25 March 1960, Volume 131, Number 3404 SCIENCE

Production and Absorption of Work by Muscle

Work absorbed in stretching a contracting muscle can reverse the chemical processes of activity.

A. V. Hill

A contracting muscle performs mechanical work by shortening against a load. Its energy is derived from chemical reactions. What the reactions are, and what their sequence is, is not precisely known, though it is certain that they occur in two main phases, initial and recovery. The initial phase is rapid and is independent of the presence of oxygen; it is known to include the splitting of creatine phosphate and it is commonly believed, though on indirect grounds, that the earliest occurrence in it is the hydrolysis of adenosine triphosphate. Other processes, not yet known, may be involved. Moreover, the formation of lactic acid from glycogen certainly occurs in normal muscles when more than a very small muscular effort is made; but since a muscle poisoned with iodoacetate may continue to contract for a time in a perfectly normal way without producing any lactic acid at all, the formation of lactic acid is now regarded as an early event in recovery. The large amount of free energy thus made available is believed to effect a resynthesis of the creatine phosphate.

The main recovery process is very slow and involves the utilization of oxygen; the free energy supplied by oxidation provides a means of reversing the previous reactions, and finally the muscle returns to the same chemical state as when it started, except that a certain amount of fuel has been burned and oxygen used. If adenosine triphosphate is in fact split in the earliest stage of contraction, the fact that its products cannot be detected chemically has to be explained by supposing that it is very rapidly re-formed with the aid of the free energy supplied by the slightly later breakdown of creatine phosphate. Unfortunately the energy changes in these three nonoxidative processes are not yet accurately known, but approximate values for the changes in enthalpy $-\Delta H$ and free energy $-\Delta F$ are given in Table 1. It would be a great service to physiology if these quantities could be more certainly determined, under the conditions existing inside a muscle fiber, but that will not be easy, for it requires a knowledge of the initial and final states, whether combined or uncombined, and the concentrations of the substances involved.

Work and Heat in Contraction

In the living muscle the energy liberated can be measured as

work + heat;

in the complete cycle, including recovery, it is about twice as great as in the initial process alone. In this article, only the initial process is considered, and no further reference is made to specific chemical reactions. The relations discussed are those between work and heat, under various conditions of shortening, lengthening, and tension, so chemical details are really irrelevant.

The processes of muscular contraction occur at constant temperature and pressure; any idea that muscle is a heat engine is nonsense—work is certainly derived at constant temperature from the free energy of chemical reactions. If no external work were done, the heat production would be $-\Delta H$, while the maximum amount of work conceivably possible is $-\Delta F$. In any actual contraction the ratio of work done to total energy used, often—though perhaps improperly—called the "efficiency," depends on several variables, particularly on the speed of shortening. The maximum value is about 0.4, so $\Delta F/\Delta H$ is certainly greater than 0.4—possibly considerably greater, for the production of work may be far from reversible in the thermodynamic sense. The values of $-\Delta H$ and $-\Delta F$ in Table 1 show that the ratio $\Delta F/\Delta H$ is rather large; it may indeed be substantially greater than 1. Then, under "reversible" conditions, if those could be realized, a muscle would cool when it did maximum work. In fact, nothing like that ever happens.

It has often been supposed that when a given stimulus has been applied to a muscle the total amount of energy liberated is then settled for good, the only point not settled being how much of this energy is turned into work, how much into heat. The question was really decided experimentally 95 years ago by Heidenhain, whose results showed (to put the conclusion in modern jargon) that a muscle contains a "governor" and that the energy used depends not only on the stimulus but on the length throughout contraction and on the load. Heidenhain's technique would be regarded today as primitive; it was subject to various errors, and the readings

---

The author is affiliated with University College, London, England. This article is the John R. Murlin lecture, presented 3 June 1959 at the University of Rochester School of Medicine and Dentistry, Rochester, N.Y.

Table 1. Heat production ($-\Delta H$) and maximum amount of work possible ($-\Delta F$) (in kilocalories per mole) for splitting and neutralization at *p*H 7.0. ADP, adenosine diphosphate; ATP, adenosine triphosphate; Cr, creatine; CrP, creatine phosphate; P, phosphate.

Reaction	$-\Delta H$	$-\Delta F$
ATP $\rightarrow$ ADP + P	5 to 10	8 to 10
CrP $\rightarrow$ Cr + P	11 to 17	10 to 15
Lactic acid from glycogen	24	39

obtained were very small. Nevertheless he arrived by it at the right answer, one of the most important in physiology. But rather little attention was paid to it, perhaps because his differences looked so small, and people went on thinking in the older terms; I did myself when I came to the subject 45 years later. The problem was not properly tackled again until nearly 60 years after Heidenhain, when W. O. Fenn joined me at Manchester in 1922. Fenn's two papers on the subject, published in 1923 and 1924 (*1*), opened an entirely new chapter in the physiology of muscle. There is no point now in recalling the details of his experiments, but their conclusion can be put into two simple statements, in Fenn's words: (i) "When a muscle shortens upon stimulation and does work in lifting a weight, an extra amount of energy is mobilized"; and (ii) Forcible "lengthening during the contraction period decreases the energy liberated. . . . When the work done by the muscle is negative the excess energy is also negative."

These conclusions still stand; they were the starting point of most of what follows.

Contractile and Elastic Elements

The "business" part of a muscle is the contractile component, which in skeletal muscle is joined to the bones by tendons forming the series elastic component. Under so called "isometric" conditions the distance between the outer ends of the tendons is constant, and when the muscle is stimulated it shortens and stretches the tendons, doing quite a lot of work on them (which can, for example, be useful in jumping). It may be that part of the series elastic component really resides in the contractile component itself—for example, in one of the bands of the sacromere—and it is certain that, when one makes experiments, part of the series elastic component resides in the connection to one's recording instruments. There are other elastic elements in muscle, making up the parallel elastic component, but if one works at a short enough length, these provide no complication and need not be referred to again.

The series elastic component, however, provides a major complication in any investigation of the mechanical work performed by a muscle and the heat it produces. By special methods (*2*), which need not be described here, its properties can be measured and displayed in a generalized diagram from which the amount of stretch under any tension, and the amount of elastic energy it contains, can be read off. A similar diagram can be constructed for the elastic properties of the recording arrangements. This stored elastic energy is important: when a muscle relaxes under tension, the elastic energy is turned into heat in the contractile component and is added to the heat previously recorded.

Activation, Shortening, and Work

When a muscle is stimulated it passes from a state of rest to one of activity. These two states differ fundamentally from one another, just as a piece of hard rubber (ebonite) after vulcanization differs from the original soft rubber. In fact, by current theories, contraction could be pictured as reversible vulcanization. The transformation from the first state to the second requires chemical change, and that results in a production of heat which we call the heat of activation, A. A is independent of whether the muscle shortens and does mechanical work, or does not. But the transformation from rest to activity quickly reverses itself, and if the stimulus is not repeated, the active state decays and the initial condition returns. In order to maintain the state of activity a succession of stimuli must be applied, and A becomes the heat of maintenance, the cost of keeping the engine going.

The next stage is this. If a muscle is allowed to shorten it gives out extra heat. For a given amount of shortening the heat is independent of whether mechanical work is done or not; it is simply proportional to the amount of shortening (*3*). The phenomenon is most elegantly displayed by releasing a muscle against a load during a previously isometric contraction. The quantity of heat is ax, where x is the amount of shortening and a is a constant of the dimensions of force (heat is always calculated in mechanical units). The constant a is directly related to the strength of the muscle—that is, to the maximum force it can exert.

The third stage is this. When a muscle shortens it does more or less work according to the load which, to quote Fenn's anthropomorphic idiom, it "discovers it must lift." The performance of this work does not affect the amount of heat liberated in the other two stages; the mechanical work (W) just appears as an extra term in the equation, which finally runs: total energy by muscle $= A + ax + W$.

The appearance of W as an extra energy term without any extra heat is striking, but it seems to be authentic. The quantity $(A + ax)$, in a sense, is "waste heat," though a better term is "overhead"; it depends, as regards A, on the duration of the stimulus and as regards ax, on the amount of shortening allowed. To get the greatest mechanical output from a given expenditure of chemical energy, the conditions must be adjusted to make $(A + ax)/W$ as small as possible. But the "overhead" cost of contraction cannot be avoided, and this suggests that it may not really be "irreversibility" (in the thermodynamic sense) that limits the ratio of work done to energy used, but the nature of the machine itself. If a muscle is to do mechanical work it has to be put in a state of readiness and then to shorten, and the energy needed for this can be regarded as "overhead" cost. The muscle can then perform mechanical work with an extra expenditure of energy no greater than the work itself. If in the underlying chemical reaction $-\Delta F$ and $-\Delta H$ were equal, this could happen if the muscular process were "reversible" in the thermodynamic sense. If $-\Delta F$ were greater than $-\Delta H$, as may well be the case, thermodynamic "irreversibility" can still occur to a certain extent; then only a part of $-\Delta F$, equal to $-\Delta H$, would be utilized in producing external work.

Stretching during Contraction

The exciting possibilities of an approach in muscle to thermodynamic "reversibility" in the production of work, together with the rather precise way in which all these relations seem to hold together, suggested a reexamination of Fenn's original result on the stretching of muscle. Could the chemical processes which are provoked by applying a stimulus really be reversed by the application of external mechanical work? Consider a storage battery and a motor which can also function in the reverse direction as a dynamo. When they are connected the storage battery provides energy which is used by the motor in doing mechanical work. When external mechanical power is applied to the motor in the opposite direction it becomes a dynamo and charges the battery. Can this sort of thing happen in a muscle when mechanical power is applied to it during contraction? One must say specifically "during contraction" because a muscle at rest does not resist stretch except by purely elastic and viscous forces. The only way in which mechanical work can be applied to the contractile portion of a muscle is by stretching the muscle while it is actively resisting.

In 1938, 15 years after Fenn, I took the question up again and came to the preliminary conclusion that during very gradual lengthening, under a load somewhat greater than a muscle could bear, the net rate of its energy liberation was rather less than during an isometric contraction (*4*). After another interval of 12 years, due to World War II and to the need for rehabilitating ideas and apparatus, the problem was tackled again, by Abbott and Aubert, who clearly confirmed the earlier result (*5*). But something far more important came out of their experiments when much more rapid stretches were applied and when heat and work were measured. It then became clear that a substantial part of the work disappeared and did not reappear as heat; we could only suppose that it was used in driving the resynthesis of chemical breakdown products of the reaction set up by the stimulus. But the results were not as decisive as they might have been, and there was no evidence of when and how the work disappeared. We were, in fact, not thinking very clearly about the subject; it is funny how long clear thinking sometimes takes! But after another 7 years the subject was taken up again (*6*). In the meantime, apparatus and methods had been somewhat improved, but, more important, we had much clearer ideas of the mechanics of muscle and of the nature of the problem.

Chemical Reversal by Stretch

Consider a muscle stretched by 11 percent or more during a single twitch or a short tetanus. The stretch occurs at any desired speed, starting not too long after the stimulus. The ergometer is provided with a tension recorder, joined to the muscle by a strong chain, and also with a device to record the distance moved. Tension and distance are displayed on the two beams of a cathode-ray tube and photographed. The work is obtained from the curve relating the two. The heat is measured by thermopile and galvanometer and recorded from a second tube.

Table 2. Contractions with stretch. H_s, total heat appearing in muscle; W_o, total work done on muscle.

Stretch (%)	H_s (gm-cm)	W_o (gm-cm)	$H_s - W_o$ (gm-cm)
	Twitches		
11	26.4	25.8	0.6*
11	31.5	26.7	4.8
11	27.9	25.2	2.7†
12	26.5	24.2	2.3†
14.5	39.5	38.8	0.7*
18	46.3	46.7	−0.4*
	Tetani (short)		
15.5	42.8	42.4	0.4*
16	72.1	66.5	5.6
16	57.3	55.1	2.2*
16.5	76.6	68.5	8.1
18	58.8	59.2	−0.4*
18	64.2	65.4	−1.2*
22	75.1	75.0	0.1*

* H_s and W_o were equal within the limits of experimental error. † The equality of H_s and W_o was doubtful.

Let us first consider total quantities—the total work done by the ergometer and the total heat produced in the muscle up to the time when it has fully relaxed (Table 2). To avoid trouble with elastic energy remaining after the end of relaxation, the length to which the muscle is stretched must not be so great that any tension is then left. With that provision, the whole of the work done on the muscle disappears; it must have gone into the muscle, for there is nowhere else it could go. Either it has been dissipated as heat and is added to the heat produced by the muscle itself, or it has been absorbed in some other form. Now here is the striking fact that emerges. In a good proportion of all the experiments made, the heat found in the muscle in the end was no greater than the work put into it. The muscle itself apparently had produced no heat at all of its own, although it had resisted the stretch very strongly. One might think that the very act of stretching the muscle somehow prevented the normal chemical processes of activity from occurring. That is certainly not so, for the muscle may produce a large part of its normal heat before the stretch begins. The only possibility is that the chemical reactions (which certainly started, as is shown by the normal early heat production) were totally reversed. In the whole process, from start to finish, the muscle liberated no energy at all; the heat observed was merely degraded work.

This is what happened in a good proportion of the experiments; in the rest the heat was slightly greater than the work, but much less than it would have been had the work been added to the normal heat production of the muscle. The reversal of chemical processes, though substantial, was not quite complete. With smaller stretches, of less than 10 percent, the heat is always greater than the work; the degree of reversal depends on the amount of stretch—that is, really on the amount of work applied. One striking result was that, within the limits of experimental error, the heat was never less than the work; this means that the chemical reversal never overshot its original mark. Such an overshoot might possibly have occurred, for the muscles were not fully recovered from previous contractions and there must always have been chemical substances at large which could conceivably have been resynthesized. A stretch, therefore, cannot reverse any chemical reaction except that of the actual contraction during which the stretch was applied.

Time Course of Heat Minus Work

This was all very odd and required closer analysis of when and how it happened. Fortunately the means for that analysis were at hand, for the instruments are capable of yielding a true picture of the course of the heat production throughout a contraction, and that, when it is compared with the mechanical events, throws much light on the matter.

Figure 1 (upper half) gives three curves obtained from a muscle stretched 3 millimeters during a single twitch; the stretch started early and continued till 360 milliseconds after the shock. These experiments were all made with toad sartorius muscles at 0°C, and in an isometric twitch the maximum tension is reached in 0.4 or 0.5 second. Curve *A* is the tension (*P*), which drops rapidly at first when the stretch ends. Curve *B* is the heat (*H*) liberated in the muscle, as obtained by analysis from the records. Curve *C* is the work (*W*) done by the ergometer. This is a good example of a contraction with stretch in which the heat converges to the same value as the applied work, so that in the complete process the muscle really liberated no energy at all. Now look at the lower half of the figure. Curve *D* is the difference between heat and work ($H - W$). As a first approximation this could be taken as the net energy liberated by the muscle. The astonishing result appears that the net energy rapidly becomes negative after the stretch begins, changes direction when the stretch ends, and then slowly returns to zero at the end of relaxation.

Such a strange result had to be regarded very critically. One obvious correction had to be made, due to the fact that, except at the very end, not all the work had gone into the contractile component of the muscle—some of it remained, until relaxation was complete, as elastic energy in the series elastic component and in the connecting chain. The elastic energy (E) could be calculated from the tension, and so the net work (W_n) could be obtained by subtracting the elastic energy from the work ($W_n = W - E$). Curve *E* is the result of subtracting the net work from the heat ($H - W_n$); this gives the net energy liberated by the muscle. The negative phase is reduced but by no means abolished; clearly it has to be taken seriously.

Figure 2 gives the results of three contractions in another experiment with a short tetanus. Here the stretch did not start very early, and a good deal of the normal heat production had occurred before it began. The ordinate in this case is the net energy liberated by the muscle. For the isometric contraction, this is the sum of heat and elastic energy ($H + E$); for the stretches it is the sum of heat and elastic energy, less work ($H + E - W$). Two stretches were applied, one quicker than the other, ending at the downward-pointing arrows. Exactly the same phenomenon is observed: soon after the stretch begins the curve of net energy turns around and passes through a long negative phase, finally becoming zero at the end of relaxation.

Figure 2 contains one effect (curve *b*) not hitherto referred to, the stretch of the contractile component. This can be derived from the tension by means of the data from which the elastic energy is derived. From the actual stretch indicated by the ergometer the calculated extension of the elastic elements is subtracted, and the difference is the stretch of the contractile component. When the stretch begins, as soon as the tension exceeds the maximum force that

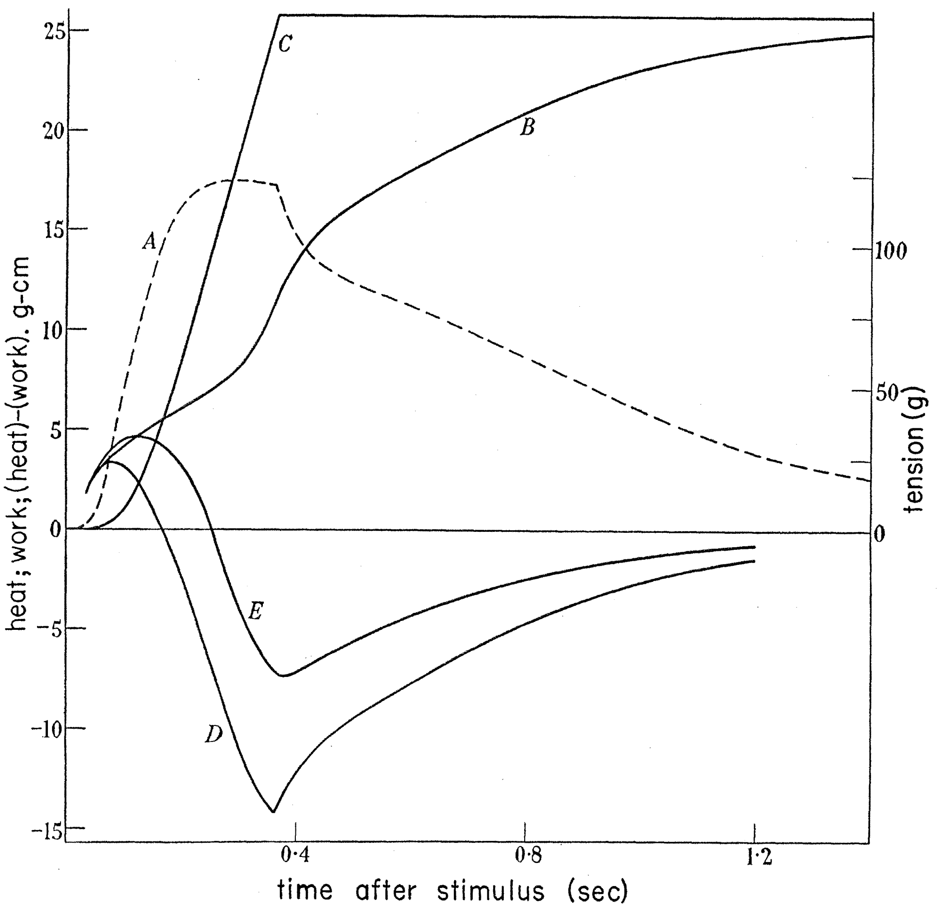

Fig. 1. Curves for tension, heat, work, and the difference between heat and work during a 3-mm stretch of a muscle stimulated at time zero (single shock, toad sartorius, 0°C). Curve *A*: tension (P); curve *B*: heat (H); curve *C*: work (W) done by the ergometer; curve *D*, difference between heat and work ($H - W$); curve *E*, difference between heat and net work ($H - W_n$), where W_n is the difference between work W and elastic energy E in the muscle and connections.

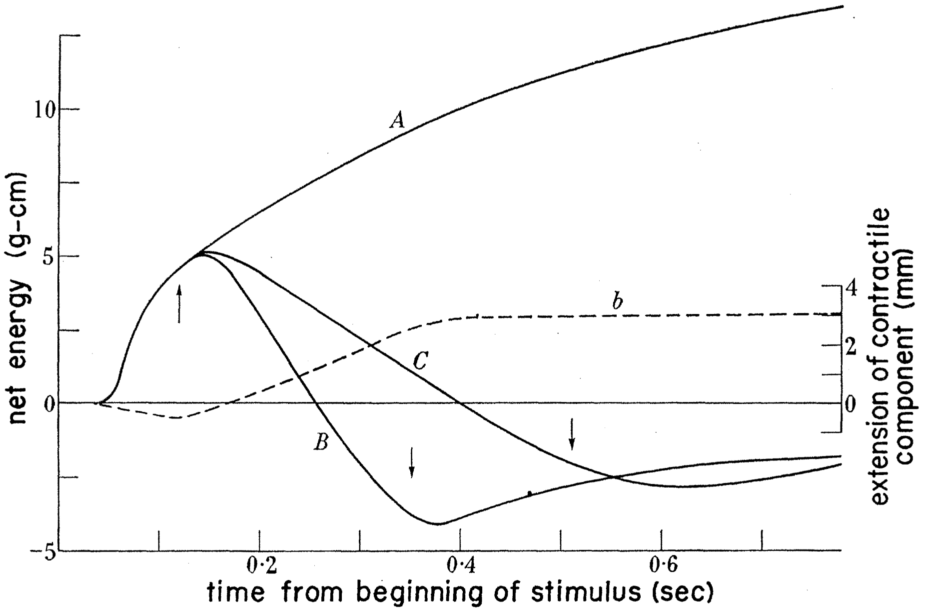

Fig. 2. Net energy liberated by muscle in isometric contraction (curve *A*) and in contractions with stretch (curves *B* and *C*). For curve *A* the ordinate is ($H + E$); for curves *B* and *C*, it is ($H + E - W$). The stretches began at the arrow that points up and ended at the arrows that point down. Curve *b* (broken line) shows the calculated extension of the contractile component of the stretch shown in curve *B*. Toad sartorius, 0.3-sec tetanus, 0°C.

the muscle can bear, the contractile component begins to be extended. It is during the forcible lengthening of the contractile component that all these interesting things happen. Curve *b* corresponds to stretch *B*; one can see that the rate of extension of the contractile component rapidly falls when the stretch ends. But the tension is still high, and the extension continues to the end of relaxation.

Figure 3 shows another experiment, a 15-percent stretch during a longer tetanus. Here the stimulus long outlasted the stretch, so the total heat greatly exceeded the work: the curve of net energy rose rapidly as soon as the stretch ended and went on rising as long as the stimulus continued. Curve *A* shows the tension before, during and after the stretch; curve *B* shows the energy liberated by the muscle, as the sum of heat and elastic energy $(H + E)$, in an isometric contraction; curve *C* shows the net energy liberated by the muscle during a stretch—that is, the sum of heat and energy, less work $(H + E - W)$. A large amount of energy had been liberated normally by the time the stretch began. Then the net energy rapidly fell, became negative for a short time, then rose quickly as the stimulus continued after the stretch ended. At the top the change in length of the contractile component is shown, before, during, and after the stretch.

Such experiments left no doubt that an absorption of energy occurs during the extension of the contractile component. This extension lasts longer than the applied stretch, for the stretch produces a high tension in the elastic elements which go on extending the contractile component right to the end of relaxation. But a puzzling dilemma remained. When total quantities in the whole cycle of contraction and relaxation are considered, the net energy produced by a muscle was never negative. How could it be so obviously negative throughout a large part of the process? No simple explanation seemed possible, but the dilemma was resolved in an unexpected way.

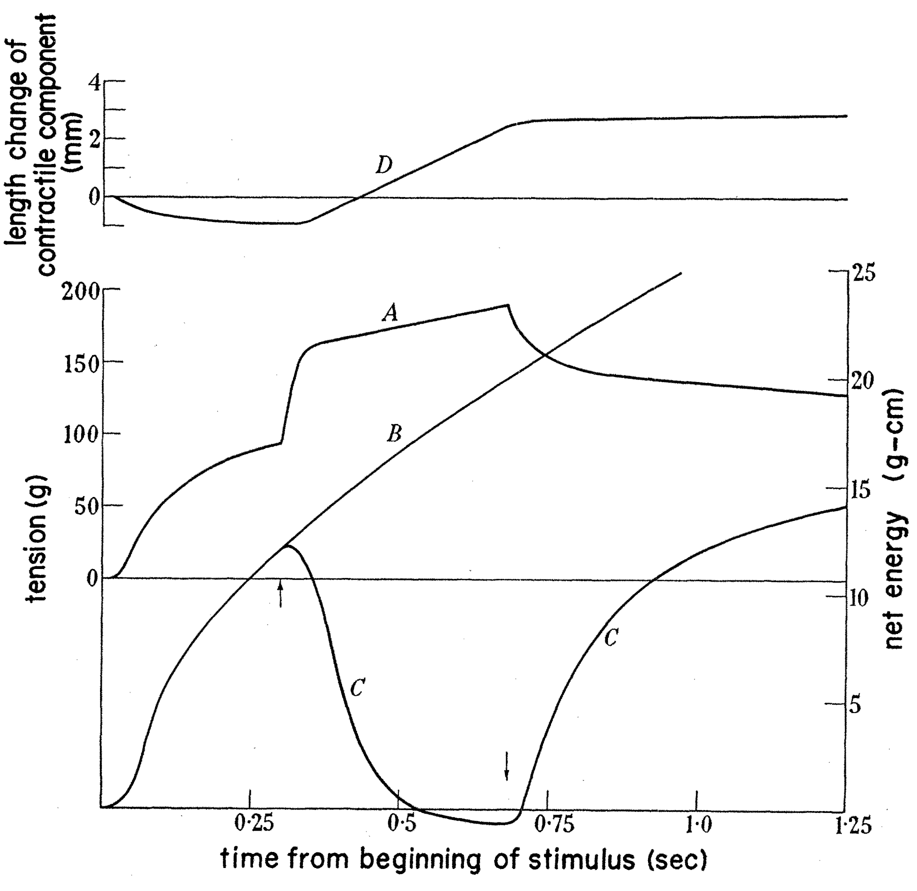

Fig. 3. Net energy liberated by muscle in isometric contraction (curve *B*) and in contraction with 4-mm stretch (curve *C*). For curve *B*, the ordinate is $(H + E)$; for curve *C*, it is $(H + E - W)$. Curve *A* shows tension (*P*) before, during, and after the stretch. Curve *D* shows the calculated change of length of the contractile component before, during, and after the stretch. The duration of the stretch is indicated by arrows. Toad sartorius, 1-sec stimulus, 0°C.

Thermoelastic Effect

It has been known for more than a century that when a tension is applied to a rod or wire, the temperature of the rod or wire falls; when the tension is removed the temperature rises again. The heat absorbed, or produced, can be calculated, in mechanical units, from the coefficient α of thermal expansion of the material, by the expression

$$\alpha T l \Delta P$$

Here T is absolute temperature, l is length, and ΔP is change of tension. In materials like thermosetting plastics, which are more like an active muscle than metal wires are, the value of α is large. The phenomenon occurs universally and in an analogous form is found in liquids. It is absent only if the coefficient of thermal expansion is zero, a rare and special case.

If this so-called "thermoelastic" effect occurred also in the filaments of active muscle, and if they had a value of α similar to that of thermosetting plastics, then the whole difficulty would be cleared up. During the phase of rising tension there would be a "thermoelastic" absorption of heat, of purely physical origin, which would neutralize some of the heat derived from physiological and chemical processes, so the real physiological heat would be greater by that amount. Conversely, during the phase of falling tension there would be a purely physical production of heat, which would add to the heat produced by chemical processes, so during this phase the real physiological heat production would be less. Now it happens that in 1953 I came upon a phenomenon of just this kind (*7*), which is illustrated in Fig. 4. The lower curve shows the mechanical effect of a sudden short release applied near the maximum tension of a twitch; the upper curve shows the immediate rise of temperature. This sort of experiment was made in a variety of ways, and the final conclusion was embodied in the formula

$$\Delta Q = 0.018\, l_0\, (-\Delta P)$$

where ΔQ is the heat produced, $-\Delta P$ is the fall of tension, and l_0 is the standard length of the muscle. This formula is the same as that referred to above for the thermoelastic effect in solids, if αT is 0.018; it gives a value of α about the same as that for ebonite.

The application of this result to the present experiments was made by adding Q in the formula to H, the observed heat; Q was calculated from the observed tension. Figure 5 shows the same experiment as Fig. 2, but Q, the thermoelastic heat, has been added to the observed heat throughout. The same downward movement of the curves of net energy is found as before—that is, energy is still absorbed by the muscle during a stretch, but the net energy never becomes negative, and the difficulty has disappeared.

This is not the place to go further into the thermoelastic effect, or to justify its use on other grounds, other than to add that its application gives a greatly simplified picture of the energy liberated during the course of an isometric contraction. The introduction of the thermoelastic heat has no effect on total quantities, since P (and therefore Q) is zero at the beginning and end of contraction.

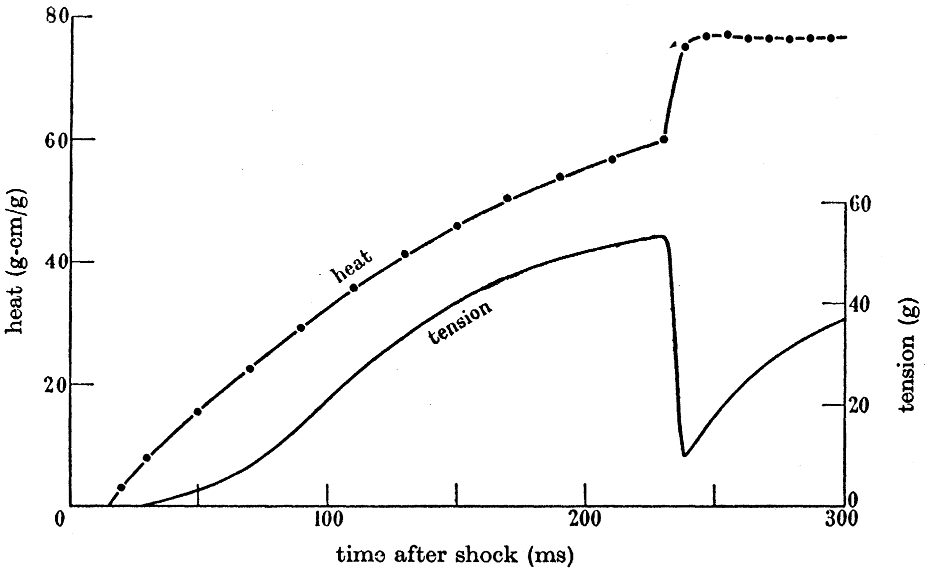

Fig. 4. Heat and tension in isometric twitch of frog sartorius muscle at 0°C, released 0.6 mm in 8 msec, 0.23 sec after the shock.

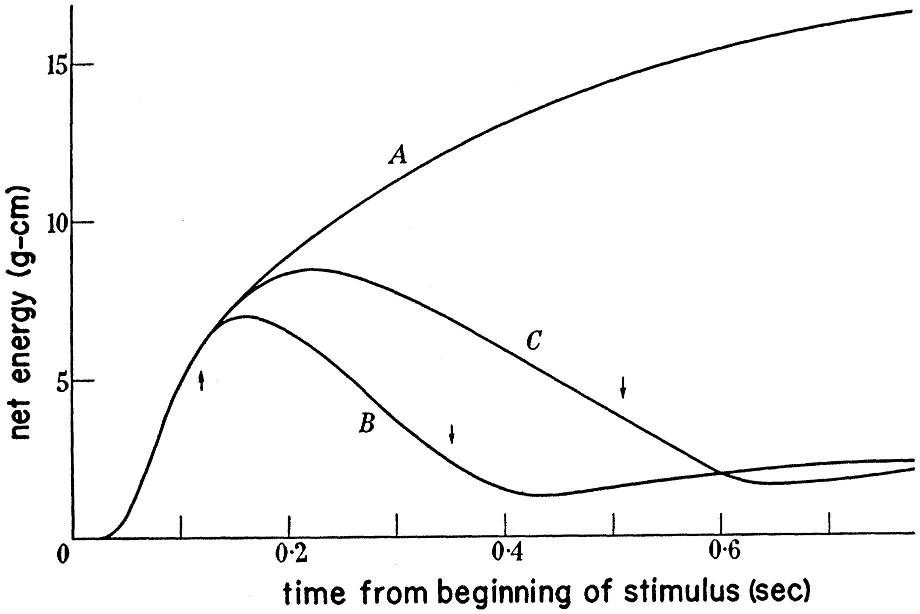

Fig. 5. Effect of a 4-mm stretch on the net energy liberated by a muscle during and after a short tetanus (0.3 sec). The experiment is the same as that illustrated in Fig. 2, but account is taken of the "thermoelastic" heat absorption associated with a rise of tension. Curve A, isometric contraction; ordinate: $H + E + 0.018 l_0 P$. Curves B and C, contraction with stretches starting and ending at the arrows; ordinate: $H + E + 0.018 l_0 P - W$. l_0, standard length of the muscle.

Mechanism of Reversal

One naturally asks, what is the actual mechanism by which the reversal of a chemical process is effected by stretching a contracting muscle? Beyond demonstrating the fact itself, these experiments throw no light on the mechanism: for that purpose, experiments of quite a different kind are required. The great strength of thermodynamics is that the results are independent of the molecular mechanism, but one cannot have it both ways or use thermodynamic results to throw light on the mechanism. It is tempting to speculate, in terms of current theories of contraction (*8*), on how mechanical work is derived from chemical free energy when filaments creep along one another, and on how chemical free energy is restored when the filaments are forcibly drawn apart. But if I were to mention the words *actin, myosin,* and *adenosine triphosphate,* attention might be drawn away from the facts under discussion, which would be rather a pity, for they *are* facts and have to be explained by any theory of muscle contraction.

The chief scientific interest of these results lies in the fact that a biochemical process, in a living muscle cell, can be reversed by the application of external mechanical work. But they do not allow any expectation that energy can be stored in this way, for there is no evidence that the reversal can ever be more than 100 percent complete—that is, that chemical substances other than those produced in the contraction itself can be reinstated.

Application to Man

There is, however, another aspect of these results to be considered—the bearing they have on the physiology of muscular work in human beings. It is always interesting to try to find out how far the results obtained on isolated living material can be reproduced in the intact animal, particularly on the best of all experimental animals, man. It is scarcely conceivable that so large and obvious an effect, once recognized, should not appear again in human muscles, when those are doing "negative" muscular work, as in lowering a weight or going down hill. This is not an unimportant matter, for lowering weights, or the body, is a common affair, and indeed the whole muscular system is guided and balanced all the time by an arrangement of antagonist muscles, one of which lengthens under tension whenever the other shortens.

Soon after the work of 1951 was finished, an attempt was made by three of my colleagues (*9*) to see how the physiological expense of "negative" work in man compares with that of ordinary positive work. At that time research workers were not so certain as they are now that stretching a muscle during contraction can cause a reversal of chemical processes, and they were more cautious in interpreting what they found than they would need to be today. Their results, indeed, were quite unexpectedly large and were certainly due in part to the fact that the force exerted by a muscle while it is being stretched is much greater than the force exerted while it is shortening at the same speed, so a smaller number of muscle units could be employed for a given force. But that is probably not the whole story, and the partial reversal of chemical reactions probably plays a substantial part. That possibility should be examined critically in further experiments on man.

The original experiments were entertaining ones to make, or to watch. Two bicycles were arranged in opposition; one subject pedaled forward, the other resisted by back-pedaling. The speed had to be the same for both, and (apart from minor loss through friction) the forces exerted were the same. All the work done by one subject was absorbed by the other; there was no other significant resistance. The main result was evident at once, without analysis: the subject pedaling forward became fatigued, while the other remained fresh. The rate of working was varied, and the physiological effort was measured by determining the rate of oxygen consumption. It was found that the slopes of the lines relating oxygen usage to rate of working differed greatly between positive and negative work. The experiment was shown in 1952 at a *conversazione* of the Royal Society in London and was enthusiastically received, particularly because a young lady doing the negative work was able quickly, without much effort, to reduce a young man doing the positive work to exhaustion. It is evident now that further investigation is necessary. But however much, or little, the results of stretching isolated muscles may explain the findings in studies of negative work in man, it is interesting to see how the experiments on man arose directly from those on toads. The moral is, if you have a bright idea, try it and see; the result may be much more amusing than you expected.

References and Notes

1. W. O. Fenn, *J. Physiol.* (*London*) **58**, 175 (1923); *ibid.* **58**, 373 (1924).
2. A. V. Hill, *Proc. Roy. Soc.* (*London*) **B137**, 273 (1950); *ibid.* **B141**, 104 (1953).
3. ———, *ibid.* **B136**, 195 (1949); B. C. Abbott, *J. Physiol.* (*London*) **112**, 438 (1951).
4. ———, *Proc. Roy. Soc.* (*London*) **B126**, 136 (1938).
5. B. C. Abbott, X. M. Aubert, A. V. Hill, *ibid.* **B139**, 86 (1938); B. C. Abbott and X. M. Aubert, *ibid.* **B139**, 104 (1938).
6. A. V. Hill and J. V. Howarth, *ibid.* **B151**, 169 (1959).
7. A. V. Hill, *ibid.* **B141**, 161 (1953).
8. A. F. Huxley, *Progr. in Biophys. and Biophys. Chem.* **7**, 255 (1957).
9. B. C. Abbott, B. Bigland, J. M. Ritchie, *J. Physiol.* (*London*) **117**, 380 (1952); B. C. Abbott and B. Bigland, *ibid.* **120**, 319 (1953).

Investigations of Natural Environmental Radiation

A profile of external dose rates, cosmic and terrestrial, has been obtained with ionization chambers.

Leonard R. Solon, Wayne M. Lowder,
Arthur Shambon, Hanson Blatz

We have reported previously the results of external environmental measurements made during the summer of 1957 by members of the United States Atomic Energy Commission's Health and Safety Laboratory (*1*). The purpose of these measurements was to establish the approximate range of population exposures to penetrating cosmic and terrestrial gamma radiation; exposure to terrestrial beta radiation was excluded.

In the present article are summarized further measurements made in the eastern United States and in New England, and a series of measurements made in Western Europe. In addition, cosmic radiation ionization intensities as a function of altitude have been obtained by several series of measurements made in an airplane. By subtracting the cosmic radiation component from the observed total radiation, estimates of the terrestrial radiation dose rates alone have been derived.

Since ground measurements were made in an automobile, an average attenuation factor for terrestrial radiation by the automobile has been determined experimentally, and all observations, including those presented in the earlier reports, have been corrected correspondingly.

Also reported are measurements made in single-family and multiple-family dwellings in the metropolitan New York area, including three boroughs of New York City, nearby Long Island, and Westchester County.

The ionization chamber used in the measurements has been described in detail elsewhere (*2*). This chamber has a gas volume of 20 liters and is filled with air at atmospheric pressure. Ionization current is measured with a vibrating-reed electrometer, connected

---

Mr. Solon, Mr. Lowder, and Mr. Shambon are affiliated with the Health and Safety Laboratory, New York Operations Office, U.S. Atomic Energy Commission. Mr. Blatz is director of the Office of Radiation Control of the Department of Health, New York City.