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Capillary density and capillary-to-fibre ratio in *vastus lateralis* muscle of untrained and trained men

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Abstract: Muscle fibre profile area (A_f), volume density (V_V), capillary-to-fibre ratio (CF) and number of capillaries per fibre square millimetre (CD) were determined from needle biopsies of *vastus lateralis* of twenty-four male volunteers (mean ± SD: age 25.4±5.8 years, height 178.6±5.5 cm, body mass 72.1±7.7 kg) of different training background. Seven subjects were untrained students (group A), nine were national and sub-national level endurance athletes (group B) with the background of 7.8±2.9 years of specialised training, and eight subjects were sprint-power athletes (group C) with 12.8±8.7 years of specialised training. Muscle biopsies of *vastus lateralis* were analysed histochemically for mATPase. Capillaries were visualized and counted using CD31 antibodies against endothelial cells. There were significant differences in the V_V of type I and type II muscle fibres in both trained groups, B (51.8%; 25.6%) and C (50.5%; 26.4%). However, in untrained group A that was treated as a reference group, the difference between V_V of type I and type II fibres was less prominent, nevertheless statistically significant (42.1%; 35.1%). There was also a significant difference in CF: 1.9 in group A and 2.1 in groups B and C. The number of capillaries per mm^2 (CD) was 245 (group A), 308 (group B) and 325 (group C). Significant differences ($P<0.05$) in CF and CD, were found only between group A (1.9; 245) and both groups of trained men, B and C (2.1; 308 and 325). However, endurance athletes (group B), such as long-distance runners, cyclists and cross country skiers, did not differ from the athletes representing short term, high power output sports (group C) such as ice hockey, karate, ski-jumping, volleyball, soccer and modern dance.

Key words: Training - Muscle - Capillaries - Exercise - Sport

Introduction

In response to resistance training, adult human skeletal muscle can substantially increase its size and force-generating capability (see *e.g.* Jones and Round, [18]). This form of muscle enlargement has been thought to be the result of increased cross-section area of individual muscle fibres without an increase in total muscle fibre number. Endurance exercise training may influence metabolic and morphological features and improve aerobic capacity of skeletal muscles. Strength and endurance training has been performed concurrently to improve the performance of athletes in various sport disciplines and the quality of life of subjects recovering from injury or cardiovascular disease [5, 22]. A common adaptive response to strength and endurance training is the formation of new blood vessels and transition of fibre types in the exercised muscles. However, these phenomena and the underlying mechanisms appear to be training regimen-specific. Studies of human muscle microvasculature have primarily been restricted to the examination of limited numbers of sedentary adults [15, 33] and endurance trained adults [15, 20]. These investigations demonstrated that the relationships between fibre size, its contractile and metabolic profile, and capillary-to-fibre ratio are consistent in healthy untrained men. Endurance training of athletes and sedentary subjects increases skeletal muscle capillarity and microvascular fluid filtration [9] and enhances percentage of type I fibres in the exercised muscles [10, 11, 12, 16, 21]. By contrast, training activities designed to improve muscle strength lead to muscle fibre hypertrophy but do not induce substantially increased capillarity [5, 9, 19, 22]. Human *vastus lateralis* muscle is a locomotor muscle

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Table 1. Morphometric estimates of muscle fibres

Groups	Volume density V_v (%) Fibre type			Surface area A_f (μm^2) Fibre type			Capillaries per fibre ratio CF	Capillaries per mm^2 CD	Duration of training (years)
	I	IIA/I	II	I	IIA/I	II			
A Physically active untrained students n = 7	42.1 SD = 9.6 SE = 3.62 CV = 23		35.1 SD = 7.5 SE = 2.83 CV = 21	4230 SD=669.1 SE=252.49 CV=16		3994 SD = 789.5 SE+297.92 CV = 20	1.9 SD = 0.3 SE = 0.11 CV = 16	245 SD = 44.9 SE = 16.94 CV = 18	
B Endurance trained athletes n = 9	51.8 SD = 11.2 SE = 3.73 CV = 22	2.9	25.6 SD = 9.7 SE = 3.23 CV = 39	4877 SD = 930.9 SE = 310.3 CV = 19	5680	4974 SD=602.9 SE=200.97 CV=12	2.1 SD = 0.4 SE = 0.13 CV = 19	308 SD = 64.5 SE = 21.5 CV = 21	7.8 SD = 2.9 SE = 0.97 CV = 37
C Trained athletes (short term, high power output sports) n = 8	50.5 SD = 9.3 SE = 3.29 CV = 18	2.9	26.4 SD = 8.0 SE = 2.83 CV = 30	4876 SD=936.0 SE=330.74 CV=19	3935	5458 SD = 932.7 SE=329.57 CV = 17	2,1 SD = 0.5 SE = 0.18 CV = 24	325 SD = 74.7 SE = 26.40 CV = 23	12.8 SD = 8.7 SE = 3.07 CV = 68

CV – coefficient of variation in %

well characterized physiologically and biochemically. Its phenotype clearly reflects any adaptive changes taking place during variety of physiological conditions such as different types of training regime [3, 4, 26, 28, 31].

The aim of the present study was to fill the gap in exercise physiology between so far presented data on world class athletes and poorly investigated national and sub-national level athletes. We would like to emphasize that our investigation is a part of longitudinal study on physiological performance of large spectrum of athletes investigated by Zoladz *et al.* [32]. We examined capillary density and capillary-to-fibre ratio in a thigh muscle *vastus lateralis* of physically active but untrained students and of national and sub-national level sportsmen, representing different sport disciplines.

Materials and methods

Subjects. Twenty-four male volunteers (mean ± SD: age 25.4±5.8 years, height 178.6±5.5 cm, body mass 72.1±7.7 kg) of different training background were classified into three groups according to their physical activity and sport discipline. Group A contained 7 physically active but untrained students of the Academy of Physical Education in Kraków, Poland. Group B included 9 endurance trained athletes specialised for 7.8±2.9 years in long distance running, cross country skiing or cycling. Group C consisted of 8 athletes (12.8±8.7 years of specialised training) performing short term, high power output sports such as ski jumping, karate, ice hockey, soccer, modern dance, volleyball and handball. Sportsmen of group B and C represented national or sub-national level in their sport disciplines. All volunteers were subjected to detailed medical interview and check-up. The Local Ethical Committee approved the investigations.

Analysis of muscle biopsy samples. After local anaesthesia (2 ml of 1% lignocaine), percutaneous muscle biopsy samples were taken from the middle part of *vastus lateralis m. quadricipitis femoris*, 15 cm above the upper margin of patella using ∅ 5 mm Bergström needle [6]. The tissue samples used for the present investigation were rapidly frozen in isopentane cooled with liquid nitrogen and stored until use. Ten μm cryostat (Shandon OT, Astmoor, Runcorn, Cheshire, UK) cross-sections were used for identification of slow type I, fast type II and hybrid IIA/I fibres by histochemical staining for mATPase after alkaline (pH 10.4) and acid (pH 4.35 and 4.6) preincubations [8, 27]. For identification of capillaries, the sections were incubated with mouse anti-CD31 monoclonal antibody, clone IC/70A (DAKO A/S, Denmark) against endothelial cells and visualised with streptavidin-biotin immunoreaction kit (DAKO LSAB2 System, Peroxidase, Denmark). Sections were incubated overnight with primary anti-CD31 antibody diluted at 1:40 with PBS and processed according to manufacturer's protocol. Thy were mounted in glycerine jelly, examined and images were recorded using an Axioskop light microscope (Zeiss, Oberkochen, Germany). For estimation of the muscle fibre number, muscle fibre volume density (V_v) and the surface area of an individual muscle fibre (A_f), the sections stained for mATPase activity after alkaline preincubation were used. The estimations of capillary-to-fibre ratio (CF) and number of capillaries per $1mm^2$ of the investigated area of muscle tissue (CD) were performed directly on sections stained with antibody against endothelial cells. All stereological variables were obtained using the square lattice test system with a total of 121 points and 0.194 mm^2 area. Three to five non-overlapping fields were analysed for each biopsy. The square lattice was inserted into the × 6.3 eyepiece [29]. Final magnification of × 200 was used.

Statistical analysis. All values are reported as mean ± standard deviation (SD) and standard error of the mean (SE). The data were analysed by one-way analysis of variance and tested for statistically significant differences. The correlation coefficient (r) was used to determine the degree of relationship between two variables. The confidence level of $P<0.05$ was chosen to indicate statistical significance.

Results

Muscle fibre type content and distribution

Muscle fibres of type I, II and IIA/I were readily identified in sections stained for mATPase after alkaline preincubation. The number of type IIA/I hybrid fibres in biopsy samples was so small that they were considered in data acquisition but not in statistical analyses. They were present only in four biopsies and are included in

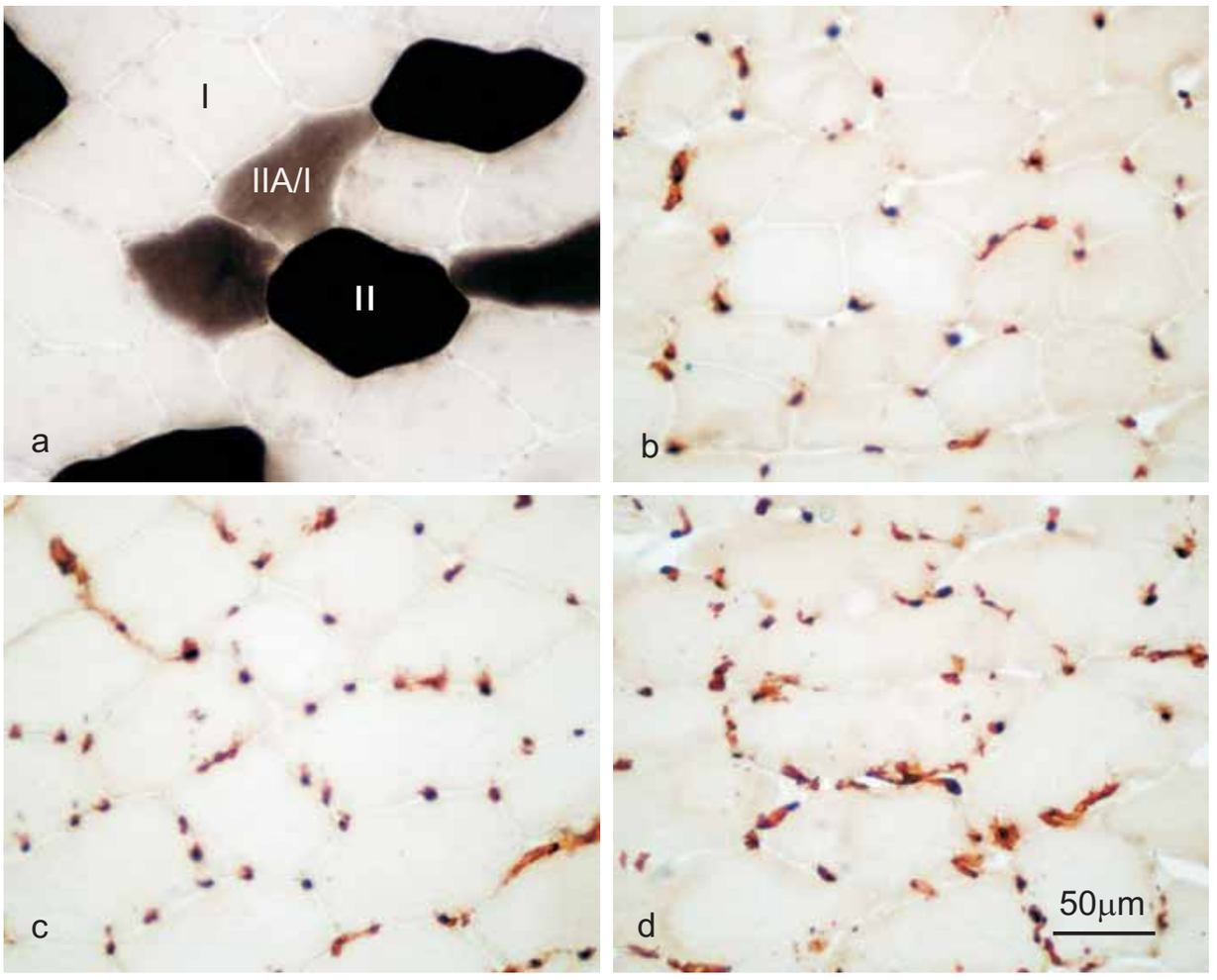

Fig. 1. Transverse serial cryostat sections obtained from the biopsy of human *vastus lateralis* muscle; **(a)** fibre typing by staining for ATPase activity after preincubation at pH 10.4. Slow type I fibre white, fast type II fibre black, and hybrid IIA/I fibres brown. Immunostaining of capillaries (red) with monoclonal antibodies against transmembrane glycoprotein CD31, **(b)** untrained but physically active student, group A, **(c)** endurance trained athlete, group B, **(d)** trained athlete representing short term, high power output sports, group C. Bar = 50 μm.

Table 1. Type IIA/I fibres displayed brown colour in contrast to the black coloured fibres of type II and white fibres of type I (Fig. 1a). Figure 2 illustrates graphically the mean number of slow I, fast II and hybrid IIA/I fibres and the significant differences between group A and the two other groups B and C for slow and fast fibres.

Significant differences were also found in muscle fibre type content indicated as a volume density and in area of muscle fibre profiles between untrained subjects of group A and the two other groups of trained subjects, B and C, for slow and fast fibres ($P<0.05$). The volume density of type I fibres in groups B and C was by 23% and 20% higher in comparison with untrained students of group A. However, the volume density of type II fibres was by 27% and 25% lower in groups B and C , respectively (Tab. 1). The size of the fibres was expressed as the surface area of their cross-section profiles (A_f). The fibre size was significantly higher in subjects of groups B and C in comparison to group A. The size of type I fibres was by 15% higher, while that of type II fibres was by 25% and 37% higher in groups B and C, respectively.

Capillary density and capillary-to-fibre ratio

Capillaries visualized by anti-CD31 antibody in the representative samples from the investigated groups are shown in Figure 1 b-d. The number of capillaries per mm^2 of muscle fibres (CD) was higher in trained than in untrained men (Fig. 3). The average number of capillaries per fibre was by 11% higher in the endurance trained than in the untrained subjects, *i .e.*, 2.1 and 1.9,

respectively (Table 1). These differences were apparently not due to the mean fibre size, since the average area of type I fibres differed by 15%, and in case of type II fibres they were even more prominent and ranged from 25% to 37%, when trained athletes were compared to untrained students. The average number of capillaries per mm^2 was 245, 308 and 325 in untrained students of group A, endurance trained athletes of group B, and trained athletes performing sprint strength sport disciplines of group C, respectively (Fig. 3).

Scatter plot of capillaries per mm^2 as a function of the duration of training is shown in Figure 4. Scatter plots of capillary-to-fibre ratio as a function of fibre type I and type II area is shown in Figures 5 and 6, respectively, and of duration of training in Figure 7.

Discussion

This study has attempted to determine whether the capillary bed of *vastus lateralis* muscle differs among athletes according to the kind of performed training. The principal finding is that in endurance trained athletes the capillary density and capillary-to-fibre ratio are higher than in untrained students. Moreover, the volume density and surface area of slow type I fibres were higher in trained than in untrained subject. However, in case of type II fibres the volume density was lower, while the surface area was higher in relation to physically active but untrained students. These results may indicate that both fibre types underwent hypertrophy, which was more prominent in fast fibres. Our findings are in agreement with a longitudinal training study by Andersen and Henriksson [2] who showed that an expansion of capillary bed in *vastus lateralis* was accompanied by fibre type transformation.

Quantitative determination of the capillary supply of skeletal muscle is beset with several methodological and theoretical problems. The capillarization of human muscle biopsy samples has been characterized using histochemical [1, 2, 25], or combined histochemical and electron microscopic methods [24]. In the present investigation, we have employed immunohistochemical method using monoclonal mouse antibody against platelet/endothelial adhesion molecule (CD31) that belongs to immunoglobulin superfamily with adhesive properties. This single chain type I transmembrane glycoprotein (130 kD) is strongly expressed by all endothelial cells [23]. Therefore, in our opinion the antibody against CD31 molecule is suitable to be used as a capillary marker in human skeletal muscle, what was demonstrated in the present paper.

The measurements of capillary density in any skeletal muscle may be markedly affected by shrinkage or swelling of the tissue during the histological procedures. Therefore, the correct values for capillary density are accurate only if the fibre size and their spatial relation in fresh-frozen sections are unaltered as compared to the native condition. Questions what the native conditions should be and to what degree the muscle tissue is affected by the histological procedures have not been so far adequately answered. Having that problem in mind, we did not attempt to investigate it but were fully aware of the fact that the degree of swelling or shrinkage may alter our results and therefore we were dealing with the over- or underestimated data. However, since the presented calculations have comparative character, we carefully followed a strictly established regime of histological process, for all 24 samples in order to obtain compatible results.

To compute and analyse our data, we assumed that even slightly over- or underestimated variables may demonstrate possible influence of training on the spatial distribution of the capillary bed. The capillary density ranged from 245 in untrained men to 308 and 325 capillaries per mm^2 in trained men of groups B and C, respectively. In spite of some discrepancy between our results and those found in the literature, some of them, *e.g.* the results of Brodal *et al.* [7] are in agreement with ours. From their Table 2 one may calculate that the endurance-trained men have 821 capillaries per mm^2 that is 40.3% more than untrained men (585 per mm^2). In our study, both trained subjects from groups B and C have 25.7% - 32.6% more capillaries per mm^2, respectively, than untrained men from group A. Brodal *et al.* [7] have suggested that the differences in the capillary supply of skeletal muscle might be an effect of heritage rather than training. The experimental studies on human muscles [13] contradict these suggestion and demonstrate that physical training leads to an increase in capillary density. In the present study, the linear regression of capillary density against duration of training in years shows positive correlation. We demonstrated that in groups A, B and C there were individual subjects whose capillary density in their muscle biopsies markedly differed from the means (170 vs. 245; 225 vs. 308; and 241 vs. 325 in group A, B and C, respectively). This may be due to individual inherited features that may favour these individuals, to sustain more intense training and to result in the future sport success. On the contrary, individuals that have innately low number of capillaries per mm^2, well below the mean, may be unable to undertake the endurance training and sport career. However, despite of the above speculations, it seems likely that the differences in capillary density between untrained and trained men were mostly due to the effect of physical training.

Capillary-to-fibre ratio

Since capillary-to-fibre ratio (CF) is not affected by swelling or shrinkage, it should therefore be more suited for comparison. The size and metabolic properties of fibres influence the number of surroundings capillaries.

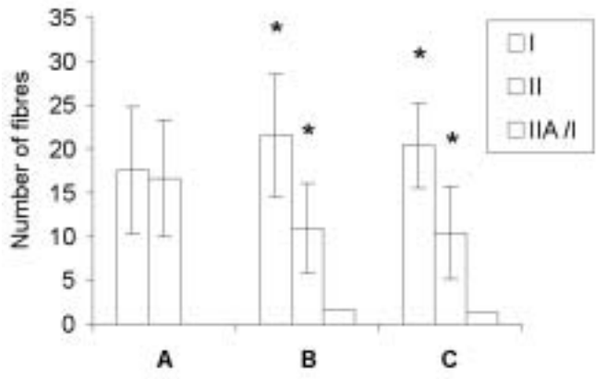

Fig. 2. Diagram showing relation between the mean number of slow I, fast II, and hybrid I/IIA + IIA/I fibres in 0.194 mm^2 of the cryostat transverse section of biopsies of *vastus lateralis* muscle of untrained students **(A)**, endurance trained athletes **(B)** and trained athletes representing short term high power output sports **(C)**. Significant differences (*) exist between group A and the two other groups B and C for slow and fast fibres ($P<0.05$).

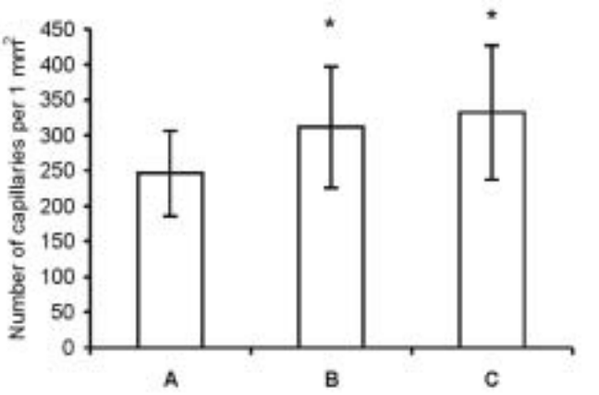

Fig. 3. Diagram showing relation between the number of capillaries per 1 mm^2 in biopsies of *vastus lateralis* muscle of untrained students **(A)**, endurance athletes **(B)** and trained athletes representing short term high power output sports **(C)**. Significant differences (*) exist between group A and the two other groups for slow and fast fibres ($P<0.05$).

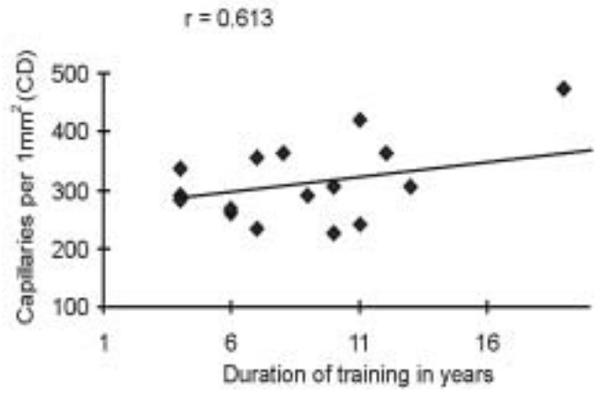

Fig. 4. Scatter plot of capillary density per 1mm^2 as a function (r = 0.613) of the duration of training. The regression line was fitted using the least square method. Significant r = 0.491.

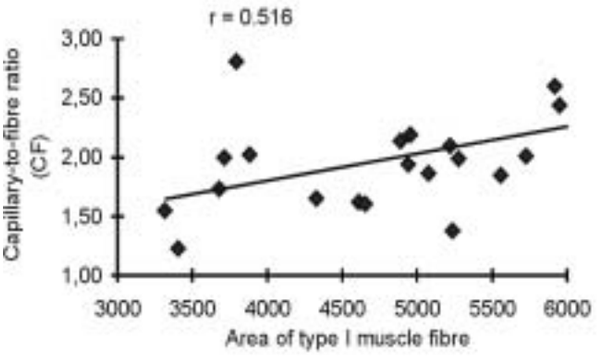

Fig. 5. Scatter plot of capillary-to-fibre ratio as a function (r = 0.516) of fibre type I area. The regression line was fitted using the least square method. Significant r = 0.466 shows the existence of relation between capillary-to-fibre ratio and the area of the type I fibres.

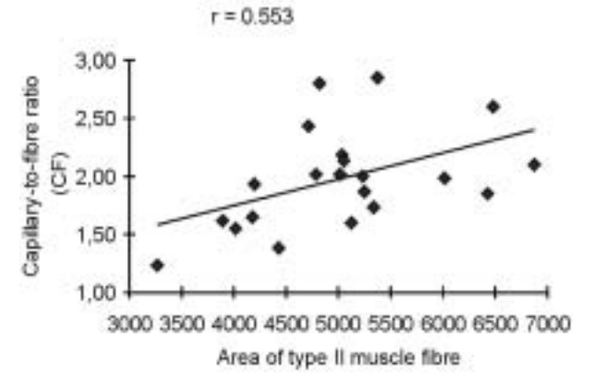

Fig. 6. Scatter plot of capillary-to-fibre ratio as a function (r = 0.553) of type II fibre area. The regression line was fitted using the least square method. Significant r = 0.468 shows the existence of relation between capillary-to-fibre ratio and the type II fibre area.

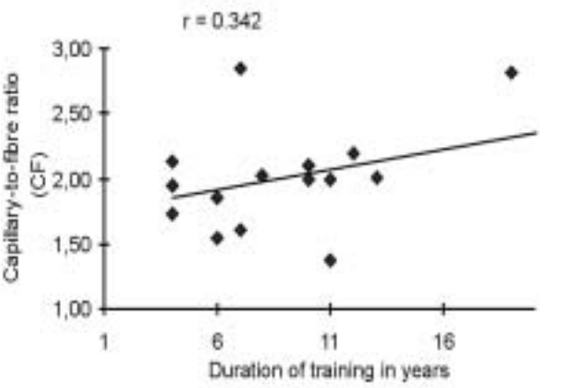

Fig. 7. Scatter plot of capillary-to-fibre ratio as a function (r = 0.342) of the duration of training. The regression line was fitted using the least square method. Significant r = 0.506 shows that there is no relation between capillary-to-fibre ratio and the duration of training.

The fibres with higher oxidative capacity are surrounded by larger numbers of capillaries than similar size fibres of lower oxidative capacity [2, 13, 20] what means that CF is higher in the region of muscle composed of oxidative fibres. The surface area of type I muscle fibres correlates positively with the capillary-to-fibre ratio. However, similar relation was noticed when type II fibres were analysed. These results indicate that type II muscle fibres also posses high oxygen delivery capacity, which may result from their recruitment during normal daily activity as well as from physical training. This is in accordance with the previous study by Ivy *et al.* [17] showing that type II muscle fibres are already activated at very low power outputs. The CF for untrained men ranged from 1.08 [14], 1.77 [7] to 1.9 in our study. The last value characterized group A that consisted of physically active students and it is by 54% higher than the mean value obtained previously in human skeletal muscle. In the present investigation, the mean CF value for both trained groups B and C was 2.1, while in other studies by Hermansen and Wachtlowa [14], and Brodal *et al.* [7] the corresponding values were relatively higher and ranged from 1.5, to 2.49, respectively. It is difficult to explain the differences between our data and those of other authors. They may be due to distribution of fibre types, degree of intensity of training, individual variation among the investigated subjects in capillary density and finally may depend on techniques used by the other investigators. Gollnick *et al.* [12] have demonstrated that the distribution of "red" and "white" muscle fibres in a biopsy from *m. quadriceps femoris* varies substantially from one untrained subject to another what may also be true for the capillary density in this muscle.

Fibre size and number of capillaries

Our study demonstrated that regardless of type of training, large fibres are surrounded by larger number of capillaries than the small ones. There was a proportional increase in capillary density and capillary-to-fibre ratio as well as increase in the size of muscle fibres in endurance trained athletes and the capillaries surrounding those fibres had the largest size or the highest level of oxidative enzymes [30]. This investigation emphasizes the numerous variables that can influence capillary density and capillary-to-fibre ratio in trained and untrained human muscle. As in untrained men, capillary number and capillary-to-fibre ratio are correlated with fibre size and metabolic profile. In the *m. quadricipitis femoris*, all the above mentioned variables are significantly higher in national and subnational level athletes representing different sport disciplines in relation to the control group of physically active but untrained students.

We would like to point out, however, that endurance athletes (group B) and sprint strength athletes (group C) have not revealed any significant differences in the composition of slow and fast muscle fibres, as well as capillary-to-fibre ratio and capillary density. A similar conclusion was reached in the previous biochemical and histochemical study [30]. The authors pointed out that muscle phenotype in both groups of these athletes (B and C) was similar showing low amount of fast myosin heavy chain isoform MyHCIIX and marked predominance of slow type muscle fibres and slow myosin heavy chain isoform MyHCI. Thus, this phenotype was adapted rather for long lasting and sustainable activities typical for endurance disciplines (group B) than for fast disciplines requiring high power output during short time (group C). Furthermore, the relative amount of the fastest MyHCIIX isoform in *vastus lateralis* muscle was significantly lower in athletes training sprint strength disciplines than in untrained students (group A). However, it is difficult to establish to what extent the expression of this slow phenotype was inborn or was the result of training volume overload, because the myosin profile before the beginning of the training process was unknown.

In conclusion, the increased capillary density and capillary-to-fibre ratio in *vastus lateralis* muscle of endurance trained athletes in comparison with untrained students is mainly a consequence of the endurance training. The enlarged profile area of type II fibres with parallelly decreased volume density of these fibres may result from muscle fibre hypertrophy.

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