

Relationship of Muscle Fibre Distribution to Body Composition in Physically Trained and Normally Active Human Males

J. MELICHNA, J. PAŘÍZKOVÁ¹, C.W. ZAUNER², L. HAVLÍČKOVÁ

Department of Physiology and ¹Biomedical Centre, Faculty of Physical Education and Sport, Charles University, Prague, Czech Republic and ²Department of Exercise and Sport Science, College of Health and Human Performance, Oregon State University, Corvallis, Oregon, U.S.A.

Received October 18, 1993

Accepted April 27, 1994

Summary

This study was designed primarily to identify relationships among indices of muscle tissue structure (m. vastus lateralis) and of somatic qualities (anthropometric parameters) in 44 untrained men and 105 well-trained athletes. The ratio of glycolytic to oxidative muscle fibres was significantly less ($P < 0.05$) in endurance athletes as opposed to both the controls and the power athletes. Correlations between anthropometric factors and indices of muscle morphology were stronger in trained men, particularly in power athletes. Relationships between body fat and muscle fibre distribution were low in trained and untrained subjects. Documented muscle plasticity may enhance relationships between somatic and muscle tissue indices. Our results suggest that the response of the three major muscle fibre types to prolonged training may be relatively high. Finally, it was proposed that enhanced oxidative capacity of skeletal muscle might be characteristic of those resistant to heart disease.

Key words

Muscle morphology – Anthropometry – Athletes – Untrained men

Introduction

Successful physical performance is the outcome of coordinated function of many supporting systems as well as nutritional, biomechanical and psychological factors. It is likely that both body build and skeletal muscle fibre distribution may play important roles in the quality of exercise performance. Muscle fibre distribution and characteristics of body composition are strongly influenced by genetic factors, even though they develop during physical training as a consequence of adaptation to various types of physical workload. As a result, studies in the last decade have led to the development of physiological profiles for description of relationships between morphofunctional parameters and sports performance (Bouchard and Lortie 1984).

One can conclude from the abundant literature that a given sports performance will be determined by factors related to physique as well as to

muscle properties. Thus, such parameters differentiate athletes in various ways. For instance, the lowest values of body mass and/or percentage of depot fat, accompanied by predominance of slow muscle fibres (type I) were found in endurance runners, while in power athletes such as weight lifters, the percentage of body fat was relatively high and muscular strength was dependent on the number of fast muscle fibres (type II) (Gollnick *et al.* 1972). Furthermore, characteristics of body composition have been found to be related to maximum aerobic power (VO_2max) and to anaerobic capacity (Wingate Test) (Wilmore 1979). Finally, multiple regression analyses demonstrate relationships among such sports performances as running speed and/or economy, and a wide range of physiological data (Foster *et al.* 1978).

In trained human subjects the character of muscle fibre pattern seems to be heavily dependent on

or reflective of the type of sports discipline (speed, power, endurance). However, in boxers, those of the highest weight categories demonstrated a greater number of slow muscle fibres in m. vastus lateralis (Melichna *et al.* 1980). Unfortunately no findings exist to evaluate such phenomena in untrained men, and studies of the interface of exercise or training habits, in this regard are also rare. However, a progressive increase in slow fibres has been observed during early postnatal development in animal and human skeletal muscles which is associated with an increase of body mass (Kugelberg 1976, Cooling-Saltin 1980).

Relative parameters such as the percentage distribution of muscle fibres are probably only partially assignable to body size, while absolute parameters, such as the area or diameter of muscle fibres, are dependent upon the size of the animal. The latter might be explained by the fact that both growth and training influence not only skeletal muscles, but also body weight. Thus, a rapid increase in cross-sectional area (size) was observed during early postnatal development of animal and human muscles which was associated with an increase in body weight. Furthermore, the ratio of muscle weight to body mass is relatively independent of age (Müller 1975).

Heavy resistance training results in an increase in cross-sectional area of both type I and type II fibres (Melichna *et al.* 1982). The greater degree of hypertrophy that occurred in the type II fibres indicates a greater relative involvement of these motor units in the adaptive response to training (MacDougall 1986). In young rats (20 days old) the average size of fast fibres tends to be smaller than for slow fibres. At the age of 34 days the fast fibres are larger. This represents hypertrophic growth of the muscle fibres (Maltin *et al.* 1989).

Significant differences are known to exist among athletic groups in body mass and body fat content (Pařízková 1977, 1985). Also, relationships among muscular strength, body mass, lean body mass (LBM) and muscle fibre area in trained men have been examined (Wilmore 1979). In untrained populations it has been observed that habitual physical activity of an aerobic nature exerts favourable influences on diabetes, elevated blood cholesterol concentrations (Siscovick *et al.* 1985) and on blood pressure (Sallis *et al.* 1988). On the other hand, those physically active demonstrated reduced risk for heart disease (Blair *et al.* 1989). Furthermore, physically active individuals have been found to have elevated percentages of oxidative muscle fibres (Macková *et al.* 1989), whereas persons with significant cardiac risk factors such as cigarette smoking (Örlander *et al.* 1979) and obesity (Bass *et al.* 1982), as well as those suffering congestive heart disease (Sullivan *et al.* 1991) have reduced oxidative capacity of muscles.

The present study was designed to:

1. elucidate the relationships among parameters of muscle morphology and of body composition in normally active men and their well-trained counterparts, and,
2. establish in a relatively large population whether or not men habitually involved in aerobic exercise training have greater muscle oxidative potential than either normally active controls or power athletes.

Methods

One hundred and five athletes and 44 normally active, healthy volunteers served as subjects. All were male. The mean subject age was 23.0 ± 6.1 years (16–42 years). Athletes had been in training for at least three years at the time of assessment, and they were participants at either the junior or senior Czech and/or Slovak national level. The number of primarily endurance as opposed to mainly power (strength or sprint) athletes was approximately equal. Seven sprint runners and 5 hammer throwers were assigned to a subgroup identified in this report as "power athletes". Similarly, fourteen cross-country skiers and 4 marathon runners were assigned to the subgroup "endurance athletes". All other athletes in this study represented sport disciplines that demand varied and subtle combinations of power and endurance competitions. Control subjects, although never having been engaged in organized sport, were moderately physically active and thus could not be classified as truly sedentary. The subject characteristics are described in Table 1.

Anthropometric parameters (body mass, body height and percentage of body fat) were assessed. We measured ten skinfold thicknesses with a modified caliper (Pařízková 1977) and calculated the value of body mass index as follows: $BMI = wt \text{ kg} / ht^2 \text{ m}^2$. The BMI is often used for the evaluation of actual body mass regarding the height. For the estimation of the percentage of depot fat, a special regression equation, derived on the basis of the measurements of body density and skinfolds in a Czech population, including athletes, was used (Pařízková 1977). Maximum aerobic power (VO_{2max} per kg of body weight) was tested by means of an incremental test *ad vita maxima* on a bicycle ergometer according to IBP method (Melichna *et al.* 1982).

Muscle fibre distribution in the m. vastus lateralis was studied. A sample was taken with a bioptic needle (Bergström 1962). It was frozen in isopentane cooled by liquid nitrogen and cross-sectioned (10 μm thick) with a microtome. Serial cross-sections were then stained for both myofibrillar ATPase after preincubation at pH 4.35, 4.60 and 10.60 and for succinic dehydrogenase activity. These procedures allowed us to identify three muscle fibre types: type I

(slow oxidative), type IIa (fast oxidative-glycolytic) and type IIb (fast glycolytic). To determine muscle fibre diameter, we used the method of the "lesser fibre diameter" measurement. Twenty fibres of each type were randomly selected and evaluated for their diameter (Dubowitz and Brooke 1973) .

Pearson Product-Moment Coefficients of Correlation were calculated to determine the relationships among all variables, except in the cases of the relationships between and among values expressed as percents or ratios which were examined by the Spearman correlation technique. The $P<0.05$ level of

probability was accepted as indicative of a significant relationship.

The significance of mean differences in the percentage of type IIb muscle fibres, type IIb diameter, type I diameter, the ratio type II fibre/type I fibre and the ratio type IIb fibre/type IIa + type I fibres between endurance and power athletes, endurance athletes and the controls and between power athletes and the controls were assessed by means of simple randomized analysis of variance (ANOVA). The Scheffé test was applied *post hoc* when the F-ratio proved statistically significant ($P<0.05$).

Table 1
Selected parameters of body composition and muscle fibre pattern (m. vastus lateralis) in controls, athletes, power athletes and endurance athletes

Parameter	Controls (n=44)	Athletes (n=105)	Power athletes (n=12)	Endurance athletes (n=18)
Age (years)	26.9±8.0	21.4±4.1	20.2±5.7	20.8±1.3
Body mass (kg)	71.6±7.2	74.8±11.9	85.2±15.7	69.2±6.7
Body height (cm)	177.3±5.6	180.2±7.4	185.0±6.0	177.8±5.3
Body fat (%)	11.1±3.9	8.5±3.0	11.5±4.2	7.8±1.9
VO ₂ max.kg ⁻¹ (ml.min ⁻¹)	51.7±9.0	58.0±10.1	45.5±4.6	69.2±5.9
Fibre type IIb (%)	24.4±13.5	23.7±16.1	41.2±7.3	7.3±7.4
Fibre ratio				
II/I	1.38±0.94	0.98±0.58	1.52±0.25	0.58±0.22
IIb(IIa+I)	0.37±0.26	0.38±0.33	0.73±0.23	0.09±0.10
Fibre diameter (µm)				
IIa	81.3±12.7 ⁴	93.2±14.4 ¹	88.7±14.8	93.4±14.1
IIb	73.9±20.4 ⁴	94.1±14.7 ²	101.7±19.6	73.6±35.5
I	67.7±15.7 ⁴	80.6±13.7 ³	79.6±14.4	82.2±11.3

¹n=102, ²n= 99, ³n=104, ⁴n= 43, VO₂max = maximum aerobic power, Means ± S.D.

Results

Using correlation methods, the significance ($P<0.05$) of relationships among anthropometric and muscle morphological data were established (Table 2).

Although a number of the relationships were statistically significant ($P<0.05$), only those between anthropometric indices and muscle morphology in the athletes were rather strong. Table 2 illustrates that power athletes showed a moderate to strong positive

relationship ($r=0.63$) between body mass and fibre type IIb diameter, between percentage of body fat and type IIb fibre diameter ($r=0.61$), and between BMI and IIb diameter ($r=0.72$). Endurance athletes had a moderate to weak positive relationship between height and fibre type I diameter ($r=0.46$). On the other hand, there were no significant correlations among parameters in the control subjects.

The results of ANOVA and *post hoc* tests are presented in Table 3. As can be seen, endurance athletes had a significantly smaller mean percentage of type IIb fibres than either the power athletes or the controls. The mean type IIb diameter was greater in power athletes than in the controls and endurance

athletes. Mean type I diameter was greater in endurance and power athletes than in controls. However, there was no significant difference in mean type I muscle fibre diameter between the two specialized groups of athletes.

The ratio type II/type I fibres was significantly greater in power as opposed to endurance athletes, and significantly greater in control subjects than in endurance athletes. On the other hand, the ratio type IIb/type IIa + type I was significantly greater in power athletes than in endurance athletes and control subjects and was significantly lower in endurance athletes than in controls.

Table 2
Intercorrelations among the variables

Variables	Fibre type (%)		Fibre ratios	Fibre diameter	
	IIb	II/I	IIb/(IIa+I)	IIb	I
Body mass (kg)					
– combined (n=149)	0.21 ⁺	0.11	0.22 ⁺	0.20 ⁺	0.14
– controls (n=44)	–0.08	–0.06	–0.03	–0.12	–0.05
– athletes (n=105)	0.30 ⁺	0.19	0.29 ⁺	0.23 ⁺	0.15
– power (n=12)	0.21	–0.04	0.20	0.63 ⁺	0.27
– endurance (n=18)	–0.25	0.25	–0.29	–0.30	0.42
Body height (m)					
– combined	0.16	0.12	0.17 ⁺	0.13	0.03
– controls	–0.02	0.10	0.02	–0.16	–0.13
– athletes	0.24 ⁺	0.19 ⁺	0.24 ⁺	0.15	0.00
– power	–0.04	0.10	–0.01	0.04	–0.01
– endurance	–0.06	–0.28	–0.08	–0.08	0.46 ⁺
Body fat (%)					
– combined	0.13	0.17 ⁺	0.13	0.00	0.01
– controls	–0.05	–0.04	0.00	0.07	0.07
– athletes	0.16	0.15	0.16	0.11	0.20 ⁺
– power	0.33	0.33	0.33	0.61 ⁺	0.43
– endurance	–0.03	0.10	–0.03	–0.12	0.04
BMI					
– combined	0.18 ⁺	0.09	0.18 ⁺	0.17 ⁺	0.17 ⁺
– controls	–0.07	–0.09	–0.04	–0.01	0.04
– athletes	0.25 ⁺	0.14	0.24 ⁺	0.22 ⁺	0.22 ⁺
– power	0.22	0.11	0.20	0.72 ⁺	0.28
– endurance	–0.37	0.08	–0.39	–0.26	0.17

IIb = fast glycolytic fibres, IIa = fast oxidative-glycolytic fibres, I = slow oxidative fibres, BMI = body mass index, ⁺ = $P < 0.05$

Table 3
Results of *post hoc* tests (Scheffé test)

	% IIb	IIb diameter	I diameter	II/I	IIb(IIa + I)
Power vs. Endurance	31.54*	4.62*	0.11	5.77*	28.36*
Power vs. Control	10.23*	5.86*	3.16*	0.169	11.74*
Endurance vs. Control	14.12*	0.001	6.32*	7.41*	9.64*

* $P < 0.05$

Discussion

Recent scientific advances have led to the development of detailed physiological profiles for athletes in different sports (Wilmore 1979). The above cited findings suggest that anthropometric characteristics and parameters descriptive of muscle fibre composition are both very important for athletic performance (Pařízková 1977, 1985, Gollnick and Matoba 1984). Moreover, it was concluded that these determinants of performance as well as the sensitivity of the organism to training are largely genotype-dependent (Bouchard and Lortie 1984). However, the relationship between body composition and muscle fibre distribution has not yet been fully elucidated.

Since we sampled the tissue from m. vastus lateralis in all subjects, differences in fibre distribution among various human skeletal muscles may be viewed as a concern. Jansson and Kaijser (1977) found no difference in the distribution of fibres in leg and arm muscles of elite orienteers. In a study of swimmers, the ratio of fast to slow twitch muscle fibres was essentially the same among vastus lateralis, latissimus dorsi and deltoideus muscles (Melichna 1990). Tesch and Karlsson (1985) reported no difference in the percentage of slow twitch fibres found in the vastus and deltoid muscles in a mixed group of athletes. However, the same authors discovered a significantly higher percentage of slow fibres in the deltoid as opposed to the vastus in kayakers, and the precise opposite in distance runners. In a report on 7 freestyle wrestlers (Melichna 1990), a high percentage of slow fibres was evident in the leg musculature but a relatively high percentage of fast fibres in the arm muscles. Finally, Boros-Hatfaludy *et al.* (1986) demonstrated a greater percentage of slow fibres in the gastrocnemius as opposed to the vastus lateralis in untrained subjects, but no such difference in high jumpers. Unfortunately, at present it is impossible to determine if differences in fibre distribution among skeletal muscles, sometimes observed in athletes, are representative of a training effect or if they are a part of the process of selection playing an important role in the choice of the sport

discipline. We believe that in a large population of athletes from a wide array of sports it is unlikely that there will be significant differences in fibre distribution between leg and arm muscles. Furthermore, for our subgroups of power and endurance athletes, subjects were selected whose sports demanded concentrated leg work.

Earlier findings indicate that in men, the body size and body composition, particularly lean body mass (LBM), are related to the anaerobic and aerobic capacity (Melichna *et al.* 1989), muscular strength (Maughan *et al.* 1983), blood circulation (Spatz 1991), blood pressure (Klesges *et al.* 1991), haemoglobin concentration, red blood cell count and haematocrit (Telford and Cunningham 1991, Hutchinson *et al.* 1991), the capillary network in skeletal muscle and blood lipoproteins (Pařízková 1977, 1989). These relationships were observed mainly in well-trained males. Significant correlations between muscle morphology and anaerobic and aerobic work capacity have been reported (Melichna *et al.* 1989). From the above mentioned findings it seems logical that the relationships among expressions of somatic characteristics and muscle composition may be strong.

Relationships among anthropometrical data and muscle morphology are presented in Table 2, with individual coefficients shown for all subjects (combined), the groups of untrained (controls) and trained subjects (athletes), and separately for power and endurance athletes. The results clearly differ between athletes and the controls and between power and endurance athletes. Significant correlations existed between BMI and most indices of muscle fibre pattern in the combined group of all subjects and in the athletes. The same was true as regards body mass. Moreover, significant correlations were also observed between body height and muscle fibre type distribution, especially in the group of athletes. On the other hand, no significant relationships were found between body fat and muscle morphology, either in untrained or trained men, except for type I fibre diameter in the group of all athletes.

It seems that the association between body characteristics and muscle morphology is not as strong as might be expected. The strongest relationships were between fibre type IIb diameter and BMI (0.72), body mass (0.63) and body fat (0.61) in power athletes. Furthermore, in all athletes, significant relationships were observed between type IIb fibre percentage and BMI (0.25), and body mass (0.30).

Higher values of body mass and body mass index were connected with a greater percentage and larger diameter of IIb fibres. It is striking that, while not statistically significant, the correlation between body mass and IIb diameter in endurance athletes is negative (-0.30) while it is reversed in power athletes (0.63). The same phenomenon is evident when the associations of IIb fibre diameter with both body fat and BMI for power and endurance athletes are examined. These findings are in good agreement with our earlier report that power athletes had greater mean muscle fibre diameter and a greater proportion of IIb fibres than did endurance athletes (Melichna *et al.* 1989). Also, it was found that among boxers in the highest weight category (over 75 kg), the smaller population of IIb as compared to type IIa fibres (m. vastus latwralis) was compensated by a very large diameter of type IIb (Melichna *et al.* 1980). Another essential difference between endurance and power athletes is illustrated by the significant positive correlation between body height and type I muscle fibre diameter in endurance athletes (0.46) which is in direct contrast to that in power athletes (-0.01).

The differences shown in this study between power and endurance athletes may be associated with their contrasting somatotype. Štěpnička (1977) showed that power athletes demonstrate greater mesomorphy while endurance athletes are more ectomorphic and sedentary subjects more endomorphic. Although Štěpnička's conclusions may partially explain some of the differences identified between athletic types, they would also lead to the expectation of some strong relationships in sedentary subjects between body fat and indices of muscle morphology. This was not the case in the present study.

Macková *et al.* (1982) showed a significant negative relationship between hydroxyacyl CoA-dehydrogenase activity and the percentage of depot fat in endurance trained athletes. It is also known that untrained men with a smaller percentage of body fat are able to achieve greater work loads at the same metabolic cost than those who must spend more energy to carry a larger body weight due to a higher percentage of body fat (Šprýnarová and Pařízková 1972). Moreover, a recent report by Kirkwood *et al.* (1991) failed to support a relationship between the metabolic rate and muscle mitochondrial morphology in untrained men, even though body fat is associated with lower mitochondrial density and a decreased oxidative capacity of muscles. In spite of the fact that

the mitochondrial content of skeletal muscles is a function of the number and size of oxidative muscle fibres (Hoppeler *et al.* 1985), we have not found a relation between body fat and the ratio of IIb/IIa+I fibres, either in sedentary or in trained subjects.

It appears that genetic influences are at least partly responsible for the muscle fibre size and proportion of fibre types, and for anthropometrical characteristics (Bouchard and Lortie 1984), but that habitual physical activity plays an important role in phenotypic expression (Schantz 1986). Perhaps because of this critical function of chronic exercise, the associations between somatic attributes and categories of muscle morphology were not as strong as our hypotheses assumed. In a previous study, it was shown that body mass was strongly and positively related to both anaerobic capacity and to oxidative power, but this did not apply to muscle mass (Melichna *et al.* 1989). This suggests that type I, IIa and IIb human skeletal muscle fibres possess great adaptability with regard to their enzymatic capacity. With a technique involving microdissection of freeze-dried fibre fragments, it was shown that metabolic changes induced in skeletal muscles by a training load may not necessarily be associated with muscle fibre type transformation (Essén-Gustavsson and Henriksson 1984). Moreover, changes in the proportion of muscle fibre types have been found to be a function of increased sympathoadrenergic activity (Taguchi *et al.* 1985), hypertension (Ben Bachir-Lamrini *et al.* 1990), hyperthyroidism (Celsing *et al.* 1986) and hypoxaemia (Hildebrand *et al.* 1991). An elevated percentage of type II fibres was observed in all these mentioned conditions. This plasticity of muscle may have an enhancing effect upon the anticipated relationships among parameters of muscle morphology and anthropometric features of the human body. Reciprocally, the present study suggests the three major muscle fibre types are responsive to a training load, since the relationships between elements of muscle morphology and of body composition are relatively low.

It has been demonstrated that increased physical activity and the degree of physical fitness correlate with the reduced risk of coronary heart disease (Blair *et al.* 1989, Leon *et al.* 1987, Paffenbarger *et al.* 1986). Others have indicated that the increased physical activity has favourable effects on diabetes and on blood and muscle cholesterol concentrations (Siscovick *et al.* 1985, Vondra *et al.* 1982) and on obesity (Klesges and Hanson 1988). Although the relationship between blood pressure and physical activity level remains equivocal (Klesges *et al.* 1991), a negative association between these two parameters in normotensive subjects has been reported (Sallis *et al.* 1988).

Men habituated to long distance running were observed to have a high percentage of oxidative fibres

in leg muscles (Macková *et al.* 1989). On the other hand, smokers were found to have a lower percentage of slow oxidative muscle fibres and a higher percentage of fast glycolytic fibres when compared to non-smokers (Örlander *et al.* 1979). Furthermore, a relatively reduced oxidative capacity in muscles of obese individuals has been noted (Bass *et al.* 1982). Sullivan *et al.* (1991) reported, among other things, decreased muscle oxidative enzyme activity in patients suffering from chronic heart failure. Thus, it would appear that reduced muscle oxidative capacity and/or a preponderance of fast glycolytic muscle fibres in non-athletic subjects may signal potential heart disease. Our

findings show that endurance athletes, a group often noted for its apparent resistance to coronary heart disease, demonstrated a lesser percentage of type IIb muscle fibres (implying a greater percentage of oxidative fibres), than in power athletes and the controls, greater type I fibre diameter than evidenced in control subjects and a significantly smaller ratio of glycolytic fibres to oxidative ones than in either power athletes or controls. These findings suggest that the dominant muscle oxidative potential may be a characteristic of those resistant to heart disease or, conversely, that a reduced aerobic muscle potential may depict those at risk for heart disease.

References

- BASS A., MACKOVÁ E., TEISINGER J., VONDRA K.: Some enzyme activities of energy supply in m. vastus lateralis of trained ski-runners and less active men. In: *Metabolic and Functional Changes During Exercise*. B. SEMIGINOVSKÝ, S. TUČEK (eds), Charles University, Prague, 1982, pp. 41–45.
- BEN BACHIR-LAMRINI L., SEMPORÉ B., MAYET M.-H., FAVIER R.J.: Evidence of slow-to-fast fibre type transition in skeletal muscle from spontaneously hypertensive rats. *Am. J. Physiol.* 258: R352–R357, 1990.
- BERGSTROM J.: Muscle electrolytes in man. *Scand. J. Clin. Lab. Invest.* 14 (suppl. 68): 1–110, 1962.
- BLAIR S.N., KOHL H.W., PAFFENBARGER R.S., CLARK D.G., COOPER K.H., GIBBONS L.W.: Physical fitness and all-cause mortality; a prospective study of healthy men and women. *J. Am. Med. Assoc.* 262: 2395–2401, 1989.
- BOROS-HATFALUDI S., FEKETE G., APOR P.: Metabolic enzyme activity patterns in muscle biopsy samples in different athletes. *Eur. J. Appl. Physiol.* 55: 334–338, 1986.
- BOUCHARD C., LORTIE G.: Heredity and endurance performance. *Sports Med.* 1: 38–64, 1984.
- CELSING F., BLOMSTRAND E., MELICHNA J., TERRADOS N., CLAUSEN N., LINS P.E., JANSSON E.: Effect of hyperthyroidism on fibre-type composition, fibre area, glycogen content and enzyme activity in human skeletal muscle. *Clin. Physiol.* 6: 171–181, 1986.
- COOLING-SALTIN A.S.: Skeletal muscle development in the human fetus and during childhood. In: *Children and Exercise*, Vol. 9. K. BORG, B.O. ERIKSSON (eds), University Press, Baltimore, 1980, pp. 193–207.
- DUBOWITZ, V., BROOKE, M.H.: *Muscle Biopsy: A Modern Approach*. W.B. Saunders, London, 1973.
- ESSÉN-GUSTAVSSON B., HENRIKSSON J.: Enzyme levels in pools of microdissected human muscle fibres of identified type. Adaptive response to exercise. *Acta Physiol. Scand.* 120: 505–515, 1984.
- FOSTER C., COSTILL D.L., DANIELS J.T., FINK W.J.: Skeletal muscle enzyme activity, fibre composition and $\dot{V}O_2$ max in relation to distance running performance. *Eur. J. Appl. Physiol.* 39: 73–80, 1978.
- GOLLNICK P.D., ARMSTRONG R.B., SAUBERT C.W. IV, PIEHL K., SALTIN B.: Enzyme activity and fibre composition in skeletal muscle of untrained and trained men. *J. Appl. Physiol.* 33: 312–319, 1972.
- GOLLNICK P.D., MATOBA H.: The muscle fibre composition of skeletal muscle as a predictor of athletic success. An overview. *Am. J. Sports Med.* 12: 212–217, 1984.
- HILDEBRAND I.L., SYLVÉN C., ESBJÖRNSSON M., HELLSTRÖM K., JANSSON E.: Does chronic hypoxaemia induce transformations of fibre types? *Acta Physiol. Scand.* 141: 435–439, 1991.
- HOPPELER H., HOWALD H., CONLEY K., LINDSTEDT S.L., CLAASSEN H., VOCK P., WEIBEL E.R.: Endurance training in humans: aerobic capacity and structure of skeletal muscle. *J. Appl. Physiol.* 59: 320–327, 1985.
- HUTCHINSON P.L., CURETON K.J., OUTZ H., WILSON G.: Relationship of cardiac size to maximal oxygen uptake and body size in men and women. *Int. J. Sports Med.* 12: 369–373, 1991.
- JANSSON E., KAIJSER L.: Muscle adaptation to extreme endurance training in man. *Acta Physiol. Scand.* 100: 315–324, 1977.
- JOHNSON M.A., POLGAR J., WEIGHTMAN D., APPLETON D.: Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. *J. Neurol. Sci.* 18: 111–129, 1973.
- KIRKWOOD S.P., ZURLO F., LARSON K., RAVUSSIN E.: Muscle mitochondrial morphology, body composition, and energy expenditure in sedentary individuals. *Am. J. Physiol.* 260: E89–E94, 1991.
- KLESGES R.C., ECK L.H., ISBELL T.R., FULLITON W., HANSON C.L.: Physical activity, body composition, and blood pressure: a multimethod approach. *Med. Sci. Sports Exerc.* 23: 759–765, 1991.

- KLESGES R.C., HANSON C.L.: Determining the environmental precursors and correlates of childhood obesity. In: *Childhood Obesity: A Behavioral Perspective*. N.A. KRASNEGOR, G.D. GRAVE, N. KRETCHMER (eds), Telford Press, New York, 1988, pp. 89–118.
- KUGELBERG E.: Adaptive transformation of rat soleus motor units during growth – histochemistry and contraction speed. *J. Neurol. Sci.* 27: 269–289, 1976.
- LEON A.S., CONNETT J., JACOBS D.R., RAURAMMA R.: Leisure-time physical activity levels and risk of coronary heart disease and death. *J. Am. Med. Assoc.* 258: 2388–2395, 1987.
- MACDOUGALL J.D.: Morphological changes in human skeletal muscle following strength training and immobilization. In: *Human Muscle Power*. N.L. JONES, N. MCCARTNEY, A.J. MCCOMAS (eds), Human Kinetics Publ., Champaign, 1986, pp. 269–288.
- MACKOVÁ E.V., NOVÁK J., MELICHNA J.: Coureurs Amateurs de grand fond. Caractéristiques d'un muscle strié (m. vastus lateralis) et réponse du métabolisme énergétique musculaire lors d'une course durant 24 heures. *Medicine du Sport*. 63: 3–10, 1989.
- MACKOVÁ E.V., BASS A., ŠPRYNAROVÁ Š., VONDRA K., BOJANOVSKÝ I.: Changes of enzyme activities of the energy metabolism due to endurance loads. In: *Metabolic and Functional Changes During Exercise*. B. SEMIGINOVSKÝ, S. TUČEK (eds), Charles University, Prague, 1982, pp. 47–51.
- MALTIN C.A., DELDAY M.I., BAILLIE A.G.S., GRUBB D.A., GARLICK P.J.: Fibre-type composition of nine rat muscles I. Changes during the first year of life. *Am. J. Physiol.* 257: E823–E827, 1989.
- MAUGHAN R.J., WATSON J.S., WEIR J.: Relationships between muscle strength and muscle cross-sectional area in male sprinters and endurance runners. *Eur. J. Appl. Physiol.* 50: 309–318, 1983.
- MELICHNA J.: *Movement and Morphological Adaptability of Skeletal Muscle* (in Czech). Charles University, Prague, pp. 1–311, 1990.
- MELICHNA J., VRÁNOVÁ J., HAVLÍČKOVÁ L., SELIGER V., BARTUNĚK Z.: Functional fitness and histochemical analysis of biopsy samples of muscle tissue in boxers (in Czech). *Teor. praxe těl. vých.* 28: 168–175, 1980.
- MELICHNA J., HAVLÍČKOVÁ L., VRÁNOVÁ J., SELIGER V., BARTUNĚK Z., BARTUŇKOVÁ S., ŠTICHOVÁ J.: Muscle fibre composition and functional performance in athletes of various sports events. In: *Metabolic and Functional Changes During Exercise*. B. SEMIGINOVSKÝ, S. TUČEK (eds), Charles University, Prague, 1982, pp. 119–122.
- MELICHNA J., MACKOVÁ E.V., NOVÁKOVÁ H., FRIČ J., NOVÁK J., ZAUNER C., ULBRICHOVÁ M.: Skeletal muscle properties in relation to anaerobic and aerobic work capacity of athletes. *Sports Training, Med. and Rehab.* 1: 227–235, 1989.
- MÜLLER W.: A method for the comparison of morphometrical data on skeletal muscles in young rats of different ages and body weights. *Histochemistry* 43: 241–248, 1975.
- ÖRLANDER J., KIESSLING K-H., LARSSON L.: Skeletal muscle metabolism, morphology and function in sedentary smokers and nonsmokers. *Acta Physiol. Scand.* 107: 39–46, 1979.
- PAFFENBARGER R.S., HYDE R.T., WING A.L., HSIEH C-C.: Physical activity, all-cause mortality, and longevity of college alumni. *N. Engl. J. Med.* 314: 605–613, 1986.
- PAŘÍZKOVÁ J.: *Body Fat and Physical Fitness*. Martinus Nijhoff, The Hague, 1977.
- PAŘÍZKOVÁ J.: Adaptation of functional capacity and exercise. In: *Nutritional Adaptation in Man*. K. BLATER, J.C. WATERLAW (eds), John Libbey, London, 1985, pp. 127–139.
- PAŘÍZKOVÁ J.: Age dependent changes in dietary intake related to work output, physical fitness and body composition. *Am. J. Clin. Nutr.* 89: 962–967, 1989.
- SALLIS J.F., PATTERSON T.L., BUONO M.J., NADER P.R.: Relation of cardiovascular fitness and physical activity to cardiovascular disease risk factors in children and adults. *Am. J. Epidemiology* 127: 933–941, 1988.
- SCHANTZ P.G.: Plasticity of human skeletal muscle. *Acta Physiol. Scand.* 128 (Suppl. 558): 1–62, 1986.
- SISCOVICK D.S., LAPORTE R.E., NEWMAN J.M.: The disease-specific benefits and risks of physical activity and exercise. *Public Health Rep.* 100: 180–188, 1985.
- SPATZ H.C.: Circulation, metabolic rate, and body size in mammals. *J. Comp. Physiol.* 161B: 231–236, 1991.
- ŠPRYNAROVÁ Š., PAŘÍZKOVÁ J.: The influence of high or low proportion of depot fat on the aerobic capacity and performance in 11-18 year-old boys. *Physiol. Bohemoslov.* 22: 440–441, 1972.
- ŠTĚPNIČKA J.: Somatotypes of Czechoslovak athletes. Growth and development, Physique. *Symp. Biol. Hung.* 20: 357–364, 1977.
- SULLIVAN M.J., GREEN H.J., COBB F.R.: Altered skeletal muscle metabolic response to exercise in chronic heart failure: relation to skeletal muscle aerobic enzyme activity. *Circulation* 84: 1597–1607, 1991.
- TAGUCHI S., HATA Y., ITOH K.: Enzymatic responses and adaptation to swimming training and hypobaric hypoxia in postnatal rats. *Jpn. J. Physiol.* 35: 1023–1032, 1985.

- TELFORD R.D., CUNNINGHAM R.B.: Sex, sport, and body-size dependency of hematology in highly trained athletes. *Med. Sci. Sports Exerc.* **23**: 788–794, 1991.
- TESCH P.A., KARLSSON J.: Muscle fibre types and size in trained and untrained muscles of elite athletes. *J. Appl. Physiol.* **59**: 1716–1720, 1985.
- VONDRA K., BRODAN V., BASS A., KUHN E., ANDĚL M., VÍTEK V., TEISINGER J.: The effect of short maximum load exercise test on some enzyme activities and cholesterol content in human skeletal muscle. In: *Metabolic and Functional Changes during Exercise*. B. SEMIGINOVSKÝ, S. TUČEK (eds), Charles University, Prague, 1982, pp. 53–56.
- WILMORE J.H.: The application of science to sport: physiological profiles of male and female athletes. *Can. J. Appl. Sport Sci.* **4**: 103–115, 1979.
-

Reprint Requests

Prof. C. W. Zauner, Department of Exercise and Sport Science, Langton Hall, Room 214, Oregon State University, Corvallis, OR 97331, U.S.A.