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THE ENERGY EXPENDED IN MAINTAINING A MUSCULAR CONTRACTION.

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It is obvious that the energy expended by a muscle increases with the strength of the contraction. There is, however, no definite information regarding the relative amounts of energy required to maintain contractions of varying strengths. This question is of considerable importance in connection with the economy of muscular activity, and is of timely interest because of the recent investigations of Adrian and Bronk(1, 2) regarding the mechanism of grading the strength of a muscular contraction.

By recording the frequency of motor impulses in single nerve fibres and the resulting contraction frequency of single groups of muscle fibres, they showed that there are two ways in which the strength of a reflex or voluntary contraction may be increased. An increased number of neuromuscular units may come into action, and a higher tension is produced in the individual fibres by a higher frequency of motor nerve impulses. Rising from a level as low as 5 or 10 a second in a weak tonic contraction to 80 or 100 in the stronger responses, the resulting contraction of the single muscle fibre changes from a series of discrete pulls to a fused tetanus. Due to the fact that the twitches of the various fibre groups are out of phase the response of the muscle as a whole in a weak contraction is smooth and fused, completely masking the discontinuous character of the unit responses. As the frequency of the twitches increases, the resulting summation produces a higher tension and an increase in tension-time. In a steady contraction the tension-time is of course the product of the tension by the time that it is maintained. In a non-uniform contraction or in a series of twitches it is the area under a tension-time curve

[1] The experimental work reported in this paper was done while the author was a Fellow in Medicine of the National Research Council, U.S.A.

or $\int T\,dt$, where T is the tension and t the time. From the point of view of a maintained contraction it is this quantity that is of importance, and in considering the relative energy expenditure in various types of contractions we will use the ratio of the tension-time to heat production or that of the tension to the rate of heat production as a measure of the economy.

The answer then to the question regarding the relative economy of maintaining contractions of varying strengths lies in a study of the energy expended in developing a given amount of tension-time (*a*) when varying fractions of a muscle are in action, and (*b*) when the muscle is stimulated at various frequencies. No attempt has been made to measure the variation in economy of contractions graded by the former mechanism, due to the uncertainty regarding the distribution of heat between muscle and thermopile in submaximal contractions and the consequent suspicion attaching to such myothermic observations. There is, however, no obvious reason why a mere increase in the number of fibres contracting should alter the ratio of tension produced to heat developed, and it seems safe to say that in so far as a stronger contraction is a result of an increased number of active fibres, the economy of maintaining a contraction is probably independent of the strength.

Previous work of Hartree and Hill(3) gives us a clue as to what we may expect to find regarding the variation in economy of maintaining tension at various frequencies. In the paper referred to they show that the heat production in the early part of a short tetanus is relatively greater than that in the later portions. This observation may be logically interpreted as indicating that it is more expensive to develop a muscular tension than to maintain it. If this be so, one would expect to find that it is less economical to produce a given amount of tension-time by a series of twitches than by a fused tetanus, and consequently that a weak contraction maintained by a low frequency of motor impulses would be relatively less economical than a strong contraction resulting from a higher frequency motor discharge.

This has been tested experimentally by stimulating the sartorius muscle of a frog (*Rana temp.*) for a given period of time at various frequencies, observing the tension-time developed and measuring the heat production during the period of stimulation. The methods employed are essentially those which have been developed by Hill during recent years(4). The excised muscle was mounted on a thermopile, placed in a glass vessel containing Ringer's solution to which was added 10 mg. p.c. of P in the form of sodium phosphate, and the whole ensemble mounted in a fairly constant temperature bath enclosed in a large Dewar flask.

After soaking in the phosphate-Ringer's fluid for about 3 hours as a precaution against loss of irritability, the solution was removed and a slow stream of oxygen passed through the vessel throughout the course of the experiment. Just maximal stimuli of various frequencies were delivered to the muscle from a condenser, which was alternately charged and discharged at the desired frequency. This method was employed after four standard contact breakers used in conjunction with a Harvard induction coil were found to involve the danger of chatter and repetitive stimuli at the higher frequencies. These same faulty contactors, when used for charging and discharging the condenser, of course did not give multiple stimulation even though the contacts chattered. The tendon end of the muscle was connected to an isometric lever, which recorded on a rapidly moving drum turned at a constant speed. The tension-time developed during any period of stimulation was, therefore, obtained by determining the area between this tracing and the base line, the lever being frequently calibrated. The initial heat production was observed by means of the thermopile and either a Downing moving magnet or a Kipp moving coil galvanometer. Due to the fact that the galvanometers had periods of from 3 to 6 seconds and the thermopile had been made slow by coating with a considerable amount of paraffin, the heat production during a 1- or 2-second period of stimulation was taken directly as the ballistic swing of the galvanometer. In certain experiments the duration of stimulation was increased to 5 seconds and the frequency reduced to one every 2 seconds. Even then it was found that the thermopile-galvanometer system could be made to sum by adding sufficient paraffin to the thermopile surface.

Provided the interval between successive stimuli is greater than 1 second there is no evident variation in economy with frequency, as is shown by Fig. 1. A further increase in the rate of stimulation, however, results in a greater economy of tension-time production, even though the successive contractions are in no wise fused. This absence of even partial summation precludes the possibility of explaining the increased economy on these grounds. It is rather to be accounted for on the basis of observations made by Hartree and Hill (5), which showed that with regard to the second of two twitches "the efficiency of the contraction, as measured by T/H, is noticeably increased as the result of a previous shock at a suitable interval." Some altered condition of the muscle resulting from the previous contraction persists and makes more efficient the succeeding twitch—thus giving rise to a true "staircase" effect.

Fig. 2 shows the variation in economy over a wider range of frequencies. In this experiment tension-time was maintained nearly three times as economically at the higher rates of stimulation. Ten other experiments showed that the economy was increased by factors of from

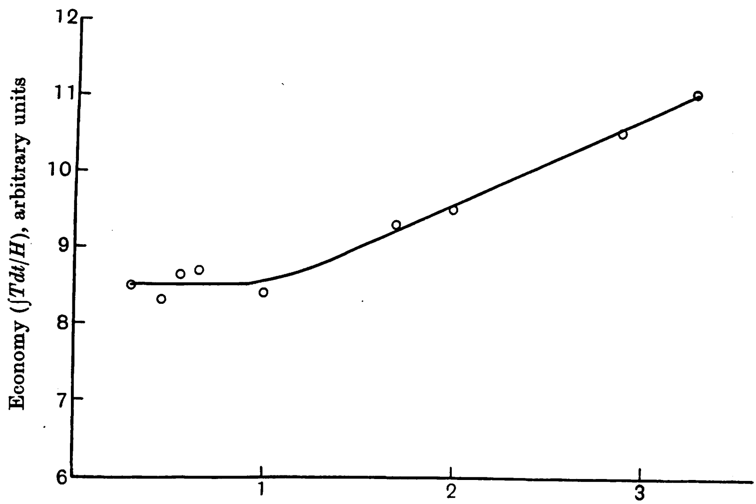

Fig. 1. Variation of economy with low frequencies of excitation. Muscle stimulated for 5-sec. periods. All contractions were discrete twitches with no evidence of summation. 18° C. 17. xii. 28.

three to five. The broken line of Fig. 2 represents the maximum tension developed by the muscle at the various frequencies. At first the tension is independent of the frequency because there is no fusion of the successive twitches; a further increase in the rate of stimulation causes a progressive increase in the degree of fusion, and a consequent increase in tension which continues until the contractions reach the stage of a fused tetanus.

A comparison of these two curves indicates the reasons for the increase in economy with increased frequency of stimulation. The rising economy at low frequencies is to be accounted for on the grounds suggested in the preceding paragraph; the larger part of the increase, however, is to be ascribed to the increased fusion of the successive twitches. This is shown by the fact that the economy and tension both increase with the frequency up to, but not beyond, the limit of complete fusion. In this connection it is interesting to recall that the frequency of motor nerve impulses in reflex contractions does not seem to go above a level adequate to produce maximal tension in the muscle. In view of the fact that the present experiments show the economy and tension to vary over much the same frequency range, we may now state that as the motor centres speed up their discharge as a result of greater excitation, maximum tension is developed at a maximum economy.

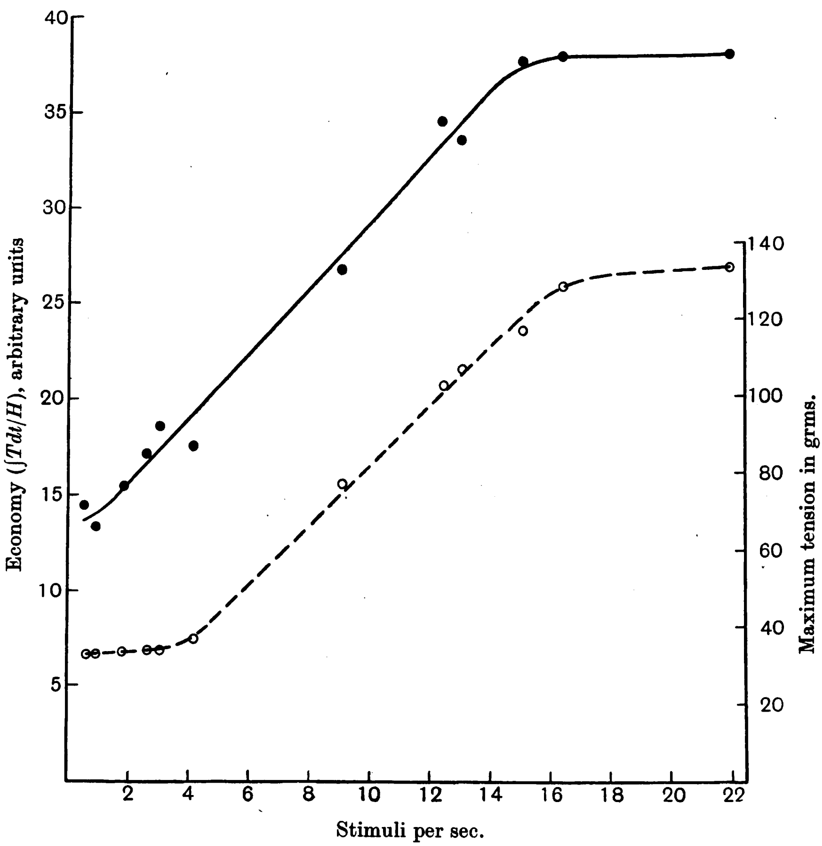

Fig. 2. Solid line: relation between economy and frequency of stimulation. Broken line: relation between maximum tension developed during each 2-sec. period of stimulation and the frequency. 18° C. 12. xii. 28.

It must also be concluded from these experiments that a weak contraction maintained by a series of discrete twitches, or by a partial tetanus of the active muscle fibres, is less economical than if the contraction were the result of complete tetanus of a smaller number of fibres. This lower economy may, however, be offset by the possible advantage of a more adequate circulation in a prolonged contraction sustained by a succession of twitches in the individual fibres. What is more to the point is the fact that the grading of contractions by an increased frequency of excitation achieves a greater economy as the strength of contraction increases, being a nicely balanced control for lowering the energy required per unit of tension in those contractions which make the greatest total energy demands.

Inasmuch as the greater economy resulting from increased frequency of stimulation is largely due to mechanical summation, we may suppose that at a relatively low rate of stimulation the economy is increased as the result of any alteration in the muscle which gives it slower characteristics. As a demonstration of this, certain experiments were performed with the muscle at 0° C. Typical results are shown in Fig. 3, from which

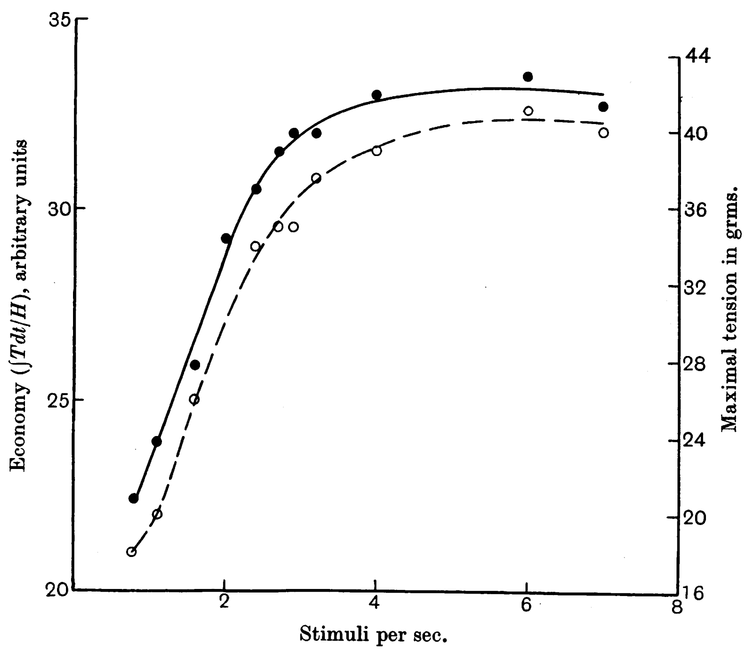

Fig. 3. Muscle at 0° C. Solid line: relation between economy and frequency of stimulation. Broken line: maximum tension developed at the various frequencies. 5-sec. periods of stimulation. 15. xi. 28.

it will be seen that the maximum economy and tension are attained at a stimulus rate of about five a second. The rate of stimulation at which the economy begins to increase is of course also much lower than in the case of a muscle at room temperature. These observations have no obvious bearing on normal reflex and voluntary contractions except in the case of cold-blooded animals. As their body temperature falls, it seems reasonable to assume that the average range of discharge frequency from the motor centres would decrease, both as a result of lowered temperature of the motor cells themselves (Cooper and Adrian(6)), and as a result of a lower frequency of afferent impulses (Matthews(7)) playing upon these centres. The result of a lower rate of motor impulses would be a contraction maintained at a greater expenditure of energy per unit of tension, were it not for the fact that the lowered temperature of the muscle causes its contractions to fuse at a slower rate and so maintains the higher level of economy.

Effect of fatigue.

An altered muscular condition of more significance in the present discussion is that resulting from fatigue. It is a well-known fact that a muscle stimulated at a frequency just below the level needed to produce partial summation will gradually go into a fused tetanus, if the same rate of stimulation be continued. The following experiments have been made to determine the amount of energy required to maintain a unit of tension throughout such a progressive fatigue.

The experimental procedure has been much the same as that outlined above. The muscle chamber was kept filled with an atmosphere of nitrogen rather than oxygen in order that the heat determinations may be less complicated by the consideration of the recovery and delayed heat. The muscle was stimulated at a frequency of three or four a second, the contraction was recorded on a fairly slow drum and the galvanometer deflection observed at 6-second intervals throughout the period of stimulation. This was continued for several minutes or until the contraction was no longer measurable. The muscle was then electrocuted, and after the system had again reached thermal stability an alternating heating current was passed through the muscle for a period of some seconds. Several such "control" heatings were made and the galvanometer deflections carefully observed. The average of these readings plotted against time gave a "control" curve which was used to analyse the deflection-time curve obtained during the prolonged stimulation of the muscle. Following the methods described by Hartree and Hill(8) this analysis gave the rate of heat production at 6-second intervals throughout the course of the stimulation.

The variation in economy of maintaining tension as a result of previous stimulation is given by dividing the tension-time developed during each of the 6-second intervals by the heat production during the corresponding period. The solid line of Fig. 4 shows that during 2 minutes of continuous stimulation at a frequency of four a second the amount of tension-time produced per unit of energy expended increased more than fivefold. This increase in economy was characteristic of each of six experiments although the rate and extent of the increase varied somewhat

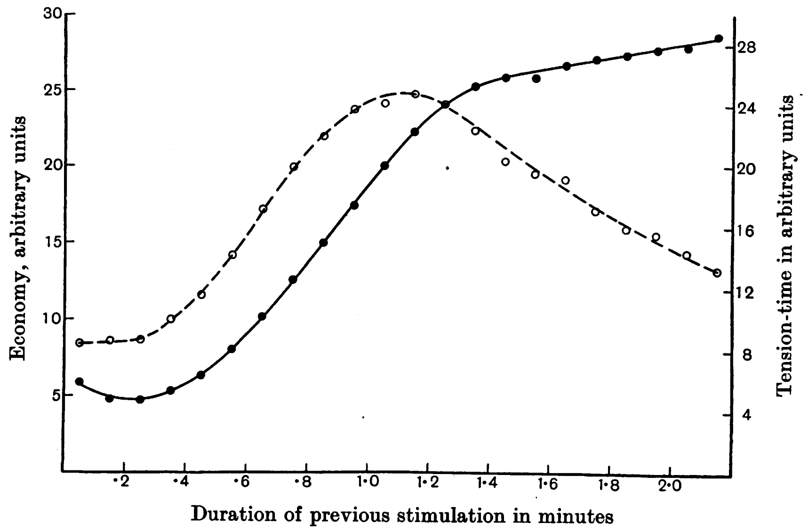

Fig. 4. Solid line: economy of maintaining muscular tension $\frac{\int T dt \text{ in interval}}{H \text{ in interval}}$ with increasing duration of previous stimulation at four a second. Galvanometer deflection analysed at 6-sec. intervals by means of a control heating curve of 5-sec. duration. Broken line: amount of tension-time developed in successive 6-sec. periods. 11. i. 29.

with the previous condition of the muscle. The broken line of Fig. 4 represents the amount of tension-time developed during successive 6-second intervals throughout the course of the stimulation. The rise is obviously due to the gradual increase in summation of the successive twitches as fatigue develops; the subsequent fall results as greater fatigue offsets the gain resulting from fusion. A comparison of these two curves shows that the most rapid increase in economy comes during the period in which the character of the contraction undergoes the most pronounced change from a series of twitches to a fused tetanus. The increase in economy associated with the changed state of the muscle resulting from previous stimulation is, therefore, to be ascribed to the lower energy requirement for maintaining a given tension as compared with that required for the development of a contraction.

Two factors might at first thought indicate the inapplicability of these findings to normal muscular contractions. It may be argued that even in long sustained maximal contractions a circulated muscle would never develop the degree of fatigue produced in these experiments on excised preparations. It is, however, to be noted that even in the early stages of this fatigue, *i.e.* during the course of the first minute, and while the muscle is still giving vigorous contractions, there is frequently as much as a threefold rise in economy. And as regards the effect of circulation it is worth recalling the suggestion previously made (2) that a fused contraction of a large number of the muscle fibres might be expected to occlude the arterioles and capillaries and so reduce the blood flow. Such an effect has indeed been described by Anrep and Häusler (9) as restricting the coronary circulation during systole. A prolonged reduction in flow through a muscle produced in this way during a long sustained contraction, would certainly increase the degree of fatigue and make possible summation at a lower frequency. But a strong contraction, during which the fatigue develops, has presumably been maintained by a frequency of motor nerve impulses sufficiently high to produce tetanic contractions of the muscle fibres. Slower characteristics of the muscle would therefore be without effect upon the economy at that same frequency. In the absence of experimental evidence regarding the frequency of motor impulses throughout the course of a long sustained maximal contraction, there can be no satisfactory consideration of this point, but it is at least probable that the frequency from the motor nerve cells would gradually decrease as a result of a prolonged high rate of activity. In that event the slower characteristics of the fatigued muscle would more or less effectively compensate for the decreased impulse frequency, checking the fall in tension and economy that would otherwise result.

Certain invertebrate muscles, as for instance the claw muscles of the crab, show a rapid slowing as a result of sustained contraction and their nerves soon fatigue at fairly high rates of stimulation. As Hill (10) has pointed out, this fatigue of the nerves may be prevented by a decrease in the frequency of the motor impulses. Due, however, to its slower characteristics the muscle would still maintain a uniform tension, and without the increase in energy expenditure that would otherwise result from a lower frequency of excitation. Such considerations indicate that the experiments referred to in this paper may give a clue to the puzzling problems regarding muscular contractions which, although rapid in their onset, are nevertheless maintained with an unusually low expenditure of energy. This question is more fully discussed by Dr Bozler in a succeeding paper.

SUMMARY.

The economy of energy expenditure in maintaining muscular contractions has been studied, at various frequencies of stimulation and in progressive fatigue. This has been done by measuring the heat production and the tension-time.

1. As the rate of stimulation is increased, the economy, or amount of tension-time maintained per unit of energy expended, increases. This is largely due to a greater degree of fusion of the separate muscle twitches, there being no further increase in economy with frequencies of a value higher than that needed to produce complete tetanus.

2. These results are discussed in relation to the findings of Adrian and Bronk, which show an increased strength of muscular contraction to be due in part to an increase in frequency of motor excitation. It may, therefore, be concluded that tension is maintained at a smaller expenditure of energy in a strong contraction than in a weak one.

3. At 0° C. the increase in economy develops at lower frequencies. In cold-blooded animals this factor would be of significance in the event that the range of frequency of impulses from the motor centres was lowered as a result of a fall in temperature.

4. A stimulation frequency not quite sufficient to give partial summation of the successive twitches will, if continued, produce a fused tetanus. Associated with this changed condition of the muscle there is a greater economy of maintaining tension. It is pointed out that this factor may play an important rôle in long-sustained contractions where there would be reason for expecting a decreased frequency of motor impulses.

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