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THE CONTENTS OF HIGH-ENERGY PHOSPHATES IN DIFFERENT FIBRE TYPES IN SKELETAL MUSCLES FROM RAT, GUINEA-PIG AND MAN

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SUMMARY

1. The contents of high-energy phosphates at rest have been measured in skeletal muscles with different fibre-type composition from rat, guinea-pig and man. All muscles studied biochemically have been characterized histochemically.

2. Fast-twitch muscles had a higher ATP/ADP ratio than slow-twitch muscles and, with the exception of the tongue in the rat, higher contents of ATP and phosphocreatine.

3. There was an inverse relationship between the content of phosphocreatine and the stainability for succinyl dehydrogenase, which is a marker enzyme for oxidative capacity.

4. The biochemical and histochemical data are discussed in relation to known morphological and functional properties of the different muscle-fibre types. It is concluded that fast-twitch fibres have a high ATP/ADP ratio favouring a fast acceleration of energy production. The content of phosphocreatine seems to be related to the glycolytic capacity but not to the contraction time. In addition to being an immediate energy source, phosphocreatine functions as a buffer against lactic acidosis.

INTRODUCTION

It has been known for more than a hundred years that the red and white colours of muscle fibres are associated with slow and fast contractions (Ranvier, 1874). This finding has been extended by the intense research during the last twenty years in order to relate different histochemical profiles of whole muscles and single motor units to physiological properties like speed of contraction and resistance to fatigue. For review of the literature and references see Close (1972) and Burke & Edgerton (1975).

In contrast to the vast number of studies on ATPase stainability and activity measurements *in vitro* of what are thought to be key enzymes in energy metabolism, very little work has been done to determine the actual contents of adenine nucleotides and phosphocreatine (PCr) in muscles with different functional characteristics. This

is somewhat surprising since ATP and PCr are the immediate energy sources at the onset of muscular contractions and the ratios of ATP/ADP and ATP/AMP are considered to be the main regulators of oxidative and glycolytic energy metabolism (Newsholme & Start, 1974; Beis & Newsholme, 1975; Williamsson, 1979).

The data concerning differences in concentrations of ATP and PCr in fast and slow muscles published so far have appeared as side observations in papers dealing with other problems (Baldwin & Tipton, 1972; Essén, 1978; Holloszy, Winder, Fitts, Rennie, Hickson & Conlee, 1978) or been treated as facts, making comparisons between different muscles more difficult (Fitch, Chevli, Petrofsky & Kopp, 1978). Beis & Newsholme (1975) made a very detailed investigation in muscles from several animal species, where they found a positive correlation between the ATP content and the ATP/AMP ratio and the capacity to accelerate energy utilization and thus energy production. However, the few mammalian muscles studied by them were not specified. In the hamster Goldspink, Larson & Davies (1970) found that muscles which fatigue quickly have higher contents of ATP at rest than fatigue-resistant muscles.

The object of the present study was to compare animal and human muscles with different fibre-type composition as to their contents of high-energy phosphates at rest. All muscles studied biochemically have been characterized histochemically, including staining for succinate dehydrogenase (SDH), which is a commonly used marker enzyme for oxidative capacity.

A preliminary account has appeared elsewhere (Hultman, Sjöholm, Sahlin & Edström, 1980).

METHODS

The present work is part of a project which has been approved by the Ethical Committee of the Karolinska Institute, Stockholm, Sweden.

Human biopsies. Six healthy volunteers (three male and three female) aged 18–34 years participated in the present study. None of the subjects was especially well trained but most of them regularly took part in some form of physical activity. In every case the nature and purpose of the study was explained to the subjects before their voluntary consent was obtained.

Tissue material was obtained from the vastus lateralis of the quadriceps femoris muscle by the needle biopsy technique described by Bergström (1962). The forceps technique of Radner (1962) was used to take biopsies from soleus. The incisions were made about 10 cm proximal to the cranial edge of patella and on the lateral part of the leg halfway between the lateral malleolus and caput fibulae. Care was taken to make the biopsies on exactly corresponding sites. The advantage of the Bergström technique is that several small pieces of muscle can be obtained in one puncture from a large muscle such as vastus lateralis. The advantage of the Radner technique is the better control of biopsy depth. This is of great importance when performing a biopsy selectively on a smaller muscle such as soleus or gastrocnemius.

The biopsy material was quickly frozen in liquid Freon maintained at its melting point (−150 °C) by liquid nitrogen. With the Radner technique two biopsies were obtained from the same incision; the first one was always used for biochemistry and the second for histochemical fibre-type analysis. With the Bergström technique the biopsy specimen was cut in two pieces after freezing.

Animal muscle specimens. Muscles from adult male guinea-pigs and adult male albino rats of the Sprague-Dawley strain were freshly frozen in the same way as the human biopsy specimens. Care was taken not to damage the muscle before it could be cut off and quickly frozen, and thus the preparation procedures were reduced to a minimum. Corresponding parts of the muscles were investigated biochemically and histochemically.

Histochemical methods and fibre typing. The freshly frozen specimens were cut in a cryostat operating at −20 °C. Cross-sections of the muscle were stained for ATPase according to Brooke

& Kaiser (1970) at pH 9·4 with or without acid pre-incubation. The muscles from man and guinea-pig were pre-incubated at pH 4·3 and 4·6 and the muscles from rat at pH 4·3 and 4·5 (Dubowitz & Brooke, 1973). Succinate dehydrogenase (SDH) was stained according to Nachlas, Tsou, de Souza, Cheng & Seligman (1957) with some modification (cf. Nyström, 1968). The profile of stainability for acid- and alkali-stable ATPase was determined by photographic recording of serial sections stained differentially, and the muscle fibres were classified as type I, IIA, IIB and IIC according to Brooke & Kaiser (1970). The fibre-type frequencies in human biopsies were based on 2598 fibres identified in soleus muscle and 4513 identified in the biopsies from the lateral vastus of quadriceps femoris muscle. No single biopsy contained less than 150 fibres which were possible to classify. The classification based on differences in ATPase stainability has a functional implication as it corresponds to differences in contraction speed in different muscle-fibre populations (Kugelberg, 1973; Burke, Levine, Tsairis & Zajac, 1973).

As the two human muscles investigated were biopsied bilaterally the fibre-type spectrum from corresponding biopsy sites could be compared and expressed as a standard deviation from duplicate determinations (S.D.) or a coefficient of variance (C.V.).

For vastus lateralis values obtained for the percentage of type I, IIA and IIB fibres were S.D. = 9·6, 8·5 and 5·3 % and C.V. = 23·4, 21·8 and 26·3 % respectively. For soleus the corresponding values for the percentage of type I, IIA and IIB fibres were S.D. = 6·2, 4·7 and 6·9 % and C.V. = 9·6, 19·6 and 76·7 % respectively. Thorstensson (1976) has performed unilateral double biopsies on vastus lateralis in ten healthy young volunteers using the Bergström technique and reported a C.V. of 10 % for determination of the frequency of FT fibres (corresponding to type II fibres).

Biochemical methods. Samples were freeze-dried, dissected and extracted with $HClO_4$ (0·5 M) as previously described (Harris, Hultman & Nordesjö, 1974). The neutralized extract was analysed for ATP, ADP, AMP, PCr and free creatine by enzymatic methods according to Harris *et al.* (1974).

RESULTS

Histochemical characterization of the muscles investigated

Man. Criteria for muscle fibre-type classification are given in the legend to Pl. 1 (left row) and the fibre-type spectra of soleus and vastus lateralis are presented in Table 1. In most biopsies type I, IIA and IIB fibres were easily identified. Type IIC fibres were identified in less than half of the biopsies and then at a low frequency, which is in accordance with earlier concepts of normal skeletal muscles (Brooke & Kaiser, 1970; Dubowitz & Brooke, 1973).

All fibres with a high or intermediate stainability for SDH were of type I and thus all type II fibres were weakly stained (cf. Edström & Nyström, 1969). Further, type IIA fibres tended to have a slightly higher activity of SDH than type IIB. This difference in SDH activity between type I and type II fibres has been confirmed by quantitative determination of SDH activity in single muscle fibres (Essén, Jansson, Henriksson, Taylor & Saltin, 1975).

As expected, the type I fibres were more numerous in soleus than in vastus lateralis and, on the basis of an interindividual comparison, all biopsies from soleus exhibited a higher frequency of type I fibres than the corresponding biopsy from vastus lateralis. The mean difference was $24{\cdot}3 \pm 5$ % which is highly significant ($P < 0{\cdot}005$). Saltin, Henriksson, Nygaard, Andersen & Jansson (1977) reported that soleus has 25–40 % more type I fibres than other leg muscles.

Animal muscles. Plates 1 (right row) and 2 demonstrate the muscles investigated from the guinea-pig and Pls. 3 and 4 the muscles from the rat, and their fibre-type spectra are presented in Table 1. The relation between the type of fibre defined on basis of stainability for ATPase and its content of SDH is more complex in these small

laboratory animals than in man. In the muscles from the guinea-pig and rat the following relations were commonly valid: type I fibres were intermediately stained for SDH, type IIA fibres highly or intermediately stained, whereas type IIB fibres typically had a low stainability.

In the guinea-pig the red part of quadriceps femoris (Pl. 2, left row) was composed of about 10 % type I fibres and a mixture of type IIA and IIB fibres. All type II fibres

TABLE 1. Frequency of fibre types in different skeletal muscles from man, rat and guinea-pig; n = numbers of volunteers and number of animal muscles investigated respectively. In man the percentage of fibres is expressed as mean ± S.D. A mean value of the two bilateral biopsies from corresponding biopsy sites are presented for each volunteer

		Fibre types (%)				
Species	Muscle	I	IIA	IIB	IIC	n
Man	Vastus lateralis	41 ± 10	39 ± 10	20 ± 6	0	6
	Soleus	65 ± 11	24 ± 7	9 ± 7	2 ± 0	6
Rat	Psoas	0	0	100	0	5
	E.d.l.	2	24	74	0	5
	Soleus	96	4	0	0	5
	Tongue	0	20	80	0	5
Guinea-pig	Quadriceps femoris					
	White part	0	10	90	0	4
	Red part	10	41	48	1	4
	Soleus	100	0	0	0	4

in this part of the muscle had, however, a high or intermediate stainability for SDH. The white part of quadriceps femoris had a dominance of large fibres with a low content of SDH (Pl. 2, right row). Soleus was a uniform type I muscle (Pl. 1, right row).

In the rat, four muscles were investigated and three were almost exclusively type II muscles with different contents of fibres with high or low stainability for SDH. Thus the part of the tongue investigated was found to be composed of only type II (mainly IIB) fibres which all had a high or intermediate stainability for SDH (Pl. 3, right row). Recent investigations on contractile properties of the tongue muscles in the cat revealed comparatively short contraction times (Hellstrand, 1979). The psoas muscle was composed exclusively of type IIB fibres, with a strong dominance for large fibres with a low content of SDH (Pl. 4, left row). Extensor digitorum longus (e.d.l.) (Pl. 4, right row) represented an intermediate muscle with a mixture of type IIA and type IIB fibres, mostly with low or intermediate stainability for SDH. In contrast to these almost exclusively type II rat muscles, soleus was dominated by type I fibres and had only a small fraction of type IIA fibres (Pl. 3, left row).

Muscle contents of high-energy phosphates

The ratio of ATP/AMP has not been calculated in this study due to a relatively large analytical error in the AMP determination.

Man. Vastus lateralis had significantly higher contents of ATP, total adenine

TABLE 2. Contents of high-energy phosphates in vastus lateralis and soleus from man. Metabolites are expressed as mmol/kg muscle. Values are means ± S.D. Significance of difference tested by Student's *t* test for paired values: $^{**}P < 0.01$, $^{*}P < 0.05$, n.s. = no statistical significance

	ATP	ADP	AMP	TAN	PCr	TCr	ATP/ADP
Vastus lateralis $n = 8$	27·05 ± 0·95	3·40 ± 0·25	0·08 ± 0·09	30·5 ± 1·2	82·1 ± 6·0	133·9 ± 7·7	8·0 ± 0·5
	*	n.s.	n.s.	*	*	**	n.s.
Soleus $n = 8$	24·30 ± 1·75	3·16 ± 0·40	0·03 ± 0·06	28·1 ± 1·8	76·1 ± 6·7	100·6 ± 8·9	8·0 ± 0·8

TABLE 3. Contents of high-energy phosphates in the white and red part of quadriceps femoris and soleus from the guinea-pig. Metabolites are expressed as mmol/kg dry muscle. Values are means ± S.D. Significance of difference between the white and red parts of quadriceps femoris and the red part of quadriceps femoris and soleus were tested by Student's *t* test: $^{***}P < 0.001$, $^{*}P < 0.05$, n.s. = no statistical significance

Quadriceps femoris	ATP	ADP	AMP	TAN	PCr	TCr	ATP/ADP
White part $n = 8$	35·3 ± 1·8	2·90 ± 0·40	0·15 ± 1·10	38·5 ± 1·9	76·3 ± 15·3	181·4 ± 6·1	11·6 ± 0·7
	n.s.	n.s.	n.s.	n.s.	*	***	*
Red part $n = 8$	34·1 ± 1·7	3·30 ± 0·35	0·23 ± 0·07	37·6 ± 1·7	57·5 ± 15·3	163·1 ± 10·5	10·5 ± 1·3
	***	n.s.	n.s.	***	n.s.	***	***
Soleus $n = 8$	19·9 ± 0·9	2·95 ± 0·35	0·10 ± 0·08	23·0 ± 1·4	55·1 ± 6·1	101·5 ± 2·8	6·8 ± 0·6

TABLE 4. Contents of high-energy phosphates in rat muscles. Metabolites are expressed as mmol/kg dry muscle. Values are means ± S.D. Significance of difference between psoas and e.d.l., e.d.l. and soleus and soleus and tongue were tested by Student's t test: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. = no statistical significance

	ATP	ADP	AMP	TAN	PCr	TCr	ATP/ADP
Psoas							
$n = 10$	29·6 ± 1·0	3·42 ± 0·43	0·20 ± 0·13	33·1 ± 1·1	93·9 ± 9·3	172·9 ± 4·4	9·0 ± 0·8
	**	n.s.	n.s.	**	*	***	n.s.
E.d.l.							
$n = 8$	28·0 ± 1·0	3·03 ± 0·33	0·19 ± 0·09	31·2 ± 1·0	82·9 ± 6·5	140·9 ± 5·8	9·4 ± 1·4
	***	n.s.	n.s.	***	***	***	***
Soleus							
$n = 7$	19·7 ± 2·3	3·18 ± 0·25	0·16 ± 0·07	23·1 ± 2·3	47·3 ± 6·6	98·4 ± 6·2	6·3 ± 0·8
	n.s.	***	*	n.s.	*	***	***
Tongue							
$n = 4$	20·3 ± 1·1	2·06 ± 0·37	0·35 ± 0·13	22·9 ± 0·9	39·8 ± 2·1	63·9 ± 4·2	9·3 ± 0·2
Heart							
$n = 12$	—	—	—	27·7 ± 1·3	—	64·0 ± 3·9	—

nucleotides (TAN = ATP + ADP + AMP) and total creatine (TCr = PCr + free creatine) as compared to soleus (Table 2). The ATP/ADP ratios were the same.

Animal muscles. It is uncertain to what extent the measured values of PCr really represent the values at rest. The muscles might have been partially activated in the course of dissection which would decrease the content of PCr. Muscle content of TCr is, however, unaffected by slight activation and it is reasonable to assume that muscles with a high content of TCr also have a high content of PCr at rest.

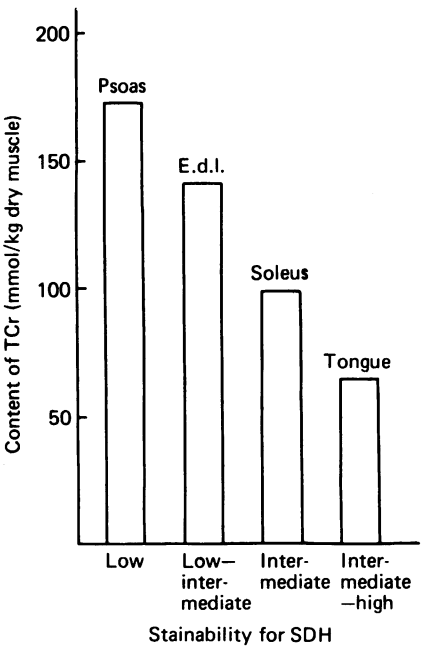

Fig. 1. Rat muscles. Stainability for SDH *versus* content of total creatine (TCr).

In the guinea-pig there was a clear difference in the metabolite content between soleus and the superficial white and deep red part of m. quadriceps femoris (Table 3).

Soleus has lower contents of ATP, TAN, TCr and a lower ATP/ADP ratio. The white part of m. quadriceps has a higher TCr content than the red part; otherwise these two parts of the same muscle are relatively similar.

In the rat we investigated four muscles representing the greatest differences possible in terms of fibre-type composition. For comparison the content of TAN and TCr in the heart are also included in Table 4. Soleus and the tongue had lower ATP contents than psoas and e.d.l. The ATP/ADP ratio was clearly lower in soleus which is a slow type I muscle compared to the other fast type II muscles where the ATP/ADP ratios were almost the same.

There was a large difference between the four rat muscles in their contents of TCr. Psoas had almost three times as much TCr as the tongue. An inverse relationship seemed to exist between the muscle-fibre stainability of SDH and its content of TCr

(Fig. 1). It is interesting to note that the heart has the same content of TCr as the tongue, which has the highest stainability for SDH of the skeletal muscles investigated, reflecting the highest oxidative capacity.

DISCUSSION

The variations in energy demand are greater in fast type II fibres designed for short-term phasic or rapidly alternating tonic activity than in slowly contracting type I fibres. The active state is shorter in fast muscle fibres (Wells, 1965) and they have a better developed sarcoplasmic reticulum (Schiaffino, Hanzliková & Pierobon, 1970; Briggs, Poland & Solaro, 1977) contributing to the shorter active state and the higher contraction and relaxation velocity. Fast muscle fibres have also higher myosin ATPase activities which, according to Barany (1967), should be the limiting step in the shortening rate. In line with that proposal, Kugelberg (1973) and Burke *et al.* (1973) found a positive correlation between speed of shortening of single motor units and the histochemical stainability for ATPase. In order to maintain the same sustained tension in fast and slow muscle fibres a higher rate of energy production is needed in the fast muscle fibres (Goldspink, Larson & Davies, 1970; Wendt & Gibbs, 1973), a fact which Goldspink *et al.* (1970) explained on the basis of the shorter active state in fast muscle fibres.

All these facts necessitate mechanisms in fast muscle fibres for a rapid acceleration of energy production. One such mechanism could be a high ATP/ADP ratio at rest, which according to Newsholme & Start (1974) is consistent with the theory of control of glycolysis, in which small changes in ATP concentration produce much larger relative changes in concentrations of ADP and AMP through the reaction catalysed by adenylate kinase:

$$2\,\mathrm{ADP} \rightleftharpoons \mathrm{ATP} + \mathrm{AMP}.$$

According to this theory, the higher the resting ATP/ADP and ATP/AMP ratios the greater the change in concentration of AMP for a given change in that of ATP and thus an increased stimulation of glycolysis. The ATP/ADP ratio in the cytoplasm is considered to be the main regulator of mitochondrial oxidative phosphorylation (Williamsson, 1979). A rapid decrease of a high ATP/ADP ratio at the onset of activity would thus also accelerate oxidative phosphorylation.

If, as proposed by Carlson & Siger (1959) and Serayderian, Mommaerts & Wallner (1962), ADP is protein bound to a large extent whereas ATP and AMP are not, the physiologically relevant ATP/ADP ratios would be much higher than the ones measured and consequently much more reduced during activity. This would increase the relevance of the theory of metabolic regulation by changes in the ATP/ADP and ATP/AMP ratios.

In the guinea-pig and rat the muscles representing different combinations of fast type II muscles had higher ATP/ADP ratios than the slowly contracting soleus muscles which contain almost exclusively type I fibres. The tongue and soleus in the rat are both oxidative muscles, and the rat tongue has a higher ATP/ADP ratio. The tongue is however a fast muscle (Hellstrand, 1979) compared to soleus.

No clear difference in mitochondrial content in different muscle-fibre types has been

shown and the mitochondrial volume in muscle is only around 5 % of the cell volume (Buchthal & Schmalbruch, 1980). The influence of the mitochondrial ATP/ADP ratio on the total ATP/ADP ratio will consequently be small.

It thus appears that fast-twitch muscles have a higher ATP/ADP ratio in the cytoplasm than more slowly contracting muscles. This will create a higher capacity for acceleration of energy production which seems to be an adaptation to the contraction characteristics of the muscle.

In the four rat muscles investigated there was an inverse relationship between the content of TCr, which would reflect the content of PCr at rest, and the stainability for SDH. Thus in fast muscles dependent on glycolytic activity there is a high content of PCr as an immediate energy source via phosphorylation of ADP. Utilization of PCr occurs via the creatine kinase reaction:

$$H^+ + PCr + ADP \rightleftharpoons ATP + Cr.$$

Breakdown of PCr will thus also liberate base and this is one of the main buffers against acidosis due to lactic acid formation during periods of high rates of glycolysis (Sahlin, 1978). Muscle fibres which possess a high glycolytic capacity thus have a high buffer capacity due to a high content of PCr. It may even be possible that there is an initial slight alkalinization at the onset of phasic activity (Steinhagen, Hirche, Nestle, Bovenkamp & Hasselmann, 1976) due to the creatine kinase reaction, which would further accelerate glycolysis (Danforth, 1965; Lowry & Passoneau, 1966).

Gauthier (1969) and Schiaffino *et al.* (1970) have reported that muscle fibres with a high stainability for SDH also have more and larger mitochondria with better developed cristae. Consequently they should be less dependent on glycolysis. A high stainability for SDH has been shown to be a good marker for resistance to fatigue (Edström & Kugelberg, 1968; Burke *et al.* 1973; Kugelberg & Lindegren, 1979). This is also valid for the heart, a muscle which hardly fatigues.

Plates 1–4 demonstrate that muscle fibres from man have a greater diameter than animal muscle fibres and also a different appearance. Moreover, different muscle fibres from man are more intermingled in the muscle as a whole compared to animal muscles which are either more homogeneous with regard to fibre type or organized in more pronounced superficial white and deep red layers. On the basis of such morphological differences it is doubtful whether similar histological staining profiles in human and animal muscles always reflect the same functional properties.

In man the ATP/ADP ratio is the same in soleus and vastus lateralis but it is not known if there are any differences in contraction time between motor units in these two muscles. Soleus has a lower TCr content which is in line with the higher proportion of type I fibres with high SDH stainability.

Recently Rehunen & Härkönen (1980) reported that there are no differences in the contents of ATP and PCr between single type I and type II fibres from vastus lateralis in man. However, the contents of ATP and especially PCr seemed to be reduced below normal in this investigation.

In conclusion, fibres which have a short contraction time, well developed sarcoplasmic reticulum and high ATPase stainability have a high ATP/ADP ratio, favouring a fast acceleration of energy production. The content of TCr (and PCr) seems to be correlated with the glycolytic capacity, inversely related to the

stainability for SDH and not related to the contraction time. It should be remembered that in addition to being an immediate energy source, PCr functions as a buffer against lactic acidosis.

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EXPLANATION OF PLATES

PLATE 1

Photomicrographs of serial sections from human soleus muscle (left vertical row) and guinea-pig soleus muscle (right vertical row). Upper sections stained for ATPase at pH 9·4, middle sections stained for ATPase at pH 9·4 after pre-incubation at pH 4·6 and lower sections stained for SDH.

In the left row (human soleus muscle) a cross indicates the position of two type I fibres with a low content of alkali-stable ATPase, a high content of acid-stable ATPase and a high content of SDH. A bar indicates the position of two type II fibres with a high content of alkali-stable ATPase and a low content of SDH. The stainability for ATPase after pre-incubation at pH 4·6 (middle section) is low in the fibre to the right (a type IIA fibre) and intermediary in the fibre to the left (a type IIB fibre).

In the right row (guinea-pig soleus muscle) all fibres have the same stainability, corresponding to a homogeneous population of type I fibres with a low stainability for alkali-stable ATPase (upper section), a high stainability for acid-stable ATPase (middle section) and an intermediary SDH content (lower section). A cross in all three sections facilitates the comparison.

PLATE 2

Photomicrographs of serial sections from guinea-pig quadriceps femoris muscle, illustrating the difference in fibre composition between the red part of the muscle (left vertical row) and the white part (right vertical row). Upper sections stained for ATPase at pH 9·4, middle sections stained for ATPase at pH 9·4 after pre-incubation at pH 4·6, and lower sections stained for SDH. In the red part (left row) type I fibres (one indicated by a cross) are dominating. As obvious from the middle section, the type II fibres are of both type IIA (unstained) and type IIB (intermediate stained) but they all have a high or intermediary content of SDH.

In the white part (right row) a large sized type IIB fibre (as indicated by o) with a low content of SDH is dominating.

PLATE 3

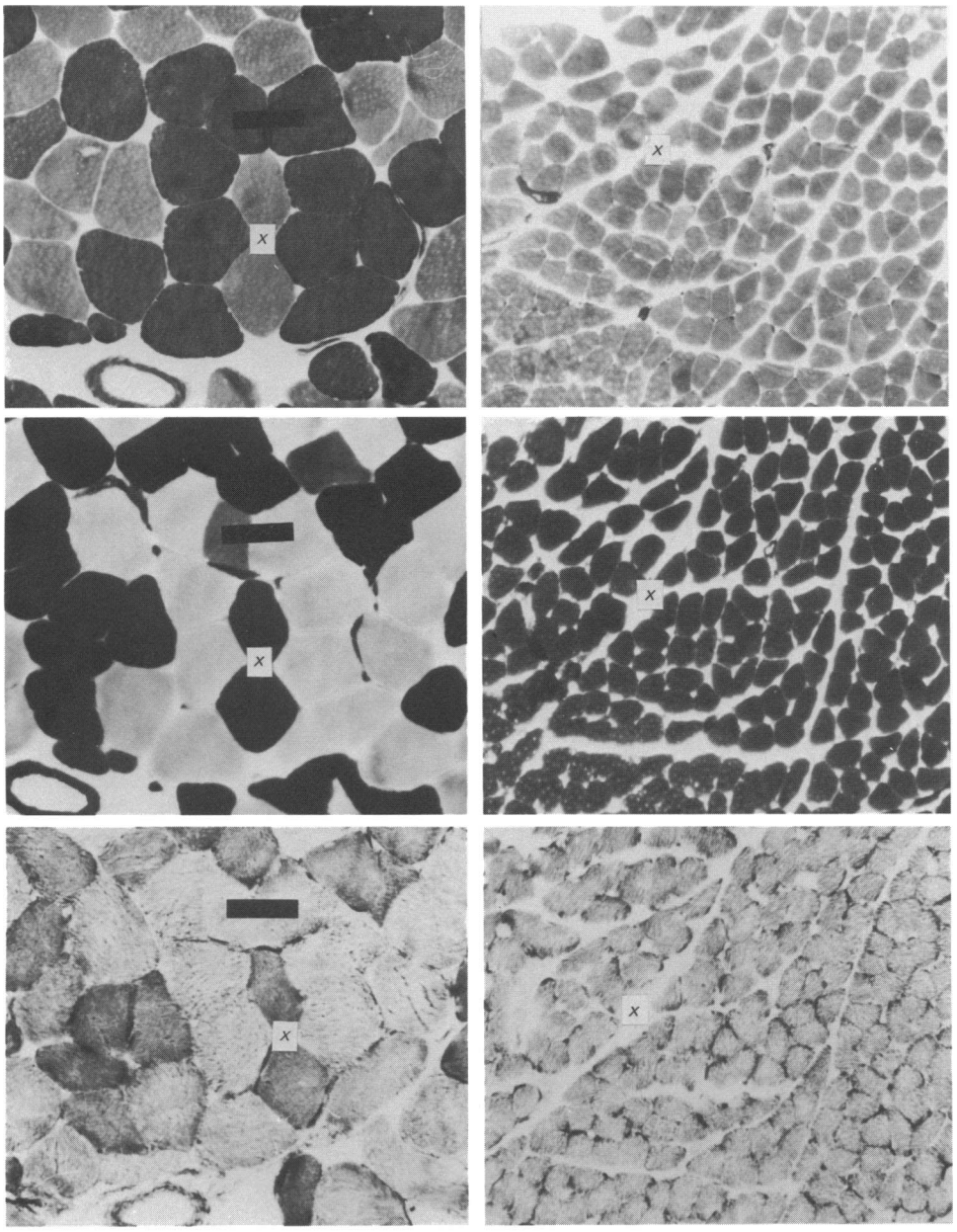
Photomicrographs of serial sections from rat soleus (left vertical row) and tongue (right vertical row). Upper sections stained for ATPase at pH 9·4, middle sections stained for ATPase at pH 9·4 after pre-incubation at 4·5 and lower sections stained for SDH.

Type I fibres are dominating in the soleus but there are also type IIA fibres (one indicated by a cross) which has a somewhat higher content of SDH than the type I fibres. In the tongue (right row) all fibres are of type II as indicated by their high stainability for alkali-stable ATPase in the upper section. Most of them are of type IIB as indicated by their intermediate stainability for acid-stable ATPase, but there are some type IIA fibres visible which lack stainability for acid-stable ATPase (middle section). All fibres have a high or intermediate stainability for SDH as illustrated in the lower section.

PLATE 4

Photomicrographs of serial sections from rat psoas muscle (left vertical row) and e.d.l. muscle (right vertical row). Upper sections stained for ATPase at pH 9·4, middle sections stained for ATPase at pH 9·4 after pre-incubation at pH 4·5 and lower sections stained for SDH. The psoas muscle (left row) is exclusively composed of type IIB fibres which are mostly of low stainability for SDH. There is a minority of small fibres characterized by a high or intermediate stainability for SDH, as shown in the fibre indicated by a horizontal arrow.

The e.d.l. muscle is also dominated by type II fibres although there are a few of type I (one indicated by a horizontal arrow). Two type IIA fibres are indicated by a vertical arrow in the upper part of the sections. They have a high content of SDH. Two type IIB fibres are indicated by a bar in the lower right part of the sections. They exhibit a low and intermediate stainability for SDH.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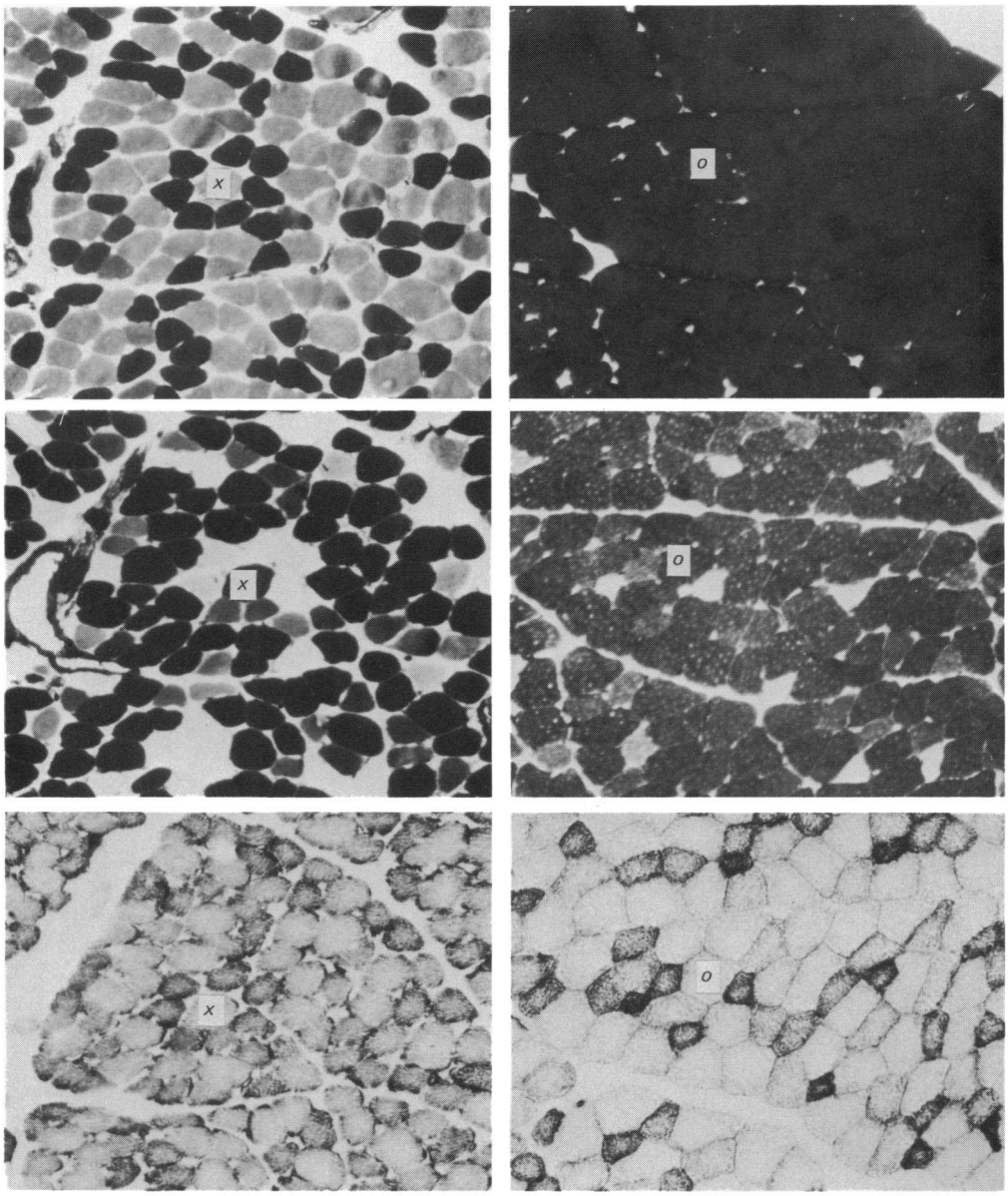
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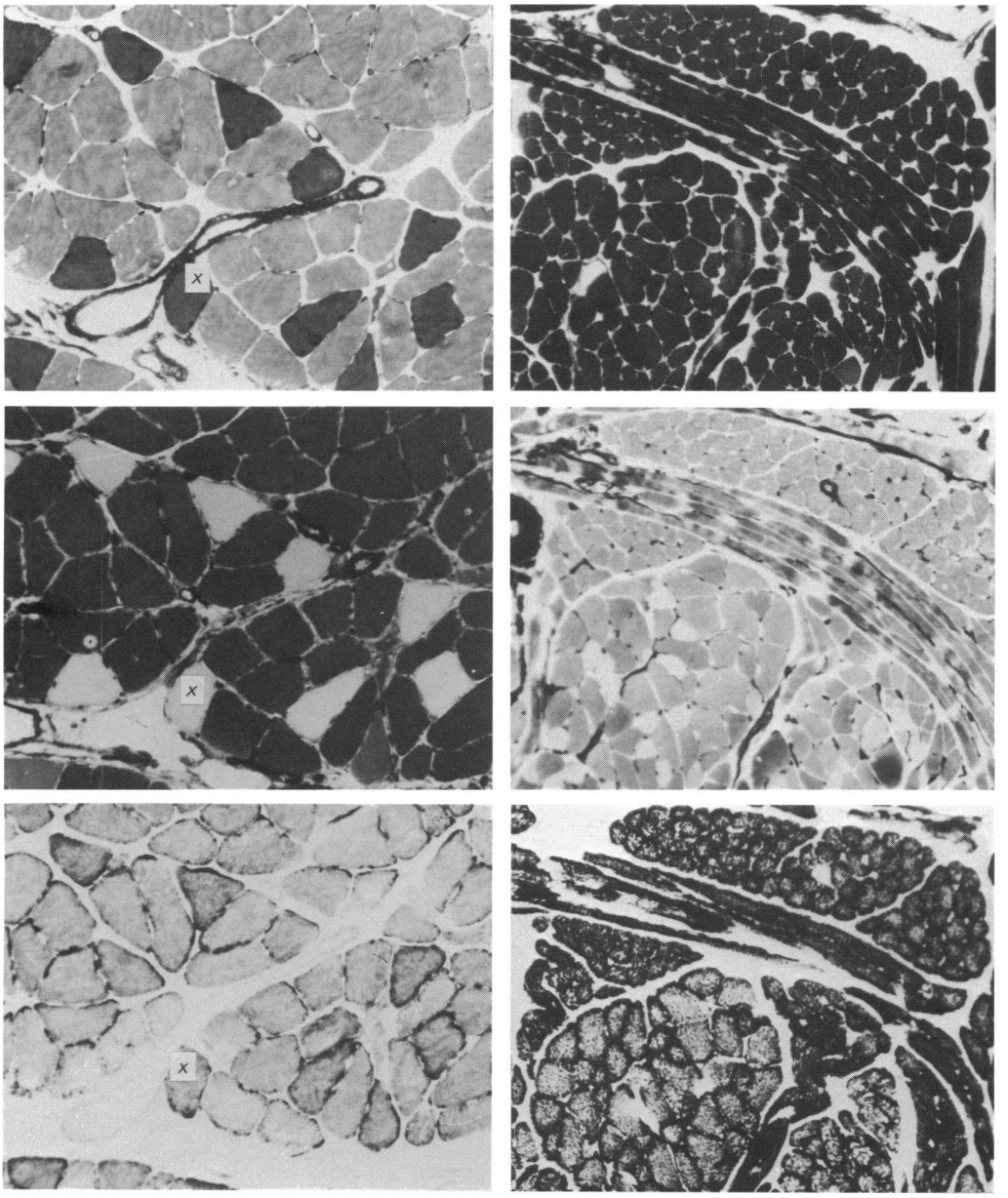
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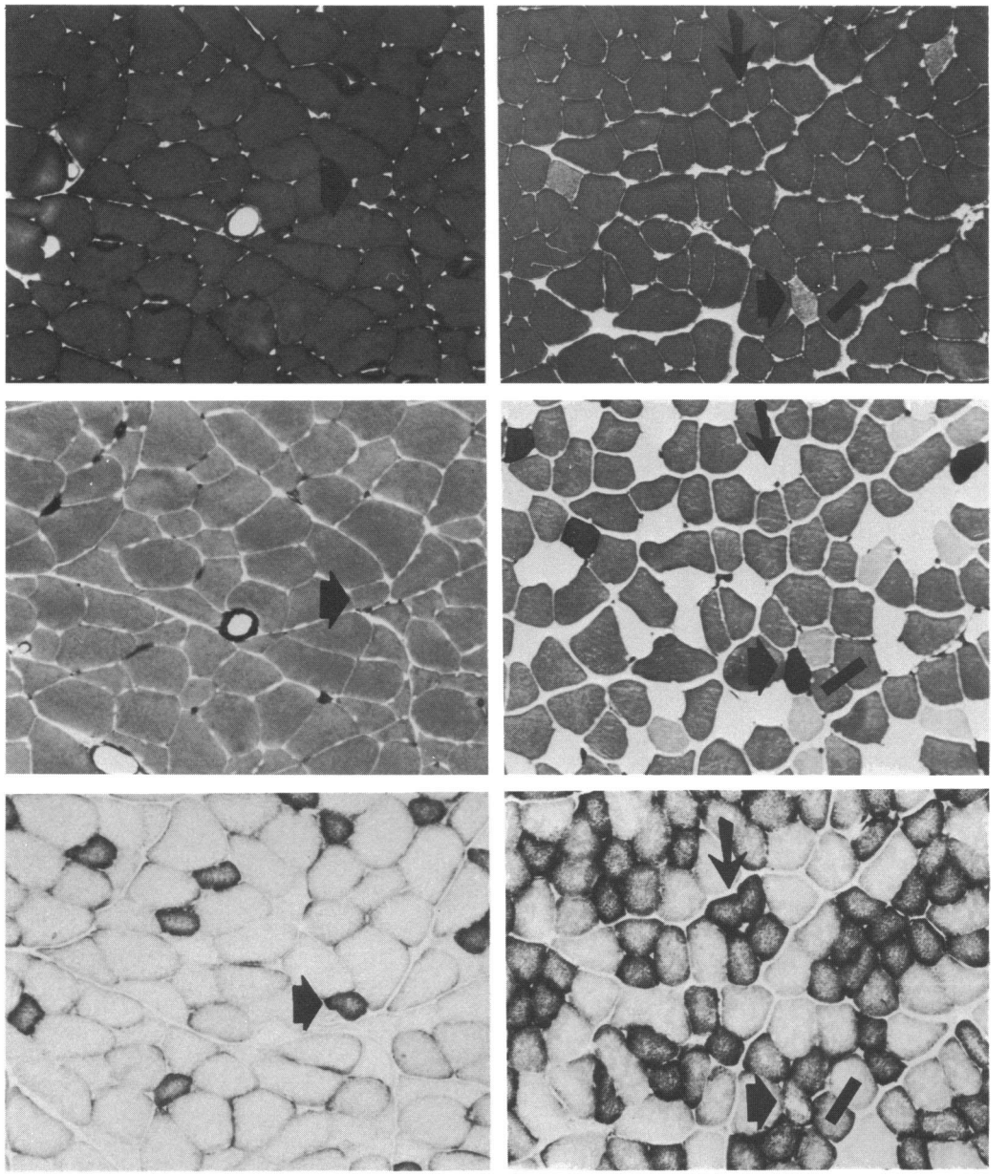

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