ANALYSIS OF MECHANICAL AND THERMAL PARAMETERS AND EFFICIENCY OF MUSCULAR CONTRACTION IN RABBITS AT DIFFERENT AGES

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Experiments on rabbits showed an increase with age in the external work of the muscle in situ during isotonic tetanus and an increase in the mechanical efficiency of the tetanus. The efficiency of the gastrocnemius muscle reaches a maximum after acquisition of the standing posture and falls slightly toward the adult state. The curve of the change in temperature in the gastrocnemius muscle during prolonged tetanus in rabbits aged 1 week is characterized by a low value of heat of shortening and a high value of the heat of maintenance of tetanus. In more adult animals the opposite result is found. The hypothesis is put forward that the increase in the efficiency of muscular contraction with age is due to a reduction of the dissipative effects.

Investigations in the writers' laboratory have shown that the skeletal musculature of mammals born immature is characterized by low lability and by constant tonic activity during early postnatal development, thereby maintaining a state of homoiothermy. After acquisition of the standing posture the skeletal musculature achieves new and high indices of lability, as the result of which it is able to maintain phasic-tetanic contractile activity [1-4, 9, 11-14].

In connections with these differences, the present investigation was carried out in order to study individual mechanical and thermal parameters of contraction and relaxation as well as the efficiency of contractile activity of the muscles in rabbits at different ages.

Results of investigations of the efficiency of muscular contraction in isolated muscles of cold-blooded animals are described in the literature [15, 18]. The muscles of adult homoiothermic mammals in situ have been inadequately studied from this standpoint [6, 7]. There is no information in the literature on ontogenetic investigations of the efficiency of muscular contractions.

EXPERIMENTAL METHOD

Experiments were carried out on rabbits of four age groups: group 1) 5-8 days, group 2) 16-19 days, group 3) 1-1.5 months, group 4) adult rabbits. The test objects were the tibialis anterior and gastrocnemius muscles. Urethane anesthesia was used and the animals' body temperature was kept at the normal level. The test muscles were kept at a constant surface temperature (32-34°C) and were moistened with warm Ringer's solution, and their blood supply was undisturbed. Square pulses of maximal strength, 0.5 msec in duration for the rabbits of groups 2, 3, and 4 and 1.5 msec in duration for group 1, were used for indirect stimulation of the muscles. When the mechanical parameters of muscular contraction were determined under isotonic conditions the frequency of stimulation (f_T) was chosen to be equal to the frequency of transition between intermittent and smooth tetanus [3, 11, 12]. This corresponded to maximal stability of prolonged tetanus. These frequencies were 10 Hz for group 1, 20 Hz for group 2, 30 Hz for group 3, and 40 Hz for group 4. When the thermal effect of isotonic tetanus for a duration of 10 msec was evaluated, the fre-

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TABLE 1. Characteristics of Contraction of Tibialis Anterior and Gastrocnemius Muscles (frequencies of stimulation f_T) in Rabbits of Different Ages (M± m)

Mechanical efficiency (in %)	M. tibialis anterior				M. gastrocnemius			
	n	P_M	$\frac{\Delta l}{l_0}$	$A_M\left[\frac{J}{g}\cdot 10^{-3}\right]$	n	P_M	$\frac{\Delta l}{l_0}$	$A_M\left[\frac{J}{g}\cdot 10^{-3}\right]$
1-(5-8 days)	6	162,0±26,4	0,102±0,005	2,57±0,36	10	62,3±5,2	0,135±0,016	1,37±0,25
P		>0,2	>0,2	<0,05		<0,001	>0,2	<0,001
2-(16-19 days)	6	153,6±2,7	0,125±0,022	6,18±1,14	7	323,0±27,5	0,162±0,031	12,16±2,20
P		>0,2	>0,2	>0,2		<0,005	>0,2	>0,1
3-(1-1 1/2 months)	7	184,2±40,2	0,103±0,003	8,62±1,62	12	188,8±10,0	0,124±0,010	8,83±0,88
P		>0,2	<0,05	>0,05		<0,001	>0,2	<0,005
4-(adult)	6	134,0±8,2	0,138±0,014	13,30±1,75	8	75,4±4,1	0,128±0,009	5,7±0,2

Legend. P_M denotes mean isotonic loads (relative to weight of muscle); $\Delta l/l_0$ represents maximal shortening of muscle during contraction (relative to initial length); A_M denotes external work (per gram weight of muscle); P) significance of differences between mean value for successive age groups.

quency of stimulation (f_0) used was that which produced maximal shortening of the muscle with an average load and enabled stable tetanus to be maintained for not less than 10 sec. For the rabbits of group 1 this frequency was 30 Hz, for groups 2 and 3 it was 50 Hz, and for group 4 it was 60 Hz. The mechanical parameters of isotonic contraction were recorded by a strain gauge [8]. Changes of temperature in the muscle during contraction were measured by a thermoelectric method with copper-constantan and Chromel-Copelium thermocouples. The parameters were recorded photographically by a loop oscillograph and VÉKS-4M apparatus. The sensitivity of the temperature-measuring apparatus was 0.01 deg/cm, and the time taken for the temperature to rise from 0 to its maximum during instantaneous heating of the thermocouple did not exceed 80 msec.

EXPERIMENTAL RESULTS

The mean relative load (P_M) for the gastrocnemius (but not for the tibialis anterior) muscle changes significantly with age, reaching a maximum in age group 2, i.e., at the time of acquisition of the standing posture by rabbits (Table 1). The external work of isotonic tetanus (A_M) showed considerable age changes both in the tibialis anterior and in the gastrocnemius muscle. The value of A_M for the tibialis anterior arose gradually during individual development, and in adult rabbits it was 5.2 times higher than in animals aged 1 week. For the gastrocnemius muscle the value of A_M reached a maximum in age group 2. A_M for adult rabbits was 4.2 times higher than for animals aged 1 week.

The values of the mechanical efficiency η were determined for the phase of development [18] of isotonic tetanus of the gastrocnemius muscle with average loads and at a frequency of stimulation of f_0. The following equation was used for the calculations:

$$\eta = \frac{A_M}{c \cdot \Delta T + A_M} \cdot 100\%,$$

where A_M is the external work (per gram weight of muscle); c the specific heat of the muscle (0.8); ΔT the rise of temperature in the muscle in the phase of development of tetanus (in °C).

The values of η (Fig. 1) increased significantly with age, and in the adult rabbit they were almost twice as high as in the animals aged 1 week.

Arshavskii [5] puts forward the hypothesis that there are two forms of excessive anabolic responses to muscular exertion in developing animals. Whereas in the first form of anabolism there is excessive accumulation of the mass of living protoplasm, the second form is manifested by an excessive accumulation of physicochemical potentials during recovery, thus increasing the subsequent working capacity of the skeletal muscles. A frequent manifestation of this second form of excessive anabolism is the development of true Wedensky inhibition and excessive relaxation by comparison with the original length of the loaded muscle, which is a char-

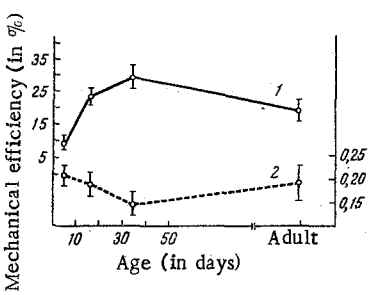

Fig. 1

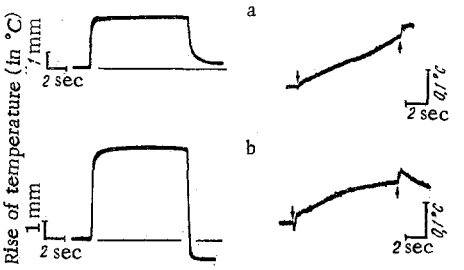

Fig. 2

Fig. 1. Mechanical efficiency (1) for phase of development of tetanus and complete rise of temperature, (2) of gastrocnemius muscle during isotonic tetanus for 10 sec in rabbits at different ages (with average loads and frequencies of stimulation f_0).

Fig. 2. Mechanical contraction (left) and changes in temperature (right) of gastrocnemius muscle during isotonic tetanus: a) rabbit aged 6 days, frequency of stimulation $f_0 = 30$ Hz, average load P = 13 g; b) rabbit aged 1.5 months, frequency of stimulation $f_0 = 50$ Hz, mean load P = 320 g.

acteristic feature of that state. In adult rabbits excessive relaxation can be observed both after true Wedensky inhibition [2, 5] and also after tetanus evoked by stimulation at the optimal frequency (Fig. 2b). In early postnatal life the phenomenon of excessive relaxation after tetanic contraction is not observed (Fig. 2a). At this age period the second form of excessive anabolism cannot take place in the animal.

Characteristic features of the curves showing the change in muscle temperature during contraction in the rabbits of group 1 were the absence of the first endothermic phase, to use Putilin's classification [10], the lower value of the heat of contraction, and the higher value of the heat of maintenance of contraction compared with adult animals (Fig. 2). The low value of the heat of contraction can be explained to some extent by the low value of the work performed [16, 17], while the high value of the heat of maintenance was evidently largely dependent upon the considerable dissipative effects in the muscles of the young animals during prolonged tetanus.

In a separate series of experiments, in order to detect the influence of the blood flow on the temperature effects of muscular contraction, the femoral artery was compressed a few seconds before stimulation and throughout the 10 seconds of tetanus of the gastrocnemius muscle. No changes were found in the temperature curves or in the amounts of work done under these circumstances.

The results of these experiments show that mechanical and energy parameters of the skeletal muscles undergo changes during individual development on account of a change in lability and conversion of the skeletal musculature from a tonic to a phasic-tetanic type of activity. This conversion differs for different groups of muscles and it depends on whether or not they perform mainly an antigravity (gastrocnemius) or locomotor (tibialis anterior) function after acquisition of the standing posture. The sharp increase in efficiency of isotonic tetanus found in these experiments in rabbits after acquisition of the standing posture can be explained by changes in the structural and functional parameters of the skeletal muscles at this period and the decrease in dissipative effects during muscular contraction.

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