

**THE RELATION BETWEEN FORCE, VELOCITY AND
INTEGRATED ELECTRICAL ACTIVITY IN HUMAN
MUSCLES**

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When a voluntary isometric contraction of a muscle is made, the electrical activity, measured by integrating the action potentials from surface electrodes, bears a linear relation to the tension that is being exerted (Lippold, 1952). This relation has been demonstrated in human subjects for most of the larger muscles and those smaller muscles with short tendons. Certain muscles, including tibialis anterior, however, follow a quadratic relation rather than a linear one (Edwards & Hardy, personal communication). This might be due to stretching of long tendons and their retinacula during strong contractions allowing substantial internal shortening. It therefore seemed desirable to investigate the problem when the muscle was actually changing in length.

Previous attempts to establish a relation between the tension in a voluntary isotonic contraction of muscle and some arbitrary feature of its electromyogram have proved abortive, probably because the velocity of the movement was uncontrolled; it might be predicted from Hill's (1938) equation relating force and velocity—which can be applied to human muscle (Wilkie, 1949)—that the faster a muscle shortens the more electrical activity would be associated with a given tension. If, on the other hand, the muscle is lengthened during its contraction, the tension is independent of the velocity (Abbott & Aubert, 1951). The recent experiments of Abbott, Bigland & Ritchie (1952) and of Abbott & Bigland (1953), on subjects whose leg muscles were working at different forces and velocities, showed that the oxygen consumption increased rapidly with increasing velocities of shortening at constant force, but remained about the same when they were being stretched. The assumption was made that any increase of oxygen consumption was a direct reflexion of the number of active motor units and their frequency of excitation.

The degree to which a muscle is excited determines both the electrical activity it displays and the isometric tension it can exert. It has been shown

that the isometric tension in submaximal contractions is proportional to the integrated electrical activity recorded from surface electrodes (Lippold, 1952) and thus the symbol P_0 , the isometric tension in Hill's equation, may be replaced by kA , a quantity proportional to the electrical activity under any conditions involving the same degree of stimulation. Thus in the characteristic equation relating force exerted to speed of shortening,

$$(P+a)V=(P_0-P)b, \quad (1)$$

P_0 may be replaced by kA : and since $a=nP_0$ and $b=nV_0$, where n is a constant (usually about 0.25) and V_0 is the velocity of shortening under zero load, the equation, after simplifying, can be written

$$kA=P\left(1+\frac{V}{nV_0}\right)\left/\left(1-\frac{V}{V_0}\right)\right. \quad (2)$$

This shows that at constant velocity V , the electrical activity A , is directly proportional to P . Under constant load P , but with varying velocity, if V/V_0 is small enough for its square and higher powers to be neglected, the equation becomes

$$kA=P\left[1+\frac{V}{V_0}\left(1+\frac{1}{n}\right)\right]. \quad (3)$$

Thus at lower velocities under constant load the electrical activity should be a linear function of the velocity. More generally it is

$$kA=P\left[1+\frac{V}{V_0}\left(1+\frac{1}{n}\right)+\frac{V^2}{V_0^2}\left(1+\frac{1}{n}\right)+\dots\right] \quad (4)$$

which starts linearly and bends upwards at the higher velocities.

The experiments reported in this paper were accordingly designed to show the relation between excitation of a muscle and its tension at different controlled velocities of shortening in voluntary contraction.

METHODS

The experimental subjects were young adult males and females. The subject was seated at the dynamometer described by Lippold, Naylor & Treadwell (1952), modified to enable voluntary isotonic contractions of the calf muscles to be made at predetermined constant velocities (Bigland, Lippold & Wrench, 1953). The foot platform, free to rotate about the axis of the subject's ankle joint, was attached to a flexible steel wire running over a large pulley, in such a manner that plantar flexion of the foot lifted a weight. A linear potentiometer attached to an extension of the bearing spindle indicated the angular rotation of the foot as a vertical deflexion of one spot on a double-beam cathode-ray tube, conveniently visible to the subject. The second spot was moved in the same axis by a calibrated, linear-sweep time-base triggered from a key pressed by the subject. With a little practice, and by the use of rhythmical movements, the subject could keep both spots in juxtaposition, thus making contractions of the required constant angular velocity. Contraction velocities of 0.1–1.0 radian/sec in both shortening and lengthening of the muscle and forces of contraction from 0 to 500 kg (calculated in the tendon) were employed.

Action potential recordings were made from the calf muscles using the surface suction electrodes and amplifiers described by Lippold (1952). Integration was performed with a modified Miller

circuit, for which we are indebted to Dr J. A. V. Bates, in which a small condenser was charged by the amplified and rectified action potentials. When its potential reached a predetermined value, this capacitor discharged, producing a pulse which was fed into a conventional scale-of-two counter. The number of pulses in a given time was proportional to the area enclosed by the action potential tracing. Certain experiments were performed where integration was carried out both by planimetry (Lippold, 1952) and by the electrical method. Comparison of these results indicated that the electrical method was at least as accurate as the planimetric method.

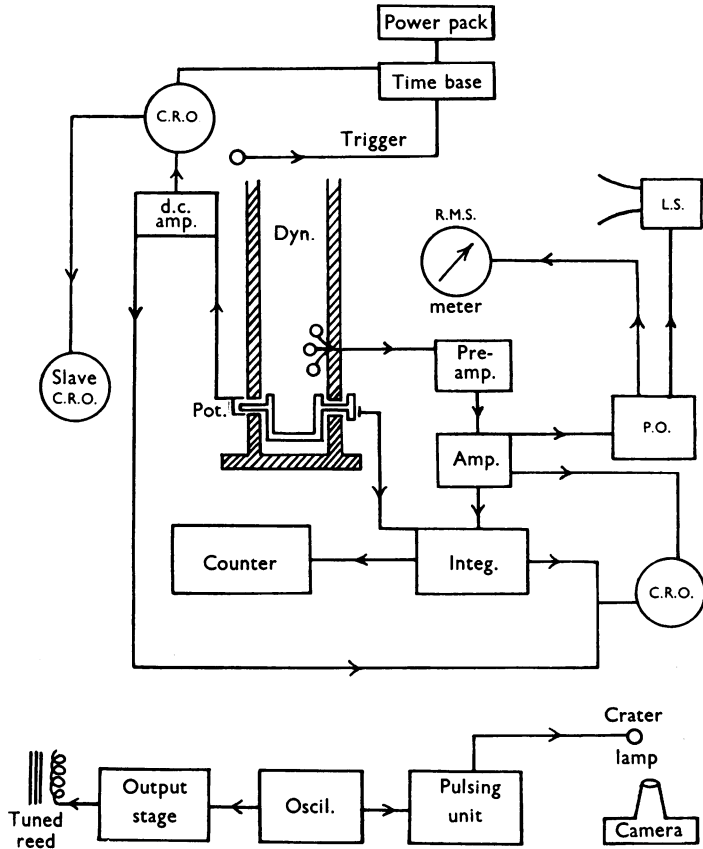


Fig. 1. Block circuit diagram of apparatus.

The integrator was switched by means of a commutator on the foot platform spindle, so that only 12° of each contraction and return was recorded. In some experiments, action potentials, position indicators, 50 c/s time trace and integrator pulses were recorded on 70 mm bromide paper running at 50 cm/sec. A master cathode-ray tube enabled the observer to reject the integrator counts of any contraction made at incorrect velocity (Fig. 1).

Other recordings were made using concentric needle electrodes (Adrian & Bronk, 1929) and three single stainless steel electrodes. The latter were constructed of No. 28 s.w.g. solid-drawn, stainless steel tubing, the earth electrodes being left bare while the two recording needles were completely insulated with twelve coats of enamel, their resistance in this condition being $10\text{ M}\Omega$ at 500 V when tested in saline with the Megger. Before insertion a small area of the tip of these

electrodes was bared with a razor blade. By varying this area, control of the volume of the muscle sampled by the needles could be exercised. In these experiments the forefinger was arranged to lift a weight from a supporting stop and subsequently to maintain it at an isometric level. Electrical activity was recorded from these needles, carefully sited within the muscle belly of extensor digitorum communis, and compared with that from surface suckers over it, on the skin.

The surface electrode impedance was measured in separate experiments using an a.c. bridge circuit at 5 kc/s. It was found to vary up to 1.0% of the effective input impedance of the amplifier during 2 hr. It was desirable to curtail the length of experiments as much as possible: each experiment was divided into three parts, the electrodes being removed and reapplied between them.

RESULTS

At constant velocity

When the force of contraction of the muscle was varied while the rate of contraction was kept constant, a linear relation was found between the integrated electrical activity and the weight being lifted. In all experiments the forces of the Achilles tendon were between 0 and 500 kg approximately. All five subjects showed the same type of relation, although the slope of the line varied between individuals and also between the different recordings from the same subject. This linear relation was elicited at any velocity within the capabilities of the particular subject but its slope varied with the velocity.

The five subjects performed this experiment sixteen times in all, the graph plotted in Fig. 2 representing the type of relation obtained. The coefficient of correlation with a straight line in this case was 0.93 and 0.88. It can be seen that the linear relation held when the muscle shortened and also when it lengthened at this constant velocity. During the lengthening, however, the electrical activity of the effort required to lower a given weight was much less than that needed to raise it.

When this experiment was repeated at different velocities a series of straight lines was obtained, each of different slope. These lines were extrapolated to meet at zero activity corresponding to no tension in the muscle. This point was at -3.5 kg tension, which was found to be equal to the weight of the platform, so confirming the predicted direct proportionality between A and P .

At constant force

In this series of observations, the force was kept constant, while the velocity was varied in steps by adjustment of the time-base which the subject was following. Over the small range of movement in which recordings were taken (6° above and below mid-position of the ankle joint) the rate of movement could be considered as representing a constant velocity of shortening or lengthening of the muscle itself.

Subjects showed an optimum velocity in terms of ability to follow the moving spot on the cathode-ray tube. This was apparent to the observer and reflected also in the increased scatter of individual points on the plotted line

when the subject had difficulty in following the desired speed. Most trouble was experienced at extremely low velocities because of frictional effects; if the subject allowed the platform to stop momentarily, the static friction in the bearings and pulleys had to be overcome in order to restart it, necessitating the output of greater forces than those needed to maintain a smooth movement

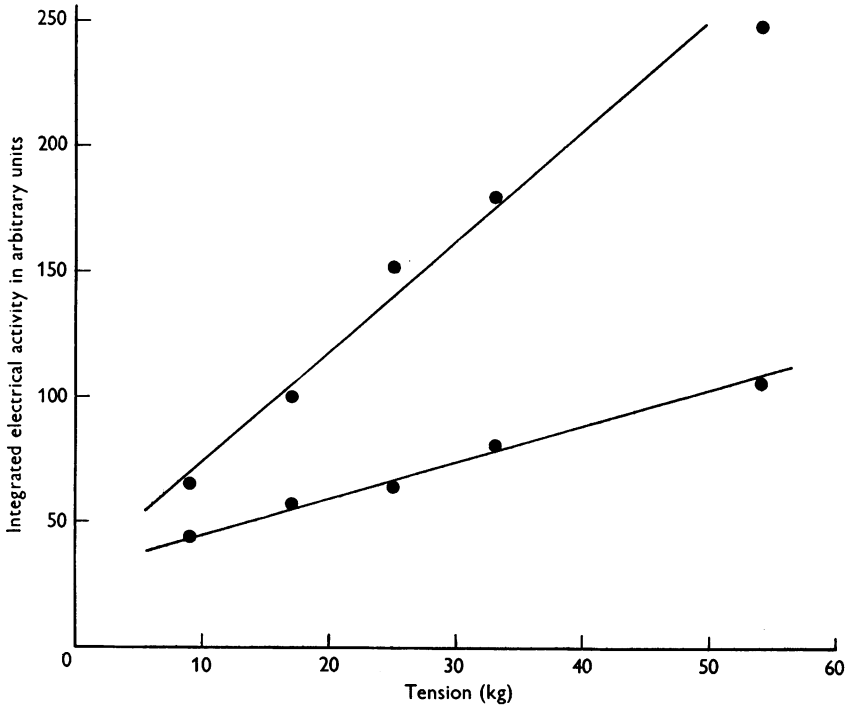


Fig. 2. The relation between integrated electrical activity and tension in the human calf muscles. Recording from surface electrodes. Shortening at constant velocity (above) and lengthening at the same constant velocity (below). Each point is the mean of the first ten observations on one subject. Tension represents weight lifted and is approximately $\frac{1}{3}$ of the tension calculated in the tendon.

against kinetic friction. Similarly, at high velocities, although rhythmical movements were employed, visual difficulties in following the spot accurately, and also in the monitoring by the observer, obtruded. In order to obtain results with the least scatter it was found necessary to let the subject spend time learning to follow the spot at various speeds and different forces.

This experiment was performed 18 times in all by the five subjects. A typical result is plotted in Fig. 3 showing a linear relation between velocity of shortening or lengthening and electrical activity. From the graph it can be seen that the electrical activity increased considerably with the speed of shortening but that in lengthening the electrical activity remained almost independent of velocity.

As before, multiple graphs could be constructed by performing the experiment at different tensions.

In both series of experiments, an interesting periodicity of motor activity in the contracting muscle was observed, occurring during the time when the muscle was lengthening under load, and occasionally when conditions were isometric. Short bursts of action potentials alternated with equal time intervals

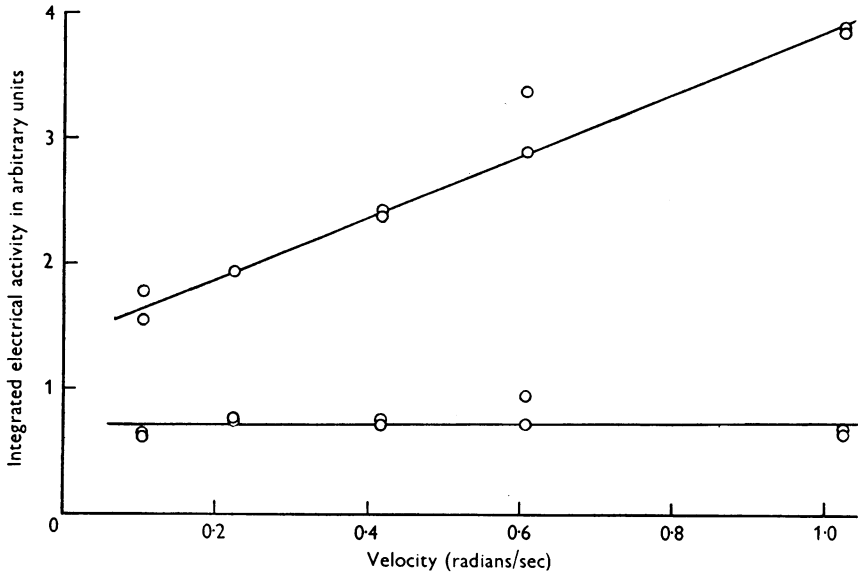


Fig. 3. The relation between integrated electrical activity and velocity of shortening (above) and lengthening (below) at the same tension. (3.75 kg). Each point is the mean of the first ten observations on one subject.

of quiescence usually at about 8 to 10 c/s. This 'clonic' activity could be seen to involve the whole muscle and was apparent in the loud-speaker and in the cathode-ray trace. A strip of this type of record is shown in Fig. 4 compared with the random activity recorded during normal shortening. The effect did not appear to influence the relation between load or velocity, and the integrated action potentials.

At constant electrical activity

When the subject followed the moving cathode-ray trace at a given velocity, the electrical activity could be made to reach any predetermined level merely by altering the weight raised. This permitted the direct construction of a family of force-velocity curves at these different levels of submaximal excitation of the muscle. Such an experiment is shown in Fig. 5(a), and in Fig. 5(b) is shown the same family of curves drawn to the same scale, but calculated from the constant velocity results. Similarly, in Fig. 6(a), the results of a constant

velocity experiment show the different slopes obtained when tension and electrical activity are plotted at different given velocities. At high velocities slopes are steeper than at low velocities. Fig. 6(b) shows the same relations

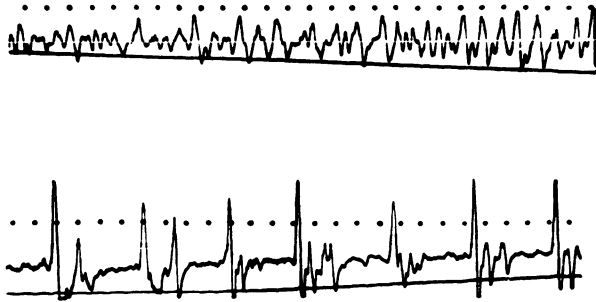


Fig. 4. Recordings taken from surface electrodes on the human calf muscles. Upper record shows normal action potential curve of shortening against resistance. Lower record obtained during lengthening. Note the periodicity of large waves at 8–10 per sec. Time markers at 50 per sec. Lower line indicates position of foot.

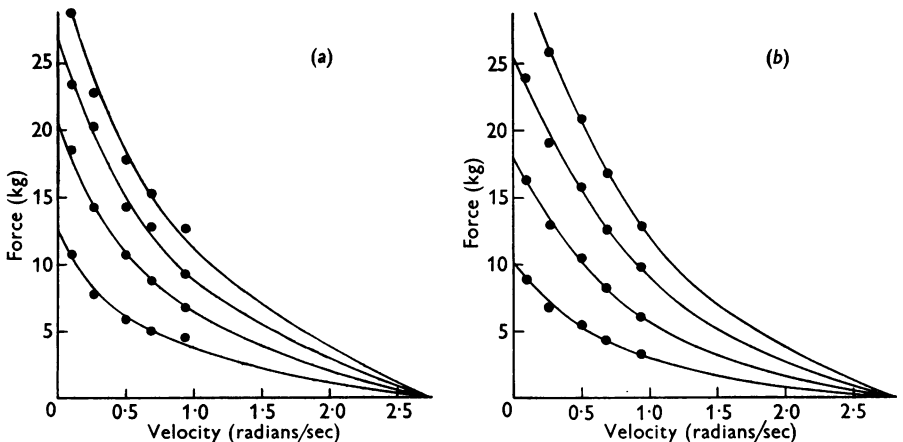


Fig. 5. (a) Force velocity curves plotted at four different levels of submaximal excitation of the calf muscles. Electrical activity was kept at a constant level for each curve by adjusting the weight lifted at each velocity plotted. (b) Shows the same family of curves calculated from the constant velocity results. Forces represent actual weights lifted and are approximately $\frac{1}{15}$ of forces calculated in the tendon.

calculated from the force-velocity curves of Fig. 5(a). The curves of Fig. 5(b) can also be derived from the constant force results, in which the variation of electrical activity is depicted at five given forces.

The series of force velocity curves can therefore be produced by three quite different methods, and are in good agreement.

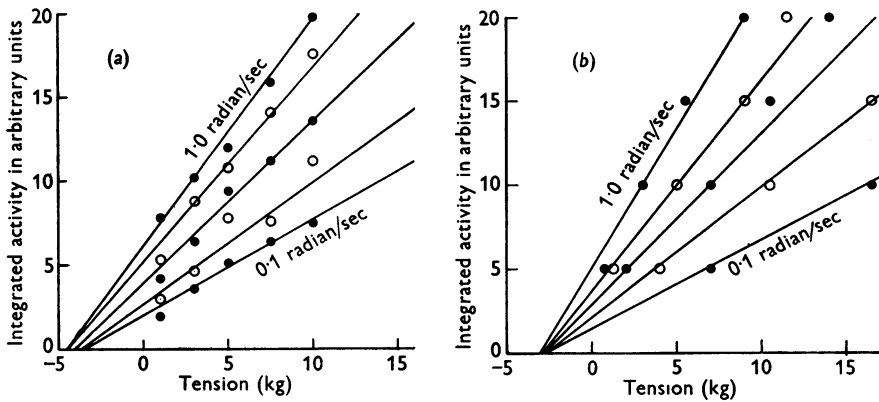


Fig. 6. (a) Graph showing the relation between tension and electrical activity plotted at five different velocities (0.1–1.0 radian/sec). (b) The same curves calculated from the force velocity curves of (a).

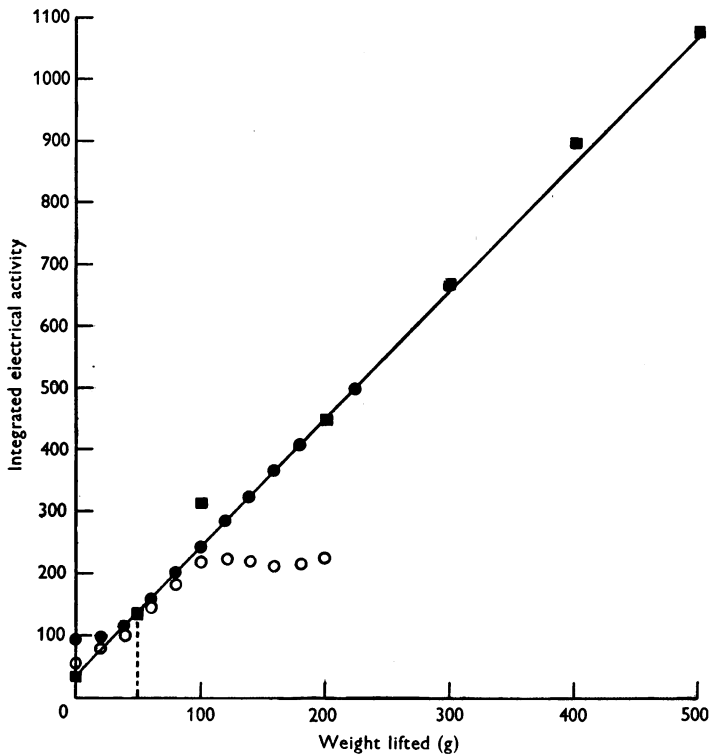


Fig. 7. The relation between electrical activity and isometric tension when recorded (a) from surface electrodes, ●; (b) from needle electrodes with large bared tips, ■; and (c) needle electrodes with small tips, ○. Amplification adjusted to give the same mean activity for 50 g wt.

Comparison of surface electrodes with needle electrodes

Recordings from the extensor muscles of the finger, using needle electrodes as well as surface electrodes indicated that at low levels of activity there was good correlation between the two methods (Fig. 7). Better correlation was obtained when the needles were arranged to record diffusely with a large area of metal exposed, than when only a minute puncture of the insulation was made at the tips. These experiments were all performed under isometric conditions.

DISCUSSION

These results show a direct proportion between the integrated electrical activity in a muscle and the tension it is exerting, during constant (or zero) velocity of shortening (or lengthening). This indicates that, as the electrical activity increases, the proportion of overlap between potentials arising in different parts of the muscle, causing addition and subtraction in the final output, remains constant. Thus at any given velocity the area under the action potential curve is a measure of the 'excitation' in the muscle.

The excitation is related to the number and discharge frequency of active units. Assuming that the fibres are randomly distributed within the muscle in terms of the size and hence of the force of contraction of each fibre, the tension developed in the muscle must be related directly to the number of units which are active. It has been shown in nerve muscle preparations that the tension developed in response to maximal shocks is directly proportional to the frequency of stimulation, until a maximum tension is reached (Adrian & Bronk, 1929; Brown & Burns, 1949). This is also true in intact human muscles (Bigland & Lippold, unpublished). Thus, within certain limits on these grounds, any changes in either the number or frequency of active units would be expected to result in a linear relation between electrical activity and tension.

The fit of the experimental points to a linear relation depends on the skill with which the subject can maintain the correct velocity. Nearly always, discrepancies in the integrated readings could be predicted by the subject, a fact which might indicate an even closer relation between actual tension and electrical activity than is evident from the experimental results.

The results also show that the slope of the relation between electrical activity and tension, in an active muscle which is being forcibly stretched at constant speed, is less than that of the corresponding curve when the muscle is shortening at the same speed. This means that the degree of excitation of the muscle required to produce a given force of contraction is smaller when the muscle is contracting at a negative velocity, than it is at the same positive velocity. Such a finding would be expected from a consideration of the force-velocity characteristic of muscle, which shows that as the velocity of shortening

decreases to zero the tension that can be exerted by the muscle increases. A further increase in tension is shown when the velocity becomes negative; i.e. when the muscle is being actively lengthened (Katz, 1939).

That this force-velocity characteristic also applied to submaximally excited muscle is evident in our results, from which typical force-velocity curves have been plotted, both by direct measurement of forces and velocities when activity was kept constant at given levels and by calculation from the constant tension and constant velocity results. These curves agree with the characteristic equation (Hill, 1938).

SUMMARY

1. Action potentials recorded by surface electrodes from voluntary contractions of the human gastrocnemius were integrated electronically during isotonic shortening and lengthening of the muscle.

2. Comparison was made of the results obtained with surface and needle electrodes.

3. At constant velocity of shortening or lengthening, the electrical activity was directly proportional to the tension, the slope of this relation being less in lengthening.

4. At constant tension, the electrical activity increased linearly with velocity of shortening, but remained almost independent of speed when the muscle was being lengthened. The relation held over the range of velocities possible in the experiments described, but would not be expected to do so at higher velocities. This result could be predicted from Hill's force-velocity equation.

5. Force-velocity curves obtained from a muscle excited by a constant submaximal stimulus (as indicated by constant electrical activity) agreed with the equation

$$(P + a)V = (P_0 - P)b$$

over the narrow range of force and velocity possible in such experiments. A similar result could be derived by interpolating for the results under (3) and (4) above.

6. Tension, velocity and electrical activity are thus interdependent, and integration of the electrical record provides a composite measure of the number of active fibres and their frequency of excitation.

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