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ALTERNATING RELAXATION HEAT IN MUSCLE TWITCHES

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When a muscle is excited directly by a single shock at a pair of electrodes, or indirectly through its nerve, its contraction is not simultaneous all over but is propagated away from the stimulating cathode, or from the neuromuscular junctions. Consequently, one part stretches another and in turn is stretched by the other (Happel, 1926; Fischer, 1926). Since the part which starts to contract first also starts to relax first, considerable inequalities may so occur (see below) in the distribution of the relaxation heat along the length of the muscle. If a muscle is excited at multiple electrodes disposed along its length, the contraction is more nearly simultaneous and presumably this mutual stretching does not occur (Abbott & Ritchie, 1951); but multiple stimulation is not practicable with a muscle on a thermopile. It has long been suspected, however, particularly from the evidence of records of heat production during an isometric, or a heavily after-loaded isotonic, contraction, that different parts of a muscle behave in different ways, quite independently of these effects due to propagation (Hartree, 1931; Hill, 1938, p. 152, 1949*a*, p. 218, 1953, p. 112). This inequality may occur not only between different regions along the length of a muscle but between different parts of the same cross-section. Such differences are inherent in a system containing many fibres of widely different diameters and therefore, probably, of different physical characteristics. Even in a single fibre, which in a frog's sartorius may be 200–1000 times as long as it is thick, it is unlikely that the contractile strength and other properties should be identical throughout.

The double thermopile described by Abbott, Aubert & Hill (1951) makes it possible to compare directly the heat production in two different regions of a muscle, and its three electrodes allow a stimulus to be applied in a variety of ways. The original simple purpose of the present investigation was to find out how large a difference of heat production in a twitch occurs between two portions ('pelvic' and 'tibial') of a frog's sartorius. The thermopile consists of two parts each about 9 mm long, with about 2 mm between them. The pelvic sample of muscle was between 3 and 12 mm from the bone, the tibial sample from 14 to 23 mm, so leaving (in a 30 mm muscle) a clear 7 mm to the tendon. The result came out consistently: in isometric, or in heavily after-loaded isotonic, twitches the total rise of temperature in the tibial region averaged about 14 % less than in the pelvic region. If the tibial part contained a rather greater proportion of tendon, the rise of temperature in it would be less for two reasons: first, because the tendon produces no heat; secondly, because the mechanical energy in the lifted load, or in the stretched tendon, would be dissipated as heat to a greater extent in the opposite region of the muscle as it relaxed.

These experiments were not very interesting, but a most peculiar phenomenon was noticed in one of them and this was followed up. Whichever of the two thermopiles was used, *in successive twitches of a regular series the heat production alternated in size.* The difference was quite large, the smaller heat being 70–80 % of the greater, under conditions where a 3 % difference would have been significant. Moreover, the smaller heat recorded by one thermopile was simultaneous with the greater heat recorded by the other. Clearly the two parts of the muscle were alternating in some way. The stimulus was maximal; increasing it did not affect the phenomenon, nor did changing the site of the stimulus.

The contraction was isotonic, with a small initial load and a large after-load, the condition for about-maximal work. If the muscle was stretched 3 or 4 mm, providing an initial load of a few grams, the alternation stopped (see Fig. 3, curve 2 and legend). If the muscle was then released to its original length and the series continued, the alternation gradually worked up again: once established, it continued indefinitely.

These observations were of the total initial heat, read on a galvanometer scale: they were extended by photographic records made with a rapid galvanometer. These showed the same alternation in total heat production: but the difference between successive records was found to reside entirely in the relaxation heat, which is derived from the mechanical energy of the load transformed into heat when the muscle relaxes. The greater part of this mechanical energy, in a series of contractions, appeared alternately first in one part of the muscle and then in the other. The ordinary initial heat (of activation and shortening) occurring in the first 0·5 sec was identical in successive contractions. In Fig. 1 *X* are two consecutive records of the heat production. In the lower, there is only a trace of relaxation heat, in the upper it is large and obvious. Why, in contractions which were otherwise identical (judging from the early coincidence of the records), should the mechanical energy be absorbed during relaxation first by one portion of the muscle and then, in the next contraction, by the other? Fig. 1 *Y* gives a more usual example of the same effect. Here, as in Fig. 1 *X*, there is identity during the contractile phase, and although the relaxation heats are obvious in both, there is a considerable difference between them.

It has long been known that in isometric twitches relaxation occurs earlier the shorter the muscle (Hartree & Hill, 1921, p. 401). In present-day jargon, the active state decays more slowly when a muscle is at a greater length. In heavily after-loaded isotonic contractions, the effect of length on relaxation is even more obvious. In Fig. 2 are three consecutive isotonic records, at initial lengths 31, 33 and 35 mm, of a pair of muscles which at 33 mm had an initial tension of 1 g. The experiment was that of Fig. 1*X*, in which the muscles had a length of 32 mm and other conditions were identical. The effect of initial length is striking. At the moment (0·50 sec) when the muscle stimulated at 31 mm had come right back to its initial length, stimulated at 33 mm it still retained about 87 % of its maximal shortening.

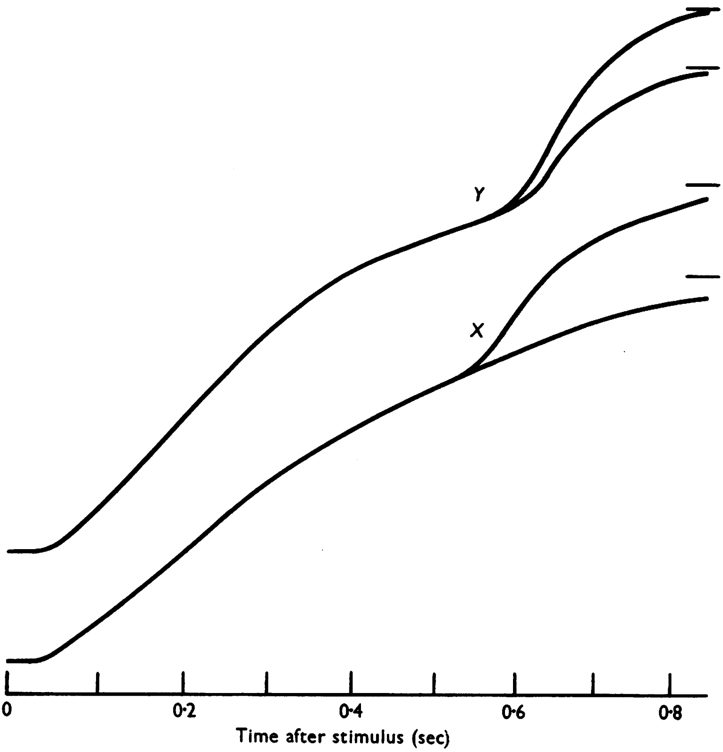

Fig. 1. Copies of records of the heat production in isotonic twitches of frogs' sartorii at 0° C, to show alternating relaxation heat. Ordinate, galvanometer deflexion, uncorrected, maxima shown by horizontal bars: abscissa, time after stimulus. Two separate experiments. *X*, muscles 170 mg, under initial load 1 g with after-load 37 g: two consecutive twitches. *Y*, muscles 235 mg, under initial load 1 g with after-load 28 g: upper, mean of records 1, 3 and 5 in the series; lower, mean of records 2 and 4.

The suddenness of the stretch by the load during relaxation, and the slower onset of relaxation in a muscle stimulated at a greater length, have nothing to do with the site of the stimulus. Fig. 2 was obtained from a muscle pair with the cathode in the tibial region and the anode at the pelvic end; but exactly similar records were obtained with a single muscle with 5 cathodes and 4 anodes distributed along it.

Consider two regions *A* and *B* along the length of a muscle which is giving regular isotonic twitches under a small initial load with a large after-load. Suppose that *A* be slightly more stretched initially than *B*. (This condition is possible in a muscle under the same tension throughout because of hysteresis. For example, when a muscle previously gently stretched out is stimulated under a small load, it remains shorter after relaxation: if gently pulled out again, it now remains longer [Hill, 1949*b*]). Then *B*, by hypothesis, being initially less stretched than *A* will, according to Fig. 2, relax earlier when stimulated: so it will be stretched by the falling load, while *A* will not be. Consequently, the conditions of *A* and *B* are reversed for the next twitch and alternation will occur. It is not necessary to start with a large difference between *A* and *B*; even a small difference tends to grow in successive contractions, until a steady state of alternation is built up. Under mechanical circumstances

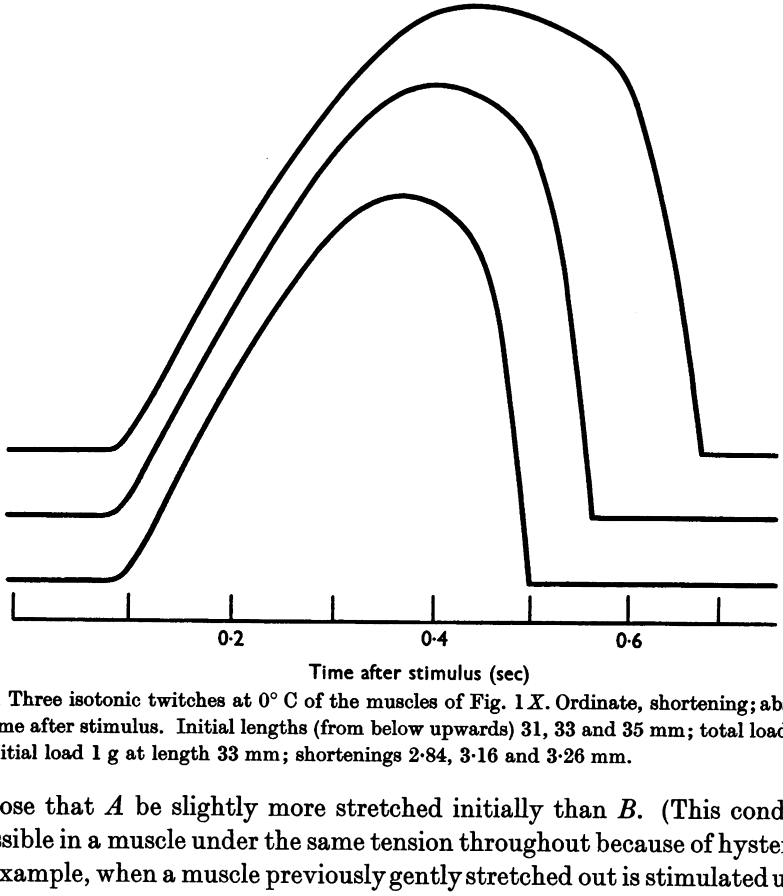

Fig. 2. Three isotonic twitches at 0° C of the muscles of Fig. 1 *X*. Ordinate, shortening; abscissa, time after stimulus. Initial lengths (from below upwards) 31, 33 and 35 mm; total load 28 g, initial load 1 g at length 33 mm; shortenings 2·84, 3·16 and 3·26 mm.

of this kind, an exact similarity of behaviour throughout the length of a muscle is an unstable condition and is bound to be replaced by alternation.

The experiments so far described were made with heavily after-loaded isotonic twitches under a small initial load, the conditions claculated to give the most striking effect. But similar alternations of heat production were found in isometric twitches under a small initial tension, though these were not so great, usually about half the size. This was to be expected, for in isometric contractions the fall of tension in relaxation is much slower than the precipitous lengthening under a large load in isotonic conditions. The gradual stretch, therefore, of one part of a muscle by another during isometric relaxation would not be so extensive as the abrupt stretch by the falling load in isotonic relaxation. The greatest effect was found when the initial tension was quite small, of the order of 0·5–1·0 g in a pair of muscles weighing 200 mg; with an initial tension of 3 or 4 g the alternations were absent. This also was to be expected, for under a greater resting tension hysteresis would not be strong enough to allow one region of the muscle to retain much, if any, of the stretch effected during the previous relaxation; so it would not relax later after the next contraction and the conditions for setting up an alternation would not exist.

The alternation observed need not be between the pelvic and the tibial halves of a muscle: it might occur between any regions and there could be many of them in one muscle. With a thermopile in contact with nearly half the length of a muscle the size of the alternation between successive isometric twitches was not more than about 12 % of the larger; with a thermopile only 5 mm long, alternations up to 20 % were observed. A long thermopile would give only an average over regions which might be in opposite phases of the alternation. A short thermopile, however, could possibly be located in a single alternating region, so in consecutive twitches it might show, in the first no relaxation heat at all, in the second much more than the proper amount.

This possibility was followed up with isotonic twitches and a single thermopile only 5½ mm in length. After various trials, it was found that, placed at 4–9½ mm from the pelvic bone between a pair of sartorii 34 mm long, this thermopile showed the remarkable alternation between (1) and (3) of Fig. 3. In (3) there is no sign of relaxation heat, in (1) it is twice the normal amount: yet up to the moment (0·50 sec) when (1) diverged from (3) the records were identical. The initial load in the alternating series was 0·8 g, the afterload 46 g, the length 34 mm. The muscles were then stretched 5 mm under the same total load: the initial load must now have been a few grams. Alternation was no longer observed, and curve (2) is the record of the heat production, the same in successive contractions. Curve (2) is identical with (3) up to the moment (0·6 sec) when the relaxation heat came on. The interval (0·1 sec) between the divergence of (1) and (2) from (3) is a measure of the delay in relaxation due to a greater length.

The same phenomenon of an excess, or deficit, of relaxation heat can be shown in another way, without spontaneous alternations. Let a stimulus be applied (best after curarization) at one end of a muscle; then the time taken in propagation of contraction (at about 35 cm/sec at 0° C) is long enough to ensure that, with the precipitous relaxation of a heavily after-loaded twitch (Fig. 2), the end near the point of stimulation has relaxed completely before the other end has relaxed at all. In this way, enormous relaxation heats can be recorded, greater even than that of curve (1) in Fig. 3. For this purpose, a small initial load is not necessary. With a long thermopile, in two halves, covering nearly the whole length of the muscle, stimulation of a curarized muscle at the pelvic end produced a large relaxation heat in the pelvic region, little in the tibial region. Stimulation at the tibial end had the converse effect. This helps to explain Rosenberg's (1934) result that the ratio of heat to tension

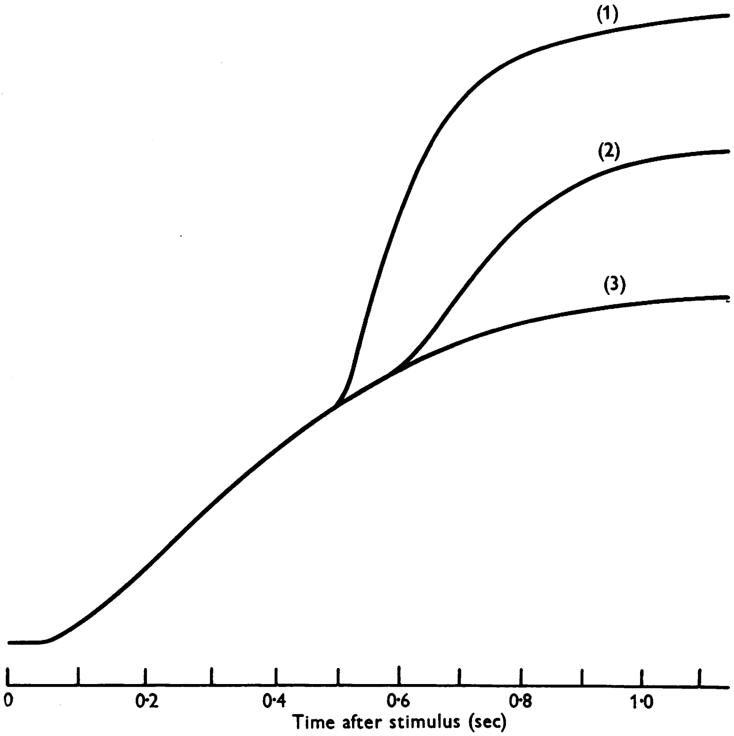

Fig. 3. Copies of records of the heat production of a frog's sartorius at 0° C, to show relaxation heat alternating in consecutive isotonic twitches under a small initial load (curves 1 and 3), and the absence of alternation under a greater initial load (curve 2). Ordinate, galvanometer deflexion, uncorrected; abscissa, time after stimulus. A very short thermopile was used, located between 4 and 9½ mm from the pelvic end. Muscle pair, weight 220 mg, at length 34 mm under an initial load of 0·8 g (curves 1 and 3), and at length 39 mm (curve 2). Total load 47 g. Stimulating cathode in the middle of the muscle, anode at the pelvic end.

in an isometric twitch was greater with stimulation at the pelvic than at the tibial end. His thermopile was in contact with the proximal part of the muscles so with stimulation at that end the elastic energy was dissipated chiefly there in relaxation and was added to the heat.

These experiments show in an unequivocal way (if it still needs to be shown) that the relaxation heat is purely of mechanical orgin. No other explanation of an alternating difference between successive twitches, like that between (1) and (3) of Fig. 3, seems reasonable. A moral to be drawn from all this is that it is dangerous to regard a muscle as a homogeneous body contracting and relaxing uniformly throughout. In examining the finer details of the twitch, it is advisable to choose the conditions (e.g. not too low an intial tension, and if possible stimulation 'all over') which give the muscle a better chance of behaving in an ideal way.

An obviously fundamental property of muscle is the large effect of initial length on the duration of the active state, as is illustrated by Fig. 2. This is shown more vividly in heavily after-loaded isotonic contractions than in any other way. The phenomenon deserves an attempt to explain it in terms of recent theories of contraction.

SUMMARY

1. During a regular series of isotonic twitches of a frog's sartorius, under a small initial load and a heavy after-load, considerable alternations may appear in the magnitude of the heat production recorded in a limited region of the muscle.

2. These are not due to fluctuations of the normal muscular response but solely to the energy of the load, transformed into heat during relaxation, appearing alternately in different regions.

3. Relaxation occurs later in any region (*A*) which was initially more extended, so the falling load stretches another region (*B*) relaxing earlier because it was initially less extended.

4. Consequently, in the next twitch, *B* in turn relaxes later and *A* earlier: *A* therefore is now extended by the falling load and the cycle is repeated.

5. A similar alternation, but of smaller amplitude, is found in successive twitches under isometric conditions with a small initial tension. With a larger initial tension, the alternations do not occur.

6. The condition of uniform distribution of the relaxation heat is unstable, unless the initial load is great enough.

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