COMPARISON OF MECHANICAL PROPERTIES BETWEEN SLOW AND FAST MAMMALIAN MUSCLES

BY J. B. WELLS*

From the Department of Physiology, University of Rochester, Rochester, N.Y. and The National Institute of Neurological Diseases and Blindness, National Institutes of Health, Bethesda, Md, U.S.A.

Ranvier (1873) first suggested that certain skeletal muscles contained functionally distinct types of fibres. He observed in rabbits a slow persistent contraction which he associated with red muscles in contrast to brisk responses from pale muscles. Subsequent investigation, based on histological as well as physiological observations, showed that the slow fibres resisted fatigue better (Ranvier, 1880) and their tetanic responses fused at lower stimulus frequencies (Fischer, 1908; Cooper & Eccles, 1930). These differences were related to the contractile properties rather than to neuromuscular transmission since the responses reported by Ranvier were directly evoked from animals poisoned with curare.

Following these more qualitative reports were those characterizing muscle activity in terms of physical systems. The non-linear relation between active tension production and the velocity of shortening was first emphasized by Fenn & Marsh (1935). Hill (1938) confirmed and expanded these mechanical studies to include thermal measurements. The result was a mathematical expression relating force and rate of energy release, the constants of which, determined by either mechanical or thermal methods, were similar. This description of the active contractile response of muscle states that the rate of total energy liberation in excess of the isometric rate is proportional to the reduction of external tension (P) below maximal isometric force (P_0). The equation is usually written

$$(P+a)v = b\,(P_0-P),\tag{1}$$

where b, with dimensions cm/sec, is the rate of energy liberated, in excess of isometric energy, for each gram of tension reduction below P_0. The constant a, with dimensions of force, is the energy liberated concomitant with external work, above that of the isometric, per unit length of shortening: v denotes velocity of shortening.

* Present address: The National Institute of Neurological Diseases and Blindness, National Institutes of Health, Bethesda, Md, U.S.A.

The relation applies, in general, to vertebrate voluntary muscle (Hill, 1950) as well as cardiac (Sonnenblick, 1962) and uterine (smooth) muscle (Csapo & Goodall, 1954). Such studies led to the concept of muscle models (Hill, 1949; Jewell & Wilkie, 1958; Pringle, 1960) consisting of three elements: (1) a contractile component, characterized by the equation stated above in series with (2) a slightly damped (Woledge, 1961) elastic element, characterized by its stress–strain properties, and (3) a parallel elastic element which may be largely avoided by maintaining the muscle at or below a length established at rest with a small initial load. Finally, the time course and intensity of the contractile capacity of a muscle, called the active state, has been shown (Hill, 1949) to be a determinant in the mechanical response. Quantitative differences are described between the mechanical responses of rat anterior tibialis and soleus muscles which have been applied to the model outlined above. These differences indicate basic diversities between the respective contractile and elastic components which may be related to function. Data on the dynamic constants of rat-limb muscles (Close, 1964) became available after the results presented here were first submitted for publication. Comparisons of parallel findings are included in the discussion.

METHODS

Preparation. The soleus and anterior tibial muscles from young, male, albino rats, weight range 180–220 g, served as representative slow and fast muscles respectively. The selection was based on the comparison of fusion frequency, the ability to maintain tetanic tension, shortening velocity and twitch duration following supramaximal stimulation of the motor nerves. Fusion of isotonic contractions was produced in soleus muscle at about 45 c/s compared to about 85 c/s in tibialis anterior. During tetanic stimulation, maximal tension declined 50 % in 143 sec in the soleus (4 expts.), while a similar decline was observed in 11 sec from the phasic muscle (4 expts.). The isotonic shortening velocity of lightly after-loaded soleus was about 1/3 that of comparably loaded anterior tibial muscle, while the twitch duration of soleus was nearly 3 times that of tibialis. These differences plus the nearly identical *in situ* lengths; 2·5 cm for anterior tibialis and 2·7 for soleus muscles, and ease of access for mechanical recording permitted a comparative study of their mechanical properties.

The animals were initially anaesthetized with diallyl barbituric acid (Dial)–Urethane 0·6 ml./kg body wt. I.P. Cannulations of the trachea and the external jugular vein were accomplished under supplemental ether anaesthesia. The appropriate muscle of the right hind limb was dissected from unnecessary surrounding tissues to avoid distortion of mechanical responses (Denny-Brown, 1929). The limb was fixed by two bone clamps, the points of which were screwed into small indentations drilled in the medial and lateral surfaces of the femur and tibia near their distal ends. The clamps were secured to an aluminium block, which also supported the supine animal, so that the muscle moved in the horizontal plane. Muscle length was indicated by the distance between knots tied with fine silk at the inside ends of the origin and insertion tendons. The isolated insertion tendon was passed through a small steel ring, folded back and tied on itself so that a minimum of free tendon separated the ring and the distal end of the muscle.

The appropriate nerve, with all unused branches cut, was separated from the sciatic

trunk, which had been severed proximal to a tie close to the spinal column, and placed on a pair of shielded silver wires for indirect stimulation.

Mineral oil was periodically placed on the nerve and Tyrode Solution, maintained at 38° C, continuously irrigated the muscle to prevent drying and cooling.

Comparison of mechanical responses between muscles of different sizes requires an estimate of cross-section area, made by dividing the muscle weight by its standard length (L_0). The standard length was obtained *in situ* while positioning the ankle joint for maximal muscle stretch and corresponded, within ± 1 mm, to the length for optimal isometric tension development. These necessary approximations, based on the assumptions that constituent fibres operate in parallel and continue from origin to insertion, are made with the knowledge that complex muscle architecture may render the values less accurate.

Apparatus. Muscle loading, with minimal inertia, was provided by a series of Neg'ator springs (Jones, 1962), each furnishing a constant force to the shortening muscle. The springs were linked to the muscle by a 20-cm length of steel tubing (o.d. 0·46 mm) to which was
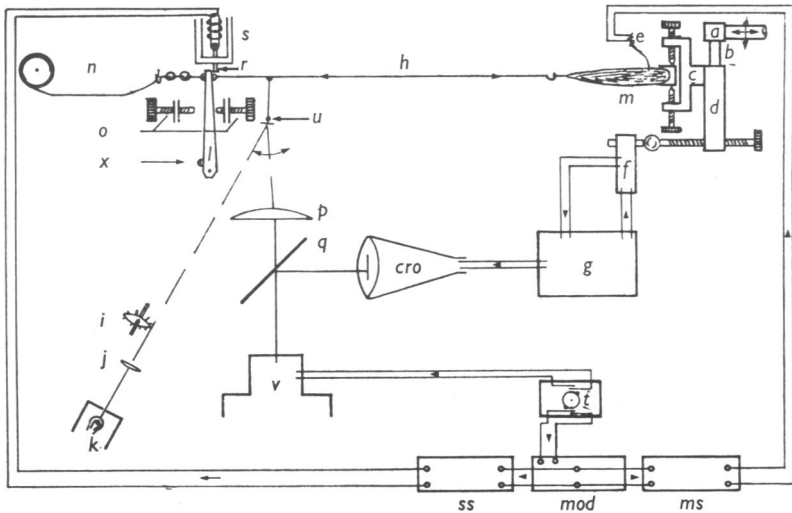

Fig. 1. Diagram of apparatus used for simultaneous recording of after-loaded isotonic shortening and tension development. Steel rod (*b*) connects rigid rack-mounted bar (*a*), secured to the base-plate and adjustable in three dimensions, to aluminium block (*d*) which receives two bone clamps (*c*) fixing the leg and muscle (*m*). The displacement of transducer pin (*f*) permitted by the rod was less than 0·03 mm for tension equal to P_0. Carrier preamplifier (*g*) feeds transducer signal to cathode ray oscilloscope (*cro*). Tension trace is then reflected by half-silvered mirror (*q*) on to moving film in camera (*v*). Muscle loading is provided by Neg'ator springs (*n*) linked to lever (*l*) at free end (as shown) or near fulcrum (*x*). After-loading and movement limitation of lever, which joins muscle via low-compliant connexion (*h*), is provided by adjustable stops (*o*). The lever as drawn is arranged for isometric recording and is rapidly released when engaging pin (*r*) is pulled by activation of solenoid (*s*). Small mirror cemented to pivoted end of short shaft (*u*) following muscle movement sweeps the reflected beam from light source (*k*), focused by lens (*j*) across plane surface of condensing lens (*p*). Spot image is recorded on moving film through half-silvered mirror. Beam chopper (*i*) provides continuous timing. Timer (*t*) simultaneously opens camera shutter and triggers modulating stimulator (*mod*) which triggers in turn muscle stimulator (*ms*) and solenoid activating stimulator (*ss*). Nerve is draped over stimulating electrodes (*e*).

fastened the free end of a light aluminium lever of the second class (Fig. 1). The lever, suspended on a bearing-mounted vertical axis (fulcrum) permitting rotation in the horizontal plane, was provided with adjustable stops for after-loading and movement limitation. The lever was fixed for isometric contraction by a pin attached to a solenoid core and could be rapidly released by energizing the solenoid.

Each spring was mounted on a bearing-suspended lucite drum which could be positioned horizontally for connexion with the lever either (1) near the fulcrum end (Fig. 1, x) (used with soleus) or (2) at the free end (used with tibialis only). The ratio of the lever arms at the respective positions was $1 \cdot 0 : 9 \cdot 3$. Spring forces were determined by static loading or dynamically by measuring the acceleration imparted to the uncoiling springs by a known
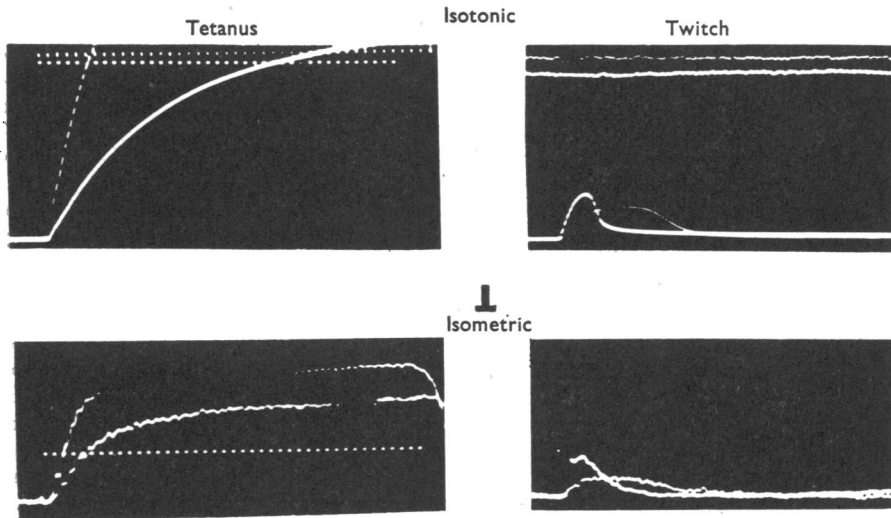

Fig. 2. Superimposed contractile responses from two animals evoked in anterior tibialis and soleus muscles by maximal stimulation of the motor nerves. In all four illustrations the tracing with shortest rise time was that of anterior tibialis. Isotonic load was 3 (4 % P_0) and 27 (6·5 % P_0) g wt. respectively for slow and fast muscles. Dots above base line are stimulus records. Isotonic beam interrupted every 4 msec. Horizontal scale is 25 msec. Vertical scale is 1 mm for all isotonic responses and 18 and 70 g wt. respectively for the soleus and anterior tibial isometric responses. Note the prolonged twitch response exhibited by soleus as compared to that of anterior tibial muscle.

force. The product of this acceleration and the total mass of the system was taken as the net dynamic force, and that subtracted from the known (accelerating) force yielded the opposing force of the spring. The values determined dynamically agreed with those derived statically within ± 3 %. The tensions exerted by the individual springs were rather evenly distributed between 5 and 60 % of P_0. The equivalent mass of the entire linkage system, excluding the springs but including bearing friction, was determined with the apparatus arranged as during experiments except that a light chain hung over a small pulley replaced the muscle. With the lever fixed by the solenoid pin the chain was loaded sufficiently to cause an acceleration of the linkage upon release. The movement was recorded optically and measured graphically. This procedure was repeated under different loads and the mass of the linkage was calculated from simultaneous equations relating net force to the product of total mass and acceleration. The average value of the equivalent mass of the

apparatus (including the extra pulley) was $1·88 \pm 0·1$ g (s.e.). Individual values determined at accelerations ranging from 0·1 to 0·5 g were constant within the variation previously given.

In a similar manner the equivalent mass of the apparatus was redetermined with the springs included; hence that of the springs could be derived by difference. Incorporation of the smallest spring into the apparatus, exerting a force of 3·0 g wt. (joined to lever near fulcrum), produced no measurable increase in the mass determination of the system. Hence the mass of this spring was assumed to fall within the standard error of that of the apparatus (0·1 g). The corresponding value for the largest spring, exerting 64 g wt., similarly coupled, was 2·6 g.

The complete apparatus was mounted on a 20 kg steel base-plate and suspended on rubber columns to reduce vibration. A short steel rod joined the limb clamp supporting the animal to a rigid but adjustable framework which was bolted to the base-plate. The compliance of the rod determined the displacement of a transducer cantilever (Grass model FT 03) which was in contact with the limb clamp and permitted continuous recording of tension applied horizontally by the muscle.

The compliance of the system, residing mainly in the steel rod (Fig. 1,b) and linkage connexions, was 0·06 mm/100 g wt., about 0·5 % L_0/P_0 and was disregarded.

Muscle displacement caused a small mirror, pivoted vertically on jewels and coupled to the muscle linkage (Fig. 1,u), to sweep a reflected light beam horizontally through the focal field of a Grass kymograph camera. The output signal of the tension transducer was fed to a Dumont model 333 dual beam oscilloscope positioned at the side of and at a right-angle to the camera field. A half-silvered mirror fixed vertically at 45° to the light beam (Fig. 1,q) and directly in front of the camera shutter, simultaneously transmitted the chopped light beam, while reflecting that of the cathode ray tube, on to the 35 mm film. The cathode ray tube was rotated, for horizontal display of the unswept vertical amplifiers, one of which monitored the output of the nerve stimulator while the other received the demodulated transducer signal (4800 c/s) via a Sanborn model 350–1100 B carrier preamplifier. Thus, the vertically moving film, automatically started by the opened shutter, furnished the sweep for the concurrent registration of muscle displacement and tension. These parameters were calibrated following each experiment by photographing the light beam spot after positioning the linkage in 1 mm steps with a micrometer screw, and recording changes in the transducer signals when weights were attached via a pulley to the muscle.

Stimulation. The motor nerves were stimulated by single or trains of square pulses, 0·5 msec duration, at a voltage 5–10 times that required for maximal response. Microswitches, operated by cams on the rotating shaft of a synchronous motor, simultaneously opened the camera shutter and activated a second stimulator which triggered and modulated the muscle stimulator.

To avoid fatigue the anterior tibial preparation was stimulated with trains of pulses to the peroneal nerve 0·5 sec in duration at 82–85 c/s (just fusion frequency). Trains of impulses delivered to the tibial nerve, innervating soleus muscle, also at 82 c/s (twice fusion frequency) were 0·7–1·0 sec in duration. The trains were delivered every 30 sec throughout the experimental period to maintain a steady state.

Force–velocity curves obtained before and after i.v. administration of tubocurarine chloride (0·4 mg/kg body wt.) showed good congruence thus implying that no difference occurred in responses evoked directly or by nerve stimulation. Nerve excitation was used exclusively to avoid hazards accompanying direct muscle stimulation.

Experimental procedure and analysis. One muscle only was prepared in each animal. P_0 was recorded before and after isotonic after-loaded contractions against each of the seven springs. Following this the stimulated muscle, which had developed full isometric tension, was rapidly released to that particular spring load. Thus each point determining the force–velocity and series elastic stress–strain curves was an average of duplicate observations.

Following these responses, additional measurements concerning series elasticity, active state decay, etc., were made in some preparations, the techniques of which are presented with the results.

Tracings of shortening were enlarged and projected on graph paper and velocity was calculated from their estimated slope. The measurements were applied to the predicted relation by plotting v against P and the constants a and b were determined graphically as described by Katz (1939). The variation between the observed values for shortening velocity and corresponding points on the curve calculated from P_0 (observed) a and b (determined graphically), averaged 4 % of maximal shortening velocity for all soleus preparations and less than 3 % for anterior tibial muscles. Means, standard deviations, and standard errors were determined for a, b, a/P_0, P_0, b/V_0, and V_0, from 15 anterior tibial and 14 soleus muscles. V_0, called the intrinsic muscle velocity by Hill, represents the speed of unloaded muscle and was calculated from equation (1) by setting $P = 0$ which yields

$$V_0 = (b/a)\, P_0. \qquad (2)$$

Summary of symbols

P = Muscle tension (g wt.).
P_0 = Maximal muscle tension (g wt.) at standard length.
v = Velocity of shortening.
v_0 = Maximal velocity of shortening.
a = Force constant (g wt.) (Hill's equation).
b = Rate constant (cm/sec) for extra energy liberation
(Hill's equation).
g = Gravitational acceleration.
L_0 = Standard length (cm) of muscle.

RESULTS

Properties of the contractile elements

Tetanic contraction characteristics. In the rat, the anterior tibialis muscle exerts about 5 times the isometric force displayed by the soleus muscle following maximal stimulation (Table 1, col. 3). However, expression of the force per unit of cross-section area (Table 1, col. 4) showed a similar tension development in both soleus and tibialis of 3259 ± 235 (S.E.) and 2781 ± 141 (S.E.) g wt./cm^2 respectively. These values are in the range generally obtained from other skeletal muscles of both amphibia and mammals (Fenn & Marsh, 1935; Hill & Woledge, 1962).

Maximal isotonic shortening, obtained at loads less than 5 % P_0, averaged 31·0 and 33·5 % of L_0 for 11 soleus and 14 anterior tibialis muscles respectively.

Similarity in the values of these parameters of maximal response suggested comparable contractile mechanisms, the components of which could be examined for possible functional differences.

Force–velocity relation. Columns 2, 5, 7 and 10 of Table 1 list the average values of a(g wt./cm^2), a/P_0, $b(L_0$/sec) and b/V_0 respectively for both muscle types. Probability values are listed in the table when the differences between means derived from phasic and tonic muscle as indicated by t test were significant at a level of $P < 0.05$. The value of a for the

anterior tibialis muscle was 1155 g wt./cm² and was rather greater than the 661 g wt./cm² obtained for the corresponding constant from soleus muscle. Similarly, a comparison of the rate constant b derived from the phasic and tonic muscles showed respective values of $2 \cdot 25 \pm 0 \cdot 24$ and $0 \cdot 40 \pm 0 \cdot 04$ (S.E.) L_0/sec. This difference between the rate constants was highly significant with P less than $0 \cdot 001$.

TABLE 1. Dynamic constants of rat muscle

|	1	2	3	4	5	6	7	8	9	10
	a (g wt.)	a (g wt./ cm²)	P_0 (g wt.)	P_0 (g wt./ cm²)	a/P_0	b (cm/ sec)	b (L_0/ sec)	v_0 (cm/ sec)	v_0 (L_0/ sec)	b/V_0
				Anterior tibialis (15 animals)						
$\bar{X}$	181	1155	438·0	2781	0·356	5·7	2·25	14·4	5·7	0·38
S.D.	82	574	91·5	522	0·136	2·2	0·88	3·4	1·4	0·12
S.E.	22	155	24·7	141	0·036	0·6	0·24	0·9	0·4	0·03
$P <$	—	0·05	—	—	0·05	—	0·001	—	0·001	0·001
				Soleus (14 animals)						
$\bar{X}$	18·0	661	91·0	3259	0·214	1·07	0·40	5·4	2·0	0·23
S.D.	6·8	258	27·0	845	0·094	0·40	0·15	2·4	1·0	0·09
S.E.	1·9	72	7·4	235	0·026	0·11	0·04	0·7	0·3	0·02

Figure 3 (top graph) shows the force–velocity curves constructed by applying the average values of a, b and P_0 obtained from phasic and tonic muscles to the characteristic relation (1). The differences in the values of shortening velocity, observed at a particular load, between the two curves mainly reflect the differences in the rate constants b. The graphs also show the general character of the force–velocity relations to be similar in both muscle types, i.e. the velocity increased non-linearly with decreased load. This confirmed for rat-limb muscle the findings of Fenn and Marsh in cat-limb muscle.

Because Hill's equation (1) is that of a rectangular hyperbola, the ratio a/P_0 should equal that of b/V_0 and indicate the shape of the force–velocity curve (Wilkie, 1950). Comparison between the ratio values, found in cols. 5 and 10, Table 1, for either muscle group shows approximate equality. However, the values of 0·36 and 0·38 for a/P_0 and b/V_0 respectively, determined from phasic muscle were higher than the corresponding figures of 0·21 and 0·23 obtained from the soleus muscle. This difference between corresponding values was especially significant in the case of b/V_0.

Figure 3 (lower graph) illustrates the variation in the ratio values by showing the differences in shape between the respective force–velocity curves obtained from soleus and anterior tibialis muscle. The curves were calculated from the same values used in Fig. 3 (top graph) but for ease of comparison both abscissa and ordinate are expressed as the fraction of maximal velocity and maximal force respectively. The interrupted curve
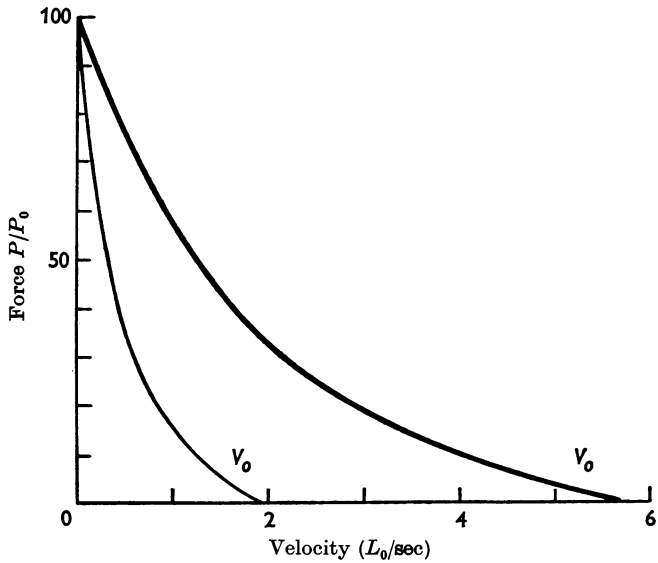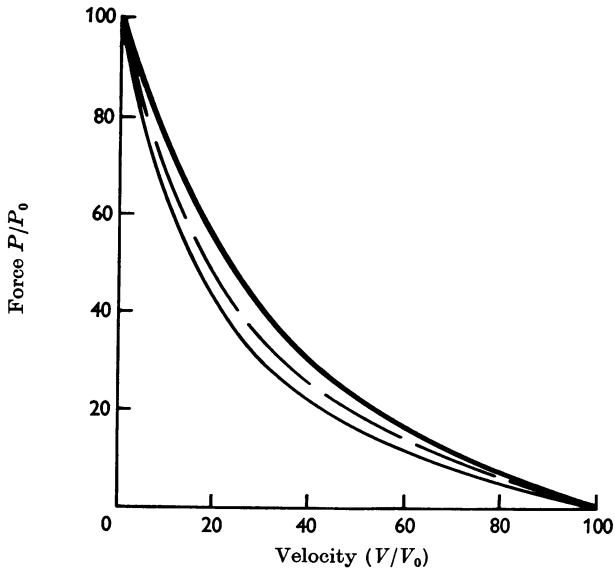
Fig. 3. Relation between force and shortening velocity derived from anterior tibial (heavy curve) and soleus muscles in rats. Curves in upper graph were calculated from average values of a, b, and P_0. Lower graph same as upper except the force is expressed on ordinate as fraction of maximal force plotted against velocity, on abscissa as fraction of maximal velocity. Note difference in curvature of solid curves. Interrupted curve was calculated from average constants derived from soleus muscles, to each of which three times the respective standard errors had been added.

was calculated with the constants obtained from soleus muscle but using the mean values of a and b to which three times the respective standard errors had been added. This curve remains different from that of fast muscle and permits rejection of the hypothesis that the contractile mechanisms, from which these force–velocity relations were derived, were sampled from the same population. The rejection is based on the premise that a difference as great as that shown by the curves would not occur by sampling variations in over 99·7 chances out of 100.

In order to determine whether other differences exist between the mechanical behaviour of these muscles, velocity measurements were made at loads greater than P_0. Under these conditions shortening was negative, or rather, the active muscles lengthened. The muscles, released at standard length to loads varying from 1·0 to 1·5 times P_0 following maximal tension development, were permitted to lengthen 2·5–3·0 mm beyond L_0. The resulting time course of elongation was the same in soleus and tibialis muscles and adequately fit the description of similar observations made on isolated amphibian muscle by Katz (1939). In contrast to the experiments reported by Katz, rat muscle did not tolerate release to loads greater than P_0. After each release an immediate, continuous decline of P_0 was observed which persisted even during muscle inactivity. Similarly, the force–velocity curves of tonic and phasic muscles, when extended into the region beyond P_0, revealed the same discontinuity reported by Katz for frog and tortoise skeletal muscle.

Properties of the series elastic components

Shortening velocity of the total series elastic elements. Determinations of the velocity of recoil of the stretched series elastic elements were made according to the following procedure, outlined by Wilkie (1956). The tetanically stimulated muscle, fixed at L_0, developed full isometric tension against the lever. Rapid release of the lever (with attached muscle) to the force of the particular spring opposing the muscle, resulted in a sudden tension drop, permitting the stretched series elasticity to recoil quickly to a new length while the more sluggish contractile element shortened little. The recoil includes that from elastic components of both muscle and apparatus but the measured compliance of the linkage was considered sufficiently small to be disregarded.

Figure 4 contains superimposed traces of elastic recoil followed by active shortening, subsequent to release of tetanized fast and slow muscle to various loads. The biphasic character of the total shortening forms the basis for the existing hypothesis of an undamped elastic body in series with the active contractile element. The recoil rates of the elastic elements were constant in either muscle (more apparent in slow muscle tracings)

regardless of load and hence were considered independent of load. Since the oscillation frequency of an undamped elastic system is inversely related to its mass, the recoil rate should be much lower during retraction against relatively heavy loads (lower traces Fig. 4A, B) than similar retractions against light loads. Also the lower rates of elastic retraction expected with heavier loads would be further reduced by the decreased amplitude of elastic recoil seen at the higher loads. Failure of the elastic elements observed here during quick release to show the predicted dif-
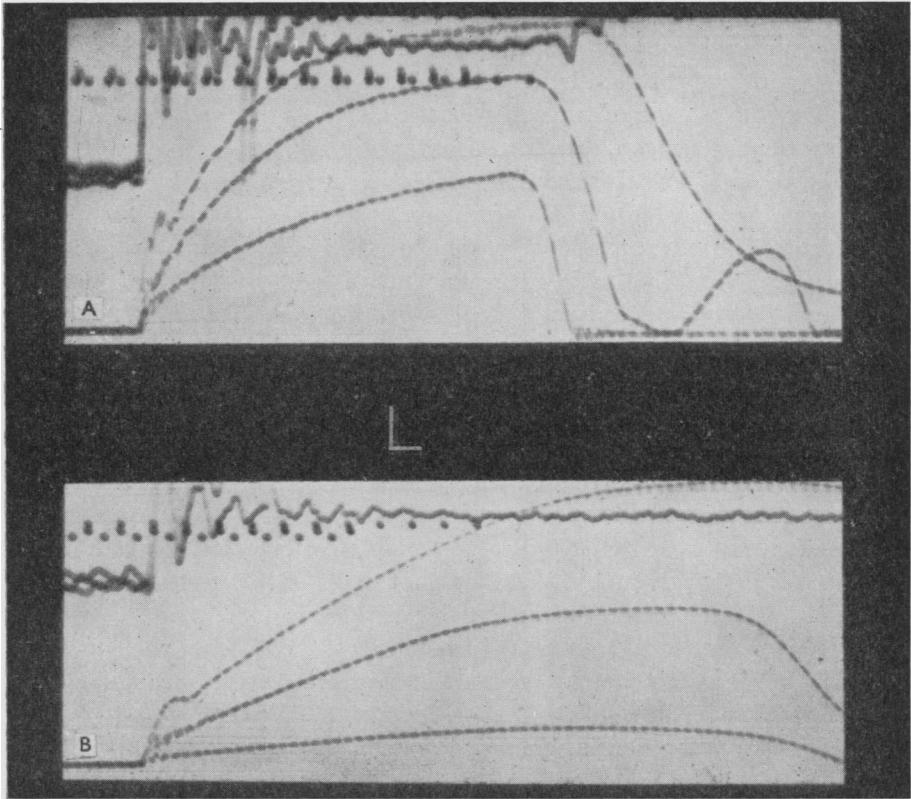

Fig. 4. Photographic reproductions of isotonic shortening of muscle at three loads following quick-release after maximal isometric tetanic tension development. Release occurrred about 140 msec before last shock of tetanus. *A*. Tracings from anterior tibialis muscle with loads 3, 27 and 100 g wt. respectively. P_0 equals 300 g wt. Activity seen in middle trace following initial relaxation was due to artifactual nerve stimulation by transients from solenoid activator. *B*. Same as *A* but derived from a soleus muscle preparation. Loads were from above down 3, 8 and 45 g wt. respectively. P_0 equals 75 g wt. Note constant recoil velocity in both muscles despite changes in load. Horizontal scale is 10 msec. Vertical scale equals 1 mm. Light beams interrupted at 4-msec intervals.

ferences in recoil rates under increasing loads suggests that elastic energy is dissipated during recoil in a form other than mechanical. Partial damping of the series elasticity is probably the simplest explanation of the above findings.

Stress–strain relation. The magnitude of elastic recoil was estimated, as illustrated by Jewell & Wilkie (1958). The method includes an allowance for active contraction during the brief period of elastic recoil. Measurements of the elastic recoil for a series of releases from full isometric tension to spring loads varying between 3 and 60 % P_0 were taken from the same responses from which the recoil rates were determined.

The difference between maximal elastic recoil (following release to the lightest load) and that occurring after release to any larger load, represents the internal extension of the series elastic elements during development of that particular tension. In Fig. 5 extension of the series elastic body, represented on the abscissa as a fraction of L_0, is plotted against corresponding tension on the ordinate, presented as g wt./cm² cross-section, for both muscle types. One of the eight soleus preparations displayed values for elastic extension (at all loads) which exceeded the corresponding means derived from the group by more than 7 times the standard error, and hence was excluded from the data.

The series elasticity of the slower muscle showed less strain per unit of stress increment than that of phasic muscle, resulting in a total series elastic extension, for development of P_0, of 3·0 and 4·8 % L_0 respectively. The extension of the series elasticity seen in the faster muscle during production of maximal tension was significantly greater than that observed in the slower muscle ($P < 0·01$). A possible explanation for this observation might be given by the fact that part of the insertion tendon of the anterior tibialis arises within the distal 0·4 of the muscle (hence is included in the measurements), whereas in the soleus the insertion tendon arises nearer the end of the fibres and is mainly excluded upon tying.

The amount of potential energy stored in the series elasticity during maximal isometric response is represented for both muscle types by the areas under the curves of Fig. 5. The estimated average elastic energy generated by the faster muscle was about twice that produced by the soleus, with respective values of $1·3 \times 10^5$ and $5·8 \times 10^4$ dyne-cm/cm² (cross-section). The increased elastic energy production seen in tibialis should not be attributed entirely to the amount of extra tendon (mentioned above). More specifically, extension of the series elasticity of fast muscle, which was only 1·4 times that of slow muscle during equal maximal tension production, was not sufficient to account for twice the elastic energy production. This suggests, as do the curves of Fig. 5, that the series elastic

body from slow muscle shows a greater coefficient of elasticity than that from the faster muscle.

The elastic energy developed during full isometric contraction is converted to at least two mechanical forms following quick release of the active muscle: (1) as work done in moving the load a distance equal to the elastic retraction and (2) kinetic energy imparted to the load, lever system,
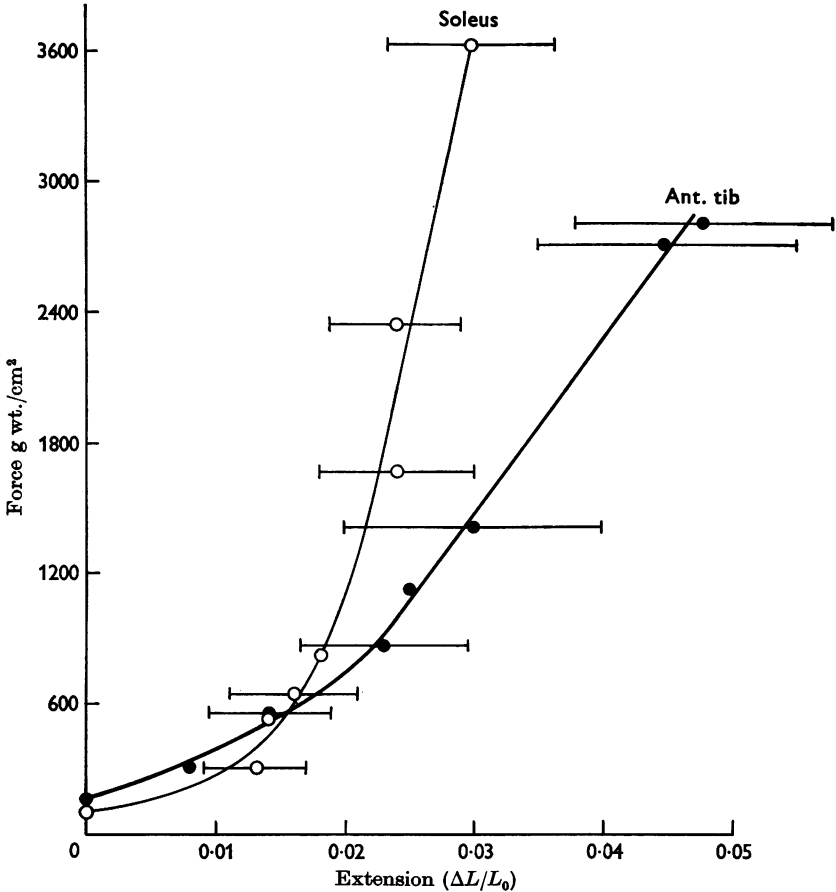

Fig. 5. Stress–strain curves of series elastic elements derived from eight fast muscle preparations and seven soleus muscles. Length of horizontal bars represent twice S.E. of mean. Open circles, soleus muscles; filled circles, anterior tibialis muscles.

and muscle itself. Estimations of the fraction of stored elastic energy converted to work and kinetic energy were made for each muscle type from averaged values of maximal velocity and displacement during elastic shortening. Fast muscle, loaded with the lightest spring (27 g wt.) recoiled an average of 0·12 cm on release, producing 3200 dyne-cm of work.

Using the value 1·7 g for the equivalent mass of spring and lever system, the muscle expended about 2400 dyne-cm (kinetic energy) in accelerating the system to the maximal velocity of 53·6 cm/sec following quick release. The energy required for the movement of the muscle itself was calculated to be less than 2 % of the total elastic energy generated and was omitted from the above estimates. Thus a total of 5600 dyne-cm of mechanical energy was recovered from $19·3 \times 10^3$ dyne-cm of elastic energy generated during full isometric contraction of the anterior tibialis. In other words, 29 % of the developed elastic energy was recovered, 17 % as mechanical work and 12 % as kinetic energy. Similar approximations for soleus muscle showed that 35 % of the developed elastic energy was recovered as mechanical energy during elastic recoil; about 15 % as work and 20 % as kinetic energy. The fact that only one-third of the elastic energy produced in an isometric tetanus could be recovered as mechanical energy following quick release supports the previous suggestion that considerable damping of the elastic element occurs during rapid recoil.

Time course of active state intensity. A distinguishing feature of mammalian slow muscle response, in addition to the relatively low shortening rate, is the prolonged time course of the twitch response. This was described by Denny-Brown (1929) for cat hind-limb muscle and is illustrated in Fig. 2 (right side). The total duration of the isotonic twitch response of the slow muscle, about 250 msec, was more than twice that of the phasic muscle and agreed with the corresponding values observed by Denny-Brown in cats. Moreover, the isotonic responses illustrated here clearly indicate the contractile element as the agent responsible for the prolonged twitch activity. This prolonged twitch response of slow muscle may be due either to a more prolonged interval of full active state intensity (plateau), or a slower decay of intensity than occurs in fast muscle.

In several experiments the time between the last pulse of a tetanic train and the first sign of relaxation was determined. The values indicated an insufficient difference in the plateau duration of the two muscle types to account for the dissimilarity in twitch duration. Similar observations have been reported in cats (Bleckmann, Jurna & Rummel, 1963). Therefore, the decay rate of the active state intensity of both slow and fast muscles was assessed using a variation of the procedure outlined by Ritchie (1954b). The method is based upon a definition of active state intensity as the capacity for maximal tension development at constant muscle length. This definition is supported by the observation that redevelopment of isometric force by a muscle rapidly released after a single stimulus to abolish tension, then refixed at a new short length, will depend on the time lapse between stimulation and tension redevelopment. In other words, the closer the release follows stimulation, the closer redeveloped tension

will approach the unreleased twitch response. It follows that only the lower range of the active state decay curve, that below twitch tension, can be determined under these conditions. If, however, the muscle is first tetanically stimulated to full isometric tension, then released at various times before the last pulse, the resulting peaks of redeveloped tension should exceed that of the twitch and outline the decay of active state intensity. By this means the active state decay curve was extended up to 80 % of P_0 (short). The procedure is also based on observations suggesting that the active state rises to full intensity abruptly after a single stimulus
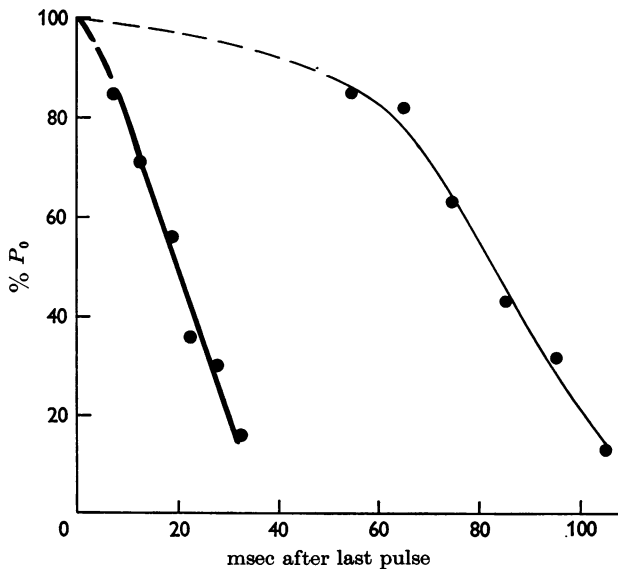

Fig. 6. Decay of active state intensity for one anterior tibial (heavy line) and soleus muscle preparation. Tension redevelopment following quick release, expressed on ordinate as % P_0 (short), is plotted against the time after the last shock for peak tension redevelopment. Broken segments of curves are projections to zero time after last shock. Details in text.

(Hill, 1951) and that repeated stimuli only increase the active state duration, not its intensity. It is assumed that the time course of the active state decay is independent of both the number of preceding stimuli and the release.

Quick releases of about 2·5 mm were applied to both fast and slow muscle (three preparations of each type) at times ranging from 100 msec before to 130 msec after the last pulse of a tetanic stimulation. After recording the value of P_0 at the released (short) length, the time course of tension redevelopment, which resulted from the release and re-engagement of the lever with its attached muscle, was recorded photographically.

A series of 30–60 responses was recorded from each muscle and evaluated by dividing the time between the last shock and peak tension redevelopment into 5 and 10 msec intervals respectively for the fast and slow muscles. The peak amplitudes of redeveloped tension, which fell in a particular time interval, were averaged and plotted, as percent P_0 (short), against the time (msec) after the last stimulus. Examples of such points taken from a soleus and tibialis muscle are illustrated in Fig. 6.

The curves show that the active state intensity of phasic muscle falls to 50 % P_0 within 20 msec after the last stimulus while the slow muscle required about 80 msec for a corresponding decrease. However, the decline of intensity from 80–20 % P_0 occurred at about the same rate in both muscles, which implies a much slower initial decay of intensity in the soleus muscle.

Thus, the most likely explanation for the prolonged twitch response and the slower relaxation rate seen in soleus muscle lies in the decreased initial decay rate of its active state intensity.

DISCUSSION

In a recent report, Hill (1964) has reaffirmed that a stimulated muscle, permitted to shorten, liberates energy above that for isometric contraction in the form of work and heat. Moreover, he found the heat of shortening α to vary directly with load so that a in equation (1) cannot precisely correspond to shortening heat although the two might be related. Since load varies inversely with velocity of shortening it is also correct to state that α varies inversely with shortening rate.

In view of the above and assuming that α and a vary directly, one might expect a, derived from slow muscle, to be relatively larger than that from phasic muscle. The results show, however, that the value of a derived from the rapid muscle is about 1·7 times greater than that from the slow muscle ($P < 0.05$). This difference was qualitatively predictable from the relation $a/P_0 = b/V_0$ when applied to the compared muscles in which P_0 was equivalent, since the faster muscle showed b/V_0 to be twice that of the slower. If the characteristic force–velocity relation extends to all kinds of muscle, with variations in the values of a and b comprising the only difference between muscle types, then the above findings suggest that a and α vary, with respect to each other, in an inverse manner.

Values for a/P_0 derived from extensor digitorum longus (EDL) and soleus muscle responses in adult rats (Close, 1964) were 0·25 and 0·17 respectively and are lower than corresponding figures of 0·36 and 0·21 from anterior tibialis and soleus muscles respectively reported here. This variation probably occurred because of the size difference between the animals. Specifically, soleus from 100-day female Wistar rats weighed

about 0·12 g while the same muscle from 200 g male rats in this laboratory averaged about 0·075 g wt. The larger muscles would be expected to develop greater maximal isometric tension resulting in a smaller a/P_0 ratio. The stimulus frequency used in this study was about one-third that employed by Close. No change in the value of P_0 was observed in this laboratory in a subsequent series of both soleus and anterior tibial muscles stimulated at the higher frequency (200–250 c/s).

a/P_0 derived from tibialis muscle was about 1·7 times that from soleus muscle and is about the same as the value obtained from similar comparison of corresponding ratios from EDL and soleus muscles. The mean value of a/P_0 calculated for anterior tibialis also agreed well with the averaged corresponding values reported by Wilkie (1950) from human-arm muscle.

The large distinction between the shortening speeds of the compared muscles reflects the highly significant difference found between the rate constants b. Values of b equal to 1·6 and 3·0 L_0/sec were estimated from data reported by Ritchie (1954a) using rat diaphragm and are consistent with the mean of 2·25 L_0/sec obtained from the anterior tibial muscle. Similarly, mean estimates of b derived from frog sartorius (at temperatures above 0° C) were reported by Hill (1938) to be 2·05 and 1·82 L_0/sec (the latter figure was calculated by Hill from the data of Fenn & Marsh). Thus several different determinations of b in a variety of phasic muscle preparations appear to yield similar values.

Maréchal, Goffart & Aubert (1963) determined the force–velocity relation in strips of sloth diaphragm muscle and expressed it in the exponential function

$$P = P_0\, e^{-v/B}, \tag{3}$$

previously described by Aubert (1956). The velocity constant B ranged from 0·6 to 0·95 L_0/sec and was similar to the value of 0·5 L_0/sec obtained when average values of P_0, P and v, derived from soleus muscle in this study, were applied to that function. The agreement between the rate constants calculated for sloth diaphragm and rat soleus muscle appears to support the contention of Maréchal that most sloth muscle is slow. The smaller rate constant, observed in slow compared to fast muscle implies a conservation of energy which could explain the greater capacity for sustained activity shown by slow muscle.

All these results support the suggestion that mammalian muscles are composed of fibres with two distinct sets of dynamic constants, which probably reflect differences in the respective contractile mechanisms. It is also suggested that values for a and b obtained for a given muscle will fall somewhere between those representative for the two fibre types depending on the percentage composition of each type in the muscle (without regard to the effects of muscle geometry).

SUMMARY

1. Two voluntary mammalian limb muscles with comparable maximal shortening and tension responses but known for their functionally different contractile behaviour have each been analysed as a two-component system; an active contractile element characterized by Hill's force–velocity equation in series with a passive elastic element.

2. Comparison of the constants a and b of the characteristic equation showed those derived from the faster contracting muscle to be significantly greater than those from the slower.

3. The stress–strain curve of the series elasticity of the slower muscle indicated a larger coefficient of elasticity than did that from the faster. Also the independence of the rate of elastic recoil of these elements from the load and the fraction of mechanical energy recoverable from their generated elastic energy suggest that they are damped during rapid elastic recoil.

4. Curves of decay of active state intensity showed a lower initial decay rate for the slower than those derived from the faster muscle which might account for the correspondingly lower mechanical fusion frequency and prolonged twitch time observed in the former.

REFERENCES

AUBERT, X. (1956). *Le Couplage Énergétique de la Contraction Musculaire.* Bruxelles: Arscia.

BLECKMANN, I., JURNA, I. & RUMMEL, W. (1963). Vergleichende Untersuchungen von Methoden zur Bestimmung der Plateaudauer des activen Zustandes am Warmblüter-muskel. Verhalten des Soleus und Tibialis anterior der Katze unter Sympathico-mimetica und Coffein. *Pflüg. Arch. ges. Physiol.* **277**, 422–433.

CLOSE, R. (1964). Dynamic properties of fast and slow skeletal muscles of the rat during development. *J. Physiol.* **173**, 74–95.

COOPER, S. & ECCLES, J. C. (1930). The isometric responses of mammalian muscles. *J. Physiol.* **69**, 377–385.

CSAPO, A. & GOODALL, M. (1954). Excitability, length tension relation and kinetics of uterine muscle contraction in relation to hormonal status. *J. Physiol.* **126**, 384–395.

DENNY-BROWN, D. E. (1929). The histological features of striped muscle in relation to its functional activity. *Proc. Roy. Soc. B*, **104**, 371–411.

FENN, W. O. & MARSH, B. S. (1935). Muscular force at different speeds of shortening. *J. Physiol.* **85**, 277–297.

FISCHER, H. (1908). Zur Physiologie der quergestreiften Muskeln der Säugetiere. *Pflüg. Arch. ges. Physiol.* **125**, 541–583.

HILL, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. Roy. Soc. B*, **126**, 136–195.

HILL, A. V. (1949). The abrupt transition from rest to activity in muscle. *Proc. Roy. Soc. B*, **136**, 399–420.

HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog.* **150**, 209–230.

HILL, A. V. (1951). The transition from rest to full activity in muscle: the velocity of shortening. *Proc. Roy. Soc.* B, **138**, 329–338.

HILL, A. V. (1964). The variation of total heat production in a twitch with velocity of shortening. *Proc. Roy. Soc.* B, **159**, 596–605.

HILL, A. V. & WOLEDGE, R. C. (1962). An examination of absolute values in myothermic measurements. *J. Physiol.* **162**, 311–333.

JEWELL, B. R. & WILKIE, D. R. (1958). An analysis of the mechanical components in frog's striated muscle. *J. Physiol.* **143**, 515–540.

JONES, R. V. (1962). Some uses of elasticity in instrument design. *J. sci. Instrum.* **39**, 193–203.

KATZ, B. (1939). The relation between force and speed in muscular contraction. *J. Physiol.* **96**, 45–64.

MARÉCHAL, G., GOFFART, M. & AUBERT, X. (1963). Nouvelles recherches sur les propiétés de muscle squeletigue du paresseux (Choloepus hoffmani Peters). *Arch. int. Physiol.* **71**, 236–239.

PRINGLE, J. W. S. (1960). Models of muscle. In *Symposia of the Society for Experimental Biology*, ed. J. W. L. BEAMENT, vol. XIV, pp. 41–68. New York: Academic Press.

RANVIER, L. (1873). *Comptes Rendus des Seances et Memoires de la Societe de Biologie* **5**, 267–268.

RANVIER, L. (1880). *Leçons D'Anatomie Generale sur le Système Musculaire*, pp. 202–219. Paris.

RITCHIE, J. M. (1954a). The relation between force and velocity of shortening in rat muscle. *J. Physiol.* **123**, 633–639.

RITCHIE, J. M. (1954b). The effect of nitrate on the active state of muscle. *J. Physiol.* **126**, 155–168.

SONNENBICK, E. H. (1962). Force-velocity relations in mammalian heart muscle. *Amer. J. Physiol.* **202**, 931–939.

WILKIE, D. R. (1950). The relation between force and velocity in human muscle. *J. Physiol.* **110**, 249–280.

WILKIE, D. R. (1956). Measurement of the series elastic component at various times during a single muscle twitch. *J. Physiol.* **134**, 527–530.

WOLEDGE, R. C. (1961). The thermo elastic effect of change of tension in active muscle. *J. Physiol.* **155**, 187–208.