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## Energy utilization by mammalian fast and slow muscle in doing external work

Recently Goldspink  $et\ al.^1$  have shown that the slow soleus muscle of hamster was about 5 times more efficient in maintaining isometric tension as far as ATP usage is concerned than the faster muscles of the same animal. The aim of the investigation reported here was to measure the efficiency of a mammalian slow muscle and a mammalian fast muscle under conditions where they are required to contract isotonically and to perform isotonic work.

There are two main biochemical methods available for measuring energy usage during contraction. These involve either inhibiting the creatine phosphotransferase using 2,4-dinitrofluorobenzene and assaying the depletion in ATP<sup>2</sup> or by inhibiting glycolysis and oxidative phosphorylation using iodoacetate and nitrogen and measuring the change in the creatine phosphate level<sup>3</sup>. Although the former method is more precise, we chose to employ the latter method as in this case the energy reserves are higher because both the ATP and creatine phosphate levels are available and the muscles are capable of doing more work.

Pairs of biceps brachii and solei muscles were dissected from mature male Syrian hamsters and placed in Krebs-Ringer bicarbonate buffer containing 1 mM iodoacetate for 30 min. The buffer was maintained at 2-4° and continually gassed with a mixture of  $N_2$ -CO<sub>2</sub> (95:5, v/v). After this 30-min incubation period the temperature of the muscles was elevated by briefly immersing them in the buffer solution maintained at 25°. One muscle of each pair was stimulated to give several brief tetanic contractions and then rapidly frozen by immersion in Freon 12 cooled to  $-160^{\circ}$  using a quick freezing apparatus as described by Cain and Davies<sup>4</sup>.

The contractions were recorded using an E.&M. isotonic lever myograph and physiograph pen recorder. The lever system was weighted with 5 g and 2 g for the biceps brachii and soleus, respectively. The other muscle of each pair acted as the control; they were treated in exactly the same way except they were not stimulated.

The frozen muscles were weighed and then pulverized, using a stainless steel tube and pestle precooled to  $-196^{\circ}$ . The muscles were then assayed for total creatine and free creatine<sup>5</sup> after extraction with cold  $HClO_4$ . The creatine phosphate levels of the muscles were obtained by subtracting the free creatine from the total creatine values. The work done by the stimulated muscles was calculated in  $g \cdot cm$  by multiplying the distance shortened by the muscle times the load.

The results of the experiment are shown in Table I. From Table I it can be seen that although the fast biceps brachii muscle used more creatine phosphate upon stimulation than did the slow soleus muscle, it also performed considerably more work. The efficiency when expressed as the work done per  $\mu$ mole of ATP was found to be more than twice as high in the case of the fast muscle (P < 0.1). The hamster biceps brachii has been shown¹ to have a rate of shortening of approx. 3 times faster than the soleus muscle. It seems that the longer cross bridge engagement time of the soleus muscle which causes it to shorten more slowly also makes the muscle less efficient for performing work. This is probably due to the fact that the myosin cross bridges that are pulling are working against those that are holding. The results support

TABLE I

CREATINE PHOSPHATE BREAKDOWN BY THE BICEPS BRACHII AND SOLEUS MUSCLES DURINGWORK

Pair No.	Muscle wt. (mg)		Creatine phosphate (µmoles/g)			Work done	
	Control	Stimulated	Control	Stimulateo	l Difference	by muscle (g·cm)	(g·cm·g <sup>-1</sup> ·μmole <sup>-</sup> creatine phosphate
Biceps brac	hii						
1	47.0	48.0	0.11	6.5	-4.5	89.0	412.0
2	52.0	52.0	13.5	6.6	-6.8	78.2	221.0
3	48.1	45.0	10.7	8.3	-2.4	98.0	493.5
4	69.0	72.0	14.6	6.6	-8.o	99.5	172.7
	64.1	62.1	14.4	6.2	-8.2	99.2	194.9
5 6	45.0	45.0	15.0	6.7	-8.3	131.0	350.7
7	59. I	70.1	8.8	4.7	-4.1	46.0	189.9
7 8	43.I	63.9	8.9	4.7	-4.2	53.2	301.3
9	48.0	61.0	8.9	5.8	-3.1	29.0	104.1
10	48.1	60.I	8.9	4.7	-4.2	70.2	356.2
Mean	·						
$\pm$ S.E.	52.3	57.9	11.4	6.0	$-5.4 \pm 0.7$	79.3	$279.5 \pm 38.8$
Soleus							
I	30.0	30.0	5.9	0.4	-5.5	II.I	66.0
2	21.0	23.1	5.5	0.4	5.1	5.3	49.4
3	23.1	25.0	4.2	0.4	-3.8	15.0	177.3
4	18.0	20.0	4.5	0.3	-4.2	23.2	306.8
5 6	31.1	31.1	4.3	0.6	-3.7	16.8	146.4
6	32.1	32.0	5.2	0.5	-4.7	15.3	102.0
7	37.0	33.1	6.4	3.9	-2.5	5.2	56.2
8	34.0	37.0	3.5	2.4	-1.1	5.2	165.7
9	31.0	35.0	4.7	2.5	-2.2	6.0	87.9
10	35.0	34.I	6.4	2.7	-3.7	12.3	99.9
Mean							
$\pm$ S.E.	29.2	30.0	5.0	1.4	$-3.6 \pm 0.4$	11.5	$125.8 \pm 22.6$

the suggestion<sup>1</sup> that the fast muscles have evolved for efficiency in performing work whilst the slow muscles have evolved for efficiency in maintaining isometric tension.

This work was supported by a research grant from the Muscular Dystrophy Associations of America. The authors also wish to acknowledge the expert technical assistance provided by Mr. S. E. Waterson.

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Received April 27th, 1970

Biochim. Biophys. Acta, 216 (1970) 229-230

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