On human muscle as a transformer of energy / John G. McKendrick.

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ON

HUMAN MUSCLE AS A TRANSFORMER OF ENERGY.

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Human Muscle as a Transformer of Energy. By JOHN G. M'KENDRICK, M.D., LL.D., F.R.S., President.

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THE principle of the Conservation of Energy has been applied with considerable success by Mayer, Joule, Hirn, von Helmholtz, Berthelot, and Chauveau to physiological phenomena, and more especially to those manifested by living muscle. Muscles liberate energy as heat and motion. Every one knows that it is by the contractions of the muscles that the levers formed by the bones and ligaments of the body are moved, and every one knows also that the body is warm, and maintains a fairly constant temperature. It is also a familiar experience that when we bring many muscles into play, as in climbing a hill, or ascending a ladder, or carrying a heavy weight, we feel warmer, and at the same time the skin becomes bedewed with perspiration. If the muscles are thus expending energy, it is evident that this loss must be compensated. Energy must be supplied to the muscles, and it scarcely requires to be said that the source of the energy must be traced to food materials and oxygen, both of which are brought to the muscles by the blood. The muscles, then, may be regarded as machines or engines or motors for the transformation of energy, and they may be compared to other well-known thermic, electric, or hydraulic motors.

This comparison has always had a fascination for physicists and physiologists, and the attempts made by many eminent men to work out the problem have been singularly fruitful to science, not only as regards the physiology of muscle, but also as regards animal heat and the applications of the laws of thermo-dynamics to living beings. As the subject has recently engaged my attention, I have thought that it might not be uninteresting to the members of the Philosophical Society to bring before them the result of my reading and reflections.

The old philosophers attributed the production of heat to the action of a vital principle. Vital heat was continually developed, and the body, they alleged, would be consumed by its own heat if it were not cooled by the process of respiration. In those days, the great thoughts had not arisen that as nothing can come from nothing, light and heat cannot spring out of nothing but only represent forms of energy. The first step towards a sound knowledge of the origin of animal heat was taken late in last century by those immortal workers who laid the foundations of modern chemistry. Priestley, Cavendish, and Black recognised that the animal body was the seat of chemical changes ; Crawford, in 1779, made the remarkable statement that " Animal heat seems to depend upon a process similar to a chemical elective attraction ;" and in the following year Lavoisier published his famous researches on respiration. There can be no doubt that the great Frenchman was the first to shed light on the problem of animal heat. Reasoning that as flame, hitherto considered as an element, was caused by the chemical combination of certain bodies with oxygen, he conjectured that respiration was for the purpose of supplying the body with oxygen, and that thus an internal combustion was produced which was the chief source of animal heat. Experiments proved that the conjecture was sound, and thus the foundation-stone of this department of science was securely laid.

Since the time of Lavoisier, by calorimetric methods, the heat produced by the combustion of many elementary, and of not a few complex substances and food-stuffs has been approximately determined ; and, by similar methods, attempts have been made to estimate the heat developed by the body of a man, both while at rest and while performing mechanical work. Finally, the heat developed by isolated muscles, while at rest and while at work, has also been measured. The great progress that has been made in thermo-dynamics has given precision to these researches, not merely as regards the development of refined experimental methods, but more especially by defining the units of heat and of work, the calorie and the kilogrammetre.*

Taking the body as a whole, attempts have been made to construct a balance sheet, showing, on the one side, the income of energy, and, on the other, the expenditure, for a period of twenty-four hours. The income consists, in the first place, of the potential energy in the food-stuffs, set free by the chemical operations occurring in the body; and it has been assumed that these operations are essentially oxidations, brought about by the interplay of these food-stuffs and the oxygen introduced by respiration.† To this must be added energy as heat coming from other sources than combustion, say, from warm fires; and from the sum must be deducted the energy still existing in excrementitious matters that have not been completely oxidised. On the other side, we place the energy liberated during, say, nine hours, as mechanical energy, and the energy represented by the heat set free during the whole period. The heat is expended in warming the food and drink, in warming the air respired, in converting into vapour the water exhaled from the respiratory surfaces, while the remainder is lost by radiation, conduction, and the evaporation of sweat. The energy represented by the so-called internal work of the body—namely, the mechanical energy of the heart in forcing the blood through the vessels, the movements of the respiratory muscles, and the frictional

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* The unit of heat or *calorie* is the amount of heat required to raise the temperature of 1 kilogramme of water 1° centigrade; or, strictly, from 15° to 16° centigrade. A *small calorie* is the $\frac{1}{1000}$th part of a *large calorie*, or it is the heat required to raise 1 gramme of water 1° centigrade. The heat unit may be transmuted into the work unit by multiplying by 425, and the reverse is accomplished by dividing by the same number, for the weight of 1 kilogramme falling 1 metre in height in one second will produce the same amount of heat as will raise 1 kilogramme of water from 15° to 16° centigrade.

† It is convenient to regard some of the chemical phenomena in the living body as oxidations, but it is probable that they are more of the nature of fermentations, or changes brought about in fermentable matter by the action of the living substance, or protoplasm.

movements of one part of the body upon the other—need not appear in the account (unless it is subtracted from the total heat), as these movements are all ultimately resolved into heat. Such attempts to strike a balance are not very successful; they lack scientific accuracy, as it is almost impossible experimentally to obtain all the data from one individual, and certain items in the account have to be supplied from other sources. Still, the balance sheet shows amounts so nearly alike on the two sides as to prove that the body may be considered from this point of view as a machine, the income and output of which, both as regards matter and energy, are controlled by the same laws as regulate the motors made by man.

Suppose we take a man of average weight, say 85 kilogrammes, (187 lbs.), and in excellent health, and place him in a properly constructed calorimetric chamber in which he will be at liberty to stand, sit, or lie down at pleasure, and without uneasiness or restraint. Let us suppose, also, that we have an arrangement by which he can perform mechanical work for nine hours of the twenty-four in which he resides in the chamber, and that the amount of this mechanical work can be measured and registered in units of heat. Suppose, further, that he receives a diet suitable for a man doing this amount of work, and that the calories obtained by the combustion of this food have also been calculated. Finally, let us suppose that the excreta passed during the twenty-four hours are collected, and their calorimetrical value also ascertained. No doubt it would be difficult to carry on this experiment for a period of twenty-four hours, but such experiments have been made by Hirn, a well-known authority on this subject, for a period of one hour in each case, and it would be a matter only involving trouble and special arrangements to maintain the conditions for twenty-four hours.

We will allow the subject of experiment a diet equal to that supplied to the Royal Engineers of the British army when they are engaged in active service. This is selected as a diet suitable for a healthy man doing vigorous work for nine hours per day. The result would probably come out in the following balance sheet, in which the figures have been calculated from data given by Hirn in his well-known calorimetric experiments on man* :—

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* For a summary of Hirn's latest views and figures, see *La Revue Scientifique*, XIII., 1887, 3^{me} série, pp. 673, 714, and 779.

INCOME.

1. *Food*—

Proximate Compounds.	Amount in Grammes. *a.*	Calories produced by Combustion of 1 Gramme. *b.*	Amount of Heat in Calories. *a* × *b*.	Total Calories.
Proteids,	144	6·250	900	
Fats,	82	9·842	807	
Carbo-hydrates,	630	4·479	2,821	
Salts,*	30	0	0	
				4,528
2. *Heat*, from external sources,				500
				5,028
Less heat obtained by combustion of matters in the urine and fæces that have not been oxidised, say,				500
Total income of Energy,				4,528

EXPENDITURE.

	Calories.		
1. *Work*, for nine hours, at 84·7 calories per hour,		762	
2. *Heat*, during nine working hours, at 260 calories per hour,	2,340		
3. *Heat*, during seven hours rest, at 140 calories per hour,	980		
4. *Heat*, during eight hours sleep, at 40 calories per hour,	320		
		3,640	
Total output of Energy,			4,402
Balance in favor of Income,			126

The total heat produced is, in calories, ...		3,640
This amount, according to the estimate of Helmholtz, is disposed of as follows :—		
1. To heat the food and drink to a temperature of 12° centigrade, 2·6 per cent. of the total, ...	94·64	
2. To heat the air respired, 2·6 per cent., ...	94·64	
3. Heat rendered latent by evaporation of water exhaled from respiratory organs, 15 per cent., ...	546·00	
4. Heat lost by radiation, and conduction carried off by fæces and urine and by evaporation of sweat, 79·8 per cent., ...	2904·72	
		3,640

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* These supply no energy to the body, and their value as food-stuffs depends on the physical modifications which they make in the media in which the chemical phenomena of life occur.

The internal work of the body, including under this term the work of the heart, the work of the respiratory muscles, and the heat produced by frictional movements, amounts to a little over 240 calories; but, as already remarked, the whole of this energy is ultimately resolved into heat, and need not therefore appear in the balance sheet. According to this computation, of the total energy supplied to the body by the food, about 17·4 per cent. is returned as mechanical work.[*] It has frequently been pointed out that the return made by the animal machine compares favourably with the results obtained from our common motors, steam and gas engines, but this view of the question will be discussed after we have considered more minutely the behaviour of a muscle.

In calculating the calories of combustion of food-stuffs, I have taken the figures from those published recently by Danilewski and Rechenberg. These figures may now be substituted in discussions on this question for the somewhat antiquated results published by Frankland [†]:—

DANILEWSKI.[‡]	Calories.
1 gramme Fibrin,	5·830
,, Casein,	5·950
,, Vegetable albumen,	6·250
,, Peptone,	4·900
,, Fat,	9·842

RECHENBERG.[§]	Calories.
1 gramme Starch,	4·479
,, Dextrose,	3·939
,, Mactose,	4·163

There is, however, another route by which we may approach the subject. If the energy of the body is derived from combustion, we should be able to calculate the amount received from the amount of oxygen used, say, in twenty-four hours; and if we find the result corresponds with that obtained by the other method, we shall feel more confidence in our balance sheet. Hirn found that during

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[*] 1 kilogrammetre = 7·23308 foot-pounds, and 1 foot-pound = ·138254 kilogrammetre. To convert the above computations into foot-pounds, multiply the number of calories by 425, and the result by 7·233.

[†] Frankland. *Philosophical Mag.*, xxxii.

[‡] Danilewski. *Pflüger's Archiv.*, t. xxxvi., p. 230, 1885.

[§] Rechenberg. "Ueber die Verbrennungswärme organischer Substanzen." Leipsig. 1880.

hard work, on an average, 123 grammes of oxygen were consumed per hour, while the quantity was reduced to 25·4 grammes per hour during the period of rest. Suppose, again, that the man worked hard for nine hours—the probable consumption of oxygen would then be for the twenty-four hours as follows :—

	Grammes.
9 hours work: 123 grammes × 9, ...	1,107
15 hours rest: 25·4 ,, × 15, ...	381
Total, ...	1,488

This is nearly double the quantity given in physiological text-books as the amount of oxygen used in twenty-four hours, but the difference is due to the large increase in the consumption of oxygen during a period of nine hours of hard labour. If we knew the amount of heat evolved by the combustion of one gramme of oxygen when used for the destruction of the different dietetic proximate compounds, we would be able to estimate the amount of heat produced by the combustion of 1,488 grammes. This information is found in the following table, which gives the number of calories set free by unit weight of oxygen consumed, of carbonic acid exhaled, of nitrogen or urea excreted, connected with or arising from the destruction of albumen, fat, starch, and dextrose :—*

HEAT OF COMBUSTION IN CALORIES OF ONE GRAMME.

	O absorbed.	CO_2 exhaled.	N excreted.	Urea excreted.
Animal albumen,	3·380	2·930	31·800	14·860
Fat,	3·370	3·460	—	—
Starch,	3·797	2·750	—	—
Dextrose,	3·695	2·687	—	—

The table reads thus :—For each gramme of oxygen consumed in destroying animal albumen 3·38 calories of heat are produced ; or, for each gramme of carbonic acid exhaled in consequence of, or associated with, the destruction of animal albumen, 2·930 calories are produced ; or, for each gramme of nitrogen excreted in the decomposition of animal albumen, 31·8 calories are set free ; or, for each gramme of urea excreted in the decomposition of animal albumen, 14·860 calories of heat are set free. Again, for each

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* Léon Fredericq. "Chaleur et travail musculaire." *La Revue Scientifique*, XIII., 1887, 3^{me} série, p. 466.

gramme of oxygen used in destroying fat, 3·370 calories are produced; in destroying starch, 3·797 calories; and in destroying dextrose, 3·695 calories. Lastly, for each gramme of carbonic acid exhaled, associated with the destruction of fat, 3·460 calories are set free; of starch, 2·750 calories; and of dextrose, 2·687 calories. It will be observed that each gramme of oxygen consumed produces almost the same amount of heat, whatever may be the nature of the substance oxidised in the body. Assuming a mixed diet, let us take the mean of these figures for oxygen, namely, 3·56, and multiply by 1,488. This gives 5,297·28 calories, a result approximately near that obtained by the other method of computation.

From the physical point of view, therefore, it is clear, theoretically, that a balance can be struck between the income and the output of energy in a living being like man. The chemical reactions occurring in the body are the source of the energy set free, either as heat or external mechanical work, or both. The physiologist, however, is not satisfied with the striking of this balance sheet. His science leads him to the study of the intermediary changes that occur between the chemical phenomena and the final production of thermal energy and of mechanical energy; and the tissue in which these changes may be most conveniently studied is muscle. Muscles work and produce heat. What is the relation existing between these two functions? Are they independent of each other; or is the heat set free in a muscle by chemical changes partly liberated as heat and partly converted into mechanical energy? These are questions that have in recent years been very fully discussed both by physicists and by physiologists, and on the answer to be given depends our conception of a muscle considered as a motor or heat machine.

Does the muscle resemble a heat machine which transforms heat into work? This question was first put and answered in the affirmative by J. Mayer, but it has been answered in the negative by the majority of physicists and physiologists, because they do not find in muscle one of the essential conditions of all such machines—namely, a marked difference of temperature between one part and another.

Let us consider shortly the arguments of those who uphold the hypothesis of the thermic origin of the mechanical energy manifested by a muscle.

The view in question is clearly put by Gavarret in an article on "Animal Heat."* "Muscle is a living motor, similar to a steam engine, utilising heat for the production of work." An internal combustion, with production of heat, opens the series of acts that end in muscular contraction. A "certain definite portion of the heat thus produced" disappears "as a thermic agent, is used up by the *internal work* which accompanies the contraction, and is *transformed into contractility.*" If a muscle in contracting does not perform external work "all the heat consumed by the *internal work* accompanying the contraction, or *transformed into contractility,* reappears in the state of *sensible heat* when the muscle is relaxed."

In a perfect steam engine, for example, which performs mechanical work by the to-and-fro movement of the piston, the essential condition is a great fall of temperature between the boiler and the condenser, favouring the return of the piston after it has been raised by the passage of steam into the cylinder. Herzen† points out, however, that a muscle cannot be regarded as a perfect machine, the piston of which moves in each direction. It is rather a machine in which the piston moves only in one direction; another cylinder and piston are required to produce a movement in the opposite direction. He calls an active muscular mechanism a single-acting machine. Thus the biceps flexes the forearm on the arm, but it cannot extend the forearm that has been flexed. To accomplish extension, the triceps muscle on the back of the arm must be brought into play. Any continuous movement, such as walking, flying, or swimming, requires two independent machines, each of which does its work without any arrangement comparable to the mechanism of a boiler and condenser. The arrangement for the movement of a limb is as if the engineer obtained a rapid to-and-fro movement of the piston, by employing two boilers, and by allowing the steam of the one to press the piston behind, and the next instant the steam of the other to press the piston in front. For these reasons, Herzen thinks that, as regards muscle, all arguments founded on the necessity of a considerable difference of temperature between two parts of the organ fall to the ground. He

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* "Chaleur Animale." *Dictionnaire Encyclopédique des Sciences Médicales.* 1re série, t. xvi., p. 79.

† "L'activité musculaire et l'equivalence des forces." *La Revue Scientifique*, XIII., 1887, 3me série, p. 257.

holds that the transformation of heat into mechanical energy really occurs, both when the muscle does work in lifting a weight, and even when it contracts without lifting a weight. When a muscle, having no resistance to overcome, contracts, it displaces to some extent its own mass, and it overcomes the internal resistance of its own substance and of its coverings. If we suppose that molecular movements occur in the muscle substance when it contracts, these must be regarded as internal work, consuming a certain amount of heat. In discussing this question one must not forget, however, the important part played by the elasticity of muscle. Like a band of india-rubber, a muscle becomes warmer when it is stretched, and it cools when it retracts. The contraction of muscle may be regarded as a sudden and strong retractile action. If so, a muscle ought then to become *colder* when it contracts. But this is apparently contrary to experience. Thermometric observations on a contracting muscle indicate a rise and not a fall of temperature. On this point there is great conflict of opinion. Some hold with Herzen that the contraction actually lowers temperature, but that the fall is hidden, and more than counterbalanced by the heat set free by the chemical changes occurring in the muscle. It is quite true that a thermometric observation gives us the temperature only at a moment of time, and that the increase may be the algebraic sum of a series of operations in the muscle having a heating effect partially neutralised by a simultaneous operation (the contraction) having a cooling effect.

According to this view, two operations occur in a muscle—a physico-vital phenomenon of contracting, which absorbs heat, and a chemical phenomenon, which produces heat. Then, if the first occurred without the second, the muscle should become colder; and if the second occurred without the first, the muscle should become hotter than it would be if a contraction had also taken place, by exactly the amount of the heat that would have been absorbed during the contraction. Here, however, experiment has given doubtful results. It is manifestly almost impossible to separate the two classes of phenomena, even supposing them to exist. Solger, Mayerstein, and Thiry have noted a slight cooling effect at the beginning of contraction, but Valentin and Heidenhain have not confirmed this observation. Herzen, with great ingenuity, suggests that in a fresh muscle the substances which are the seat of chemical changes exist in large amount, and that when such a muscle contracts the heat produced by these changes is so great relatively to the heat absorbed by contraction as to make it impossible to observe any cooling, and he thinks that the cooling effect would probably be discovered in fatigued muscles in which the heat-producing substances have already been used up.

Certain experiments made by Heidenhain in his well-known research appear to favour Herzen's hypothesis. He found that as a muscle became fatigued the quantity of heat set free diminished much more rapidly than the energy of the contraction, as measured by the amount of work done. Thus, in one series of experiments on a muscle, the first observation, made when the muscle was fresh, indicated 190·5 gramme-millimetres of work, and 6·5 degrees on the scale of the thermal galvanometer, while the last experiment registered 117 gramme-millimetres, and only 1 degree on the galvanometer scale. In another series, the first experiment recorded, of work 517, and of heat 7·5, and the last, of work 324, and of heat 2·5; and in a third series, the first readings were 1,080 of work and 12 of heat; and the last, 380 of work and 2·5 of heat. Thus the production of heat fell off at a much more rapid rate than the production of work, so that, in the same time, the heat diminished to about one-fifth, while the work was reduced by only about one-half or one-third. Herzen is of opinion that if Heidenhain had prolonged these experiments he might have reached a point when the heat would have disappeared, and a real cooling effect might then have been observed.

Another series of experiments by Heidenhain has been brought into court in support of the contention that contraction produces a cooling effect. Heidenhain caused a muscle to lift to a given height the same weight three times in succession. Suppose that the positive work of raising the weight was exactly compensated by the negative work of lowering it, so that negative work restored to the muscle the heat absorbed by it while doing positive work. If we subtract from the heat observed by Heidenhain the thermic equivalent thus restored, at the close of the series the figures of the experiments would become negative; that is to say, if the positive work had not been entirely compensated, the galvanometer would have shown a slight cooling effect at the time of contraction. In addition, as a muscle becomes warmer when stretched, it is evident that some of the heat observed might be due to the extension of the muscle when the weight pulled it out after contraction. This heat should also be subtracted from the heat actually observed. Danilewski has succeeded in making an experiment by which this somewhat difficult point is made clear. He caused a muscle to lift a weight a certain height, but the weight in falling was detached from the muscle and allowed to descend by an india-rubber thread. The heat effect was observed by a thermal pile and a galvanometer; and he found that in these circumstances the heat evolved became much less in amount, and in some experiments he obtained a distinct cooling of the muscle. That is to say, according to theory, heat was used up in the contraction of the muscle, and as it was not restored by the falling weight, and, as the muscle was not made warmer by extension, it became colder in proportion to the mechanical work accomplished. Blix has also investigated this question, using refined appliances, with the general result that when the muscle contracts without performing mechanical work; that is to say, when it has no weight to lift, no resistance to overcome, it becomes warmer; but when it contracts, and does positive work by lifting a weight or overcoming a resistance, the muscle becomes colder.

Danilewski has also made the important observation that the muscles which were the subjects of his experiments had a high thermic equivalent relative to the positive external work actually done. They used more heat than could be accounted for by the work done. The excess of heat thus absorbed is probably used up in the internal molecular work, associated, in some way not yet unveiled, with contraction of the molecular substance.

Certain of the statements made in the foregoing argument may be admitted, while others are open to objection. According to Carnot's theorem, a thermic motor can only act continuously when a difference of temperature has been produced at one portion of it so that a certain amount of heat flows from the point where the temperature is high, to another point where the temperature is low, and a portion of this heat may be employed in working the machine. No motor suitable for continuous work can operate without a difference at two points in the intensities of the dynamic element in the motor. Thus, in electro-dynamic machines, a current can only be produced when there is a difference of electric potential at two points of the conductor. A hydraulic motor also requires a difference of water level. The same must hold true of an organic motor like a muscle, although we may not be able to define the two points at which there is a difference in the intensity of the dynamic change. The nervous influence causes the muscles to contract, and either at the point where the nervous influence originates, or where it acts on the muscle, there must be a difference in the intensity of the dynamic flow, or current, or stimulus, from the intensity of the change in the muscle itself. It is not easy to prove this statement; but if heat is produced in the muscle by chemical changes, as all admit, it cannot be denied that, possibly, the muscle, considered as a machine, may not also work in consequence of a difference of temperature, and that Carnot's theorem is also applicable to it. This statement is made in view of the well-known fact that the action of the nerve is that of a liberator of the energy of the muscle. All that is implied is that there may be a dynamic difference in the change occurring in the nerve centre from that in the motor end-plates, and that it is in consequence of this difference that there is a flow of energy from the former to the latter.

The muscular machine, however, presents certain remarkable differences from ordinary motors. This has been clearly pointed out by Hirn in several suggestive papers in *La Revue Scientifique.** Every machine which acts as a continuous motor can exercise an influence on another body, and then return to its original condition. It can perform work, and after the accomplishment of the work it reverts to the state in which it was before it performed the work. As an example, take a simple form of steam engine. This machine can raise in 24 hours 864,000 kilogrammes of water into a reservoir 10 metres above the lower level. If the stroke of the piston is short and the pressure on the piston is small, this work can only be accomplished by a large number of strokes of the piston. Taking 60 per minute, or 86,400 per day, each stroke will raise 10 kilogrammes 10 metres, or 100 kilogrammes 1 metre. To obtain this work, however, each time the piston rises to its full height, we must prevent the weight of the water raised by the stroke from again descending, and we must remove the pressure of the steam underneath the piston, and allow the latter to fall by its own weight, or aided by the impulse of a beam placed overhead. These arrangements secure continuous work. The reduction of pressure under the piston is

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* *Op. cit.*

brought about by allowing the steam to return to the condition of water. The act of condensation is essential to every steam engine.

Take now an illustration of the working of a living motor. Place a series of weights (each of 20 kilogrammes) on the table. Suppose we resolve to raise each weight with the arm to a height of 50 centimetres. We seize hold of the weight and, in obedience to an effort of will, the muscles of the arm pass into a state of contraction or tension, proportional to the weight to be lifted. This condition is brought about by a flow of nerve energy along nerves from the seat of the will in the brain to the muscles. The contraction or tension of the muscles influences the jointed levers forming the framework of the arm and hand; and the force, transferred to the weight of 20 kilogrammes, raises it to the height of 50 centimetres. The work has now been accomplished, and, by another act of volition, distinct from the first, we arrest the flow of nerve energy, restrain the action of the muscles, and we then place the weight on a support intended for its reception. If we had ceased to exercise volition during the raising of the weight, or when the weight had been raised to the required height, the weight would have fallen. After placing the weight on the support intended to receive it, we loose hold of the weight, and allow the arm to descend. Hirn compares the latter action to the condensation of the steam in a simple steam-engine, or to the stoppage of the current that has been employed to magnetize a bar of soft iron. Each of the weights of 20 kilogrammes may be raised in the same way, 10 kilogrammetres of work being done in each case. Work is done by letting go each weight after it has been raised. A dynamic influence or forth-putting of energy, of the nature of which we know little, throws the muscles into a state of contraction or tension; this tension causes the dynamical effect desired, and when the work has been accomplished, the muscles return to their original state.

The action of the human motor, however, can be varied. Thus, suppose the weight to be raised is light, or, in other words, considerably within the limits of our muscular power, we can raise it easily and we can vary at pleasure the rapidity of raising it. This means that we can alter at pleasure the intensity of the volitional effort or dynamic influence that causes the muscular tension, and thus we can produce dynamic effects of great delicacy and nicety of adjustment. Another peculiarity of the human motor is that it can readily produce a dynamic effect of the opposite kind. Thus, we can, by a voluntary effort, again seize hold of one of the weights, excite muscular tension proportional to the weight, move the weight from its support and let it descend, with a rapidity which we can vary at pleasure, by a relaxation of the muscles. When we reach the lower level, the muscles have either already become completely relaxed, or we voluntarily arrest the muscular tension; and, when the arm becomes free, it can again be raised to the height from which it started, by a new volitional effort. Few motors can in this way reverse their action. In lifting the weight we perform positive work, and in lowering it we perform negative work. Now, if work is derived from heat, the questions arise—Do the muscles absorb heat in doing positive work and give it out in doing negative work? Is the mechanical work of raising the weight done at the cost of a certain amount of heat-energy; and does the negative work of lowering the weight restore heat-energy to the muscle?

This mode of discussing the subject has been carried out with great lucidity by Hirn in the paper already noticed. It appears to me, however, that he has erred in neglecting, to some extent, the internal work done in a muscle. There can be no doubt that work is done in lifting the weight, but work is also done in lowering the weight. During the process of lowering, the muscles pass from a greater to a less contracted condition, and contraction always implies physiological work. If the muscles had not remained partially contracted during the process of lowering the weight, the latter would at once have fallen to the ground. From this point of view, so-called negative work is as much work in the physiological sense as positive work. For example, in ascending a ladder, a man raises the weight of his body, by a series of consecutive muscular efforts, a certain height. In descending, he lowers his body gradually through the same height by another series of muscular efforts. In both cases, work—that is to say, work in the physiological sense—is done, and if work is derived from heat, heat would be evolved both in ascending and in descending the ladder. In descending, less expenditure of energy is probably necessary, and consequently less heat will be evolved. The action of the nervous and muscular systems in lowering the weight, to my mind, resembles the action of a steam crane in gradually lowering a heavy load after it has lifted it to a given height. The weight descends by its own gravity, but it is allowed to descend slowly by tension of the chain being kept up by the action of the engine.

We must, therefore, now inquire a little more minutely into the phenomena that occur in a contracting and relaxing muscle. Two phenomena are apparent, namely, contraction and an evolution of heat. It is also well known that the evolution of heat is less when there is positive external work. So long ago as 1843, Joule stated that if an animal were caused to gallop in a circus or to ascend a mountain, we may expect that in proportion to the amount of muscular effort there will be a diminution of the heat set free in the body by any given chemical action. A given chemical action occurring in the muscle, and connected with contraction, always produces an evolution of energy, one part of which appears as sensible heat and the other part as external mechanical work. The performance of mechanical work never entirely prevents a heat production; it only causes it to diminish. The investigations of Becquerel and Breschet, of Béclard, of Heidenhain, of Fick, and of Danilewski have all demonstrated this production of heat and its relation to work. One strong objection, apart from experimental evidence, must be urged against an exclusive theory of the thermic origin of work. Whatever be the source of the mechanical work, it cannot be denied that a muscle accumulates heat when it is caused to do hard work. The muscle thus accumulates potential energy, and it seems curious that it does not utilise it if it has the power of converting some of this heat into the energy of contraction. Why, as has been asked by Chauveau, does it not convert part of this heat energy into physiological work? Why does it go on producing more and more heat? It seems strange that when a muscle develops more heat than it can transform into work, it should still continue to produce more and more heat.

Suppose we now alter our position, and regard the contraction itself as a mode or manifestation of energy. We must not forget that a muscle is elastic as well as contractile. If we attach a weight to a muscle in a state of repose the muscle becomes stretched, and when we remove the weight it returns to its former length. A muscle, in the language of physiological text-books, is said to be feebly but perfectly elastic. Further, when a muscle is contracted a lighter weight will stretch it to the same length, and, consequently, it is said that during contraction the elasticity of a muscle is diminished. If, however, we distinguish between the elasticity of a muscle at rest from its peculiar condition when contracted, and if we view the latter condition as an elastic state brought about by contraction; if we use elasticity in this sense, we see that it then has a dynamic value. Contractility may be said to be the cause of the dynamic elasticity of the muscle. The contractility comes first, and it calls the elasticity into action in proportion to the effort required to overcome a given resistance. This view of the question has recently been strongly put forward by Chauveau,* and it appears to me to throw new light on this difficult subject. In developing his theory he gives, in the first place, the following illustrations to show the difference, as regards expenditure of energy, between various forms of elasticity:—

1st. Suppose we place a weight on a piston which is supported by a certain pressure of steam acting on the under surface of the piston. If we remove one-half of the weight, the piston will ascend until the steam underneath has become so much rarified as to come to equilibrium with the new charge on the piston. Work has been done, and the piston and its charge will remain in the new position without any further loss of energy, if the apparatus is covered so as to prevent the loss of heat.

2nd. Suppose a band of india-rubber fixed by one end and having a weight attached to the other end. The weight will stretch the band to a certain length. If we now suddenly remove one-half of the weight, the remaining half will be raised by shortening of the india-rubber band until equilibrium has again been established, and there is no further expenditure of energy.

In both of these cases, the arrest of the free play of the force of an elastic body supports a weight, and thus performs mechanical work. The tension of the elastic body is exactly equal to the weight to be supported, and no external energy requires to be supplied for keeping up the equilibrium.

Now take the case of a muscle. Suppose we hold a weight in the hand by keeping the forearm flexed by the action of the biceps muscle at a certain angle and rigidly fixed, and also that we do not alter the volitional effort put forth with the view of

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* Chauveau: "Du Travail Physiologique et de son Equivalence." *La Revue Scientifique*, 1888. Also, "Le Travail Musculaire et l'Energie qu'il représente." Paris, 1891.

supporting the weight. If we now suddenly remove a part of this weight, the muscle will raise the remainder up to a certain height, and the upward movement will cease when the muscular tension descends to the value of the weight still remaining on the hand. It is an essential condition of the experiment, however, that nervous action does not, in the meantime, alter the amount of elasticity which it at first called forth in the muscle. The elasticity of the muscle in this experiment appears, on a superficial examination, to play the same part as the elasticity of the steam, or as the elasticity of the india-rubber band. But there is a remarkable difference between the two cases.

Suppose the weight has taken up the new position in each of the three experiments under consideration. The elasticity of the steam and the elasticity of the india-rubber maintain this position without further loss of energy; but the elasticity of the muscle is maintained by chemical changes going on in its substance in connection with the physiological state of contraction. These chemical changes constitute physiological work; and it follows that the elasticity is kept up by physiological work. The mere maintenance of the weight at a certain height, while it may not be work in the physical sense, is truly work in the physiological sense, as there is a constant expenditure of energy. Thus, the behaviour of the muscle, as regards the maintenance of its elasticity, is quite different from that of either the steam or of the india-rubber band. The fact that a feeling of fatigue slowly comes on, if the weight be held up for a sufficient length of time, proves that changes are occurring, not only in the muscle, but also in the nerve centres, whence emanates the nervous energy that maintains the contraction of the muscle. But even when a muscle has no weight to lift, it does work in contracting. The proof of this is that when a muscle contracts, whether it lifts a weight or not, the flow of blood through it is accelerated, and the absorption of oxygen and the elimination of carbonic acid are increased. We see, then, that when a muscle sustains a weight by its elastic tension, there is a continual consumption of energy, because the elasticity is created or is brought into play by the contractility of the muscle. Contractility may therefore be regarded as a special mode of energy, directly related to the chemical phenomena occurring in the muscle. In a muscle the phenomena may be conceived to be as follow:—(1) Chemical changes, which liberate energy; (2) this energy is directly converted into contractility; (3) this part of the process, the bringing about of contractility, is true physiological work; (4) the immediate effect of the contractility is to develop the elasticity which, in turn, accomplishes the mechanical work of lifting a weight or of overcoming a resistance; (5) the result of the physiological work (contractility producing elasticity) is to perform external mechanical work, along with the evolution of heat arising from the molecular changes upon which contractility depends.

Thus, instead of supposing that the chemical changes liberate energy entirely as heat, and that a portion of this heat is converted into mechanical work, the remainder appearing as sensible heat, it seems more reasonable to hold that at least a portion of the chemical energy is resolved at once into physiological energy, or, in other words, into contractility. The sequence of events may thus be expressed:—(1) Potential chemical energy changed into kinetic chemical energy; (2) actual chemical energy changed into internal physiological work, or contractility; and (3) the internal physiological work of contraction converted into sensible heat, with or without external mechanical work. From this point of view, the production of heat must be regarded as the final, and not as the first, link in the cycle. When the production of physiological work is very active, a large amount of heat is finally evolved, and if it does not escape from the body with sufficient rapidity, it accumulates to such an extent as to be positively injurious. Thus, animals hunted to death die with symptoms resembling those manifested by animals which have had their temperatures raised by five or six degrees. The animals which bear severe muscular exercise with comparative impunity are those which lose heat most readily. The heat thus produced is not, however, to be regarded as absolutely useless. A certain mean temperature is one of the conditions of existence of warm-blooded animals. Thus, a living motor, a muscle, produces heat, and this is one of the conditions of its own existence.

Various attempts have been made to measure the relative amounts of work and of heat produced by a muscle, considered in relation to the chemical operations of which it is the seat. One of the most recent of these attempts is that of Chauveau and Kaufman, made in 1887.* The problem was as follows:—To

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* Chauveau: *Comptes Rendus*, t. cv., p. 296; also, "Le Travail Musculaire," *op. cit.*, p. 263.

determine, for a given weight of living muscular tissue in normal physiological conditions: (1) the quantity of blood flowing through it in a unit of time for purposes of nutrition; (2) the weight of oxygen absorbed by the tissue, together with the amount of carbonic acid produced in a unit of time; and (3) the weight of the substances furnishing the carbon of the carbonic acid. The muscle chosen was the elevator of the upper lip of a horse. This muscle is accessible; it can easily be studied at rest or when in action; and, from the arrangement of the vessels, the blood passing into it can be readily measured and collected for the analysis of its gases. The "specific activity or the co-efficients of the nutritive and respiratory exchanges" can be calculated from the data obtained by experiment, and stated for one gramme of muscle and one minute of time. The results are highly instructive. Each gramme of muscle was traversed in one minute by ·8 gramme of blood which was heated from 0·47° to 0·49° C. Supposing the capacity of blood for absorbing heat to be the same as that of water, the heating effect amounts to from ·000375 to ·000392 calorie. These figures represent the thermic equivalent of the work of the muscle, per gramme; or, in other words, the amount of energy required to give the necessary elasticity to the muscle. Can we account for this evolution of energy by considering the chemical phenomena happening in the muscle? Each gramme of muscle absorbs in one minute, when it works, ·00012 gramme of oxygen *above* the amount absorbed at rest. Supposing all this oxygen went to form carbonic acid by uniting with carbon, the amount of heat so produced would be ·000365 calorie, a figure remarkably near that obtained by the other method (a mean of ·000383).

Take, finally, the amount of carbonic acid in the blood escaping from the muscle, and from it calculate the amount of heat evolved in its formation. The amount of carbonic acid per gramme per minute is ·00020 gramme, representing in heat ·000440 calorie. This is greater than ·000365 by ·000075—that is to say, the respiratory quotient $\frac{CO_2}{O}$ is greater than unity during muscular work. As a rule, the respiratory quotient is less than unity when a muscle is at rest.

In this remarkable experiment, no account has been taken of any other chemical phenomena in the muscle except the production of carbonic acid, because our knowledge of these phenomena is very obscure; but if we were able to take them all into account, the balance between the energy set free by the chemical exchanges, and the heat produced would be complete. We may take it, then, that the thermic equivalent of the physiological work of one gramme of the elevator muscle of the lip of a horse is in one minute ·000380 calorie. This is the energy set free by one gramme in one minute, when the muscle had only to move itself. When it was caused to do external work, the energy appearing as heat was ·000335 calorie, so that the external work absorbed ·000045 calorie. The ratio then of the total physiological work to the external mechanical work was about 8 : 1; or, in other words, to produce a given amount of work, the muscle was supplied with about eight times more energy than was required for this work. According to Chauveau's theory, all the physiological work is required to produce the requisite amount of elastic tension, but this elastic tension only utilises as work one-eighth part of this energy, the remaining seven-eighths going off as heat.

It is thus shown that the energy consumed in producing the elastic tension of the muscle is much greater than that appearing as effective work. We have no right, however, to assume that the ratio of 8 : 1 is constant, even for the same muscle at different times, and still less for muscles having different mechanical arrangement of their fibres. Finally, there is a striking difference between the behaviour of a band of elastic india-rubber and a muscle. To develop and maintain the elasticity of the muscle, a much larger amount of energy is consumed than to develop the elasticity in the india-rubber band. Chauveau states that to give an elastic band a tension necessary to raise a weight of 1 kilogramme to a height of 1 decimetre, energy must be expended to the extent of $\frac{1}{4250}$ calorie; while an equal amount of muscular tissue would only acquire the same elastic tension by an absorption of *eight* times more energy, or $\frac{1}{532}$ calorie.

So long ago as 1869, Professor Fick, of Würzburg, stated that the amount of energy transformed into mechanical work by a muscle was about 33 per cent. In 1878, he announced that more elaborate and accurate experiments had obliged him to reduce the estimate to 25 per cent.* His experiments were made on isolated

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*A. Fick: "Experimentellen Beitrag zur Lehre von der Erhaltung der Kraft bei der Muskelzusammenziehung," 1869; also "Ueber die Wärmeentwickling bei der Muskelzuckung," 1878.

muscles of the frog, and to some extent were vitiated by the conditions in which the muscles were examined. Chauveau has reinvestigated the question by ingenious experiments on the muscles of living men in natural conditions. These experiments are fully described in the elaborate work recently published, entitled "Le Travail Musculaire et l'Énergie qu'il représente," a work which will sustain the fame of the great French physiologist. These researches oblige Chauveau to reduce Fick's estimate and to give the total effective work as only from 12 to 15 per cent. This is less than was expected, and it indicates that, contrary to what is often stated, a single muscle, considered as a machine, returns about the same effective work as a steam engine of the best construction.

How is this statement to be reconciled with the calculations based on the results obtained by the calorimetric observations of Hirn already described, in which he measured the total heat evolved by the body of a healthy man while engaged in performing mechanical work? The amount of efficient work was stated to be at least 17·4 per cent. of the total energy. This is somewhat greater than the results reached by Chauveau's method, but the difference is not striking, and it may be at least partially accounted for by errors of experiment. We must also bear in mind that there may be a considerable difference between the effective action of a muscular machine, made up of many muscles moving a complicated system of levers, and a single muscle. Work is done by such a machine by mechanical arrangements, all of which may have the effect of utilising, in the best possible way, the available energy.

Let us now endeavour to obtain a glimpse of the phenomena happening in a living muscle. In the first place, we must note the fact that even while at rest it consumes oxygen, produces carbonic acid and other substances—some nitrogenous and others non-nitrogenous,—and gives off heat. It is supplied by a nerve, the fibres of which, on the one hand, originate from nerve cells in the brain or spinal cord, and, on the other, terminate in the individual fibres of the muscle. When the nerve cells act, a current or change of some kind is transmitted along the nerve fibres to the fibres of the muscle; and this current of nervous energy excites chemical changes in the muscle-substance, one result of which is a larger consumption of oxygen, and a larger production of carbonic acid and of other waste substances. These chemical changes liberate energy in the form of a movement called a contraction, and at the same time there is an evolution of heat accompanied by certain electrical phenomena. The contraction, no doubt, is the result of the chemical changes; the molecules, or molecular fibrous network of the contractile substance, taking up new positions, and the fluid in the interstices of the fibrous network, or bathing the molecules, streaming in such a way that the muscular substance becomes more tense and develops elasticity in proportion to the resistance offered to the contracting muscle by its attachments to bones. As already pointed out, the energy appears as heat and movement, and the old question again presents itself:—What is the relation of the chemical phenomena to the energy thus liberated in a two-fold way?

It seems clear that the muscle cannot transform heat into movement. It is the seat of chemical changes, and internal or physiological energy is set free. This energy is transformed into contraction of the muscle-substance, and this, in turn, develops elasticity (the elasticity of contraction, as we may term it), and, by this elasticity of contraction useful external mechanical work is accomplished. Associated with this contractile and elastic state, we find the remainder of the energy appearing as sensible heat. The elasticity is, from this point of view, a passing or transitory form of energy. None of the energy set free by the chemical changes is useless. Its dissipation is regulated by the internal work of the muscle—that is to say, by the effort which the muscle makes to change its form when it is obliged to overcome resistance. This change of form produces a special elastic force, the value of which is determined by the amount of muscular shortening, and by the resistance to be overcome, and the remainder of the energy not used up in performing external work appears as heat. Such is the most modern theory advanced to explain the action of "Muscle as a Transformer of Energy."