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Composantes multiples de la fatigue du muscle isolé révélées par l'analyse mécanique et thermique de la contraction,

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Translated from French.

Multiple Components of Isolated Muscle Fatigue

Revealed by the mechanical and thermal analysis of the contraction,

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In a somewhat schematic way we can distinguish in the phenomena of peripheral fatigue the disorders related to the transmission of the nerve impulses to the muscle and the localized disorders in the level of the muscular fiber (see SCHERRER, LEFEBVRE and BOURGUIGNON, 1957). We have recently shown that this so-called contraction fatigue was itself complex: simultaneous analysis of heat production and mechanical force at different times of contraction allows the recognition of several apparently distinct mechanisms (MARÉCHAL and AUBERT, 1958). New observations, extended to the phenomena of recovery after fatigue, allowed us to better define these components.

TECHNICAL.

All our observations concern the muscles sartorius of Rana temporaria at the temperature of 16 to 18°C. Each hour, they are tetanically excited in the air, at constant length, for 2 to 15 seconds, by means of alternating charges and discharges of capacitor (frequency, 50 / s, time constant, 5 ms) . Between the contractions the muscles bathe in an oxygenated RINGER solution, supplemented with H-tubocurarine (1.5 mg / 100 ml).

Force is measured by strain gauges, and heat production by a thermocouple and galvanometer system with photoelectric amplification. The two phenomena are represented simultaneously on a two-beam oscilloscope. The details of these techniques can be found in Aubert (1956).

RESULTS.

The force sustained by a muscle subjected to long tetanus evolves in two characteristic phases (see Figure 1, central tetanus). After rapidly reaching a maximum, the force decreases slowly by 10 to 20 per cent. This first phase has a very constant duration at a given time, from four to seven seconds depending on the season. The myogram then presents a point of inflection which marks the beginning of the second phase: the force drops sharply from 20 to 50 per cent. in a few seconds, then continues to fall at decreasing speed until muscle exhaustion.

During a series of tetanus the same characteristic evolution is found, but the form of the myogram changes little by little: while the fall in force becomes weaker in the first phase, it

accelerates during the second moment of the tetanus. When transition between the two phases occurs is not, however, markedly affected by the repetition

Despite the considerable drop in force observed during long tetanus, the muscle can recover almost entirely its initial strength during the rest interval between contractions. This recovery also takes place in two phases, as shown in the example of FIG. 1. The muscle was tetanized at one hour apart for 4, 15 and 3 seconds, respectively. One second after each main tetanus, a short tetanus is administered to check the possible recovery of the force. In all three cases, this one rises to about the same level as the first phase of the evolution described above. In the case of long tetanus, for example, the force dropped from 108 to 85 g during the first phase, reaching 37.5 g at the end of the tetanus. A second later, the muscle is able to develop 82.5 g: the force drop of the second phase is thus recovered almost entirely. After one hour of rest, the developed force reached 101 g, that is to say approximately the initial maximum.

One can thus distinguish between immediate recovery and recovery late. While the sudden drop of force during the second phase of tetanus

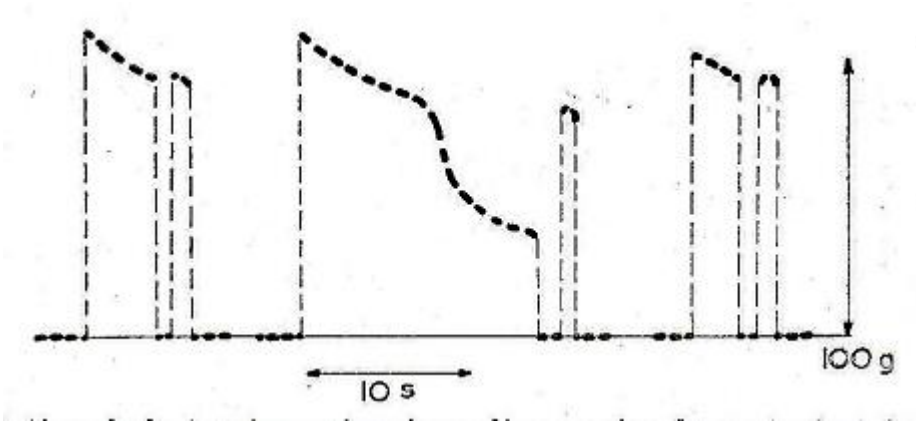

FIG. 1. Evolution of the mechanical force of a pair of frog sartorius for three tetani of 4, 15 and 3 seconds, administered at intervals of one hour. One second after each tetanus, the muscles undergo a new maximum excitation of one second. Observe the characteristic fall in force and the importance of recuperation in the case of the second tetanus Time marker : 1 sec.

Is erased in one second or less, recovery from early force drop is a much slower phenomenon. The figure shows that after the two short tetani, which show only this first phase of fatigue, there is virtually no immediate recovery. It took an hour of rest in the RINGER to see the force build up.

The study of thermogenesis confirms the complexity of the mechanisms of contraction. During the first phase of the mechanogram, the heat flow rate remains constant or decreases little, at any rate less than the force. During the second phase, on the contrary, the heat and the heat flow evolve at the same time, so that the heat produced per unit time and per gram of force remains constant. The most remarkable phenomenon is that this coefficient of proportionality between heat and force decreases from one tetanus to the next, even though the recovery of the force appears complete; The fatigued muscle thus dissipates less heat to maintain a force equal to that of a fresh muscle. However, the reduction in the heat / force ratio does not occur if the previous tetanization has not exceeded the first phase of the force evolution. It thus appears again that the contractile machine is the seat of new phenomena from the point of inflection of the mechanogram.

DISCUSSION.

The previous results lead us to define different types of contraction fatigue. We will first distinguish short-term fatigue, which occurs during tetanus contraction, from long-term fatigue, which is during a series of successive tetanus. Short-term fatigue is itself dissociable into two phases of very different properties.

During the first phase the force decreases feebly, and the heat produced hardly changes; Recovery of the force drop is slow, and may require washing in the RINGER. It does not modify the thermogenesis in subsequent contractions. We are tempted to explain this apparent fatigue by an internal shortening of the contractile units at the expense of passive elastic elements in series with them. The shortening accounts for the force drop, while the persistence of all the active elements explains the stability of the heat production. The following observation makes at least plausible the intervention of this mechanism: when a muscle is tired by a series of short tetani in the air until its force has fallen to 10%. of its initial value, it is enough to extend it by 6 mm so that it recovers more than 70%. of its contractile force (MARÉCHAL, 1957). In this type of experiment, prolonged rest in the RINGER liquid may also bring force back to normal: this late recovery completes the analogy with the first phase of fatigue in the short term.

During the second phase, the force decreases rapidly at the same time as the thermogenesis, which suggests the progressive elimination of the active elements. An interruption of the propagation of muscular action potentials, a decoupling between the excitation of the membranes and the activation of the contractile mechanism, or the inability of the chemical mechanisms of restoration to satisfy a massive and prolonged demand. Three arguments seem to argue in favor of the latter hypothesis: the rapid recuperation of the deficit in less than a second; the relative constancy of the moment of tetanus in which it appears; and finally the traces of permanent disturbance of metabolism that are manifested in long-term fatigue.

The mechanical effects of long-term fatigue are not very characteristic, but the thermogenesis is modified in a particular way as soon as the previous activity caused the force in the second phase of the mechanogram. None of the preceding mechanisms can explain the gradual increase in the muscle economy during successive contractions. This must result from a slowing down of the chemical reactions within the elements generating the force. BRONX (1932) has pointed out that in the muscle of Maia's forceps, the increasing economy of successive contractions, estimated by the measurement of total heat, goes hand in hand with a slowing down of the force rate increase. In the case of the striated muscle, our experiments reveal a paradoxical phenomenon: the slowing down of the muscular metabolism does not occur during the contraction itself, but after the interval of rest that follows. It is possible that the excessive use of the immediately available energy reserves favors the development of abnormal recovery reactions, which are responsible for this situation.

In conclusion, the drop in force during a fatigue test of the isolated muscle may be due to at least three mechanisms: the distension of the passive elastic elements in series with the contractile units; the progressive elimination of these units; and the slowing down of the chemical reactions responsible for the development and maintenance of force within these units

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