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*Original paper* ■

# Fiber Type Composition and Size of Fibers in the Rat Tibialis Anterior Muscle

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**SUMMARY**

**Muscle fiber types and their metabolic and size properties, key determinants of muscle function, can be altered by variety of factors. The aim of this study was to evaluate and compare the fiber type composition and size of fibers in the tibialis anterior (TA) muscle of young adult male and female rats, using histochemical and morphometric methods. Combined myofibrillar ATPase after preincubation at pH 4.3, 4.5, 9.4 and 10.4, and metabolic enzyme histochemistry were performed on serial cross-sections of TA from 10 rats (12- week-old).**

**Three main fiber types (I, IIA, and IIB) and IIX-like fibers were identified by myofibrillar ATPase histochemistry. These fiber populations showed differences in their oxidative potential, too. The succinate dehydrogenase activity decreased in the rank order IIA>I> IIX-like>IIB. There was no significant difference between males and females in the fiber-type composition. The TA muscle of both groups contained 48.5% type IIA and IIX-like fibers (the proportion of which was approximately equal), 47.2 % type IIB and only 4.3% type I fibers.**

**In conclusion, this study demonstrates that there is no sex-related difference in fiber type composition of the rat TA muscle and confirms an inverse correlation between fiber size and oxidative potential, and that IIX-like fibers make a significant population of fast-twitch fibers.**

***Key words:*** **skeletal muscle, fiber types, myofibrillar ATPase, succinate dehydrogenase, morphometry, fiber size, rat**

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## INTRODUCTION

The phenotypic differences among muscle fiber types, their potential of adaptability and the underlying mechanisms that control the range of fibers' heterogeneity and adaptability have been a topic of study for several decades. Most mammalian skeletal muscles are heterogeneous in composition, containing mixtures of fiber types with different morphological, contractile and metabolic properties (1-5).

In histochemical studies of skeletal muscles, the fibers are usually categorized into three main types based upon differences in myofibrillar adenosine triphosphatase (mATPase) activity. They have been designated as slow-twitch type I and fast-twitch type IIA and IIB according to the classification of Brooke and Kaiser (6). A second tripartite classification based on the use both mATPase and mitochondrial enzyme activities, and fiber types referred to as slow-twitch oxidative (SO), fast-twitch oxidative glycolytic (FOG) and fast-twitch glycolytic (FG) (1). It has been suggested that there is a close correlation between the fiber types as defined with the two classification systems (7).

By applying combined methodology, a new fast-twitch group of fibers was identified and referred as FOG-acid resistant (8), fast-twitch oxidative (FO) (4), and IIBd (9). Lind and Kernell (9) suggested that IIBd fibers probably correspond to the type IIX fibers of Schiaffino et al. (10), which has the myosin heavy chain (MHC) isoform different from those found in IIA and IIB fibers (10).

The fiber type composition varies among muscles in respect to their function. Hence, the slow soleus muscle of the rat is composed predominantly of slow-twitch type I fibers, while fast limb muscles are composed predominantly of fast-twitch fiber types (4, 11-17). The relative proportions of each fiber type vary between homologous muscles of different species (11, 15), and even in different regions of the same muscle (12-14, 16, 18). The muscle regionalisation may be related to functional requirements, suggesting that the expression of this phenomenon gives some kind of functional advantage for the animal (19).

Although fiber type composition of the rat tibialis anterior muscle (a fast-twitch dorsiflexor of the ankle) has been extensively investigated, reported data vary considerably and could result from the use of different methods of quantitative analysis and for muscle fiber typing by various investigators (4, 11-14, 16, 18, 20, 21). The influence of age and strain of the animals studied should also be considered. The age-related changes in muscle fiber composition and their size of nine rat muscles (including the tibialis anterior muscle) have been investigated (4). However, a comparison of these parameters between male and female animals of the same age has received less attention.

Thus, the aim of this study was to undertake a comparative investigation of fiber type composition and size of fibers in the tibialis anterior muscle of young adult male and female rats to determine whether these morphometric parameters vary according to the sex of animals.

## MATERIAL AND METHODS

Ten young adult Wistar rats (5 male and 5 female), weighing 200-250 g (12 weeks old), were used in this study. The tibialis anterior (TA) muscle was removed under ether anesthesia. The muscle samples were rapidly frozen in isopentane cooled to -160 °C by liquid nitrogen. Serial cross-sections (10μm thick) were cut from the midbelly region of each muscle in a cryostat at -22 °C.

The sections were stained for mATPase activity after preincubation at pH values of 4.3, 4.5, 9.4 and 10.4 (6, 22) combined with formaldehyde fixation for alkaline preincubation at pH 10.4 (23). Additional sections were stained for succinate dehydrogenase (SDH), NADH-tetrazolium reductase (NADH-TR) and α-glycerophosphate dehydrogenase (α-GPDH) activities (22).

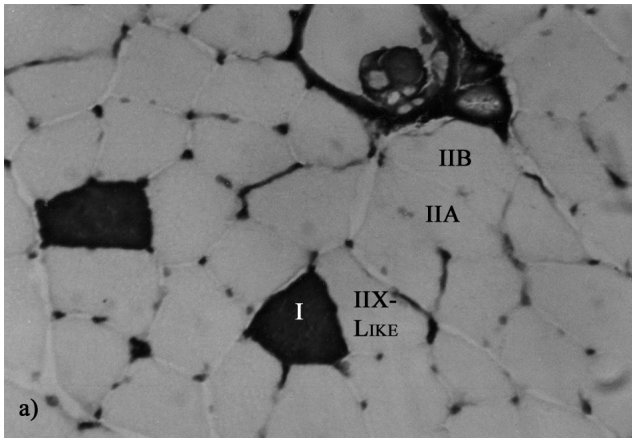
The histochemical profile based on staining reactions of each fiber type in serial sections was established and classified as type I, IIA, IIB (corresponding to SO, FOG, and FG fibers, respectively). However, the fibers displaying an intermediate behavior between type IIA and type IIB fibers were also found. These fibers we provisionally refered as IIX-like, and with regard to their histochemical profile and size were included within the type IIA fiber class for purpose of quantitative analysis.

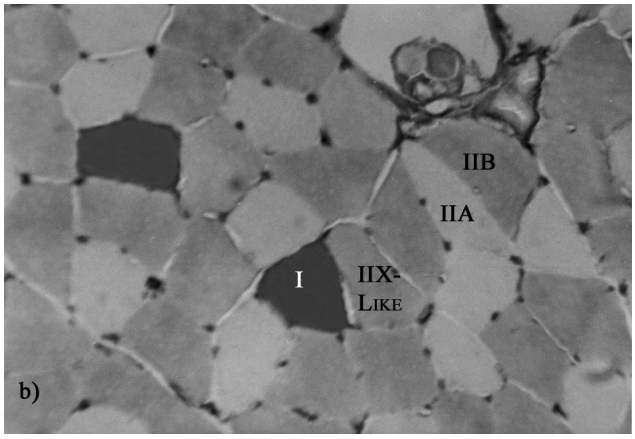
For the morphometric analysis, the image of the TA muscle (in cross-section) was projected on to the screen of a demonstration microscope and magnified to a constant size. Serial sections of muscles stained for mATPase and SDH were analyzed. The relative proportion of fiber types for each muscle was determined from direct counts of fiber numbers in 20 square areas of defined size (showing 80-120 fibers), including both, deep-red and superficial-white muscle portions. The pooled data obtained from each measurement were used to determine the mean proportion of each fiber type.

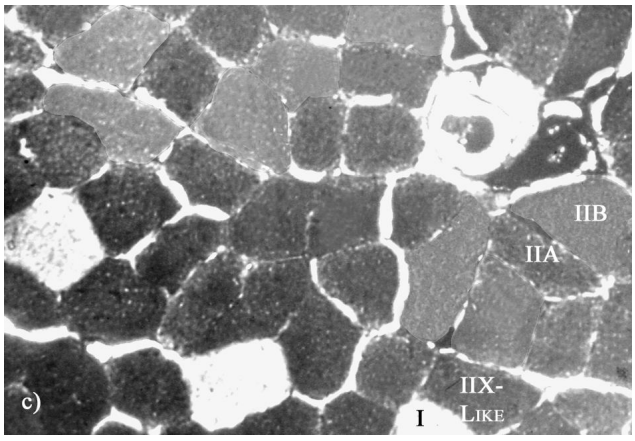
The size of the muscle fiber types was determined by measuring the "lesser fiber diameter", since this measurement is the least affected by obliquity of the section or kinking of the muscle fiber (22). Measurement was performed on 100 fibers of each type on the demonstration screen of the microscope. The pooled measurements obtained for each fiber type were used to calculate the mean values. Group values of morphometric parameters are expressed as means ±SD. The differences between the mean values for male and female groups were analyzed by Student's t test. Differences were considered statistically significant at $p<0.05$.

## RESULTS

Three main fiber types (I, IIA, and IIB) and IIX-like fibers were identified in the rat TA muscle by mATPase histochemistry. Type I fibers stained dark after acid preincubation (pH 4.3 and pH 4.5) and light after alkaline preincubation (pH 9.4 and 10.4) (Figure 1a-c). The reverse was true for type IIA fibers. Type IIB and IIX-like fibers stained light after preincubation at pH 4.3 and medium after preincubation at pH 4.5, but IIX-like fibers stained darker than IIB fibers after alkaline pretreatment (pH 10.4), as being formaldehyde-resistant (Figure 1a-c).



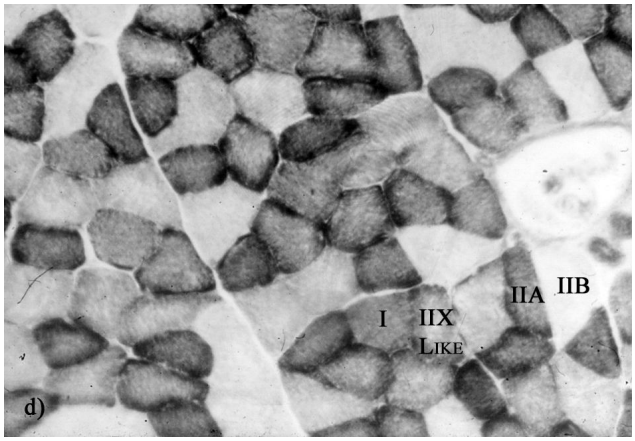




***Figure 1.*** *Serial cross-sections of rat tibialis anterior muscle stained for myofibrillar ATPase (mATPse) after preincubations at pH 4.3*
*(a), pH 4.5*
*(b) and pH 10.4*
*(c) and for succinate dehydrogenase (SDH)*
*(d) The fibers are labeled coresponding to type I, IIA, IIB and IIX-like fibers (Bar=50μm)*

The fiber types identified on the basis of mATPase activity were compared to the fiber's SDH (and NADH-TR) and α-GPDH activities that provided an indication of their oxidative and glycolytic potential, respectively. In general, type IIA fibers showed high SDH and intermediate α-GPDH activity (Figures 1d and 2). Type I fibers exhibited moderate to high SDH but the lowest α-GPDH activity, whereas type IIB fibers which possessed the highest α-GPDH activity were almost uniformly low in oxidative enzyme activity (SDH, NADH-TR) (Figures 1d and 2).

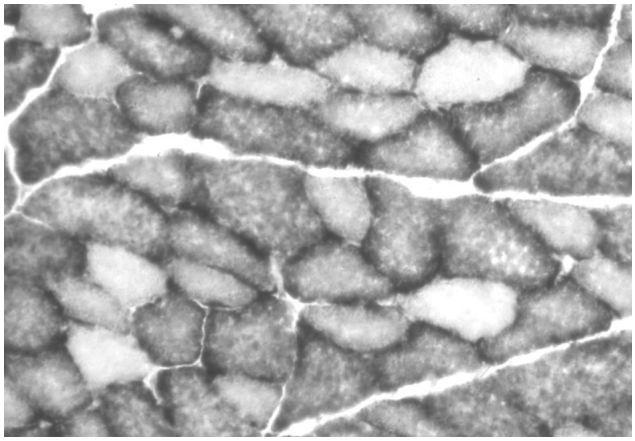


***Figure 2****. Cross-section of rat tibialis anterior muscle stained for α-glycerophosphate dehydrogenase (α-GPDH) (Bar=50μm)*

IIX-like fibers generally showed moderate activities of SDH and NADH-TR. Their α-GPDH activity appeared to be rather variable. SDH activity as an indicator of

oxidative potential of fibers was ranked such that IIA>I>IIX-like>IIB.

The results of quantitative analysis showed that fast-twitch fibers predominated in all TA muscle samples (Table 1), the average being 48.5% for type IIA with IIX-like (the latter make abut 50% of the estimated fiber proportion) and 47.2% for type IIB. Type I fibers were in the minority (4.3 %) and were located in the deep regions of the muscle. The type IIB fibers, solely, the most frequent type of fibers, predominated in the superficial mucle regions. There was a larger variation in the proportion of fast-twitch fiber types in the TA muscle of male in comparison to female rats, but there was no difference in fiber type distribution between two groups (Table 1).

In the TA muscle of both male and female rats, type IIB fibers were found to have the largest diameter, type I fibers were intermediate in size and type IIA fibers were the smallest (Table 2). The size of type I and IIA fibers was almost the same in males and females or was slightly higher in males, respectively. The type IIB fibers had generally a greater size in males (Table 2). These fibers also demonstrated the largest heterogeneity in respect to fiber diameter, but the difference in the mean values between male and female rats was not statistically significant.

***Table 1.*** *Muscle fiber type percentages in the rat tibialis anterior muscle*
*Values given are means±SD*

| Sex | N | Fiber type (%) | | |
|---|---|---|---|---|
| | | *Type I* | *Type IIA** | *Type IIB* |
| M | 5 | 4.32±1.60 | 48.52±4.16 | 47.16±4.00 |
| F | 5 | 4.33±1.47 | 48.48±3.52 | 47.19±3.15 |

*Designates IIX-like fibers make about 50% of the estimated fiber proportion as described in text

***Table 2.*** *Muscle fiber size (diameter) in the tibialis anterior of the rat*
*Values given are means±SD and CV*

| Sex | N | Type I Diameter (μm) | CV | Type IIA Diameter (μm) | CV | Type IIB Diameter (μm) | CV |
|---|---|---|---|---|---|---|---|
| M | 5 | 36.74±4.14 | 11.27 | 35.18±3.32 | 9.44 | 55.22±5.67 | 10.27 |
| F | 5 | 36.01±4.11 | 11.41 | 34.38±3.32 | 9.66 | 53.65±5.97 | 11.13 |
| p-value | | ns | | ns | | ns | |

CV, coefficient of variation in %; ns, not statistically significant

## DISCUSSION

The TA muscle examined was found to contain predominantly fast-twitch fiber types (IIA with IIX-like and IIB) while slow-twitch type I fibers were in the minority. Muscle fiber types identified by mATPase histochemistry showed differences in both their SDH (and NADH-TR) and α-GPDH activities, although the staining intensity of α-GPDH reaction was less consistently (Figure 2).

Based on the histochemical profile, type I, IIA, and IIB fibers corresponded to SO, FOG, and FG fibers, respectively (1), while IIX-like fibers were similar to FOG -acid resistant fibers of Soukup et al. (8) and to FO fibers of Maltin et al. (4).

Immunohistochemical and biochemical analyses demonstrated that histochemically-defined fiber types I, IIA and IIB exspress myosin heavy chains I, IIa and IIb, respectively (10, 24). In addition, MHCIIx (or IId) has been identified (10, 24), and corresponding population of fibers has been histochemically characterized and designated as type IIX (10) or IID (24). Hence, this fiber has been referred to as type IID/X by Delp and Duan (20). In this study, IIX-like fibers resembled type IIB in

their acid-mATPase activity, but they had a higher alkali-stable mATPase activity (resembling to type IIA) and were more oxidative and smaller. The histochemical profile of these fibers corresponded to IIBd fibers (9) and to type IIX fibers (10, 25).

Delp and Duan (20) reported on the mATPase-based fiber type distribution and size from different muscles of the rat. Type IID/X fibers was shown to make up a significant portion of the adult rat muscle mass and with regard to size and oxidative potential they are intermediate to type IIA and IIB fibers (20). The present results agree with those cited above even though we did not separately quantified this fiber type and do not have the fiber-mass data. In addition, it has been observed that muscle fiber types expressing different MHC isoforms (MHCs) also showed important differences in both their SDH and α-GPDH activities and their cross-sectional area values (26).

The four fiber types contain different MHCs that are responsible for their different mATPase activities and speed of contraction (5, 21, 26, 27). The MHCs are encoded by a multigene family, and four isoforms (i.e. I, IIa, IIx/d, and IIb) have been identified in adult skeletal muscles of small mammals including the rat, as well as in muscles of some large mammals such as the pig and the llama (5, 10, 24, 26-28), but MHCIIb isoform is not expressed in humans (29). The fibers expressing more than one MHC isoform termed as "hybrid" fibers were found to exist in normal rat limb muscles (including TA and gastrocnemius muscles) making an important population of fibers (21). The hybrid fibers have also been found in other studies, but they made up a minor portion (<5%) of the total number of fibers (20, 30). In addition to the four "pure" fiber types (I, IIA, IID and IIB), hybrid fibers (type IC, IIC, IIAD and IIDB) can be delineated by applying rafined mATPase histochemical methods, as well (21).

The proportion of different fiber types varies among muscles and is likely related to their function. Indeed, the TA of the rat is a fast-twitch muscle, so that slow-twitch type I fibers constitute only a minor population of fibers in relation to fast-twitch fiber types (>95%), among them type IIB fibers solely predominated. The young adult male and female rat TA muscles examined were found to contain 48.5% type IIA and IIX-like fibers (the proportion of which was approximately equal), 47.2% type IIB and only 4.3% type I fibers, and exhibit the uneven distribution of different fiber types. It is particularly true for type I fibers, which were only observed in deep regions of the muscle. This is in accordance with previous results for male rats using the stereological methods (16), and is in general agreement with previous studies (12, 13, 18, 19). Furthermore, it has been demonstrated that numerous skeletal muscles of the rat, such as biceps brachii, triceps brachii, gastrocnemius and tibialis posterior are regionalized (15, 16, 19, 20).

Discrepancies in reported data about fiber type composition of the rat TA muscle appears to be due to differences in classification of type IIX (or IID) fibers (11-13, 31). When the method of Peter at al. (1) was used, these fibers were classified as FOG rather than FG fibers**,** as a result of the greater oxidative capacity than the latter ones (11) (Figure 3). However, when the method of Brooke and Kaiser (6) was used, IIX (or IID) fibers were classified as type IIB rather than type IIA fibers, as a result of the similar acid-mATPase activity (31) (Figure 3).

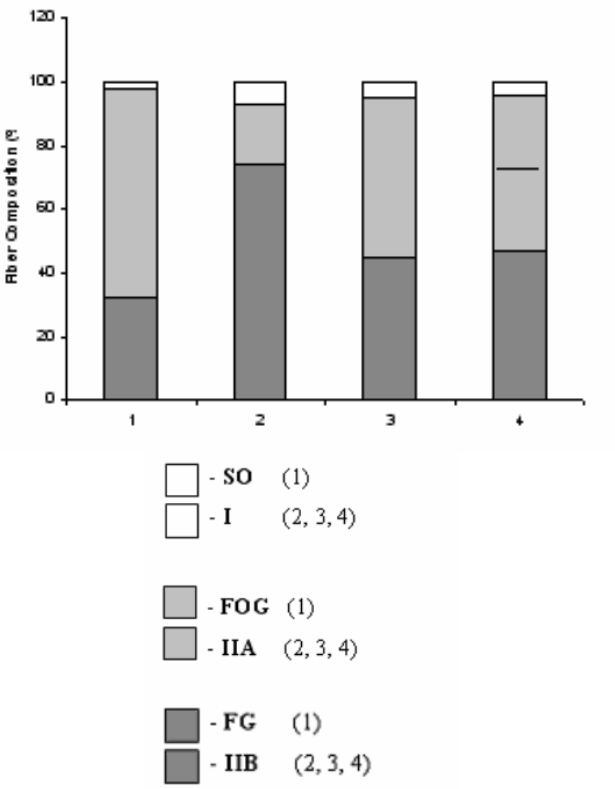



***Figure 3.*** *Fiber type composition of the rat tibialis anterior muscle determined by Ariano et al. (11; column 1), Cornachione et al. (31; column 2), Pullen (12; column 3) and by the authors of this study (column 4, - designates that IIX-like fibers make about 50% of the estimated fiber proportion). SO, slow-twitch oxidative; FOG, fast-twitch oxidative glycolytic, FG, fast-twitch glycolytic*

Moreover, the variation in fiber type composition for the rat TA muscle also exists between the studies in which type IIX (or IID) fibers were separately classified (20, 21). The influence of age and strain of rat on fiber type composition should be taken into account. In addition, muscle fibers are capable of transforming from one to another fiber type in response to altered functional demands, changes in neural input or in hormonal signals, suggesting the plasticity of muscle fibers (5, 29).

The present results regarding the fiber type composition of the TA muscle from both groups are similar to the data previously published by Pullen (12). Pullen (12) reported the fiber type composition of the TA

muscle in young adult rats of both sexes to be 49.6% type IIA, 45% type IIB and only 5,1 % type I. It seems likely that in his study, by applying mATPase method combined with formaldehyde fixation for alkaline preincubation, type IIX (or IID) fibers were included within type IIA fiber class. This author found no differences between males and females in respect to fiber type composition of the TA muscle, and the present findings agree with this. To our knowledge, there are no other data which indicate that sex differences exist in the fiber type composition of the TA muscle. Skeletal muscles are not overtly sexually dimorphic (32). In rodents the fiber type composition of the masseter muscle, but not limb muscles, was shown to be susceptible to sex differences (32).

Although it is difficult to compare fiber size data between studies based on the use of different strain, age and sex of rats, the size of type IIA fibers was the smallest and type IIB the largest in the adult rats of either sex and various strains, even if the different parameters of fiber size (cross-sectional area or diameter) were used (12, 18, 20, 21, 31). In this study, the lesser diameter was used as an index of muscle fiber size. The fibers of type IIA were found to be also the smallest and type IIB the largest in diameter in both male and female rat TA muscle (Table 2). The type I fibers were slightly larger in size than type IIA. These data indicate the inverse relationship between fiber size and oxidative potential. This relationship may reflect the economy of energy expenditure (14).

The mean values for the size of fiber types obtained for female group in this study are smaller than those found by Cornachione et al. (31) (for control I group) studied female Wistar rats, 118 days of age, while Wistar rats we used were younger (12 weeks of age). Wistar rats were also studied by Pullen (12), but presented results of fiber type sizes are based on pooled data from both sexes.

The size of muscle fibers is influenced by the number of factors such as activity and innervation, growth, hormones and nutrition (2, 3, 5, 22, 29). The muscles of the adult male in most mammalian species tend to be heavier for body size, owing to larger fiber sizes, than those in the adult female. In adult male subjects, type II fibers are usually larger than type I fibers, in contrast to females where type I fibers tend to be larger. These differences are explained as due to greater physical activity and anabolic effects of androgens. The effects of androgens are demonstrated in the animal models by either male castration or administration of androgens to female animals. Despite their observable effects, the response of skeletal muscle to androgens is less than in the male accessory sex tissues because of low concentrations of hormone receptors and generally the absence of 5α-reductase which converts testosterone to its more active congener, dihydrotestosterone (33).

In the male rat, as in man, testosterone appears to have a selective effect: type II fibers are larger in the male than in the female (34). In the study of hypogonadal mice type IIB fibers was found to be the most dependent upon sex hormones for appropriate development (33). Sciote et al. (33) observed no significant difference in the size of fiber types in the mouse gastrocnemius muscle between normal males and normal females 8 weeks of age (mice of this age represent postpubescence and young adulthood). In fact, all fiber types were slightly larger in female group, indicating faster growth of fibers in females. In the present study no significant difference in the size of type I and IIA fibers was found between males and females, although type IIA fibers were slightly larger in males. The type IIB fibers had generally a greater size in males than those in females (Table 2), but the difference was not statistically significant, indicating a small gender differences in body mass for young adult rats used in this study. The influence of other factors, such as the conditions under which the rats are maintained must be considered.

Finally, because muscle fiber types and their size and metabolic properties are key determinant of muscle function, an understanding of these variables for the same muscles in male and female rats provide a basis for comparative investigations of physiological and/or pathological responses induced by various factors.

## CONCLUSION

The results of this study demonstrate that three main fiber types (I, IIA, and IIB) and IIX-like fibers identified in the rat TA muscle by mATPase histochemistry show differences in their oxidative and and glycolytic potential, although the later was less consistent. SDH activity decreased in the rank order IIA>I>IIX-like>IIB.

The results also demonstrate no sex-related differences in fiber type composition of the rat TA and confirm an inverse correlation between fiber size and oxidative potential, and that IIX-like fibers make up a significant population of fast-twitch fibers.

Further comparative studies of the male and female rat TA muscles during growth are needed, by applying the methods for improvement in accuracy of muscle fiber typing and for successful detection of age- and sex-related changes.

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# KOMPOZICIJA TIPOVA VLAKANA I VELIČINA VLAKANA U MUSCULUS TIBIALIS ANTERIOR-u PACOVA

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**Sažetak**

**Tipovi mišićnih vlakana i njihova metabolička svojstva i veličina, ključne determinante mišićne funkcije, mogu se izmeniti pod uticajem različitih faktora.**

**Cilj ovog rada bio je ispitivanje i komparacija kompozicije tipova vlakana i veličine vlakana u m. tibialis anterior-u (TA) mladih odraslih mužjaka i ženki pacova, primenom histohemijskih i morfometrijskih metoda. Na serijskim poprečnim presecima TA 10 pacova (12 nedelja starosti) primenjena je miofibrilarna ATP-aza sa preinkubacijom pri pH 4,3; 4,5; 9,4 i 10,4 i enzimi metabolizma.**

**Tri glavna tipa vlakana (I, IIA i IIB) i tipu IIX-slična vlakna su identifikovana primenom miofibrilarne ATPaze. Ove populacije vlakana pokazale su takođe razlike u oksidativnom potencijalu. Aktivnost sukcinat dehidrogenaze vlakana opadala je u odnosu IIA>I>tipu IIX-slična>IIB. Nije nađena značajna razlika između mužjaka i ženki pacova u kompoziciji tipova vlakana. Utvrđeno je da TA za obe grupe sadrži 48,5% vlakana tipa IIA i tipu IIX-slična (čija je proporcija bila približno ista), 47,2% tipa IIB i 4,3% tipa I.**

**U zaključku, ovo istraživanje pokazuje da nema razlike u kompoziciji tipova vlakana TA prema polu pacova i potvrđuje inverznu korelaciju između veličine vlakana i oksidativnog potencijala, kao i da vlakna tipu IIX-slična čine značajnu populaciju brzo-kontrahujućih vlakana.**

***Ključne reči:*** **skeletni mišić, tipovi vlakana, miofibrilarna ATPaza, sukcinat dehidrogenaza, morfometrija, veličina vlakana, pacov**