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MUSCULAR FORCE AT DIFFERENT SPEEDS OF SHORTENING.

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In a study of the mechanics of human muscle Hill [1922] came to the conclusion that a muscle could be represented mechanically by a spring working in a viscous medium. As the speed of shortening (v) of the muscle increased he found that the work done or the tension exerted (W) fell off linearly according to the equation $W=W_0-kv$. Although the equation represented the experiments very satisfactorily it should be mentioned that the observations may have been complicated by reflex changes in the degree of innervation of the muscles in the supposedly maximal voluntary contractions (though Lupton [1922] with a quick-release mechanism obtained the same result). Moreover, the experiments of Gasser and Hill [1924] on isolated frog muscles showed that this simple linear relation did not generally obtain under these conditions.

These experiments were followed by some observations of Levin and Wyman [1927] on the relation between the force and the speed of shortening or the speed of stretching of muscles of dogfish and other animals. The expected linear relation between force and speed was not found and the authors concluded that the muscle represented a system of two components, an undamped elasticity and a damped elasticity, the latter behaving according to the equation suggested by Hill. When the muscle was suddenly released the undamped system could shorten instantaneously and could keep the tension from falling rapidly as it otherwise would. This two-component system has been widely used by subsequent workers [Bouckaert, Capellen and de Blende, 1930; Mayer and Bouckaert, 1932; Petit, 1931; Sulzer, 1928].

The work of Bouckaert, Capellen and de Blende [1930] is of special interest in this connection. They arranged to measure the rate of shortening of a muscle when the load was suddenly decreased, the inertia of the system being reduced as much as possible by the use of two levers in tandem. Their results showed that the muscle shortened a certain distance almost instantaneously while the remaining shortening took place slowly along a logarithmic curve. The results were apparently satisfactorily interpreted by means of the same two-component model, the instantaneous shortening being due to the undamped elasticity and the slow shortening being due to the damped elasticity. It appeared possible, however, to test this interpretation by another method.

Consider a muscle model such as that suggested by Levin and Wyman [1927] consisting of two springs (S and S_v) in series, one of them (S) being undamped and non-contractile, and the other (S_v) being imbedded in a viscous medium. Let the model be attached to a weight (W) which is supported outside until shortening begins. To represent the contractile process let the elasticity of S_v be suddenly increased. S will then be stretched by S_v until its tension equals W. Not until this has occurred will the external tension equal W. Hence when the load starts to rise the length change of the undamped spring (S) will be complete and it cannot participate further in the mechanical events of shortening. Therefore, under the conditions of isotonic after-loaded contractions an undamped elastic non-contractile component cannot change in length, *i.e.* if its force is constant its length must be constant. It is therefore possible to study the mechanical properties of a muscle deprived of any participation of any possible non-viscous elastic component by the simple device of observing the speed of shortening under different isotonic loads (after-loaded) varying from zero to the maximum which can be lifted. Under these conditions the muscle should follow the equation of Hill. The results showed, however, that the relation between speed and force is not linear. Hence it must be concluded that the simple two-component model does not represent the muscle correctly.[1]

Two series of experiments were performed, the first series using cat muscles (by B. S. M. in 1930–2) and the second series on frog muscles (by W. O. F. in 1933 and 1934). For the latter series an optical lever was used which much improved the accuracy of the determinations and led to the

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[1] It might of course be argued that the muscle contains an undamped contractile component which could participate in the shortening, but it cannot be assumed that the whole contractile mechanism is undamped and such an assumption would not help to explain why the contractile mechanism as a whole (S_v) when isolated from S does not follow Hill's equation. Further, an undamped contractile mechanism is practically inconceivable and the photographic records give no indication of an initial very rapid (instantaneous) shortening.

theoretical interpretation suggested. These results will therefore be reported first. The data on cat muscles are adequate, however, to show that the same formula applies in this case.

EXPERIMENTS ON FROG MUSCLES.

Method.

The sartorius muscles of *Rana pipiens* were used throughout except for a few experiments on the gastrocnemius. The muscles were mounted on a rigid support in a glass vessel immersed in a thermos bottle for a water bath. At the beginning of the experiment this vessel was filled with Ringer's solution which could be withdrawn when desired. The muscles could be stimulated either directly or indirectly. In most of the experiments the former method was used but no differences could be detected in the results if nerve stimulation was employed. For stimulation the interrupted current from the secondary of a Harvard induction coil was used, the duration (usually 0·2 sec.) being controlled by a rotary contact breaker. The strength of the current was adjusted to give a maximal contraction.

The effects of inertia were minimized by the use of two isotonic levers in tandem as suggested by Bouckaert. The long arm of the second lever is attached close to the axis of the first lever and the actual weight is hung close to the axis of the second lever. The first lever magnified 10 times and the second one 5 times so that the actual velocity of movement of the weight itself was reduced 50 times and the weight was 50 times as heavy as the tension on the muscle. The muscle was attached 8 cm. from the axis of the first lever by means of a fine glass rod. A pulley 8 mm. in radius was attached to the axis of the first lever for the thread to which the tip of the second lever was attached. A light mirror, attached also to this axis, permitted the record of the shortening by optical means with a magnification of about 8 times. Time was recorded by a tuning fork interrupting the beam of light. The velocity of the surface of the drum was usually 90 cm. per sec.

The records were for the most part smooth without any sign of vibration. Slopes could be measured to 1° of arc with an ordinary celluloid protractor placed tangent to the curve. With the high speed drum and the large magnification, this provided a measurement of speed of considerable precision which was highly satisfactory for the purpose. Velocities were always measured near the beginning of the shortening where the slope was constant and maximal and there was no acceleration or deceleration. Actually most of the curve corresponds to this requirement for the period of acceleration is scarcely visible in the records and shortening takes place at a nearly constant speed for a considerable period of time. This also served to eliminate any small effects of inertia which persisted in spite of the two levers. For this reason no attempt was made to calculate the magnitude of the inertia. Since there is no velocity change the tension in the muscle must be equal to the load.

At the close of the experiment the weight and length of the muscle were measured. The force was then calculated per $cm.^2$ cross-section and the velocity of shortening in cm. per sec. per cm. length of muscle. Since measurements were always made at the beginning of contraction, a stimulus of 0·2 sec. was ordinarily long enough, although longer stimuli up to 2 sec. were sometimes used for the low temperatures. The muscle carried an initial load of about 1 g. or less. Greater loads were carried on a supporting screw (after-loaded) until the muscle began to shorten. In most experiments the muscle was stimulated at a series of loads increasing in steps from the minimum to the maximum and then decreasing in the reverse order.

We have measured, therefore, the maximum speed of shortening under a series of different loads, the measurement being made always at the same length within a few millimetres, *i.e.* just after shortening begins and at nearly the resting length so that the resting tension can be neglected. The theoretical importance of making all the observations at a constant length should be stressed because the maximum isometric tension which can be exerted varies with the length.

Results.

Tracings of a typical set of records obtained with varying loads are shown in Fig. 1, all accurately placed with respect to the beginning of the tetanic stimulation which lasted about 0·4 sec. In taking the records the light was cut off by a signal magnet until the moment when stimulation began so that the beginning of the record marked the beginning of stimulation. The white lines made by the tuning fork crossing the light beam 200 times per second were omitted in tracing. The graphs are not S-shaped but start almost straight from the base line and continue nearly at the same velocity for a considerable time. Obviously under these conditions there is little difficulty in measuring a maximum velocity for all the loads at nearly the same length. In these particular tracings the larger loads were recorded last and there was some fatigue so that the lower velocities are relatively too small.

With the larger loads shortening begins somewhat later than with the light loads. It might be argued that the velocity with the light loads

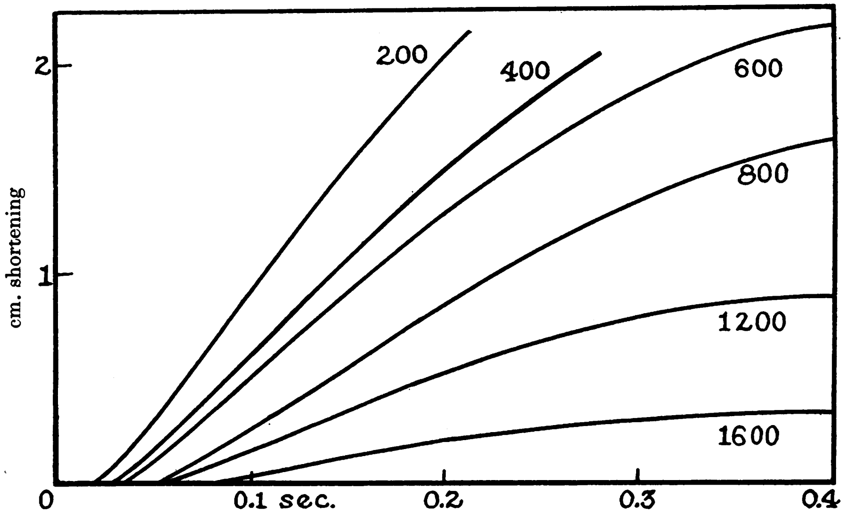

Fig. 1. Tracings of typical photographic records of shortening under different loads after rearranging so that the base lines and the points of beginning of stimulation coincide. Sartorius muscle at 0° C. Length 3·2 cm., weight 218 mg. June 14, 1935. Figures on the graph show the weight on the lever in grams, this being 50 times the weight on the muscle.

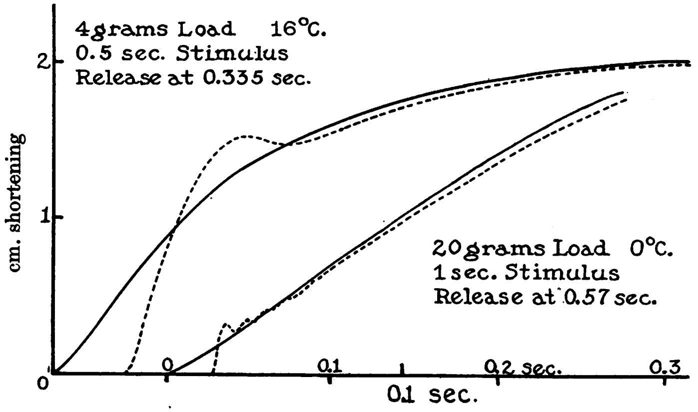

Fig. 2. Two tracings made from the photographic records of muscles shortening under the same loads; solid lines, free shortening; broken lines, delayed shortening. The relative horizontal positions of the two curves of each pair are arbitrary.

would have been still larger if the muscle had been prevented from shortening until maximum tension had been developed, and had then been suddenly released. If this were the case any interpretations based on the velocities measured in free isotonic contractions would be invalidated. We have accordingly tried some experiments in which the lever was released later in the contraction at or near the point of maximal isometric tension and have compared the subsequent velocity of shortening with the velocity of shortening of the same muscle under the same load and the same length when shortening was not interfered with. In many such comparisons we have never observed a greater velocity in the delayed shortenings after the first sudden fling of the lever is over. If there has been any consistent difference it is in the other direction, the delayed shortenings being less rapid than the free shortenings. Tracings of two comparisons of this sort are shown in Fig. 2. The result is particularly clear in the lower tracing at 0° C. The low temperature reduces the sudden fling of the lever and leaves a greater length of shortening for comparison. The dotted line represents the delayed contraction. It has been arbitrarily placed in such a position that the two records coincide shortly after the oscillations due to the fling of the lever have subsided. From the close similarity of the velocities in these curves and many others like them we feel justified in concluding that the velocities which we have measured on muscles shortening freely represent correctly the maximum velocity of which the muscle is capable at any stage of the contraction. This means that the contractile state is fully developed as far as ability to shorten is concerned as soon as the tension in the muscle is sufficient to balance the load. This may be taken as further evidence that the point of maximal isometric tension does not indicate the time when the contractile state is at a maximum, as Gasser and Hill [1924] have shown in other ways. The fact that the velocity of shortening under the light loads does not tend to increase as shortening proceeds (as shown in Fig. 1) is further indication that the contractile state is already fully developed when shortening begins. We may suppose then that, when shortening begins, the processes associated with shortening which tend to dissipate tension become promptly equal to the processes which are causing the development of tension so that shortening proceeds in a steady state from the very beginning.

The velocities of shortening measured at different loads in a typical experiment at 18·5° C. are shown in Table I and the graphs are plotted in Fig. 3. The lower curve shows the force or load plotted as ordinates against the velocity of shortening. It is obvious that no portion of this curve is linear but it is rather logarithmic in shape. To test this, the logarithms of the load are plotted against the velocity in the upper dotted

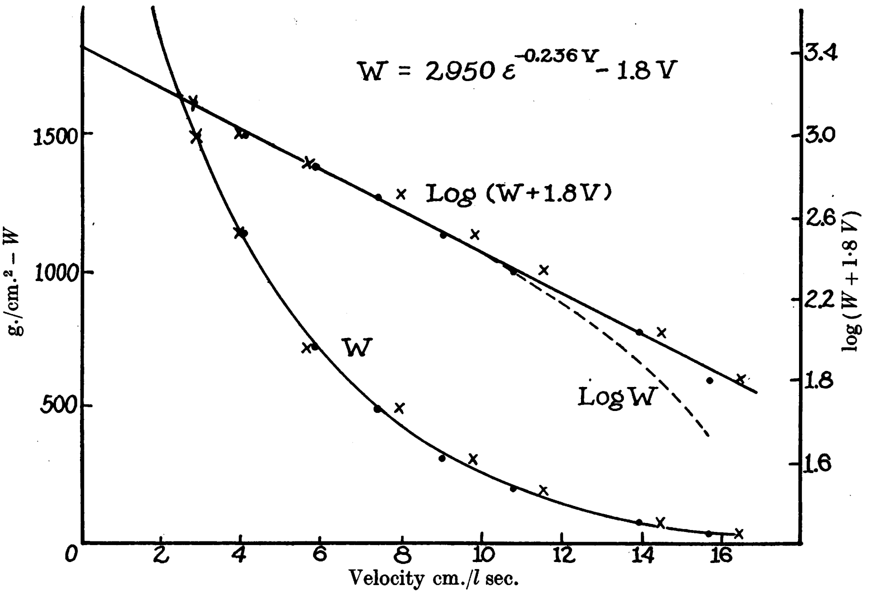

Fig. 3. Maximum velocity of shortening as abscissæ plotted against isotonic load in grams per cm.² cross-section as ordinates in lower graph. Log of load (*W*), broken line, and log (*W* + 1·8*v*), solid line, in upper graphs. Frog sartorius muscle, 114 mg., August 30, 1934. Temp. 18·5° C. Data Table I. Decreasing loads indicated by • ; increasing by ×. Experimental points for log *W* are omitted.

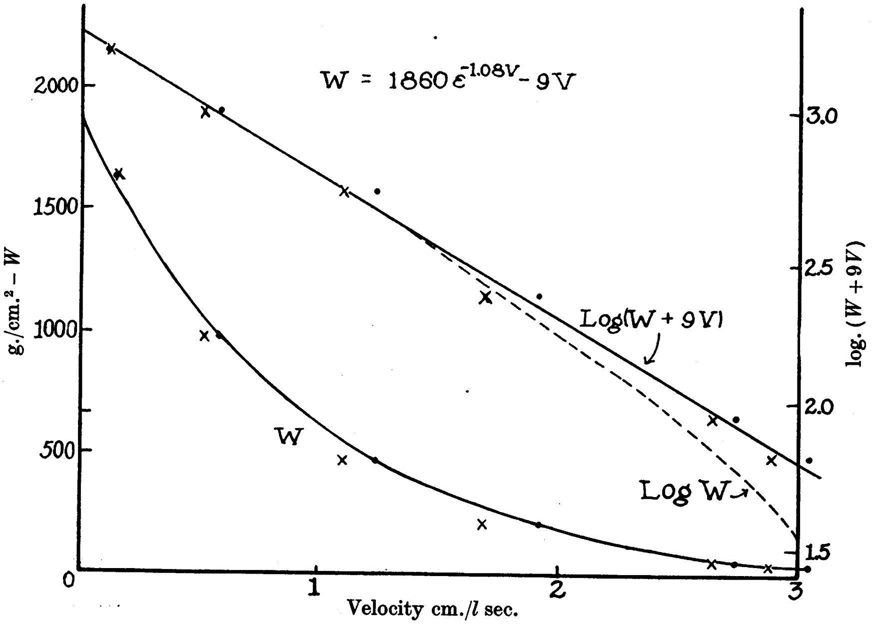

Fig. 4. Same as Fig. 1. Sartorius muscle 118 mg. September 5, 1934. Temp. 0° C. Data Table I.

TABLE I. Original force-velocity data.

Force (W) g./cm.^{2}	Velocity (V) cm./l sec. (a)	Velocity (V) cm./l sec. (b)	Force (W) g./cm.^{2}	Velocity (V) cm./l sec. (a)	Velocity (V) cm./l sec. (b)
35	16·45	15·71	38	3·04	2·88
82	14·25	13·95	64	2·73	2·63
200	11·57	10·79	218	1·92	1·68
318	9·82	8·95	474	1·23	1·09
494	7·93	7·40	986	0·58	0·52
729	5·62	5·89	1628	0·15	0·15
1140	3·95	4·07			
1493	2·94	2·95			

Sartorius at 18·5° C. (Fig. 1) Sartorius at 0° C. (Fig. 2)

Velocities under (*a*) were observed first, followed by (*b*) in reverse order. The velocity measured is the maximum rate of shortening in cm. per unit of length of muscle (l) per second.

curve. This curve is straight until it reaches the large velocities where it falls off sharply. The same result is seen in another typical experiment (at 0° C.) in Fig. 4 and Table I.

If the muscle is represented accurately by a viscous elastic system this force-velocity curve should have been linear, the loss of force being always proportional to the velocity. The slope of the curve would then represent the coefficient of viscosity. Evidently the slope of this curve is not constant and it is impossible to say what slope to take for the viscosity. The force-velocity curves of Levin and Wyman have a similar shape but they were able to invoke a non-viscous elastic component to explain them. To explain the same shape where the possibility of the participation of such an undamped component is impossible requires some quite different interpretation.

If W is the tension exerted by the muscle (*i.e.* the weight) and kv is the force expended against viscosity, then

$$W+kv=F, \qquad \text{......(1)}$$

where F is the true internal muscle force. In Hill's formula it was assumed that F is independent of the velocity of shortening, but the curves of Figs. 3 and 4 suggest that it decreases with increase in velocity in such a way that the amount of force lost for a given increase in velocity is proportional to the amount of F already present,

$$-\frac{dF}{dv}=aF \quad \text{or} \quad F=F_0e^{-av}, \qquad \text{......(2)}$$

and finally,

$$W=W_0e^{-av}-kv, \qquad \text{......(3)}$$

since $W_0=F_0$ when $v=0$.

It is impossible at the present time to give a more fundamental derivation of this equation in terms of the mechanism involved, but it can be shown at least that it empirically expresses the data with a satisfactory degree of accuracy. Taking logarithms,

$$\log (W+kv)=\log W_0 - av \log e. \qquad \ldots\ldots(4)$$

The solid upper graphs in Figs. 3 and 4 represent values of log $(W+kv)$ plotted against v and it is evident that the addition of the term kv with an appropriate value for the constant k has turned the non-linear dotted line into a very acceptable straight line, the slope of which gives the value of $a \log e$. This constant (a) may be called for convenience the "coefficient of tension loss". Since it does not vary in proportion to the velocity it cannot be a coefficient of viscosity nor even behave like viscosity. The viscous force (kv) is actually an almost negligible item and even at the highest velocities with minimum loads is usually less than the external force exerted by the muscle.

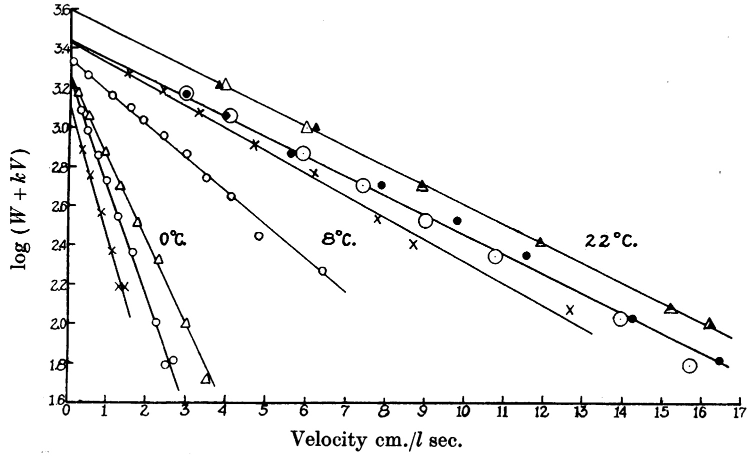

Fig. 5. Graphs of log $(W+kv)$ against velocity of nine different frog sartorius muscles at different temperatures, showing with what uniformity straight lines are obtained in this way. Two sets of points for the same graph represent ascending and descending series on the same muscle. In some cases ascending series only are included. To avoid confusion the upper of the 0° C. and of the 22° C. graphs have been raised 0·3 and 0·2 unit respectively.

The equations to the curves for W, plotted against the velocity, are given in Figs. 3 and 4 with their appropriate constants, and the curves have actually been drawn to comply exactly with these equations. They evidently fit the experimental points as well as could be expected.

To show that the experiments of Figs. 3 and 4 are not the only experiments which fit the equation, nine other experiments have been represented in Fig. 5. These have been selected at random, taking care only to pick curves which do not overlap in the graph. All of the graphs conform accurately to the straight lines. The much steeper slope at the low temperatures is very evident. The low temperatures evidently slow up the chemical reactions which are responsible for the production of energy for shortening to such an extent that the tension cannot be redeveloped so rapidly in relation to its rate of loss with shortening, and a steady state is therefore reached at a lower velocity.

A summary of the constants of the equations of all our experiments is given in Table II. Most of the values were obtained at 0° C. with a few at 22° C. and a few on the gastrocnemius muscle. The values of a, the

Table II. Summary of coefficients of tension loss (a), of viscosity (k), and of isometric tension (W_0).

W_0	a	k	W_0	a	k
	Sartorius 0° C.			Sartorius 22° C.	
2040	0·76	15	2190	0·255	5
2158	0·72	15	3090	0·331	0
1515	0·702	26	2400	0·205	0
1478	0·715	15			
2150	0·386	23·1	3630	0·264	1
2290	0·387	12	2240	0·252	0
1950	1·26	25	3720	0·270	1
1995	0·995	17	3090	0·288	2·2
			2750	0·255	4
1738	1·23	10			
1515	1·12	4	Av. 2888	0·265	1·6
1319	1·40	3·4			
1259	1·47	4			
794	1·30	10		Gastrocnemius 23° C.	
1380	1·9	0	3160	0·382	4
2400	1·104	9	2290	0·72	6
			2510	0·705	13
1122	0·87	25	4900	0·537	30
1202	0·852	11			
			3470	0·45	0·7
Av. 1665	1·01	13·2	2630	0·616	1·0
	Q_{10} for sartorius		Av. 3160	0·568	9·1
+1·22	−1·83	−2·58			
				Gastrocnemius 12–13° C.	
			1995	0·527	47
	Q_{10} for gastrocnemius		2510	0·92	38
			1950	0·901	26
+1·47	−1·38	−4·06			
			Av. 2152	0·783	37

The values for W_0 (g./cm.^{2}) were obtained by graphical extrapolation.

Figures between spaces were obtained on the same muscles. Variations are due to varying degrees of fatigue and recovery in Ringer.

coefficient of tension loss, are fairly uniform from one muscle to another for each temperature. The values of k, the coefficient of viscosity, are extremely variable. This is due to the fact that k has only a small effect on the curve, even at high velocities, and is therefore very difficult to measure with precision. Possibly it undergoes real variations corresponding to changes in the size of pores or the viscosity in different muscles.

The value of k is determined empirically by calculating approximately what value would be necessary to make the dotted lines ($\log W$) of Figs. 3 and 4 coincide with the straight lines ($\log (W+kv)$). This approximate value of k is then tried and the results ($\log (W+kv)$) are plotted and further adjustments in the value of k are made until the best fit is obtained. In reality this is merely an empirical process of fitting an equation containing a suitable number of constants to a curve. The fact remains, however, that the experimental results can be fitted by this equation and can almost be fitted by a simple exponential equation without the viscosity term, and furthermore that they cannot be fitted equally well by any equation which has hitherto been suggested in explanation of the force-speed relation.

Three additional experiments were performed in which the force-speed relation was measured by this method at two different temperatures on the same muscle; first at 0° C., then at room temperature, and then again at 0° C. with periods of rest in Ringer's solution in between. The results are shown in Table III. If the two values for 0° C. for each experiment are compared, the general reproducibility of the results can be judged. Averaging all the results and the temperatures together the corresponding values of Q_{10} given in the last line may be calculated. The

Table III. The effect of temperature in three sartorius muscles.

	Temp. ° C.	W_0	a	k
	0	1071	0·705	15·7
	22	2690	0·189	2·5
	0	1412	1·02	14·0
	0	1860	1·15	9·0
	21·5	4260	0·237	3·8
	0	1950	1·3	9·0
	0	1820	1·0	5·0
	18·5	2950	0·236	1·8
	0	1413	1·08	10·0
Av.	0	1588	1·042	10·4
	20·7	3300	0·221	2·1
	Q_{10}	+1·43	−2·11	−2·17

values of the coefficient of tension loss are the most accurate and give a Q_{10} of $-2{\cdot}1$. The averages of all the other values for these two temperatures from Table II give a Q_{10} of $-1{\cdot}83$ for the sartorius and a less accurate figure of $-1{\cdot}38$ for the gastrocnemius. The coefficient of viscosity has also a negative temperature coefficient of $-2{\cdot}17$ in Table III and $-2{\cdot}58$ and $-4{\cdot}06$ for the sartorius and gastrocnemius respectively in Table II. The isometric tension is always greater at the higher temperature, Q_{10} being 1·43 (Table III), 1·22 and 1·47 (Table II).

Discussion.

It was shown by Fenn [1924] in Hill's laboratory that in order to shorten and do work a muscle must liberate an extra amount of energy more or less in proportion to the work done in shortening. This fact was held to cast doubt upon the theory that a muscle is simply an elastic body. In spite of this objection subsequent authors have continued to explain phenomena observed in shortening muscles on the basis of simple mechanical models. The present experiments show again that these simple models are inadequate for the purpose, and it seems most likely that they are inadequate for the same reason that muscle is not an elastic body. A stimulated muscle shortens *pari passu* with the development of "shortening energy", and the rate of development of this energy from chemical potential energy must be of paramount importance in determining how fast it can shorten under a given load or how much tension it can exert for a given speed of shortening. The temperature coefficient of $-2{\cdot}1$ which was found for the coefficient of tension loss (a) may be taken to indicate that some chemical reaction is involved in determining the diminution of tension with increase in speed, and this tends to confirm the interpretation which has been suggested above. The main problem still remains unsolved, however, until an explanation is offered for the exponential decrease of F with increase of velocity. One method of attack upon this problem may now be suggested.

The theory of constant power output in shortening.

One of the suggestions which has been offered in explanation of the decrease of force with increase of speed is that of Stevens and Metcalf [1934] who showed that in a muscle shortening against an inertia device the power output (Wv) was approximately constant for a considerable part of the contraction. If Wv is constant then W must decrease in proportion as v increases. In explanation of this constancy of Wv, it seems possible that there may be a limiting value to the rate of development of excess heat for shortening which would be proportional roughly to the rate of work or to Wv. This is not, however, an adequate explanation for our curves, for if the power output (Wv) is calculated for each of the points in Figs. 3 and 4, the results are not constant but pass through a maximum at intermediate velocities. The force-velocity curve in other words is not a rectangular hyperbola. A better case can be made out for the theory that the total power output (internal plus external) is constant. The total power is given by the expression $(W+k'v)v$ or $Wv+k'v^2$.

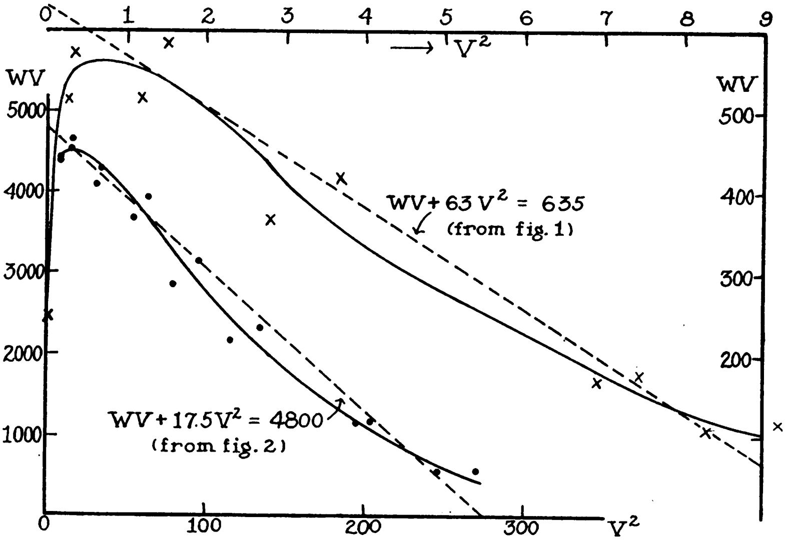

Fig. 6. Tests of the constant-power theory according to which Wv plotted against v^2 should give a straight line. Broken lines represent the best straight lines that can be drawn through the points. The equations for these straight lines are given. The continuous lines follow the experimental points and must start at the origin.

If this value is constant then Wv plotted against v^2 should give a straight line, $k'v^2$ being the power which is wasted internally in overcoming viscous resistance during shortening. The graph of Fig. 6 shows that this does actually give nearly a straight line of slope equal to k' for all the higher velocities, but as the velocities approach zero the power must also approach zero so that some other factor must be invoked to explain this part of the curve. Since this constant-total-power theory applies only to about half the curve without supplementary hypotheses we have abandoned it. It may be worth mentioning further that the value of k', the coefficient of viscosity, as deduced from the constant-power theory is considerably greater than the value of k as calculated from the exponential relation. Thus in Fig. 6 the values of k' found are 63 as compared to $k=9$ in Fig. 3 for the same data and $k'=17{\cdot}5$ in Fig. 6 as compared to $k=1{\cdot}8$ in Fig. 4. On either basis the k is almost negligibly small in comparison with the initial slope of the force-velocity curve.

EXPERIMENTS ON CATS.

Method.

The animals were anæsthetized with 0·5–0·6 c.c. dial per kg. body weight injected intraperitoneally, and were not allowed to recover. Most of these experiments were performed on the gastrocnemius muscle. The calcaneus bone was bisected, freed from all attachments with the exception of the Achilles tendon, and was fastened rigidly to the lever. The animal lay on its back and the muscle pulled directly downwards when it contracted. The femur was fixed firmly to a rigid upright by means of a small clamp screwed directly on to the bone. The clamp was introduced through a small slit in the skin on either side of the leg and lay between the adductor femoris and the semimembranosus on the medial side and between the semitendinosus and the vastus lateralis on the lateral side. The sciatic nerve was cut near the sciatic notch and was stimulated peripherally by shielded electrodes. For a few experiments on the sartorius and quadriceps muscles a somewhat similar preparation was used except that the pelvic girdle was fixed rather than the femur.

The levers were substantially built in order to carry the heavy loads which were necessary. The first lever recorded directly on a revolving drum with smoked paper and magnified the movement of the muscle 1·9 times, the muscle being attached 15 cm. from the axis. The linear speed of the surface was 50 cm. per sec. Time was recorded for each contraction by a 60 cycles per sec. tuning fork turned on simultaneously with the stimulating current. Stimulation was caused by the secondary of an inductorium operated by hand and was continued until shortening was complete.

The end of the second lever (27 cm. long) was attached by a strong flexible braided wire 1·5 cm. from the axis of the first lever and the weight was hung from a pulley of 4·5 cm. radius on the axis of the second lever. In this way the tension on the muscle was one-sixtieth of the weight. Since the isometric tension in a cat's gastrocnemius muscle may be greater than 10 kg. it was difficult to obtain weights large enough. In some experiments the second lever was dispensed with and the weights were hung directly on the first lever. The period of acceleration on the records seemed scarcely any longer under these conditions. With both levers in use weights greater than 300 kg. were used. For this purpose a strong scale pan was hung by a stout wire cable from the lever and one end of a 12-ft. beam was placed on the scale pan, the other end resting on a stool. On this beam could be placed various large weights including at times as many as three persons standing close to the scale pan. With the levers provided all this was readily lifted by most cats.

These preparations, having their normal blood supply, kept very well for several hours without sign of fatigue and many records were obtained with each load. The loads were usually progressively increased and then decreased as in the frog experiments. The maximal slopes of the graphs were measured and the values averaged together for each load. Each point plotted in the graphs represents the average of four to ten individual measurements. On account of the small magnification and some troublesome vibrations in the records the results were not so accurate as in the frog experiments. At the end of the experiment the length, maximum diameter, maximum circumference and weight of the muscle were measured. The maximal cross-section area as calculated from the circumference and diameter was used in calculating the force per cm.^{2} without regard to the physiological cross-section.

Results.

Since the figures obtained are not so precise as in the frog experiments it will suffice to present the results entirely in the form of graphs. Fig. 7 illustrates in detail one experiment on the quadriceps muscle and corresponds to Figs. 3 and 4 for frog muscles. This experiment was especially suitable for publication because the range of weights used was wide enough to show both ends of the curve fairly well. Determination of all the constants was rendered impossible in about half the experiments because only a small portion of the curve was represented in the data. In such cases the value of a, the coefficient of tension loss, was the only one which could be determined.

Graphs of log $(W+kv)$ for four other experiments are shown in Fig. 8 and the lines are evidently quite straight. Constants for all the other experiments which were complete enough for the purpose are included in Table IV together with data concerning the dimensions of the muscles used. The first four experiments of Table IV are those plotted in Fig. 8.

The constants for the gastrocnemius are the most reliable, especially the value of 1·42 for *a*. In addition to the figures listed in Table IV we have six other experiments which do not cover a sufficient range of loads to permit of a determination of *k* but which give a fair value for *a*, the results being 1·79, 1·89, 1·17, 1·73, 1·23 and 1·34 with an average of 1·52, in good agreement with the value of 1·42 from the seven other determinations. Two experiments on the cat's sartorius muscle gave values of 1·06 and 0·38 for *a*, the force-velocity curves being definitely logarithmic rather than linear, although the data were not good enough for a more complete analysis.

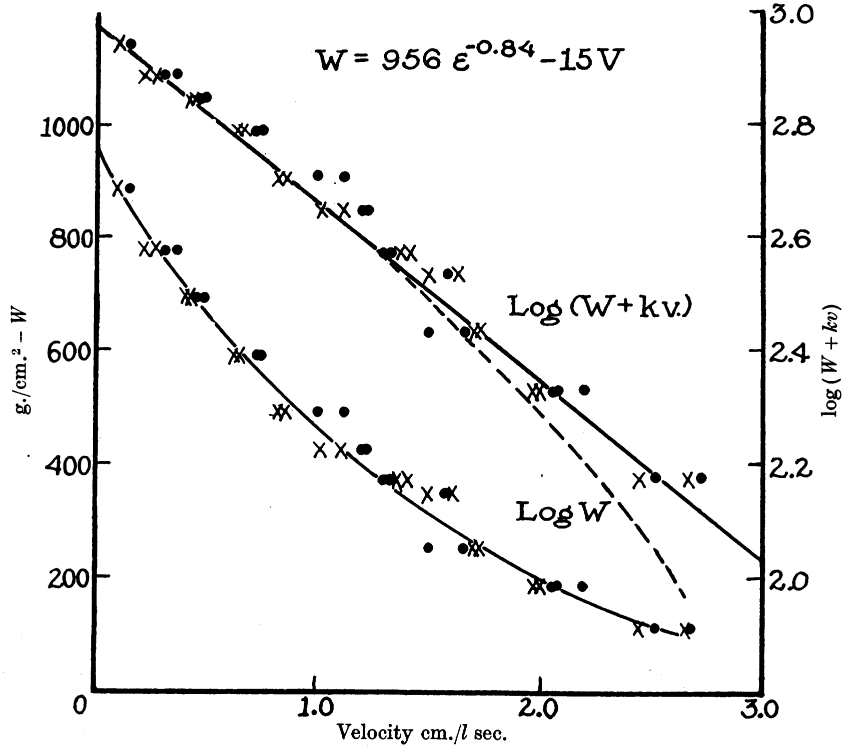

Fig. 7. Force-velocity relations in cat quadriceps muscle. See No. 7*a*, Table IV. Experimental points for log *W* are omitted. The lower graph is drawn to fit the equation derived from the straight line in the upper graph. Two ascending and two descending series are indicated by • and × respectively.

The constants for the quadriceps muscle are all smaller than those for the gastrocnemius but the experiments are hardly numerous enough to make the comparison reliable. Differences in the structure of the muscle

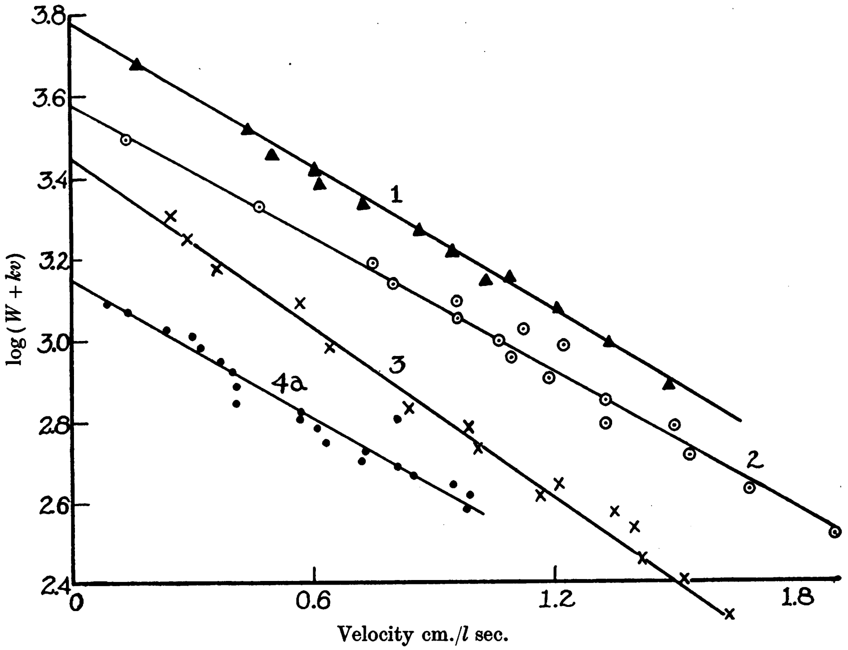

Fig. 8. Graphs of log ($W + kv$) against velocity for four cat gastrocnemius muscles to show the straight lines so obtained. Numbers on graphs correspond to numbers in Table IV where the constants are given. To avoid confusion the upper curve has been raised and the lower curve lowered 0·2 unit.

TABLE IV. Force-velocity constants in cat muscles.

	Muscle dimensions					
No.	Length cm.	Section cm.^{2}	Weight g.	W_0 g./cm.^{2}	a	k
			Gastrocnemius			
1	6·3	2·23	8·35	3800	1·42	110
2	9·0	3·26	18·50	3890	1·28	55
3	9·2	7·18	23·0	2820	1·61	40
4*a*	8·5	1·61	5·6	2240	1·32	220
4*b*				1740	1·23	250
5	10·0	4·84		1096	1·22	100
6	9·3	3·36	19·0	2510	1·85	100
			Av.	2585	1·42	125
			Quadriceps			
7*a*	12·0	4·84	54·3	956	0·841	15
7*b*				1122	0·856	14
8	9·4	4·84	26·9	776	0·70	0
			Av.	952	0·799	10

might explain the low values in the quadriceps since both *a* and *k* are dependent upon the values of *v* which are calculated per cm. length of the muscle. A more parallel-fibred muscle would therefore give higher velocities for the same total length and hence smaller values of both *a* and *k*. Comparison of the velocities in Figs. 7 and 8 shows that the quadriceps did attain higher velocities than the gastrocnemius. The value of *k* is also dependent upon the values of *W* which in turn depends upon the cross-sectional area of the muscle, but *a* is independent of the absolute values of *W* and depends only upon the percentage change in *W*.

The figures for the gastrocnemius of the cat at body temperature may also be compared with those for the gastrocnemius of the frog at 23° C. from Table II. The isometric tension is not very different in the two cases, but both *a* and *k* are higher in the cat muscles in spite of the higher temperature. This would indicate that the frog muscle is fundamentally a "faster" muscle either for mechanical and structural reasons, which would explain the lower *k* values, or for chemical and energy reasons, which would explain the lower values of *a*. From Fig. 3 it may be seen that a frog sartorius muscle at 18·5° C. can shorten with a velocity of 16 cm. per sec. per cm. muscle length while the cat's quadriceps reaches only a velocity of 3 in similar units.

Comparison with previous experiments.

Some comparison of these constants with other values from previous work may also be made. Fenn and Garvey [1934] determined a coefficient of viscosity for passive movements of the "resting" human leg. The resistance to movement to-and-fro at the knee was calculated as if it were all due to the muscles involved in this movement. In this case, the force increased more or less linearly with increase in speed, a relation which might be expected in a resting muscle where energy requirements for shortening do not enter in. The slope of this force-velocity curve represents then a coefficient of viscosity and had a value of 28 g. per cm.^{2} for an increase of velocity of 1 cm. per sec. per cm. length of muscle. The units are therefore identical with those of *k* in Table IV where values of 128 and 10 for the gastrocnemius and the quadriceps muscles were found. It may be concluded that all these values are of approximately equal order of magnitude, the differences being referable to structural differences.

Fenn, Brody and Petrilli [1931] in studies on the movement of the human leg after quick releases found that after the release the decrease of tension amounted to 31 p.c. for an increase in the speed of shortening of 100 p.c. of the length of the muscle per second, or 1 cm. per sec. per cm. of muscle length. The fact that the result was expressed as a percentage loss of tension for unit increase of velocity indicates that these authors anticipated the results of this paper, *i.e.* that the loss of tension with increasing speed is logarithmic rather than linear. Since this experiment involved a contracting muscle the loss of tension with speed is chiefly referable to the value of a. Neglecting any part which k may have had it is possible to calculate the corresponding value of a from equation (4):

$$\log W_0 - \log W_1 = \log 100 - \log(100\text{–}31) =$$
$$2 - 1{\cdot}839 = 0{\cdot}161,$$
$$0{\cdot}161 = av \log e \quad \text{and} \quad a = 0{\cdot}371, \quad \text{since } v = 1.$$

This figure is somewhat smaller but of the same general order of magnitude as the figure 1·42 for the gastrocnemius and 0·799 for the quadriceps of the cat (Table IV).

Hill's experiments with human arm muscles were recalculated by Fenn, Brody and Petrilli in terms of the probable dimensions of the muscles involved, and the conclusion was reached that in the flexion of the arm at different speeds the decrease in tension with unit increase in speed amounted to 73 p.c. The corresponding value of the coefficient of tension loss (a) is 1·31 which checks very well with the average value of 1·42 found for the cat's gastrocnemius. It should be pointed out, however, that Hill's data showed actually a linear relation between speed and force so that the percentage loss of tension would depend entirely upon the starting point chosen. The above figure represents the percentage decrease in W_0. From the value obtained it may be argued that nervous relaxation did not play a large role in Hill's experiments since equally large values were obtained in the denervated cat muscles. Such nervous effects may nevertheless have helped to produce a linear force-velocity relation by decreasing the tensions exerted at high speeds.

In the paper of Gasser and Hill [1924] it was possible to estimate values of force and velocity from their Fig. 2, curve II. With these data it is found that log F against velocity gives a fair straight line from which a coefficient of tension loss of $a = 0{\cdot}473$ was calculated (for room temperature?) which is intermediate between our values for 0 and 22° C. for the sartorius muscle.

The average value for the coefficient of viscosity for the frog sartorius at 0° C. found by Bouckaert, Capellen and de Blende on the basis of their analysis of their quick releases was 1120 at 0° C. which is nearly 100 times as large as the average value of 13·2 found in Table III. This high value, however, is of about the same order of magnitude as the initial slopes of the force-velocity curve of Fig. 4 which gives a value of 1690 for 0° C., *i.e.* 1690 g. per cm.^{2} loss of tension for unit increase of velocity. This agreement is perhaps to be expected, since Bouckaert, Capellen and de Blende derived their constant from the secondary shortening of the muscle where the velocities were relatively low.

It would appear from this that they were not actually dealing with a constant coefficient of viscosity but rather with the coefficient of tension loss (a).

DISCUSSION.

It cannot be said from these results that it is necessary to abandon altogether the theory that a muscle contains a component of relatively undamped elasticity. The necessity for such an assumption is, however, rendered doubtful and the conception of a two-component system as originally described has to be abandoned since the damped component, when isolated and studied by itself, does not have the properties originally ascribed to it. It is now necessary to enquire whether the new properties of the muscle as described in this paper can account for the phenomena observed in the quick release experiments. This probably means that it is necessary to take more seriously into account the energy requirements of a shortening muscle. The loss of tension on increasing the speed of shortening is due chiefly to a chemical rather than to a mechanical delay (friction).

SUMMARY.

1. The force exerted by muscles at increasing velocities of shortening was investigated by measuring the rate of shortening of muscles of cats and frogs in isotonic contractions under different loads.

2. In a freely shortening muscle the speed of shortening is shown to be the same as in a muscle released after tension is fully developed.

3. As the speed of shortening increases, the force decreases, not in a linear fashion as would be the case if viscosity alone were concerned, but rather in an exponential fashion, a small hypothetical correction being made for a true viscosity effect.

4. The relation between force (W) and velocity (v) can be expressed by the formula $W = W_0 e^{-av} - kv$; where a is the "coefficient of tension loss" and k is the coefficient of viscosity.

5. It is concluded that this exponential relation is concerned in some way with the processes of developing extra energy for the work of shortening and that a muscle cannot properly be treated as a simple mechanical system.

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REFERENCES.

Bouckaert, J. P., Capellen, L. and de Blende, J. (1930). *J. Physiol.* **69**, 473.
Fenn, W. O. (1924). *Ibid.* **58**, 175, 373.
Fenn, W. O., Brody, H. and Petrilli, A. (1931). *Amer. J. Physiol.* **97**, 1.
Fenn, W. O. and Garvey, P. H. (1934). *J. clin. Invest.* **13**, 383.
Gasser, H. S. and Hill, A. V. (1924). *Proc. Roy. Soc.* B, **96**, 398.
Hill, A. V. (1922). *J. Physiol.* **56**, 19.
Levin, A. and Wyman, J. (1927). *Proc. Roy. Soc.* B, **101**, 218.
Lupton, H. (1922). *J. Physiol.* **57**, 68.
Mayer, P. and Bouckaert, J. P. (1932). *Arch. int. Physiol.* **35**, 9.
Petit, J. L. (1931). *Ibid.* **34**, 113, 139.
Stevens, H. C. and Metcalf, R. P. (1934). *Amer. J. Physiol.* **107**, 568.
Sulzer, R. (1928). *Z. Biol.* **87**, 472. Cf. also **88**, 604 (1929).