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Skeletal Muscle Characteristics of Young Standardbreds in Relation to Growth and Early Training

B. ESSÉN-GUSTAVSSON, A. LINDHOLM, D. McMIKEN, S. G. B. PERSSON and J. THORNTON

Department of Medicine I, College of Veterinary Medicine, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden.

Summary

Muscle biopsies were obtained from both the left and right middle gluteal and semitendinosus muscles of ten Standardbred colts six to eight months of age. All ten colts were raised at the same farm during the following year and five of them (T-group) were subjected to regular controlled exercise four to five days per week, while the only physical activity of the other five foals (C-group) consisted of that usually occurring in a group of yearlings. Muscle biopsies were again obtained from all ten yearlings at four and ten months after the first biopsies had been taken. No difference in either fibre composition (type I, IIA, IIB) or oxidative and glycolytic enzyme activities were found when the two groups were compared at the time when the biopsies were taken. However, large variations in muscle characteristics existed among the yearlings. The type I/type II ratio did not change with age, but type IIA/type IIB ratio increased in both groups. Fibre areas increased by 30 to 70% in all fibre types. The oxidative enzyme citrate synthase showed a significant increase with age only in the T-group, while 3-OH-acyl CoA dehydrogenase was unchanged in both groups. The glycolytic enzymes, triose phosphate dehydrogenase and lactate dehydrogenase, were significantly decreased (20–40%) in both groups. No significant training effect was detected in this study since the yearlings in the T-group that were physically activated demonstrated an almost similar adaptation in muscle to the yearlings in the C-group. This does not exclude the possibility of other training régimes influencing muscle characteristics. Furthermore, the potential for adaptation in skeletal muscle may depend on hereditary factors since large variations in muscle characteristics existed among the foals even prior to training.

Introduction

In an attempt to maximize performance capacity many horses are subjected to increased levels of physical activity by 1.5 to 2 years of age. Training régimes which improve performance in man and animals have been shown to induce changes in the cardiovascular system and also in the skeletal muscles involved in exercise. Where

exercise is prolonged and of submaximal intensity the affected skeletal muscles tend to increase their oxidative capacity (Holloszy *et al.*, 1970; Barnard *et al.*, 1970; Saltin *et al.*, 1976), while improvements in glycolytic capacity are much more difficult to induce and have only been reported after high-intensity interval training in man (Roberts *et al.*, 1982). There are few reports on the effects of training on the metabolic capacity of skeletal muscle in Thoroughbred and Standardbred horses, but the oxidative capacity has been shown to increase, while the glycolytic capacity either has increased or decreased (Guy and Snow, 1977; Snow and Guy, 1979; Nimmo *et al.*, 1982; Lindholm *et al.*, 1983).

It is generally believed that the ratio of slow contracting type I fibres to fast contracting type II fibres does not change with physiological stimuli (Barnard *et al.*, 1970; Gollnick *et al.*, 1973). However, the type IIA/type IIB ratio has been shown to increase after intensive endurance training and to decrease following inactivity (Andersen and Henriksson, 1977; Green *et al.*, 1979; Saltin 1977). Old Standardbred trotters and those actively racing show higher type IIA/type IIB ratios than young and inactive Standardbreds (Essén *et al.*, 1980; Essén-Gustavsson *et al.*, unpublished), and in addition, young Thoroughbreds increase the ratio of type IIA/type IIB fibres in response to training (Lindholm *et al.*, 1983). Thus, apart from growth, it appears that physical activity is also an important factor in the development of skeletal muscle characteristics, as both type IIA/type IIB ratio and oxidative capacity may be affected. The aim of the present investigation was to study the adaptive response in skeletal muscles involved in locomotion in young growing Standardbreds and to determine any superimposed effect of early physical activity during this growth phase.

Material and Methods

Ten clinically normal Standardbred colts, two from each of five different breeders, were used in this study. In December 1980, when the colts were seven to eight months old, the breeder assigned one of his two colts to a control group (C-group) and the other to a group that would be subjected to regular controlled exercise (T-group). All ten colts were raised at the same farm and subjected to repeated clinical examinations during the subsequent year.

C-group: The five control foals were treated in the same manner as the other young foals on the farm. During the first two months the foals were kept outdoors for five to six hours per day and from February to May 1981 for six to eight hours per day. In June, the colts were taken out to pasture with 20 other yearlings, where they remained until the end of September 1981.

T-group: The five foals in this group were treated similarly to those in C-group until May 1981, from which time they were on pasture eight hours a day until August, after which they were outdoors 24 hours a day. These foals commenced their training programme in December 1980, which, due to prevailing weather conditions, was carried out in a riding house. The training programme consisted of regular and increasing workouts at a trot or canter four to five days a week, with the colts working in pairs at a slow pace. After first warming up for five minutes, the foals initially trotted approximately 1800 metres in December 1980. This was increased progressively to 3600 metres in April 1981. In May 1981, the colts began trotting outdoors at a slow tempo in a sulky over

3000 metres four to five days per week. This type of training continued with ever increasing tempo until October 1981. From July faster trotting over 1600 metres was included once a week, and by the end of September 1981 these colts were all able to trot at 500 m/min or faster over 1600 metres. The training programme varied somewhat between individuals, according to their motivation and responsiveness.

Muscle biopsies. Using the needle biopsy technique described by Lindholm and Piehl (1974), muscle samples were obtained from the left and right middle gluteal and the left and right semitendinosus muscles. The muscle biopsies were taken when the colts were seven to eight months old (December 1980), 11 to 12 months old (April 1981) and 17 to 18 months old (October 1981). On each occasion two samples were obtained from each biopsy site. One sample for biochemical analysis was immediately frozen in liquid nitrogen, while the other for histochemical analysis was oriented and mounted in embedding medium (Tissuetek II) on a chuck and frozen in isopentane cooled in liquid nitrogen. Both samples were then stored at -80°C until analyzed.

Histochemical analysis. Serial sections ($10\ \mu\text{m}$) were cut in a cryostat at -20°C and stained for myofibrillar ATP-ase after both acid (pH 4.3 and 4.6) and alkaline (pH 10.3) pre-incubation (Brooke and Kaiser, 1970). From photomicrographs of the stained sections the muscle fibres were identified as type I, IIA, IIB and IIC (Brooke and Kaiser, 1970).

Fibre area analysis. The cross-sectional areas of type I, IIA and IIB fibres were determined with the MOP digiplan analyser (Kontron) by measuring the areas of 25 randomly selected fibres of each type from a photomicrograph of the section stained for myofibrillar ATP-ase after acid pre-incubation (pH 4.6).

Biochemical analysis. The muscle tissue was freeze-dried and dissected free of connective tissue, fat and blood. The muscle (250–1000 μg) was then weighed and homogenized with an ultrasound disintegrator in cooled 0.1 M phosphate buffer at pH 7.3 (dilution 1 : 400).

The activities of citrate synthase (CS), 3-OH-acyl-CoA dehydrogenase (HAD), lactate dehydrogenase (LDH), hexokinase (HK) and triose phosphate dehydrogenase (TPDH) were assayed on the homogenate. Citrate synthase, HAD and TPDH were measured as previously described (Essén *et al.*, 1980). The assay mixtures for LDH and HK were as follows:

LDH: TEA-buffer 50 mM, pH 7.6, EDTA 6.0 mM, NADH 0.05 mM, pyruvate 1.0 mM.
HK: TEA-buffer 50 mM, pH 7.6, EDTA 5.0 mM, MgCl_2 8.0 mM, NADP 0.15 mM, glucose 1.0 mM, glucose-6-phosphate dehydrogenase 5 $\mu\text{g}/\text{ml}$, ATP 0.5 mM.

All enzyme activities were analyzed on part of the homogenate at 25°C with the aid of a Farrand fluorimeter and the Lowry technique (Lowry and Passonneau, 1973).

Statistics. Results in the figures are given as means (right plus left side) \pm SD. Standard statistical methods were used in the analysis of data. The coefficient of variation between right and left side is expressed as

$$\text{CV} = \sqrt{\frac{\sum d^2}{2n}} \cdot 100/\bar{x}$$

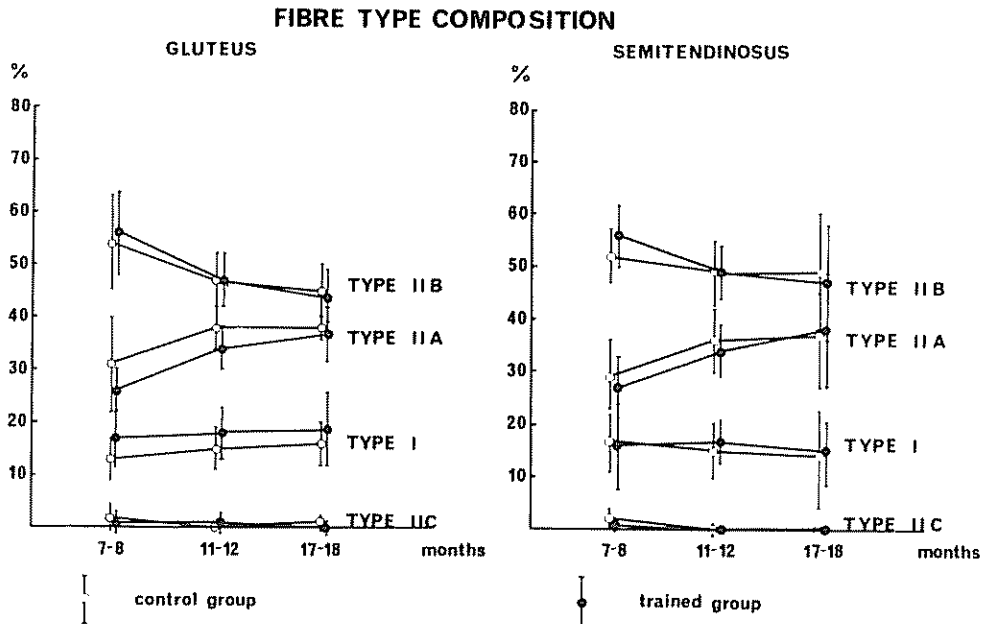
where \bar{x} is the mean, d the difference and n the number of pairs of data.

Results

Body weight. In December 1980 the mean weight of the colts in the T-group was somewhat greater (251 ± 13 kg) than that of the C-group (229 ± 23 kg). In both groups the increase in mean body weight was smaller from December 1980 to April 1981 (36 ± 6 kg in C-group, 34 ± 4 kg in T-group) than from April 1981 to October 1981 (105 ± 7 kg in C-group, 95 ± 16 kg in T-group). In October 1981 the mean body weight was greater in the T-group (394 ± 14 kg) than in the C-group (358 ± 25 kg, $p < 0.05$).

Fibre composition. There was no significant difference in fibre composition between the left and right sides for either middle gluteal or semitendinosus muscles. The results in the figures are therefore expressed as the mean of the values from both right and left sides. In the middle gluteal muscle the CV between left and right sides was 22.5% for type I fibres, 16.4% for type IIA fibres and 14.5% for type IIB fibres ($n = 30$). In semitendinosus muscle the CV was 24.7% for type I fibres, 18.5% for type IIA fibres and 13.6% for type IIB fibres ($n = 30$). A great inter-individual variation in fibre type composition was seen in both groups in December 1980, when both middle gluteal and semitendinosus muscles had less than 20% type I fibres, approximately 30% type IIA fibres and over 50% type IIB fibres. By April 1981 the percentage of type IIA had increased significantly to 38% in the C-group ($p < 0.05$) and to 34% in the T-group ($p < 0.01$) while the percentage of type IIB fibres had decreased similarly to 47% in both groups ($p < 0.05$) (Fig. 1). In the semitendinosus muscle a similar pattern with a significant change was seen only in the T-group which had 34% type IIA and 49% type IIB

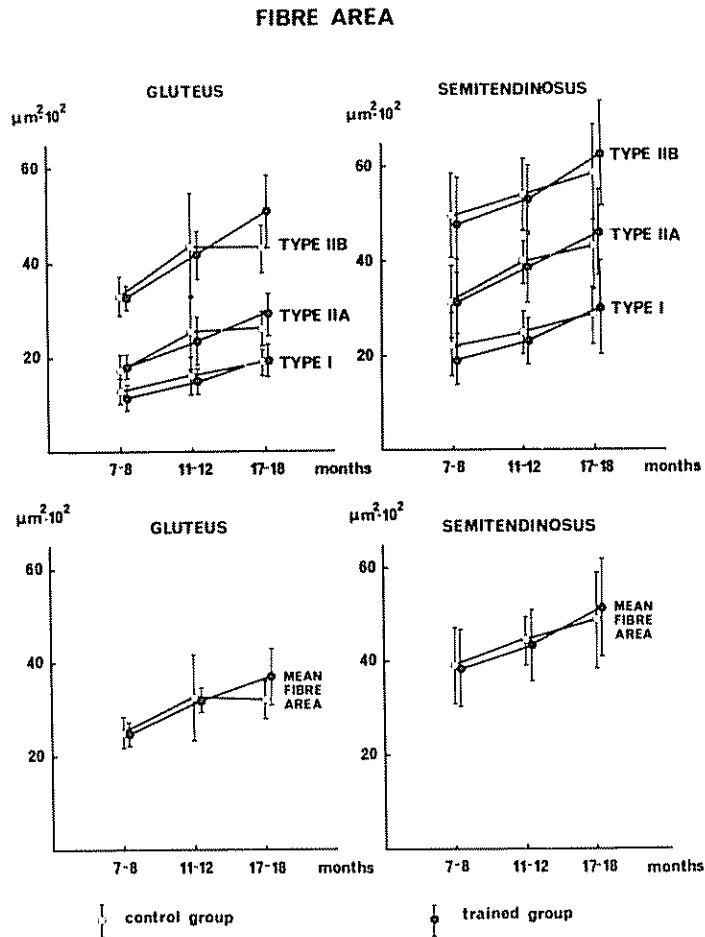
FIGURE 1. Mean values and SD are shown for fibre type composition in the middle gluteal and semitendinosus muscles in relation to age.



fibres by April 1981 ($p < 0.05$). From April to October 1981 no further significant change in the type IIA/type IIB ratio occurred in either muscle of either group. In October 1981 both muscles had a mean of approximately 38% type IIA fibres, while the middle gluteal had 45% type IIB and the semitendinosus 48% type IIB fibres.

A small number of type IIC fibres was found in both the T-group and the C-group in December 1980, whereas in October 1981 none were found in the semitendinosus muscle and only three of the ten colts had type IIC fibres in the middle gluteal muscle.

FIGURE 2. Mean values and SD are shown for fibre areas in the middle gluteal and semitendinosus muscles in relation to age.



Fibre areas. There was no difference in cross-sectional area of each fibre type or in the mean fibre area between left and right side of the muscles except for a significant difference in type IIA ($p < 0.05$) and type IIB ($p < 0.01$) fibres in the semitendinosus

muscle by October 1981. The CV was 16.3%, 13.2% and 14.1%, respectively, for type I, IIA and IIB ($n = 26$) fibres in the middle gluteal muscle and 20.3%, 18.7% and 18.1%, respectively, ($n = 26$) for type I, IIA and IIB fibres in the semitendinosus muscle. The CV for the mean area was 12.6% for the middle gluteal and 18.2% for the semitendinosus muscle. The figures show the mean of the values from left and right sides. In the semitendinosus muscle the mean cross-sectional areas of type I and type IIA fibres were 1.7 to 1.8 times larger while the mean cross-sectional areas of type IIB fibres were 1.5 times larger than the equivalent fibres in the middle gluteal muscle (Fig. 2). In the middle gluteal muscle the areas of all fibre types increased significantly ($p < 0.001$) from December 1980 to October 1981, with a greater mean increase in those of the T-group (type I 72%, type IIA 65%, type IIB 56%) compared to those of the C-group (type I 49%, type IIA 52%, type IIB 31%). By April 1981 a significant increase had only occurred in the type IIA (C-group, $p < 0.01$; T-group, $p < 0.001$) and type IIB fibres (C-group, $p < 0.05$; T-group, $p < 0.001$) in both groups of foals. In the semitendinosus muscle significant increases in the fibre areas only occurred at the October 1981 sampling when type IIA fibres of the C-group ($p < 0.01$) and type I ($p < 0.05$), type IIA ($p < 0.01$) and type IIB fibres ($p < 0.05$) of the T-group had increased significantly.

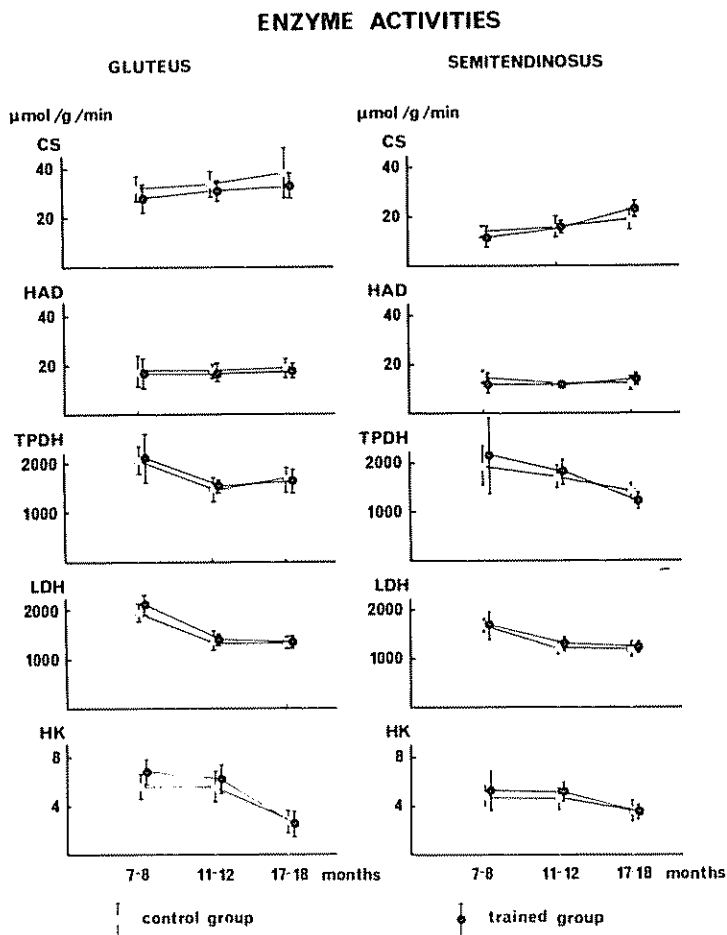
The mean fibre area increased significantly over the whole period (December 1980 to October 1981) in both middle gluteal (C-group 29%, $p < 0.001$; T-group 50%, $p < 0.001$) and semitendinosus muscles (C-group 24%, $p < 0.05$; T-group 35%, $p < 0.05$). From December 1980 to April 1981 the increase in the mean fibre area in the middle gluteal muscle alone was significant (C-group 29%, $p < 0.05$, T-group 30%, $p < 0.001$) and twice as large as the non-significant (14%) increase in the semitendinosus muscle. From April 1981 to October 1981 the mean area of all fibre types and the area of individual fibre types did not change significantly in either muscle.

Enzyme activities. The two mitochondrial enzymes CS and HAD (chosen as markers for oxidative capacity) had higher activities (CS two times, HAD 1.5 times higher) in the middle gluteal muscle than in the semitendinosus muscle (Fig. 3). Of the enzymes used as indicators of glycolytic capacity (TPDH, LDH and HK) TPDH had similar activities in both muscles, while LDH and HK were somewhat higher (1.2 times) in the middle gluteal muscle (Fig. 3).

There was no difference in enzyme activities between the left and right sides for either middle gluteal or semitendinosus muscles. The results in the figures are therefore expressed as the mean of the values from both right and left sides. The CV between the two sides was 13.3% for CS, 21.2% for HAD, 9.2% for TPDH, 7.4% for LDH and 12.5% for HK ($n = 30$) for the middle gluteal muscle and 15.4% for CS, 15.8% for HAD, 14.1% for TPDH, 9.1% for LDH and 13.5% for HK ($n = 30$) for the semitendinosus muscle.

Neither the C-group nor the T-group showed any age variation in HAD activity in either the middle gluteal or semitendinosus muscles. The CS activity did not change in the C-group, but had increased significantly in the T-group by October 1981 in both the middle gluteal (18%, $p < 0.05$) and semitendinosus muscles (92%, $p < 0.001$). In the semitendinosus muscle a significant increase was already present in April 1981 (33%, $p < 0.05$). In both groups LDH activity had decreased significantly by April 1981 in both the middle gluteal (C-group 30%, $p < 0.001$; T-group 33%, $p < 0.001$) and semitendinosus muscles (C-group 27%, $p < 0.001$; T-group 24%, $p < 0.001$) with no further change seen from April to October 1981. TPDH activity showed a similar pattern in the middle

FIGURE 3. Mean values and SD are shown for enzyme activities in the middle gluteal and semitendinosus muscles in relation to age.



gluteal muscle with a significant decrease by April 1981 (C-group 27%, $p < 0.001$; T-group 26%, $p < 0.001$), whereas in the semitendinosus muscle a significant decrease only occurred from April to October 1981 (C-group 19%, $p < 0.001$; T-group 32%, $p < 0.001$). HK activity did not change from December 1980 to April 1981 but then decreased significantly from April to October 1981 in both the middle gluteal (C-group 48%, $p < 0.001$; T-group 58%, $p < 0.001$) and semitendinosus muscles (C-group 19%, $p < 0.001$; T-group 27%, $p < 0.001$).

Discussion

The fibre type composition of the foals in the present study agrees with the data obtained from an earlier study (Essén *et al.*, 1980). In both of these studies a large inter-individual

variation was found in fibre type composition and also in the oxidative and glycolytic potential of both the middle gluteal and semitendinosus muscles. These findings probably reflect the importance of the genetic endowment of muscle characteristics. Of interest are the similar variations in type IIA/type IIB ratio and enzyme activities seen in both the C-group and T-group of the present study, despite there being only five foals in each group. One apparent reason for this similarity was that the foal with the lowest percentage of type I and IIB fibres in the C-group came from the same breeder as the foal with the lowest percentage of these fibre types in the T-group. As five breeders contributed two foals each, one to the C-group and one to the T-group, this suggests that environmental influences as well as genetic factors are of importance in the determination of muscle characteristics.

Early training of young foals did not seem to alter markedly the characteristics of the muscles from those usually seen with growth alone, as similar mean values were obtained at all stages in both the T-group and the C-group. The slight, but significant, increase over the whole period in CS, type IIA/type IIB ratio and fibre areas in the semitendinosus muscle in the T-group may indicate that, apart from growth, there was a specific adaptation of this muscle to training. The increase in fibre area might reflect increased muscle tension due either to gait changes or to additional stress imposed on the semitendinosus muscle by sulky training. The difference in fibre areas between left and right sides seen in this muscle at the end of the training programme is hard to explain. As training was performed on a straight track, influences on both left and right sides should have been equal.

It seems that not only the semitendinosus but also the middle gluteal muscle in the T-group responded to training with an increased oxidative potential, although the increase in CS was more marked in the semitendinosus muscle. An improved oxygen utilization of the muscles is consistent with the cardiorespiratory and blood lactate response seen in these horses. (Persson *et al.*, 1983). However, the type of training used in the present study appears to have had only a minor effect on muscle characteristics, while the effect on the cardiorespiratory system was apparently greater (Persson *et al.*, 1983). It is possible that a more intense or different type of training could have induced greater differences in the skeletal muscles.

Growth itself and the spontaneous activity, rather than any kind of controlled superimposed activity, seem to be the most important factors inducing the changes in muscle characteristics. It is interesting to note that in both the C-group and the T-group the greatest change in type IIA/type IIB ratio, type II fibre areas and enzyme profiles in the middle gluteal muscle occurred in the period between December 1980 to April 1981. During these first four months, the mean fibre area of the middle gluteal muscle increased by as much as 30%, but only by 0 to 15% during the following six months. Thus the effects of growth on the semitendinosus seemed to be less marked than those in the middle gluteal muscle, as a significant increase in mean fibre area was only found in October 1981. Since the increase in body weight was only 15% from December 1980 to April 1981 but 40% during the rest of the period, this indicates that when foals are one to two years old, part of the increase in body weight is due to muscle growth and development of the middle gluteal muscle in particular. The functional demands of the different muscles are probably altered during this period of growth, which may induce changes in muscle characteristics.

Spontaneous activity is another important factor to consider regarding the changes seen in muscle characteristics in different muscles. The foal is introduced to a new environmental and behavioural pattern when it is weaned at the age of six months. The foal is then normally stabled by itself but pastured with other foals, and this introduces a new type of activity pattern which may be sufficient stimulus to induce the changes seen in muscle characteristics. It is interesting to note that the foal with the greatest increase in CS was found in the C-group which suggests that this foal may have had an enhanced level of activity during the growth period when compared to the other foals.

Even though the percentage of different fibre types was similar in both middle gluteal and semitendinosus muscles in December 1980, these muscle groups differ in both oxidative capacity and fibre areas. The mean fibre area of the semitendinosus muscle was already larger in December 1980 than that of the middle gluteal by October 1981. Mean fibre areas in the middle gluteal muscle, when these foals were 1.5 years old, agree well with those of 1.5-year-old Thoroughbreds (Lindholm *et al.*, 1983). The low oxidative capacity of the semitendinosus muscle is in part explained by the fact that this muscle is composed of larger type IIB fibres than those found in the middle gluteal muscle. Type IIB fibres are known to have the lowest oxidative capacity (Essén *et al.*, 1980).

The changes in enzyme activities that occurred with growth could to some extent relate to the changes seen in fibre areas. The enlargement of muscle fibres is due to an increase in the myofibrillar content (Goldspink 1970). Thus the decrease in TPDH activity in the middle gluteal muscle by approximately 30% could be explained by a dilution of the enzyme, as the increase in fibre areas was also nearly 30%. On the other hand, the oxidative enzymes are located in the mitochondria, and as these probably increase in size and number in parallel with the myofibrils, the enzymes do not change with growth. The different response seen in enzymatic changes between the middle gluteal and semitendinosus muscles is most likely related to different functions of these muscles and the relative area occupied by a certain fibre type.

In the middle gluteal muscle of a young foal the relative area of type IIB fibres was as high as 70 to 75%, decreasing to 60% after one year of growth. In older inactive Standardbreds the corresponding area is 50%, while in racing Standardbreds with a performance of around 1:16 min/km it is only 15% (Essén-Gustavsson and Lindholm, unpublished). In a good racehorse, the largest part of the mean fibre area is thus made up of type I and type IIA fibres. These fibres are known to have a high oxidative capacity (Essén *et al.*, 1980). Furthermore, the CS activity levels in the middle gluteal muscle were two to three times higher in the racing Standardbreds compared to the older inactive Standardbreds which had values similar to those found in the foals in the present study. The question then arises whether foals selected early for a high type IIA/type IIB fibre ratio and a high oxidative capacity in their muscles are more likely to achieve good performance times in the future.

The advantage of a superimposed training programme during the growth phase in order to get an early adaptive response in the muscles of a foal may be questionable, as similar adaptations occurred with growth alone. This may suggest that it is preferable to start training foals when they are 1.5 to 2 years old, as by this time the muscles are probably close to full development and have adapted to their normal function and specific movement in connection with growth. The alterations seen in the muscles after this time are then presumably influenced by a change in the level of physical activity. The potential

for adaptation in muscle may also depend on hereditary factors since large variations in muscle characteristics existed among the foals even prior to training.

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