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THE RELATION BETWEEN FORCE AND INTEGRATED ELECTRICAL ACTIVITY IN FATIGUED MUSCLE

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It has been shown by Lippold (1952) and Bigland, Hutter & Lippold (1953) that the force of an isometric contraction of a mammalian muscle is proportional to the voltage-time integral of the electrical activity recorded from it. For practical use to be made of these observations, it is necessary to determine the limits within which this relationship holds.

If, for instance, a voluntary contraction is to be maintained at a constant tension, it might be expected that more motor units would be recruited as the tension developed by fatigued units declined. Such an occurrence would alter, with the degree of fatigue, the proportionality between electrical activity and tension. Other factors in fatigue may well influence the relation, such as neuromuscular block (Brown & Burns, 1949) or the effect of activity on the size of action potentials (Brown & von Euler, 1938).

The experiments to be reported here were designed to investigate the relation between the electrical activity and the tension of isometrically contracting human muscle under conditions of fatigue.

METHODS

The tension in the calf muscles of human subjects was measured as described before (Lippold, Naylor & Treadwell, 1952). Action potentials were recorded by means of silver suction electrodes placed over the medial border of soleus muscle, where this is subcutaneous, and were integrated electronically, the integral being displayed by a Dekatron scaling unit. Calibration confirmed that the count in 5 sec was proportional to the input voltage, within the range utilized in the experiment. A parallel channel recorded the electromyogram and its integral (as pips) on moving paper to enable a subsequent check to be made.

RESULTS

Subjects were first required to make 5 sec periods of isometric contraction at a series of constant tensions. These were usually in steps of approximately 3 % over a range of 9–45 % of the maximum voluntary strength. During each 5 sec period the electrical activity was recorded. After this procedure a continuous contraction at about 25% of maximum was maintained for about 4 min in order to fatigue the muscle, 5 sec periods of recording being taken every 10 sec. At the end of this period, without relaxation of the calf muscles, 5 sec counts of the same series of tension values were recorded in exactly the same manner as before. After 15 min rest, the experiment was usually

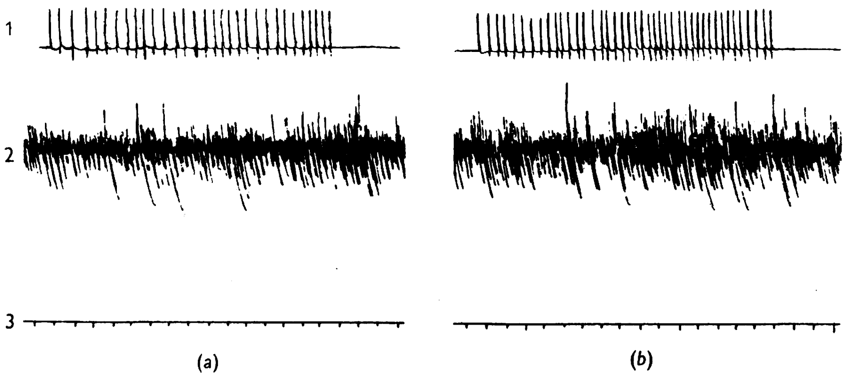

Fig. 1. Records of electrical activity (*a*) 10 sec after the commencement of, and (*b*) approximately 15 sec before the end of a 4 min period of isometric contraction at 25% maximum voluntary tension. From above downward are shown (1) the output of the integrator (each pip represents ten output pulses), (2) the action potential recording, and (3) time marking at 12 c/s. Surface electrodes over soleus muscle.

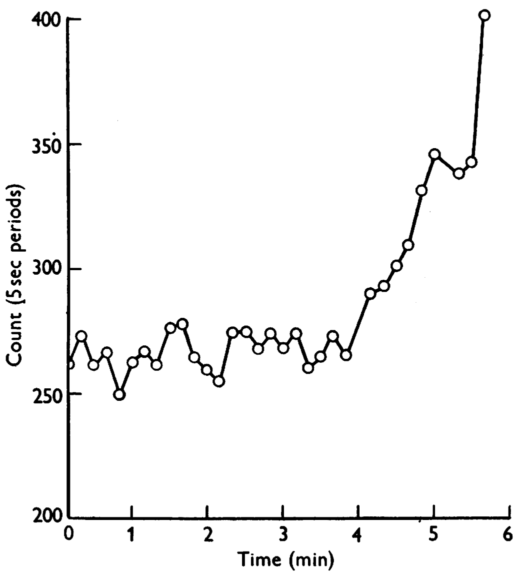

Fig. 2. Recordings of integrated activity from soleus during continuous isometric contraction at 25% maximum voluntary tension.

repeated. Eight subjects, male and female, performed fifteen experiments which produced comparable results. The first part of the experiment always showed a linear relation between activity and tension. It was, however, necessary to take precautions to prevent shortening of the muscle, as this produced a length-tension effect, destroying the linearity at high tension values.

During the fatiguing contraction, the electrical activity always fell slightly during the first minute and then increased to above the resting level to an extent varying with the subject and the strength of the contraction relative

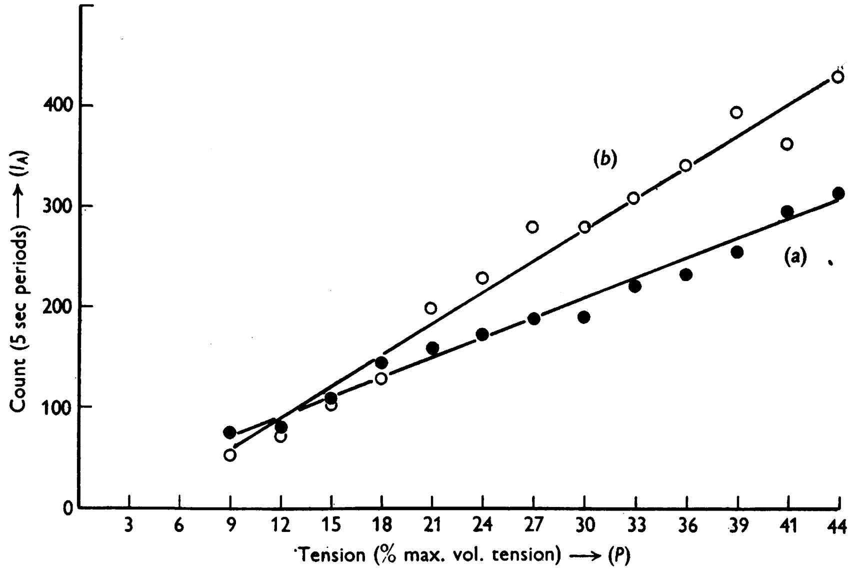

Fig. 3. Comparison of relation between integrated electrical activity and tension in soleus muscle (*a*) before and (*b*) after a 4 min fatiguing contraction. Tension values are given as a percentage of maximum voluntary tension; electrical activity in counts/5 sec. Curve (*a*) $Y = 19{\cdot}1X + 18{\cdot}2$, $r = +0{\cdot}987$ (correlation with a straight line). Curve (*b*) $Y = 31{\cdot}32X - 35{\cdot}1$, $r = +0{\cdot}985$.

to the voluntary maximum (Figs. 1, 2). After 3 or 4 min the subject usually experienced unpleasant sensations in the calf, but the onset of this could not definitely be related to any change in the action potential count.

When the electrical activity–tension recordings were repeated in the fatigued state, it was found that the counts were higher than before, as might have been expected from the behaviour of the integrated activity as fatigue progressed. In all experiments a straight-line relation resulted, usually with a correlation as good as that found before fatigue. A typical result is given in Fig. 3, from which it can be seen that in fatigue the slope of the relation

I_A/P is increased. The difference in slopes seemed to depend on the degree of fatigue evoked by the fatiguing contraction, as indicated by the rise in the activity during it.

DISCUSSION

The increase in electrical activity of the fatigued muscle, required to maintain the same voluntary tension, is an indication that in this type of contraction, fatigue must be due to a decrease in the contraction strength of the muscle fibres. As the contraction continues more fibres become active. This is in agreement with general views on fatigue of muscle (Bartley & Chute, 1947), and with the experiments of Merton (1954) on small hand muscles under similar isometric conditions.

The fact that the relation between tension and electrical activity is still linear, but with a steeper slope after fatigue, is in accordance with the view that the general properties of the muscle fibre are unaltered in fatigue, apart from a decrease in the tension that it is able to exert when excited.

Factors other than this simple increase in the number of active units during fatigue may play a part in altering the relation between activity and tension. The ratio I_A/P in the single muscle fibre is probably altered during fatigue through effects on both I_A and P, as the following two considerations show.

(*a*) It is known that potassium leakage from active muscle fibres does occur (Fenn, 1937), while Brown & von Euler (1938) have shown that after a close arterial injection of KCl the action potential recorded from a muscle decreases in height. From these results and others (Lippold, unpublished) it is reasonable to infer that the area of an action potential from a muscle fibre decreases during fatigue.

(*b*) Repetitive stimulation increases the duration of the active state in muscle (Ritchie & Wilkie, 1955), and this is responsible for the increase in efficiency of fatigued muscle described by Bronk (1930). Thus the tension-time developed by the fatigued fibre, when it is excited, is increased.

Neuromuscular block might occur; this cannot however be responsible for part of the effect, for a blocked fibre would not exert tension, hence the net effect on the ratio I_A/P, as far as any change during a continuous submaximal contraction is concerned, must be nil.

Whether the fatigue produced by this type of continuous isometric contraction is strictly comparable with muscular fatigue occurring during normal activity is debatable. In continuous voluntary movements of human calf muscles, under nearly isometric conditions, Barcroft & Dornhorst (1949) found that the blood flow to the muscle was nearly stopped when the contraction exceeded a certain strength. It may well be that the effects we have described here are due to circulatory arrest in the active muscles, and although this undoubtedly occurs in certain kinds of muscular exercise, it cannot be held responsible for fatigue under all conditions.

SUMMARY

1. The relation between integrated electrical activity and tension has been investigated in the human calf muscles under conditions of isometric voluntary contraction, in the normal and fatigued states.

2. After a period of continuous isometric fatiguing contraction the relation is still a linear one but of different slope. More electrical activity is associated with the maintenance of a given tension in the fatigued state.

3. During the course of a continuous isometric contraction of given strength, the electrical activity progressively increases. This is due to recruitment of motor units taking place to compensate the decrease in force of contraction occurring in the fatigued muscle fibres.

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