his colleagues of the complete applicability of the "all or none" principle, when expressed in the form that the size of the impulse in a nerve fibre is a function only of the condition of the fibre and is independent of the stimulus strength or of the distance the impulse has travelled, we may assume that all the impulses actually started in the nerve traverse the whole of the nerve and are not abolished by decrement. Kato⁽⁴⁾ in his second monograph, chapter VIII, deals with "the recovery of nerve," and proves, p. 115, what is important for the present purpose, that in the case of three shocks given in succession the second least interval for muscular summation is equal to the first least interval, and therefore that "the refractory period due to the first disturbance of normal size evoked in normal resting nerve is equal to the refractory period due to the second disturbance of subnormal size evoked in the incompletely recovered nerve." If this conclusion can be generalised we are justified in following the process of recovery, as we have done above, by employing a rapid succession of stimuli, instead of a single pair. Kato's result, moreover, suggests (p. 116) "that the nerve, if it will respond at all to a stimulus, will discharge all that is available at the moment, independently of the strength of the stimulus and independently of whether it is in the resting condition or in the relatively refractory period."

Let us imagine that the total energy available in a nerve for immediate discharge is liberated suddenly on the application of a shock and that as soon as the "explosion" dies down the nerve begins to recover its power of liberating energy along the curve shown in Fig. 3, or, in the case of a single fibre, along one of the elementary curves of which the curve of Fig. 3 is compounded. Let us imagine also that the impulse cannot propagate itself at all unless there is a certain amount of energy

available in it. A simple physical analogy is a train of gunpowder which will conduct a wave of burning, if ignited at any point, provided that the thickness of the train is sufficient. If the train be too narrow the combustion will die away at once and will not be transmitted. If this analogy be valid we obtain a simple picture of nerve activity, namely, that after an impulse a recovery process (presumably anaerobic) has to go on, restoring the nerve, as regards energy, to its initial condition and taking 50σ or more (or in the case of the individual fibres, 20 to 80σ) in the process; and that the absolutely refractory period is due to the fact that the wave will not propagate at all unless there be a certain amount of energy available.

The energetics of the recovery of nerve to its initial condition following a stimulus (apart altogether from the delayed process which lasts for ten minutes or more after stimulation) provide an interesting problem. In the case of muscle we know that contraction is accompanied by a large and sudden liberation of heat, while relaxation, which occurs more slowly, is also accompanied by a liberation of heat which seems to follow the course of relaxation, at any rate approximately. In their paper on the nature of the isometric twitch Hartree and Hill (5, fig. 6, p. 406) describe the return of muscle, following a shock, to its initial state of capacity for liberating energy. The return of heat liberating power in a frog's muscle at 10° C. is complete in about 0.2 sec., which is just about the time taken in complete relaxation at that temperature. It would seem likely that this "recovery" in muscle is associated in some direct way with relaxation, and, since we know that relaxation is accompanied by heat production, it may well be that in nerve the return to its initial condition will also be accompanied by a production of heat. Thus, the process of "recovery" exhibited by the curves of Fig. 3 may not be one involving no change of energy; indeed upon general grounds it would seem more likely that the chemical reactions involved in the restoration of nerve to its original condition would be accompanied by a liberation of heat, *i.e.* by a wastage of energy. Thus, in saying that in the initial process of a single impulse a nerve liberates about one ten-millionth of a calorie per grm., we do not imply that the whole of this energy liberation is confined to the interval during which the action current occurs, since there may be an initial rapid outburst of heat, as there is in muscle, followed by a slower liberation of heat occurring during the "recovery," which is analogous to relaxation, and takes 50σ or more (20 to 80σ) to complete. In this sense, therefore, there may well be, as in muscle, *three* phases of liberation of heat, namely, an initial and

very rapid phase concerned with the process which produces the rise of the action current, a second phase concerned with the restoration of the nerve to its original condition of excitability and conductivity and complete in 50σ or so, and a third phase lasting for 10 minutes, during which eight-ninths of the total energy is liberated. It is impossible at present by direct methods to analyse the heat as between these first two phases. In the case of muscle, where the heat is much larger, and contraction and relaxation may be considerably displaced in time from one another by taking appropriate slow muscles and by lowering their temperature, the analysis is technically possible. In the case of nerve, where the heat in one impulse is very small and the whole process lasts only 50σ or so, there would seem to be no chance of an experimental isolation of these two first phases from one another. On the somewhat uncertain basis, however, of an analogy with muscle one may imagine the return of the capacity of the nerve for liberating energy to correspond to relaxation of the muscle, and so to be accompanied by a production of heat.

SUMMARY.

1. The relation has been determined between the heat production of a nerve stimulated by a sequence of maximal induction shocks and the frequency of stimulation. The heat production per second continues to increase with the frequency but at a diminishing rate, the heat per impulse falling off as the interval between stimuli gets less. At a frequency of 280 shocks per second, as employed in the experiments of Downing, Gerard and Hill, the heat per impulse is not much more than one quarter of what it is at a very low frequency. From the relation observed it is possible to calculate the heat in a single isolated impulse. In frog's nerve the initial heat for a single maximal impulse is about one ten-millionth of a calorie per gram, and the total heat about one millionth of a calorie per gram.

2. From the results obtained it is possible to calculate a curve giving the return of the power of liberating energy, in a nerve impulse started by a maximal shock, as a function of the interval between it and its predecessor. This curve is of a composite nature, since some of the fibres of a frog's sciatic nerve take about four times as long to recover as the most rapid ones. Perhaps for this reason the curve is very different from that for the return of excitability as determined for the most rapid fibres by a second stimulus following a first one.

3. The "total action current" (the negative variation of the injury current), as determined by an ordinary galvanometer for a given period

of stimulation, bears a relation to the frequency of stimulation which is very similar to that shown by the heat liberated.

4. It is pointed out that the "initial recovery" of nerve following a stimulus is probably accompanied by a liberation of energy just as the process of relaxation in muscle is. There are probably three phases in nerve activity, corresponding to contraction, relaxation and "delayed recovery" in muscle.

5. It is suggested that, after an impulse has traversed a nerve, an anaerobic recovery process (analogous to relaxation in muscle) has to go on, restoring the nerve to its initial condition as regards power of liberating energy; and that the absolutely refractory period is due to the fact that a wave will not propagate at all unless there be a certain amount of energy available.

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