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The Thermo-Elastic Properties of Muscle

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V.—*The Thermo-elastic Properties of Muscle.*

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(1) Introduction.

The thermal effects of applying a stress to a body were first studied by Weber (1), who found that when an iron wire was stretched a thermal effect was produced, and that the thermal change was proportional to the stress. Lord Kelvin (2) deduced the general equations of thermo-elasticity from the laws of thermodynamics, and proved that with stresses of the most general type the thermal effect is proportional to the applied stress, provided the material remains perfectly elastic. In a body which expands on being warmed, the effect of an extension is a *fall* of temperature, while a body which shortens on being warmed will show a *rise* of temperature on extension. It will be remembered that Engelmann found that some substances (*e.g.*, catgut) containing doubly refractive particles contract on heating; such bodies, therefore, would be expected to show a rise of temperature on being loaded, and the experiments given below prove that muscles and rubber belong to this class.

The phenomena of thermo-elasticity have been employed to demonstrate the stresses set up in structures on loading them; all that is necessary is to place the "warm" junctions of a suitable thermopile against the part it is desired to investigate, and then, on loading the structure in any desired manner, the magnitude and sign of the stress in that part can be determined at once from the deflection of a galvanometer. This method, which is quite reasonably simple to employ, appears to deserve a wider application than it has received. It could be applied to a variety of substances under a variety of conditions, *e.g.*, to the materials employed in the construction of aircraft, ships, guns, etc., in which considerable stresses have to be borne by structures which have to be kept as light as possible. It might even be employed in physiology to determine the distribution of stresses in the skeleton, and

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it would certainly be of interest to make an extensive investigation of the thermo-elastic properties of elastic colloidal materials.

A further application is that of determining the elastic limit of a material. When an ordinary steel wire is stretched there is a fall of temperature; as the load is increased the fall of temperature increases at a proportional rate; at the elastic limit, however, the cooling is replaced by a warming due to the work done by the load being transformed irreversibly into heat instead of into elastic potential energy. The load at which this change occurs corresponds to the elastic limit of the wire.

Various applications of the method to engineering problems have been described by Coker (5 and 6).

It would seem that the employment of the light and sensitive thermopiles now obtainable, together with photographic recording as used in our experiments, might considerably increase the variety and importance of such applications. It should be remembered that metals and many other materials can bear enormously greater stresses, and so give greater thermal effects than can muscles or rubber, so that the high sensitivity of the galvanometer required in the experiments described here could be exchanged for a more rapid response, enabling a very accurate time-record of the thermal effects to be made. A more rapid response also could be secured by employing thinner insulation on the thermopile.

Our attention was first called to the subject by Mr. C. C. Mason, of the Cambridge and Paul Instrument Company, and it seemed desirable to investigate the phenomena of thermo-elasticity in living tissues. Assuming that (like catgut) a muscle shortens on warming, one would expect that on loading it there would be an evolution and on unloading an absorption of heat. These phenomena we have observed, but the results of our experiments are much more complex than those found in the case of an ordinary elastic body such as a steel wire, owing to the peculiar elastic properties of the muscle. The experiments throw considerable light on these elastic properties—which belong not only to muscles, but to many kinds of material—and, moreover, the purely physical thermal phenomena described here, if unheeded, may considerably interfere with or distort the physiological thermal changes associated with muscular activity.

Exactly similar results have been obtained in live and in dead muscles, and analogous results in the case of a rubber band, and it appears certain that the phenomena described are purely a consequence of the elastic properties of the material, and in no way dependent on the life or structure of the muscle.

The elastic property of a muscle which differentiates it from a steel wire is that, for any load, although well within the elastic limit, the muscle does not immediately attain its new length when the load upon it is changed. For example, when a weight is hung on a muscle, the muscle continues stretching for some time; when the load is removed, it returns only slowly to its original length. The same property is true of a jelly, or of a piece of rubber, and, of course, is well known to all who have studied the properties of materials. The implications of it, however, are peculiar, and lead to complex and interesting thermal effects of applying a stress to the body concerned. The elastic property described is presumably due, in the case of a muscle, to the existence of an elastic network, colloidal or otherwise, containing a viscous fluid in its interstices. The final equilibrium value of the extension caused by a given load is presumably a characteristic of the network. When, however, the load is suddenly altered, the viscous fluid has to change its position within the network, and, if the alteration of load is rapid, the new equilibrium length is not attained until the viscous fluid has had time to reach its new position. Consequently, if the material be unloaded and allowed to shorten rapidly, doing work, the work done will be less than the work put into it in stretching it, and the difference between the two will cause an irreversible production of heat, complicating the reversible changes predicted by the thermodynamical reasoning.

The thermal effects of passive lengthening or shortening are by no means small. They are not as large as those of stimulating a live muscle, but they are large enough to afford a notable complication in the case of any contraction in which the muscle is allowed to shorten. A discussion of these complications is given below: one obvious means of avoiding them, and the one which—fortunately, though for other reasons—has been adopted by us in most previous work, is that of making the contraction isometric. In any experiments, however, in which a muscle is initially stretched, and allowed to shorten on excitation, the purely *physical* thermal effects consequent on the shortening and the subsequent extension during relaxation, must necessarily be superimposed upon the *physiological* thermal effects attending the chemical reactions set up by the stimulus.

(2) Methods and Results of Thermal Experiments.

The instruments employed have been those described elsewhere (3). The use of the combined muscle-chamber and thermopile, immersed in well stirred water in a large double-walled vacuum flask, has ensured an absence of differences of temperature at different points on the muscle which were the stumbling block in all previous experiments in which the muscles were allowed to move over the junctions (4). The uniform temperature of the whole thermopile and muscle eliminated the possibility of a movement bringing cooler or warmer parts of the muscle on to the junctions. The muscles (a pair of sartorii from *Rana temporaria*) were fitted on the thermopile in the chamber, and a long thread taken from their upper ends, through the tube holding the chamber, up to one arm of a pivoted lever; to the other arm of the lever was tied a thread carrying a pan, in which were placed the weights required to load the muscle. The lever itself had a small weight, usually of the order of 5 grm., fixed directly to it, to provide a small constant tension on the muscle. The loading or unloading of the muscle was carried out by hand, by gently raising or lowering the pan in which the weights

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were placed. For example, if it were desired to investigate the effects of loading the muscles with 60 grm., the weights were placed in the pan and the pan held in the hand with the thread attaching it to the lever loose; the muscle was then subject only to the load of the 5 grm. providing the small constant tension. When all was ready, and the photographic arrangements running, on a given signal, recorded on the photographic paper, the pan, with its weights, was gently lowered so as to hang on the lever, and subject the muscle to an additional tension of 60 grm. The deflection of the galvanometer was recorded on the paper and the record allowed to run as long as required, usually for about 30 seconds. To investigate the effects of *unloading*, the load was allowed to hang on the lever for some time, say 2 or 3 minutes, until the length of the muscle had become appreciably constant; on a given signal, the pan with its weights was gently lifted, and the photographic record made as before. Typical records are shown in fig. 1. It should be noted that the load was lowered *gently* on to the muscle and gently removed, particular care being taken to avoid anything in the nature of a jerk.

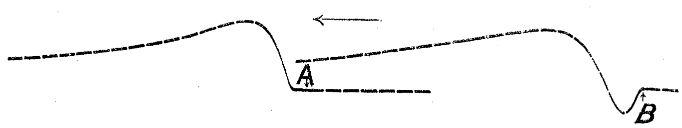

Fig. 1.—Pair of sartorius muscles from *Rana temporaria*. Permanent load 5 grm. At A on the left hand curve 155 grm. was hung gently on the muscle: the temperature rose. At B on the right hand curve, after the 155 grm. had been hanging on the muscle for some time, it was gently removed: the temperature fell rapidly (the reversible effect) and then rose (the irreversible "viscous" effect) and finally fell again (the physical loss of heat by conduction). Time in secs. shown on the curves. N.B.—These and all other records given here read from right to left.

In order to obtain satisfactory records, it was usually desirable to increase the sensitivity of the galvanometer to about $1\frac{1}{2}$ times that employed in the case of experiments on the heat-production of stimulated muscles.

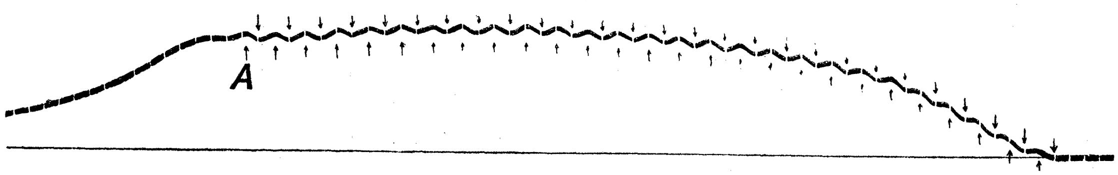

Fig. 2.—Dead muscles at 11° C. 163 grm. load "on" and "off" at intervals of 1 sec. (*i.e.*, load on—1 sec. interval—load off—1 sec. interval—load on—etc.). 50 ohms in galvanometer-thermopile circuit to reduce sensitivity, which in this experiment was about 0·26 of that in the experiment shown in fig. 1. Notice (*a*) the rise of temperature on loading followed by (*b*) the fall of temperature on unloading; superimposed upon (*c*), the gradual steady rise of temperature to a maximum (determined by a balance between heat produced and heat lost). Of these (*a*) and (*b*) are the reversible thermodynamic effects; (*c*) is the irreversible effect due to the viscous flow accompanying extension and shortening. The arrows above the curve indicate the moments at which loading occurred: the arrows below the curve indicate the moments at which unloading occurred. Time marks in secs. on the curve. At A the muscle was unloaded finally, and after a short delay began to cool down by simple loss of heat.

Various other procedures were adopted to illustrate the phenomena. For example, in some experiments the pan containing the weights was raised and lowered gently at regular intervals of, say, one second. Fig. 2 is a record of the thermal effect of such a procedure. In other experiments the muscle was loaded and then unloaded after a certain definite interval, the effect of which is shown in fig. 3.

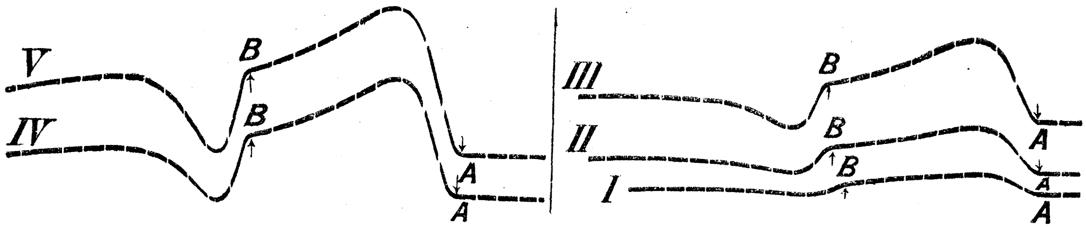

FIG. 3.—Dead muscles at $-0{\cdot}6^{\circ}$ C. Various loads "on" and "off" at an interval of 10 secs. At A on each curve the load was put "on," at B it was taken "off." Curves I–V show respectively the thermal effect of loading and unloading with 20, 50, 95, 155, and 200 grm. Time marks in secs. on the curves. Notice (*a*) the sudden rise of temperature on loading, and (*b*) the sudden fall of temperature on unloading, followed by (*c*) a subsequent rise. The shape of the curves is determined largely by loss of heat through conduction. Note also that the thermal effect increases as the load is increased, but not quite proportionally.

Exactly similar results were obtained with live and with dead muscles, and there is no evidence to show that the phenomena are in any way connected with the life or mechanism of the muscle. To make the more certain of this, the observations were repeated with a narrow strip of an old Dunlop rubber tyre (inner tube), more or less of the shape and size of a pair of muscles, and lying upon the junctions of the thermopile in the same way. In order to make the motion of the rubber over the junctions more free, a drop of paraffin oil was placed upon the thermopile. The phenomena shown by the rubber were similar in type to those shown by the muscle, though quantitatively different. Fig. 4 shows the characteristic effects of loading and

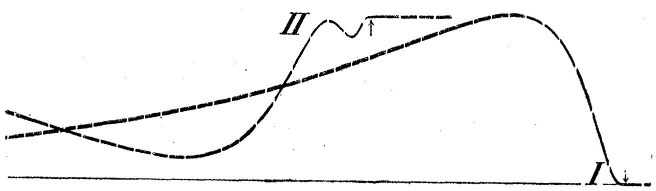

FIG. 4.—Strip of old rubber tyre, 3·5 cm. long, mass 0·59 grm., of the general shape of a pair of sartorius muscles, placed upon the thermopile in the muscle chamber at 11° C. Permanent load 150 grm. Time shown in secs. on the curves. Curve I shows the rise of temperature on loading the rubber with a further 550 grm. Curve II shows (*a*) the fall; (*b*) the rise; and (*c*) the subsequent further fall of temperature on removing the 550 grm. NOTE.—In curve I an extra 25 ohms was put in the galvanometer-thermopile circuit in order to reduce the sensitivity; consequently Curve I is on 2·4 times the scale of Curve II.

unloading the rubber. In this case there was a permanent load of 150 grm. on the rubber, and an extra load of 550 grm. was put on and taken off. Fig. 5 shows the effects of loading followed by unloading at various intervals—1, 2, 4 secs. and "infinity."

The sensitivity, expressed in degrees Centigrade per millimetre deflection, was

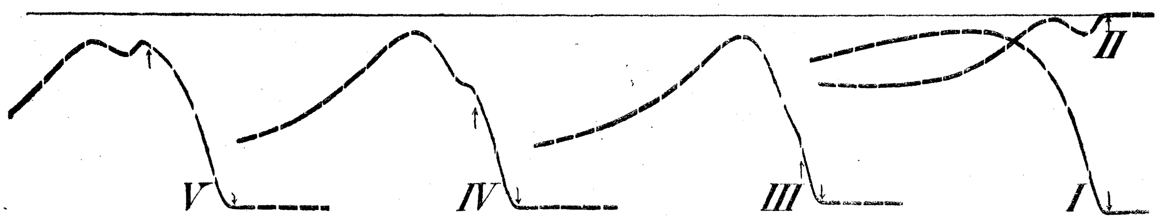

FIG. 5.—Strip of old rubber tyre, as in fig. 4. Permanent load 150 grm.

Curve I shows the rise of temperature on loading with a further 300 grm.

Curve II shows (*a*) the fall; (*b*) the rise; and (*c*) the subsequent further fall of temperature on removing the 300 grm., after it had hung on the muscle for an "infinite" time.

Curve III shows the effect of loading with 300 grm., and then unloading again after 1 sec.

Curve IV shows the effect of loading and unloading again after 2 secs.

Curve V shows the effect of loading and unloading again after 4 secs.

By an analysis of the curves of fig. 5, taking the deflections of I and II at every 1 sec. and then adding them together algebraically with an interval ("phase difference") of (*a*) 1 sec., (*b*) 2 secs., and (*c*) 4 secs., it is found that as regards the *initial* shape of the curve—*i.e.*, up to 5 or 6 secs.—there is good agreement between the results so calculated and the observed Curves III, IV, and V respectively. Afterwards, however, in all the later stages, much less heat is actually given out than would be calculated from the addition of I and II with the appropriate "phase difference": in fact—as would be expected—the irreversible processes leading to a loss of potential energy and the production of heat, are much less in extent when the load is left on for a shorter time. The same thing is shown by the fact that the total heat production in the complete cycle of loading and unloading, given very nearly by the areas of the Curves III, IV, and V, obviously increases as the interval between loading and unloading increases.

determined in the case of the experiments on muscles by means of a direct calibration, as described in another paper (3). It was about the same in the various experiments on muscles and may be taken to be approximately (in the original records)

$$1 \text{ mm.} = 6 \times 10^{-5\circ} \text{ C. or } 0{\cdot}00006 \text{ calories per grm.}$$

One is, of course, working to a high sensitivity in these thermal measurements, as the records are reliable to about 0·1 or 0·2 mm., which means that one is reading to about 10 millionths of a degree. A less sensitive arrangement would not show to sufficient accuracy the rather small quantities involved.

[The curves as reproduced in figs. 1 to 5 have been reduced to about 40 per cent. of their original size.]

In the case of the experiments on the rubber strip a direct calibration was not possible, as the rubber is a non-conductor of electricity, and so no warming current could be applied to it. We may, however, assume for the purposes of a rough calculation of the coefficient of thermal expansion that the sensitivity in degrees Centigrade was the same as in the muscle experiments.

The sensitivity of the arrangement may be expressed also in the following form, by employing the mechanical equivalent of heat:—

1 mm. = 2·5 grm.-cm. of work per gramme of muscle.

This means that, for a pair of muscles weighing 0·16 grm., 1 mm. deflection is given when 0·4 grm.-cm. of work is absorbed by the muscles and degraded into heat. A full deflection of 6 cm. could be produced, therefore, by the absorption of mechanical work to the extent of 24 grm.-cm. This is a more expressive way of stating the sensitivity, as it is clear that 24 grm.-cm. is of the same order of size as the work done in stretching the muscle 1 cm. with a load (say) of 100 grm., whereas 0·0036 calories has at first sight no obvious relation to the same quantity.

In most of the experiments the thread connecting the muscle to the lever was free in the tube; in a few of them, however, the narrow part of the tube (about $\frac{3}{4}$ mm. diameter) was filled with vaseline and the thread moved in the vaseline. The vaseline had the effect of reducing the irreversible rise of temperature following the reversible fall of temperature caused by unloading the muscle. This fact is of interest in confirming the theory as given here, and will be discussed below.

(3) Discussion of Thermal Experiments.

Since the phenomena described are susceptible to some degree of an exact treatment by the methods of thermodynamics, it may be well to put on record here a deduction of the equations for a finite extension of an elastic string. We have thought it better to employ the conception of "free energy," rather than that of "entropy," as being more intelligible to the average reader. The principle involved is to calculate A, the free energy, *i.e.*, the maximum work which could be done by an extended string, and then, by the second law of thermodynamics, to equate dA/dT to Q/T, where T is the absolute temperature and Q is the heat absorbed in the process. If the coefficient of thermal expansion be known, dA/dT can be calculated, and therefore Q is obtained directly from the equation

$$Q = T\frac{dA}{dT}. \tag{1}$$

Let an elastic body shorten from length l_1 to length l_2, doing work, and suppose the length is l for a tension P. Then the free energy of the change is

$$A = \int_{l_2}^{l_1} P\,dl.$$

Differentiating with respect to T

$$\frac{dA}{dT} = \int_{l_2}^{l_1}\left(\frac{\partial P}{\partial T}\right)_l dl, \tag{2}$$

where $\left(\frac{\partial P}{\partial T}\right)_l$ is the rate of change of P with respect to T when l remains constant.

Now l is a function of two variables, and of two variables only, P and T: hence we may write, when l remains constant,

$$\delta l = 0 = \left(\frac{\partial l}{\partial P}\right)_T \delta P + \left(\frac{\partial l}{\partial T}\right)_P \delta T$$

from which

$$\left(\frac{\partial P}{\partial T}\right)_l = -\left(\frac{\partial l}{\partial T}\right)_P \Big/ \left(\frac{\partial l}{\partial P}\right)_T. \tag{3}$$

Now, if the coefficient of thermal expansion α be independent of the tension P, we have

$$\left(\frac{\partial l}{\partial T}\right)_P = \alpha l. \tag{4}$$

In this case, from (2), (3) and (4), we have

$$\frac{dA}{dT} = -\int_{l_2}^{l_1} \alpha l \left(\frac{\partial P}{\partial l}\right)_T dl.$$

Integrating by parts

$$\frac{dA}{dT} = -\alpha\,(P_1 l_1 - P_2 l_2) + \alpha \int_{l_2}^{l_1} P\,dl.$$

Hence from (1) above, the heat absorbed is given by

$$Q = \alpha T\,[\text{work done} - (P_1 l_1 - P_2 l_2)]. \tag{5}$$

This is the most general form of the result but, if we may assume that the body is perfectly elastic, we may write

$$\text{work done} = \tfrac{1}{2}\,(P_1 + P_2)\,(l_1 - l_2)$$

in which case

$$Q = -\tfrac{1}{2}\alpha T\,(P_1 - P_2)\,(l_1 + l_2). \tag{6}$$

In other words, when the tension is diminished heat is *evolved* equal to

αT (diminution of tension) (mean length),

and when the tension is increased, heat is *absorbed* equal to

αT (increase of tension) (mean length).

It should be noted that here we have measured everything, including the heat, in dynamical units; if the heat be measured in calories, the tensions in grams-weight and the lengths in centimetres, the heat absorbed becomes

$$\frac{\alpha T\,(\text{increase of tension})\,(\text{mean length})}{4{\cdot}24 \times 10^4}\ \text{calories.}$$

If we consider the fall of temperature in an adiabatic extension instead of the heat absorbed in an isothermal one, the fall of temperature $(-\delta T)$ is given by

$$-\delta T = \frac{\alpha T\,(\text{increase of tension})\,(\text{mean length})}{(\text{mass})\,(\text{specific heat})\,4{\cdot}24 \times 10^4}. \tag{7}$$

In the case of most substances α, the coefficient of thermal expansion, is positive and of the order 10^{-5}. In the case of muscle and of rubber it appears to be negative, but of the same order of size. With these substances there is an initial rise of temperature on increasing, and an initial fall of temperature on decreasing, the tension.

We have assumed in the preceding argument that we have to deal with a perfectly elastic body undergoing a reversible change. In the case of a substance like muscle the change will be reversible only if carried out infinitely slowly, for otherwise an irreversible degradation of potential energy into heat under the action of viscous forces will occur. This matter also can be treated by means of thermodynamical reasoning. In fig. 6 are shown curves relating the extension of a muscle to its

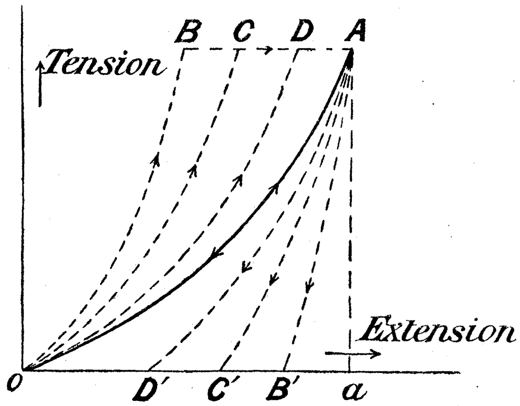

FIG. 6.—Relation between tension and extension in a muscle. The full curve OA corresponds to a very slow process of unloading or loading the muscle from or to a given tension, and represents a "reversible" process. The dotted curves represent "irreversible" processes carried out more or less rapidly. The curves OBA, OCA, and ODA correspond to *loading* carried out rapidly, the most rapid being OBA, and the least rapid ODA. The curves AB′O, AC′O, AD′O, correspond to unloading carried out rapidly, the first being the most and the last being the least rapid. The potential energy possessed by the stretched muscle corresponds to the area OAa: the work done in stretching it rapidly along (say) the curve OCA corresponds to the area OCAa: the work obtained from it on unloading it rapidly corresponds (say) to the area AC′a: the work lost and degenerated into heat irreversibly in the complete cycle corresponds therefore to the area OCAC′.

[NOTE.—The curves are illustrative only and do not represent an actual observation.]

tension. The curve OA represents the relation of extension to tension when the tension is increased exceedingly slowly from the value zero to the value Aa, and the work done in extending the muscle is represented by the area OAa. The process of passing from O to A or from A to O is strictly reversible, and no work or potential energy is degraded into heat in the process. If, however, the tension be increased more or less rapidly from zero to the value Aa, the relation between extension and tension follows one or other of the curves OBA, OCA, or ODA: OBA representing the more rapid change and ODA the less rapid. In the case of the rapid change corresponding (say) to OCA, the work done in stretching the muscle corresponds to the area OCAa, which is greater by the area OCA than the *greatest* amount of work which can be recovered on allowing the muscle to shorten again. Hence in this rapid stretching the work done re-appears in the muscle, partly as mechanical potential energy corresponding to the area OAa, and partly as heat corresponding to the area OCA. The more rapidly this stretching process is carried out the greater will be the amount of work re-appearing irreversibly as heat in the muscle. The irreversible transformation of work into heat is presumably caused by the rapid flow of viscous fluid inside the network, colloidal or microscopic, of the muscle. Hence, on stretching the muscle rapidly by increasing the tension on it, there will be a production of heat under two headings—

(*a*) The reversible thermodynamic effect given by the formula deduced above,

$$Q = \tfrac{1}{2}(-\alpha)\,T\,(P_1 - P_2)\,(l_1 + l_2)\,;$$

(*b*) The irreversible effect corresponding to the area OCA in the diagram.

These effects are of the same sign and additive.

When the muscle is unloaded a similar process takes place. If unloaded infinitely slowly, the extension-tension relation follows the curve AO. If unloaded more or less rapidly, it follows one or other of the curves AB′O, AC′O, AD′O. The *maximum* work obtainable from the stretched muscle is given by the area AO*a*. The work obtained in a rapid shortening corresponds to one or other of the areas AD′*a*, AC′*a*, AB′*a*, the area AB′*a* corresponding to the more rapid process. Consequently, in shortening rapidly along (say) the curve AC′O work is lost corresponding to the area AC′O, the potential energy of the stretched muscle re-appearing partly as external work equal to the area AC′*a* and partly as heat equal to the area AOC′. This irreversible transformation of potential energy into heat also is presumably due to the flow of viscous fluid inside the elastic network of the muscle. Thus, on unloading the muscle rapidly there will be two different thermal effects :—

(*a*) The reversible thermodynamic effect given by the formula deduced above, viz., an absorption of heat equal to

$$\tfrac{1}{2}(-\alpha)\,T\,(P_1 - P_2)\,(l_1 + l_2)\,;$$

(*b*) The irreversible production of heat corresponding to the area AC′O in the diagram.

These effects are of opposite sign and lead to the complex curves of unloading shown in figs. 1 to 5.

A further interesting case arises in the alternation of loading and unloading at a finite interval, as shown in figs. 2, 3, and 5. Here the relation between tension and extension follows a set of curves more or less similar to those shown in fig. 7. When the muscle is loaded, the extension follows the curve OA; as it remains loaded it stretches at constant tension from A to B, from A to C, or from A to D, according as a shorter or a longer interval is given. If the muscle be unloaded a short time after it is loaded, the complete cycle is represented by the curve OABG; if the interval be longer, by the curve OACF; if still longer, by the curve OADE. Thus, if the interval between loading and unloading be short, work corresponding only to the area OABG is degraded into heat, while if the interval be greater more work is lost, corresponding to the area OADE. In any case, however, some work is lost. Thus, in addition to the reversible thermodynamic effects corresponding to loading and unloading, there is an irreversible production of heat, corresponding in each cycle to

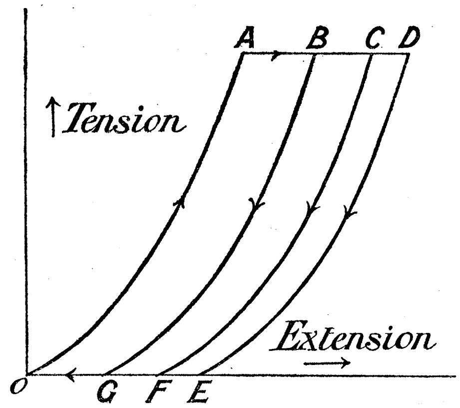

FIG. 7.—Curves relating tension and extension in the case of a complete cycle made up of a rapid process of loading and a rapid process of unloading separated by a finite interval. OA represents the loading curve; BG the unloading curve after a short interval; CF the unloading curve after a longer, and DE after the longest interval. The work degraded into heat irreversibly in the complete cycle, OACF, corresponds to the area OACF, and is clearly greater the greater be the interval between loading and unloading.

[NOTE.—These curves are illustrative only and do not represent an actual case.]

(say) the area OACF, and appearing in fig. 2 as the steady displacement of a curve on which are shown oscillations corresponding to the reversible alternations of heat production and absorption. The same phenomenon is shown in another way in fig. 5. Here the thermal effects of loading and unloading are shown in curves I and II, III, IV, and V, with intervals between them of "infinity" and of 1, 2, and 4 seconds respectively. It can be shown, both experimentally and theoretically, that the total heat produced corresponds fairly accurately to the area of the photographic record, and it is obvious that the areas of curves III, IV, and V are in ascending order of magnitude, corresponding to the increasing interval between loading and unloading. This is a strong incidental verification of the theory sketched above.

A further verification of it is shown by the following observation. In most of the experiments the thread connecting the muscles to the load passed up freely through a narrow dry tube, but in those few in which the tube was filled with vaseline, and the thread passed through the vaseline, it was obvious that the secondary and irreversible rise of temperature following unloading was far smaller than in the other experiments. The reason is simple. It required a definite, if small, force to pull the thread through the vaseline at a finite rate, so that the unloading process really took place very much more slowly, the muscle being held to some extent by the vaseline, and giving up its potential energy gradually in warming the vaseline instead of warming itself. By allowing the muscle to shorten even more slowly, the method might be extended and the irreversible thermal effects eliminated almost completely.

By means of the method of analysis described in another paper (3) it is possible to determine the rate of heat-production at all moments subject to loading or unloading and to exhibit it in a curve. The details of such an experiment are given below and the results are shown in fig. 8.

Experiment.—Pair of sartorius muscles. Permanent load, 7 grm. Extra load of 50, 100, 150, or 200 grm. put "on" or taken "off." Control curves made by electrical warming with 7, 57, 107, 157, and 207 grm. on; the initial shapes of the five sets of control curves agreed exactly. By means of the control curve the loading and unloading curves were analysed. The unloading curves are complex, owing to the mixture of production and absorption of heat; the analysis of them is difficult, and in such a case the results are necessarily rather indeterminate. The loading curves, however, are easy to analyse, and the following analysis of the thermal effects of loading with 200 grm. is typical. Heat production is given on an arbitrary scale in units per $\frac{1}{4}$ second:—

Time, secs.	0	$\frac{1}{4}$.	$\frac{1}{2}$.	$\frac{3}{4}$.	1.	$1\frac{1}{4}$.	$1\frac{1}{2}$.	$1\frac{3}{4}$.	2.	$2\frac{1}{4}$.	$2\frac{1}{2}$.	$2\frac{3}{4}$.	3.
Heat production .	56	14	8	4	3	2	2	2	2	3	2	2	1

After 3 seconds the heat production continued more or less uniformly at the rate of 1 unit per $\frac{1}{4}$ second for some time. The results are shown in fig. 8. The analysis of the unloading curve shows that there is an absorption of heat, following more or less the type of relation shown in fig. 8, but having superimposed upon it a production of heat starting later and falling more rapidly. The absorption of heat is initially the faster, then becomes the slower, and finally the faster again.

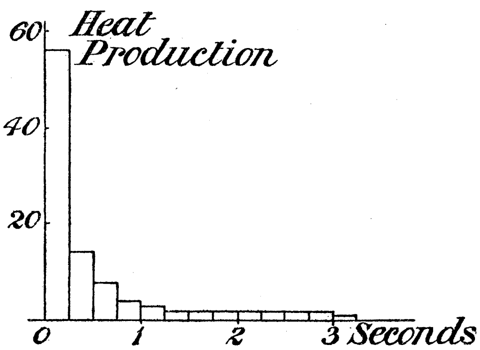

Fig. 8.—Pair of sartorius muscles, permanent load 7 grm., loaded with extra 200 grm. Record analysed and heat production shown in arbitrary units at every $\frac{1}{4}$ sec. following loading. For description of experiment see above.

(4) Results and Discussion of Mechanical Experiments.

A further experimental confirmation of the theories described above may be gained by the use of the inertia system of obtaining the maximum work described by one of us recently (7). A muscle, alive or dead, is connected to the inertia lever by a long thread: the lever is then loaded with a small rider to record the work performed, and a large rider to stretch the muscle. The large rider hangs from a long thread, and, when all is ready, is suddenly lifted off the lever; the stretched muscle immediately proceeds to shorten, and gives out all the work of which it is capable in accelerating the lever; the work done is measured by the distance through which the small rider is lifted. If the moment of inertia of the lever were infinite, the stretched muscle would shorten infinitely slowly, and give out all its elastic energy as work; the moment of inertia, however, being relatively small, the muscle shortens rapidly, and therefore gives out considerably less work. By loading the muscle with different weights and noting the extension produced, it is possible to construct a curve relating extension to load, such as the curve OA in fig. 6. From this, the potential energy corresponding to any given load can be read off as an area. This potential energy can then be compared with the actual work performed on the inertia lever in an ordinary rapid shortening consequent on release. It is found that the actual work done in a rapid shortening may be very considerably less than the potential energy of the muscle, *i.e.*, than the work which would be done in a very slow shortening; consequently, in a rapid shortening, a large part of the potential energy is wasted, and can only reappear as heat. The following Table gives typical results:—

Table I.—Comparison of the work done in the rapid shortening of a passively extended muscle, with the elastic potential energy possessed by the muscle in virtue of its stretched condition.

Note.—The action of the muscle pulling on the inertia lever is similar to that of the muscle pulling horizontally on, and so accelerating, a mass, M, suspended freely by a long string. The "equivalent mass," M, of the inertia system was varied in the following experiment, in order to vary the rate at which the muscle shortened; the greater the "equivalent mass," the more slowly will the muscle shorten. We should expect, therefore, to find more work done when the "equivalent mass" is greater, and this proves to be the case.

The potential energy is calculated from the area of the curve relating tension to extension; this and the work done are expressed in grm.-cm.

Experiment 1.—Pair of Sartorius Muscles of *Rana Temporaria.*

Load on Muscles, grm. weight.	$5\frac{1}{2}$.	7.	$8\frac{1}{2}$.	11.	$17\frac{1}{2}$.	27.	42.	57.	82.
Work done, M = 520 grm. . . .	0·7	1·0	1·3	1·5	2·2	3·2	4·6	6·1	8·8
Work done, M = 910 grm. . . .	0·8	1·0	1·3	1·7	2·5	3·5	5·0	—	—
Work done, M = 1300 grm. . .	1·0	1·3	1·6	2·0	2·9	4·2	5·9	7·6	10·1
Potential energy (M = ∞) . . .	1·0	1·4	1·9	2·5	3·8	6·0	9·4	14·2	20·8

Experiment 2.—"Equivalent Mass," M = 2900 grm.

Load on Muscles.	8.	10.	13.	17.	26.	40.	63.	86.	123.
Work done	1·3	1·8	2·3	2·9	4·1	5·5	8·4	10·9	14·7
Potential energy . . .	1·3	1·9	2·7	3·6	5·5	9·0	16·2	23·4	37·2

We see from these experiments that *the work done by a muscle in shortening rapidly when suddenly unloaded is less than the potential energy it contains*, and considerably less for large loads; moreover, Experiment 1 shows that, as the rapidity of shortening diminishes (with increasing "equivalent mass"), so the amount of work obtained increases. These facts confirm the theory discussed in connection with fig. 7 above, and have a considerable bearing on the mechanics of muscular contraction, as will be shown later.

There seems, therefore, to be little doubt that the theory employed to explain the thermal effects of loading and unloading, as shown in figs. 1–5, is correct.

(5) Application to Physiological Problems.

The importance of the phenomena described here can be discussed best under two headings: (*a*) in relation to the heat-production of muscles, and (*b*) in relation to the mechanics of muscular contraction.

(a) *Heat-production.*

Only if a muscle be held rigidly isometric will the heat produced in consequence of a stimulus be free from the complicating effects of the thermo-elastic phenomena described above. If the muscle be allowed to shorten, even as little as 1 mm., the effect will be seen. In analysing the time-course of the evolution of heat in the earlier stages of a muscular contraction (3), we have noticed more than once that, in addition to the ordinary thermal effects, the analysis required a small evolution of heat, followed by an equal small absorption of heat, corresponding in time to contraction and relaxation respectively; and it was noticed in all such cases that the muscle had been able, by reason of being tied by a long and somewhat extensible thread, to shorten 1 mm. or 2 mm., instead of being, as in most experiments, held rigidly isometric by direct attachment to the upper end of the thermopile. It is clear, therefore, that, where possible, it is safer and simpler to employ rigidly isometric contractions in all investigations of the heat-production of muscles. It is advisable also, when employing a "tension lever," to record the tension set up in an isometric contraction, to ensure that only the minimal shortening is necessary in order to work the lever,* and that the connections to the lever are as inextensible as possible (*e.g.*, not made of silk thread, which stretches considerably). If such precautions be taken, it is possible to avoid largely, if not entirely, the errors and complications caused by the phenomena described here.

In many experiments, however, and in the very important experiments in which work is actually done by the muscle, it is not possible to employ isometric con-

* In order to avoid any appreciable shortening of the muscle it is advisable to adopt a photographic device giving high magnification of movement for recording the tension developed by a muscle. Such a device was used in making the curves shown in fig. 12, of the paper (3) describing the methods employed in this investigation.

tractions. In all such cases, the actual heat-production observed is the resultant of the thermal effects of mechanical shortening or extension, and of the physiological effects set up by the stimulus. This is still further complicated by the fact that, during relaxation, the part of the potential energy set free on excitation which has not been used up in doing work is irreversibly degraded into heat. The matter can, however, be made rather more intelligible by the consideration of a physical analogy. It will be seen from this that, if a muscle, whether excited or not, be released and allowed to shorten, we may expect to find an absorption of heat, in addition to the absorption of mechanical potential energy transformed into work. If the muscle be subjected to a high initial tension, we may expect the initial absorption of heat to be greater. If the tension in an unexcited muscle carrying a weight be provided by one part (A) of the muscle, while the "active" physiological increase of tension consequent on excitation is provided by another part (B), *e.g.*, if the initial tension be taken by inactive connective tissue fibres, while the development of tension is due to active muscle fibres, then the problem is simple, for it is clear that each part can be considered separately; in this case, it is obvious that, when the whole system shortens, doing work, the usual *physical* thermal consequences of shortening must take place in the part (A) of the system, in addition to the combined physical and physiological effects in the part (B). If, however, (A) and (B) be the same, *i.e.*, if the passive tension of the loaded but unexcited muscle be provided by the same fibres or network as develop the extra tension on excitation, the matter is not so simple, and we must consider the thermal consequences of shortening in the excited muscle as a whole. The correct way of regarding the question then is best made clear by considering the following physical analogy.

A Physical Analogy.

Consider a soap-bubble of radius r, consisting of a film with surface-tension β. The surface energy of the bubble is then $4\pi\beta r^2$, and the maximum work obtainable, by allowing the bubble to contract from radius r_1 to radius r_2, is $4\pi\beta(r_1^2-r_2^2)$. Thus the bubble is analogous to an unexcited muscle subjected to an initial tension, and is capable similarly of doing work, if allowed, at the expense of its stored potential energy. There is, moreover, a further analogy with the muscle. Surface-tension, in general, diminishes with rise of temperature, and, from this, it can be shown thermodynamically that there is a reversible production of heat when the bubble contracts, and similar absorption of heat when the bubble expands; these thermal effects are analogous to those shown on loading or unloading a muscle.

The free energy, A, of the contraction of the bubble is given by

$$A = 4\pi\beta(r_1^2 - r_2^2).$$

Employing the thermo-dynamic equation

$$Q = T\frac{dA}{dT}$$

we find that the heat *absorbed* is given by

$$Q = 4\pi T (r_1^2 - r_2^2) \frac{d\beta}{dT}.$$

But $d\beta/dT$ is negative for actual films of fluid (8) and may be put constant and equal to $-k$, so that the heat *produced* is given by

$$Q = 4\pi k T (r_1^2 - r_2^2).$$

Consider now the case of a soap-bubble which, by some active process, following what (to make the analogy clearer) we will call "excitation," increases its surface tension from β to β'. Many such processes might be considered, *e.g.* :—

(*a*) The oxidation of a surface film of some substance, such as oil, which previously lowered the surface tension of the water composing the bubble;

(*b*) The neutralisation of an electric charge on its surface (in this case the mathematical statement is slightly different from that given here);

(*c*) The liberation of some chemical bodies, raising the surface tension.

There is little advantage, however, in discussing specific cases, as it is not being suggested here that any one of them represents the processes underlying muscular contraction. It is sufficient for us at present to gain a clear *general* idea of the nature of muscular activity, and to leave the description of specific processes to a day when our knowledge is more adequate. We will proceed, therefore, to consider the general problem, and will make the analogy clearer by employing physiological terms.

(A) The "resting" bubble possesses potential energy: if allowed to "contract" it can do work,

$$A = 4\pi\beta (r_1^2 - r_2^2).$$

(B) The "excited" bubble possesses more potential energy: if allowed to "contract" it can do more work,

$$A' = 4\pi\beta' (r_1^2 - r_2^2),$$

where β' is made greater than β by some process undefined. If not allowed to "contract," but made to respond "isometrically," the pressure inside the bubble rises from $2\beta/r$ to $2\beta'/r$.

(C) If the "resting" bubble be allowed to contract, doing maximum work, there is a reversible thermal effect, leading to a rise of temperature; if it be made to expand, there is a similar fall of temperature. The heat produced in the contraction is

$$4\pi k T (r_1^2 - r_2^2),$$

where k is the temperature coefficient of the surface tension.

(D) If the "excited" bubble be allowed to contract, there are similar reversible thermal effects, the heat produced on the contraction being

$$4\pi k' T (r_1^2 - r_2^2),$$

where k' is the temperature coefficient of the new surface tension.

This heat must be added to any produced by the chemical or physical processes leading to the increase of surface tension.

The analogy with the muscle, therefore, is clear, and we should expect that there would be a reversible thermodynamic evolution of heat equal to

$$\tfrac{1}{2}\alpha \mathrm{T}(\mathrm{P}_1-\mathrm{P}_2)(l_1+l_2)$$

when the excited muscle shortens from length l_1 (and tension P_1) to length l_2 (and tension P_2). In this case, however, α, the coefficient of thermal expansion, is that of the excited muscle; it would be difficult to devise a direct means of determining this quantity, but there is no reason to doubt its reality. It is presumably negative, as in the unexcited muscle, so that there is then a reversible absorption of heat on contraction, in addition to the transformation of mechanical potential energy into work.

The thermal phenomena described here have no considerable bearing on results *hitherto* obtained on the heat-production of muscles. Most previous work in which the muscles were allowed to shorten over the junctions must anyhow have been vitiated to an unknown degree by differences of temperature along the muscle's length, and conclusions from it are of doubtful value. Most of the more reliable work on the subject was performed on muscles excited isometrically. In the future, however, it will be necessary, as soon as the simpler problem of the isometric contraction has been properly explored, to consider the case of muscles fulfilling their natural, though more complicated, function of shortening; and in that consideration it will be necessary for the investigator to be alive to the difficulties and complications provided by the purely physical thermal effects consequent on the shortening of an extended elastic body.

(b) *Mechanics.*

In considering the mechanics of muscular contraction, the fact that all the potential energy put into a stretched elastic body can be recovered as work *only* if the shortening be infinitely slow is very important. Consider first the case of a muscle passively stretched. If the muscle be *stretched* from a length l_2 to a length l_1, and if the tension P be required to stretch it to any length, l, *then* P *is greater the more rapidly the stretching is carried out.* Consequently, for a given amount of stretching (*i.e.*, for a given final amount of potential energy) the faster the stretching the greater will be the work required and the more wasteful will be the process. Similarly, if the muscle be allowed to shorten from l_1 to l_2, doing as much work as possible, the tension P exerted at length, l, is *less* the more rapidly the muscle is allowed to shorten; consequently, for a given amount of potential energy available, the more rapidly the muscle shortens the smaller is the amount of external work done and the more wasteful the process. What is true of the elastic properties of the unexcited muscle is true also of those of rubber, and in all probability of those of the excited muscle. In that case one very important conclusion follows: *the more slowly a muscle be allowed to contract (in a single twitch) the more work can it be made to do.* This statement should be clearly understood, especially as it may have a practical application in our study of the heart and other muscles. It should be noted that the contraction considered is supposed to take place between the same geometrical limits in the rapid and in the slow contractions; in the case of the straight muscle it shortens from length l_1 to length l_2 in either contraction, or in the case of the heart it contracts from volume v_1 to volume v_2 in either contraction; with this provision, however, in the case of a twitch (or beat) excited by a single given stimulus, *the work done will be greater the slower the contraction is allowed to go on.* The gain in efficiency merely by slowing down the process of shortening may be relatively considerable.*

A further important application is to the case of a muscle contracting under a relatively heavy initial load. When an inactive muscle is loaded heavily, it possesses a considerable amount of potential energy; when the muscle is excited more potential energy is developed as the result of the physiological processes following a stimulus: if the muscle be allowed to shorten, both of these forms of potential energy are available presumably for the production of work, and it would seem natural to subtract the potential energy of the inactive stretched muscle from the total work done, in order to determine how much of the work was done by the muscle in virtue of its own physiological activity. The results of this paper show that such a procedure is not correct, and, indeed, if the initial load be high, may lead to very erroneous results. When a muscle is excited, it contracts rapidly, and when the stretched inactive fibres of the muscle are allowed to shorten rapidly we have shown above that there is a considerable degradation of potential energy into heat, only a fraction of it appearing as external work. Thus the work actually produced by the excited muscle by virtue of its own internal activity is greater, and may under heavy initial loads be considerably greater, than the quantity calculated as described above; while the heat produced by the muscle, by virtue of its internal activity, is less than the heat actually observed, because of the transformation of some of the potential energy into heat when the muscle shortens. If a correct calculation be desired of the work and heat liberated by the unaided internal activity of the muscle, it is necessary to measure:

(*a*) A, the potential energy possessed by the stretched inactive muscle;

(*b*) W, the maximum work obtainable from a mechanical shortening of the inactive muscle *at the same rate of shortening* as obtained in the active twitch.

Then W, and not A, must be subtracted from the work done in the active twitch, in order to get a fair estimate of the share of the work provided by the internal activity of the muscle; while (A — W), expressed in heat units, must be subtracted from the heat-production observed in order to find what amount of this heat is due to the same internal causes.

* This statement must not be misapplied, nor taken from its context.

(6) The Coefficient of Thermal Expansion of Muscle.

It is interesting to calculate the value of α, the coefficient of thermal expansion, from the formula

$$\text{rise of temperature on loading} = -\frac{\alpha T (P_1 - P_2)(l_1 + l_2)}{\text{(mass) (specific heat) (mechanical equivalent)}}.$$

On the right side of the formula we can measure everything directly except α, while our records enable us to determine the rise of temperature. As a matter of fact, it is necessary, in the records, to separate the reversible thermodynamic production of heat from the irreversible "viscous" one. We have not succeeded in doing this by any rigidly accurate method, but a more or less approximate value can be estimated from the records. The result comes out that α is negative (*i.e.*, the muscle *shortens* on warming) and in size between 10^{-5} and 10^{-4}. Why the muscle has a negative temperature coefficient it is difficult to say. Rubber appears to have the same, and of about the same order of size. It would be of interest to repeat the observation on jellies and on other kinds of rubber or elastic colloidal material. It is striking, however, that the value of α (lying between 10^{-5} and 10^{-4}), calculated for muscle from the experiments described here, agrees in magnitude, though not in sign, with the values given in Tables for a number of materials. For example, in metals α usually lies between 10^{-5} and 2×10^{-5}, gutta-percha is given the value 2×10^{-4}, glass about 10^{-5}, and various woods about 5×10^{-5}.

(7) Summary.

1. Photographic records, obtained thermo-electrically, are given of the thermal consequences of stretching a muscle, and of releasing a stretched muscle. When a muscle, alive or dead, is passively *stretched*, heat is liberated in large amount at first, but at a rapidly diminishing rate. When a stretched muscle is *released*, the first effect is an absorption of heat, but this is followed, after a short interval, by a production of heat masking the absorption. In a complete cycle of lengthening and shortening the net result is a production of heat, which is greater the greater be the interval between the two processes.

2. These thermo-elastic phenomena are in no way related to the life or visible structure of the muscle, as they are shown by live and dead muscles alike, and, in a modified degree, by a rubber band.

3. The order of size of the thermo-elastic effect may be gathered from the statement that a load of 150 grm., added to a pair of sartorius muscles of *Rana temporaria*, weighing, say, 150 mgr., would raise their temperature by something of the order of 1 to 3 thousandths of a degree, this being a fifth to a half of the rise produced by a strong twitch. These thermo-elastic effects, therefore, are of a size which makes a knowledge of them essential in experimental work on the energetics of muscular activity.

4. The phenomena depend upon the elastic and thermo-elastic properties of the muscle, and may be credited to the simultaneous action of the following two factors :—

(i) The muscle, like catgut, shortens on being warmed; conversely, the second law of thermodynamics tells us that it will warm on being stretched, and will cool on being released from a stretched state, both processes being "reversible." This explains the initial effects.

(ii) The muscle, like other elastic colloidal jellies, takes some time to reach an equilibrium length on being subjected to a tension; consequently, on stretching it, *more* work is done, and, on releasing it, *less* work is obtained, than is accounted for by the potential energy existing in it when extended. The balance in either case is liberated irreversibly as heat in the muscle. This explains the later effects.

5. The initial thermal effect—the reversible one, see 4 (i)—enables us to calculate an approximate value for the coefficient of thermal expansion of frog's muscle, and leads to values lying between -10^{-4} and -10^{-5}; we may assume, therefore, that the sartorius muscle of *Rana temporaria*, subjected to a constant load, shortens by 1 part in something between 10,000 and 100,000 for every 1° C. rise of temperature. The coefficient is of the opposite sign to that for most materials, which lengthen on heating, but is of the same order of size.

6. Experiments are described in which, by means of an inertia system for the determination of the maximum work, the elastic potential energy of the *passively stretched* unstimulated muscle is transformed into work during an elastic contraction occurring at various rates. It is found that the work done is greater the slower is the contraction, but is always considerably less than the potential energy used up. For an infinitely slow contraction, the work done would become equal to the potential energy. The balance of potential energy is used up in irreversible processes, leading to the secondary thermal changes described in 4 (ii) above.

7. It is suggested that the elastic properties of the muscle, leading to the irreversible transformation of work into heat, are the result of its microscopic, ultra-microscopic, or colloidal structure. The relation between tension and extension, as usually found, *i.e.*, leaving the load on till the muscle has settled down to its full extension, is the elastic characteristic of some network; the spaces between the parts of the network, however, are filled with a viscous fluid, and, when the shape of the muscle is changed, by pulling or releasing it, the viscous fluid has to find a new position inside the network. If the change be very slow indeed, little energy is lost by internal friction; if, however, the change be rapid, the loss of energy, which increases with the velocity of the fluid, may become large, and lead to a considerable production of heat. The force exerted by the stretched body in such a case is

employed partly in pushing the viscous fluid into its new position inside the network, and partly in doing external work. Naturally, therefore, the external work is less.

8. It is concluded that in order to avoid these complex thermal changes in investigating the heat-production of muscles, it is advisable, whenever possible, to work with rigidly isometric contractions.

9. It is shown that, when an active muscle is allowed to shorten, we may expect to find the thermal changes due simply to shortening superimposed upon those due to the physiological activity (chemical breakdowns, etc.) of the muscle.

10. When a muscle, excited by a single shock, is allowed to shorten from one fixed length to another (or, in the case of the heart, from one fixed volume to another), we may expect to find the external work done greater the slower is the shortening; this may have a practical application in the study of the heart and other muscles.

11. When a muscle is stretched passively by a load, and then excited, the work done is not equal to the potential energy existing initially in the muscle *plus* the work resulting from the internal physiological activity of the muscle. It is less than this by the amount of the potential energy degraded into heat by the viscous processes associated with its rapid change of form. This is of theoretical importance because, in an investigation of the mechanical efficiency of the muscle, it is necessary to determine the work done by the muscle by virtue of its own internal activity, after allowance for work done at the expense of its initial elastic energy; and it is not fair to the muscle to assume that more than a fraction of this potential energy reappears as work.

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