Postnatal development of the oxidative enzyme activity in equine locomotion muscles and the influence of exercise

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Summary

To study the effect of age and exercise on the citrate synthase (CS) activity, we took biopsies from the deep gluteus medius and superficial semitendinosus muscle at four ages in 37 Dutch warmblood foals, divided over three training groups. The CS activity is higher in gluteus medius than in semitendinosus muscle. At birth, the CS activity in gluteus medius and semitendinosus muscle is positively correlated. CS activity decreases from 0 to 22 weeks. An exercise effect was not detected. The succinate dehydrogenase (SDH) activity was studied in four fibre types of the gluteus medius in biopsies of 13 foals, divided over the training groups, at birth and 22 weeks. At birth, SDH activity in IId fibres is lower than in other types. At 22 weeks SDH activity in IId fibres is lower than in Ia and I, but still higher than in IId fibres. SDH activity increases in I and Ila and decreases in IId fibres. The decrease in IId fibres is largest in the boxrest group. We conclude that the normal capacity of equine locomotory muscle to use oxygen for energy production for contraction and relaxation decreases in the postnatal period. Restricted movement results in underdevelopment.

Keywords: horse, citrate synthase, succinate dehydrogenase, gluteus medius, semitendinosus, exercise, biochemistry, histochemistry
Introduction

Muscular fatigue often causes exercise intolerance in horses (Valberg 1996). For a proper muscle function, fatigue must be prevented and therefore, substrate needs to be converted into energy. Energy for the muscle comes in the form of adenosine triphosphate (ATP), which can be most efficiently produced by oxidative phosphorylation. The activity of succinate dehydrogenase (SDH) predicts the maximum rate of oxygen consumption (oxidative capacity) and therefore correlates with energy production (van der Laarse et al. 1989). Pette (1962) described a proportional relation between oxidative capacity-related enzymes. The activity of citrate synthase (CS), another oxidative enzyme, can also be used as a measure of tissue energy production.

Citrate synthase is an enzyme in the mitochondria which catalyses the conversion of acetyl coenzyme-A and oxaloacetaat in coenzyme-A and citrate in the citric acid cycle. SDH is an enzyme which is also located in the mitochondria and catalyses the conversion of succinyl-CoA in succinate in the citric acid cycle. Pool et al. (1979) have developed a quantitative histochemical method to measure succinate dehydrogenase activity in individual muscle fibres.

Age and exercise are known to increase the oxidative capacity in the muscles of horses (Guy and Snow 1977; Snow and Guy 1979; Hodgson et al. 1986; Roneus et al. 1992; Roneus 1993). It is also known that in horses, type I and IIa fibres generally show a higher oxidative capacity than type IId fibres (e.g. Valberg et al. 1985, 1988) but that this can vary markedly within one type of the different fibres. Especially in the population of type IId fibres, investigators found oxidative enzyme activities varying between low and as high as in type IIa fibres (Valberg and Essen-Gustavsson 1987). Most of these studies were performed on adult or young adult race horses. Some authors describe a decrease in oxidative capacity in the first months after birth due to decreasing percentages of oxidative fibres (Bechtel and Kline 1987, Kline and Bechtel 1990). However, direct information about the oxidative capacity in the muscles of new-born horses and the development during the first year of life is still lacking.

The aim of this study was to investigate enzyme activities, as predictors of the oxidative capacity, in locomotory muscles of Dutch warmblood foals in the first year of life. Furthermore, we wanted to investigate if exercise, given in such an early phase of life, could influence the normal pattern of age related maturation of the oxidative capacity.

Material and methods

Foals
The investigation was performed in a group of 37 Dutch warmblood foals. They were bred, raised and trained for an experiment focusing on the effects of exercise at a very early age on the development of the equine musculoskeletal system (in particular osteochondrosis) as described by van Weeren and Barneveld (1999). All procedures were approved by the
animal experiments committee (DEC) of the Faculty of Veterinary Medicine (Utrecht, The Netherlands). After birth, all foals remained with the mares in a paddock for one week, after which they were randomly divided into three groups that were subjected to different exercise regimens until weaning at five months. Two groups (boxrest, n = 12 and training, n = 11) were individually housed with the mare in 3 x 3.5 m box stalls. They were fed freshly cut grass ad libitum, along with the mother’s milk. The third group was kept at pasture with the mare 24 h a day (pasture group, n = 14). At 22 weeks of age 21 foals (7 foals from each group) were euthanized for other purposes. The remaining 16 foals were joined in one single group which was kept in a loose house with access to a small paddock. All foals were subject of investigation in the determination of the CS activity but, due to the labour intensiveness of the method, only 13 (boxrest n = 6, training n = 3, pasture n = 4) of them were used for the determination of the SDH activity.

Exercise protocol
Until 22 weeks, the boxrest group was kept in the box stall for 24 h/day. The training group was also kept in box stalls, but was given an increasing number of gallop sprints in a paddock of 48 x 15 m with a concrete floor covered by a sandy top layer. The exercise was given by two persons at the far ends of the paddock who chased the mares in between them. The foals followed the mares. Exercise started the day when they were allotted to the training group (day 7) and consisted of 12 sprints. From day 8 the number of sprints was increased to 16 which remained so till day 24. From day 25 to day 38 they made 24 sprints and from day 39 till weaning at 22 weeks 32 and 16 sprints on alternating days. Exercise was given 6 days a week. The sprints lasted for about 6 seconds (≈ 6.5 m/s) and a pause was kept after each sprint to prevent exhaustion. After the sprints, the foals were allowed an additional 0.5 hours of free exercise in the enclosure. The pasture group received voluntary movement. After 22 weeks up to 48 weeks, none of the foals was further trained, so all got the same exercise regimen.

Muscle biopsies
Two locomotory muscles (i.e. gluteus medius and semitendinosus muscle) were chosen as a model. These two muscles are subjects of investigation in many studies, mainly because of their important propulsive role, but also because taking biopsies from these muscles is relatively easy.

Percutaneous muscle biopsies were taken from each foal according to the protocol of Lindholm and Piehl (1974) in the first week after birth (day 3 on average) and at the age of 4 and 22 weeks. From half the foals, biopsies were also taken at the age of 48 weeks. To cause as little as possible discomfort, the young foals were handled by their caretakers in the presence of their mares and sedation was not necessary. After local anaesthesia, biopsies were taken as described by Dingboom et al (in press). Biopsie from the deep gluteus medius muscle were taken on an imaginary line drawn from the coxal tuber to the sacral tuber, at one third distance from the sacral tuber, perpendicular to the skin. They were taken as deep as possible (until resistance from the iliac wing) because it was expected
that at this site, the percentage type I fibres was high enough to demonstrate age- and / or exercise effects. Biopsies from the superficial semitendinosus were taken on a line drawn from ischiadic tuber to popliteal area, at two third distance from the ischiadic tuber, at a depth that was reached just after the muscle fascia was penetrated. This location was chosen because of the expected homogeneous type II population on this site. A part of each sample (for CS activity determination) was frozen and stored at −80°C. For SDH activity determination, a part of the samples from the gluteus medius muscle were rolled in talcum powder, mounted on cork blocks with the use of OCT embedding medium and oriented in such a way that the fibres could be sectioned transversely. Transverse serial sections (10 µm) were made with a cryostat at −20°C.

**CS measurement**

*Work reagens*  
1.0 ml 5,5'-dithio-2-nitrobenzoaat (DTNB; 1 mM: 0.79 mg DTNB in 2.0 ml 1 M Tris (pH 8.1)), 400 µl acetyl coenzyme A (7.5 mM) and 250 µl Triton X-100 (2 %) was put together in 7.6 ml H2O. The pH was between 7.4 and 9.0.

*Homogenate*  
The muscle biopsy was defrozen in cooled SETH (4.3 % sucrose ; pH 7.4; osmolarity between 280 and 310 mOsm / kg) buffer (10 %: 10 mg muscle tissue in 100 g SETH) and was kept cool on ice. The defrozen sample was cut with a pair of scissors and desintegrated ultrasonically to become a homogenate. To destroy the mitochondria, in order to release the enzyme, 50 µl of the homogenate was frozen (in liquid nitrogen) and defrozen (in a waterbath of 25 °C) twice and kept on ice until the spectrophotometical measurement.

Spectrophotometry measurements of CS activity was done with a spectrophotometer\(^1\) connected to an Olivetti computer, with Ultro spec III (enzyme kinetics) software was used. Duplicate measurements were carried out at 25 °C. The absorbance was measured at 412 nm. The measuring time was set to 7 minutes. The work reagens (925 µl) was put in the calibrated spectrophotometer and equilibrated to 25 °C. Then, the homogenate (25 µl) was added and mixed carefully with the workreagens before measuring the absorption. To establish the zero activity, we followed the absorption for 90 seconds. Next, we added 50 µl oxaloacate (10 mM in 0.1 M Tris (pH 8.0)) and followed the absorption for at least 5 minutes. The CS activity is measured as mU/ml, which is the amount of enzyme, in 1 ml homogenate, that converts 1 nmol oxaloacatate per minute. To standardise the results, the enzyme activity is expressed in mU/mg protein content of the homogenate (protein measurements according to Lowry).

**SDH measurement**

Staining sections (10 µm) for muscle fibre type determination were incubated with monoclonal antibodies (Mab’s) raised against certain myosin heavy chain isoforms (Dingboom *et al.* 1999). Adjacent sections (10 µm) for histochemical SDH staining were incubated, immediately after sectioning (within 24 hours after taking the biopsies), in 37 mM sodium phosphate buffer, 74 mM sodium succinate and 0.4 mM tetra nitro blue tetrazolium (TNBT) at pH 7.6 for 30 minutes at 37 °C; a formazan deposit is formed. The reaction was stopped by immersing the sections in 0.01 N HCL, followed by two rinses.
with water. The sections were mounted in glycerin-gelatin. Stained sections were stored at 4 °C in darkness until measurement (Pool et al. 1979).

In series of Mab- and SDH stained sections of one biopsy, muscle fibres were typed in I, Ila, IId or IId fibres with a certain SDH staining intensity. The muscle fibres were classified into type I, type Ila, type IId, type IId/a on basis of their reactions with the Mabs (Dingboom et al. 1999). The SDH activity of the four different fibre types was determined by measuring the absorbance of the TNBT formazan deposit by means of microdensitometry at 660 nm (van der Laarse et al. 1989). The mean staining intensities of duplicate measurements of five fibres from each type were pooled. The sections were studied with a Leica DMRB microscope fitted with calibrated grey filters. The images were obtained with a 10x objective and a monochrome Charge Coupled Devises camera, connected to a LG-3 frame grabber in an Apple Macintosh computer. Images were analysed using the public domain NIH Image 1.61 program.

Statistics
For both CS and SDH activity, the program for general linear model-repeated measures (SPSS 10 for Windows) was used to test the effects of age and exercise. Time was used as within subject factor and exercise as between subject factor and was defined at four levels (0, 4, 22 and 48 weeks) for CS or at two levels (0 and 22 weeks) for SDH. Analysis of variance (ANOVA) was used to test if there were differences already existing at birth. We analysed the data from 0 to (4 and) 22 weeks to establish the effect of exercise and from 22 to 48 weeks to see if exercise effects persisted. To analyse if the differences between the gluteus medius and the semitendinosus muscle in CS activity at 4 ages were significant, 'Muscle' was used as a second within subject factor.

To test if the CS activity of the gluteus medius and the semitendinosus muscle is correlated, we performed Spearman’s bivariate correlations.

ANOVA was used to test if the four fibre types are different with respect to their SDH activity at birth and at 22 weeks.

In all tests, differences were accepted when p < 0.05.

Results
CS activity
Table 1 shows the results of the CS activity (expressed in mU/mg protein) in the gluteus medius and semitendinosus muscle in the three training groups separately. Figure 1 shows the results of the CS activity in the total group. From this table and figure it can be observed that the standard deviations are rather large.

In general, at all four ages, the CS activity in the gluteus medius muscle is higher than in the semitendinosus muscle (p < 0.001). At birth, the CS activity in the gluteus medius muscle is positively correlated with the CS activity in the semitendinosus muscle (figure 2; correlation 0.63, p < 0.001).
In both muscles there is a statistically significant decrease (p < 0.02) of the CS activity in the postnatal period, but the time course of the decrease differs. In the semitendinosus the CS activity decreases immediately after birth (from 0 to 4 weeks of age); in the gluteus medius it occurs later, in the period from 4 to 22 weeks. After 22 weeks, the CS activity remains stable in both muscles.

An effect of exercise could not be detected.

Table 1. The mean (+/- standard deviation) of the CS activity (expressed in mU/mg protein) from the deep gluteus medius and superficial semitendinosus muscle in the three training groups and the total group at 0, 4, 22 and 48 weeks of age. (boxrest n = 12; training group n = 11; pasture group n = 14). * age effect compared to the previous age-column; p < 0.001.

<table>
<thead>
<tr>
<th></th>
<th>0</th>
<th>4</th>
<th>22</th>
<th>48</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gluteus medius</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Boxrest</td>
<td>158.4 (49.7)</td>
<td>181.1 (58.6)</td>
<td>117.1 (36.7)</td>
<td>114.0 (33.3)</td>
</tr>
<tr>
<td>Boxtraining</td>
<td>171.5 (38.8)</td>
<td>191.4 (74.6)</td>
<td>115.9 (38.0)</td>
<td>123.7 (18.7)</td>
</tr>
<tr>
<td>Pasture</td>
<td>166.7 (78.0)</td>
<td>192.4 (81.9)</td>
<td>119.4 (31.6)</td>
<td>114.9 (30.6)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>165.6 (55.5)</strong></td>
<td><strong>188.3 (71.7)</strong></td>
<td><strong>117.5 (35.4)</strong> *</td>
<td><strong>117.5 (27.5)</strong></td>
</tr>
<tr>
<td><strong>Semitendinosus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Boxrest</td>
<td>104.4 (21.3)</td>
<td>76.5 (23.6)</td>
<td>68.5 (26.6)</td>
<td>72.6 (7.7)</td>
</tr>
<tr>
<td>Boxtraining</td>
<td>115.3 (32.2)</td>
<td>76.0 (28.1)</td>
<td>116.4 (22.5)</td>
<td>101.7 (29.0)</td>
</tr>
<tr>
<td>Pasture</td>
<td>153.9 (70.9)</td>
<td>121.2 (43.3)</td>
<td>81.7 (24.6)</td>
<td>81.8 (12.5)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>124.5 (41.5)</strong></td>
<td><strong>91.2 (31.6)</strong> *</td>
<td><strong>88.8 (24.6)</strong></td>
<td><strong>85.4 (16.4)</strong></td>
</tr>
</tbody>
</table>

**SDH activity**

Figure 3 shows an example of the combination of the results from the muscle fibre classification and the histochemical SDH staining, in order to determine the SDH activity in the four different fibre types.

Figure 4 shows the results of the SDH activities (expressed as the absorbance at 660 nm) in the four different fibre types in the gluteus medius muscle at 0 and 22 weeks of age in the boxrest, training and pasture group and in the three groups together (total). At birth, the SDH activity in type IId fibres is low compared to the other three types. At 22 weeks of age the SDH activity in type IId fibres is also lower than in type IIA and type I fibres, but remains higher than in type IId fibres.
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Fig. 1. The mean and standard deviations (y-error bars) of the CS activity from the gluteus medius and semitendinosus muscle in the total group at 0, 4, 22 and 48 weeks of age (n = 37). * age effect; p < 0.02. ** age effect; p < 0.001.

Fig. 2. Scatter plot of individual CS activities from gluteus medius and semitendinosus muscle that show a statistically significant correlation at birth. Correlation 0.627, p < 0.001.
Figure 3. An example of the combination of the results from the histochemical SDH staining (top) and the muscle fibre classification after immunohistochemical MHC staining (bottom), in order to determine the SDH activity of the four different fibre types. Gluteus medius muscle of a 22 weeks old foal. The type I and type IIa fibres stain dark, the IIad fibres stain intermediate and the type IId fibres stain light.
Fig. 4. The means of the SDH activities in the four different fibre types (grey bar for type I, blocked bar for type IIa, white bars for type IIad, striped bar for type IId) in the gluteus medius muscle at 0 and 22 weeks of age in the boxrest- (n = 6), in the training- (n = 3), in the pasturegroup (n = 4) and in the three groups together (total). * age effect; p < 0.01.
Fig. 5. The means of the SDH activities of the glutus medius muscle in the boxrest- (bold solid lines, n = 6), in the training- (dotted lines, n = 3) and in the pasture group (thin solid lines, n = 4) demonstrated per fibre type. * exercise effect, p < 0.04.
From the graph of the total group (figure 4) we conclude that from 0 to 22 weeks there is a significant age effect \( (p < 0.01) \) i.e. an increase of SDH activity in fibre type I and IIa and a decrease in fibre type IId.

Figure 5 reviews the changes in the mean SDH activities per fibre type and per training group. The increase of SDH activity in type I and IIa fibres appears not to be present in the boxrest group. The effect of age on the SDH activity in fibre type I and IIa seems to be counteracted by the lack of exercise but this is not statistically significant \( (p = 0.069) \). Furthermore, we see that the overall decrease of SDH activity in type IId fibres is caused by the decrease in the boxrest group. This exercise effect is statistically significant \( (p = 0.032) \).

**Discussion**

**CS activity**

**General:** The CS activity in the gluteus medius muscle is higher than in the semitendinosus muscle which is in line with the results of other investigators (e.g. Essen *et al.* 1989) but may also be due to the dissimilarity of the sampling site in both muscles. From the gluteus medius, the biopsies were taken as deep as possible and from the semitendinosus muscle as superficial as possible. From other studies we know that these sites differ in their muscle fibre type composition (aerobic versus anaerobic; e.g. Dingboom *et al.* in press), capillarity (high versus low; unpublished data) and presumed function (postural role plus propulsion versus solely propulsion). The higher CS activity in the gluteus medius corresponds with the high oxidative demand on the deep portion of this muscle. The CS activities of the two muscles show a significant positive correlation at 0 weeks of age. Such correlations were previously found in the same group of animals for muscle fibre type composition and capillarity. Not only do the average values for a number of parameters differ between the two muscles, they also correlate positively across the individuals. This suggest that this variation is genetic. Results from other investigators also point in this direction. For example, (Lopez) Rivero *et al.* (1991, 1996) found evidence that proportions of type I and type II fibres are highly stable within a given horse breed and significantly correlate with genetic factors. Other investigators found that the fibre type composition of human muscle (Simoneau *et al.* 1995), pig muscle (Szentkuti and Schlegel, 1985) and mice muscle (van der Laarse *et al.* 1984) is also mainly determined by the genetical background.

The large standard deviations found for the CS activities in both muscles are also described by others (e.g. Valberg *et al.* 1988). These authors showed that the CS activity in the muscle fibres of different horses could vary as much as twofold.

**Age effect:** The CS activity decreased in the first five months after birth. Apparently, the need for oxidative enzymes decreases in the course of time. A possible explanation is that equine muscles grow excessively during the first months of life and therefore need sufficient enzyme activity to deliver the substrates and energy for the biosynthesis of muscle proteins. After the growth of the fibres has levelled off, the enzyme activity is
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allowed to decrease. In our study group the peak growth rate appears before 20 weeks of age (unpublished data). Similar effects were found for capillarity parameters in the same group of foals (unpublished data). The fact that the CS activity in the semitendinosus muscle decreases immediately after birth while in the deep gluteus medius the decrease occurs later, might be related to the postural role of the latter. It has been stated that foals have a higher glycolytic and a lower oxidative capacity (and therefore higher resting lactate levels) than older horses (Lindholm and Piehl 1974; Essen et al. 1980). Apparently, later in life the oxidative capacity increases again, probably when the horse begins to work.

Exercise effect: The decrease of the CS activity in this study was the same for the three training groups, so an exercise effect could not be demonstrated. Other investigators concluded that training (e.g. Essen-Gustavsson et al. 1989: five-week regime of controlled intensive daily training on a high-speed treadmill) rapidly increases the CS activity in the gluteus medius muscle tissue of (young) adult horses. Therefore, despite the younger age of our horses, the absence of an exercise effect was unexpected. A reliability test on our data revealed that, to be detectable, an exercise induced difference must exceed 14%; possibly a small exercise effect was present but undetectable.

Measurements of whole muscle CS activity do not provide information about the distribution of the oxidative capacity among the fibre types. Different fibre types belong to different motor units (Burke et al. 1973; Nemeth et al. 1986) and their recruitment depends on the activity level of the muscle (Henneman, 1981). It is therefore possible that our exercise regimen led to a fibre-type-dependent effect on the oxidative capacity. It is for this reason that, when a subtle exercise effect must be demonstrated, investigation at the level of the fibres is recommended.

SDH activity

General: The higher oxidative enzyme activity in type I and IIa fibres compared to the activity in IId fibres is an expected finding (e.g. Valberg et al. 1988) but the similar result for the activities in type I and IIa fibres is rather surprising. Although in some studies (e.g. Rivero et al. 1998; rat) other orders are found, in most species, type I fibres have the highest oxidative capacity and type IIa fibres are usually intermediate between type I and IId (or IIB in older studies) (Essen et al. 1975 (human); Essen-Gustavsson and Henrikson, 1984 (human); Reichmann and Pette, 1984 (mouse and rabbit); Valberg and Essen-Gustavsson, 1987 (horse)). Our foals are very young. Maybe, the mature order becomes visible later in life.

Age effect: Further diversification between the fibre types I and IIa on the one and IId on the other hand occurs during growth: increase of the SDH activity per surface unit in type I and IIa fibres and decrease in type IId fibres. It is conceivable, that differential growth of the four types leads to different degrees of ‘dilution’ of the enzyme activity. To check whether this is a possible explanation for the different age effects in the fibre types, the increase in cross-sectional area was compared (table 2, unpublished data). The growth factors of the fibre types did not differ much. Therefore, growth differences cannot be held responsible for the different age effects.
Table 2. The mean cross-sectional area’s (in m²) of the four different fibre types at 0 and 22 weeks of age. The growth factor was calculated from the increase.

<table>
<thead>
<tr>
<th>Type</th>
<th>0</th>
<th>22</th>
<th>Growth factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type I</td>
<td>351.7</td>
<td>1256.4</td>
<td>3.6</td>
</tr>
<tr>
<td>Type IIa</td>
<td>334.9</td>
<td>1291.4</td>
<td>3.9</td>
</tr>
<tr>
<td>Type IIad</td>
<td>386.8</td>
<td>1573.1</td>
<td>4.1</td>
</tr>
<tr>
<td>Type IIId</td>
<td>797.0</td>
<td>2983.4</td>
<td>3.7</td>
</tr>
</tbody>
</table>

Table 3. VO2max and cross-sectional area (CSA) from the four different fibre types of the gluteus medius muscle at 22 weeks of age. Determination VO2max from the SDH activity; thickness of the slide: 10 μm; incubation time: 1800 seconds. (van der Laarse et al. 1998)

<table>
<thead>
<tr>
<th>SDH activity (abs. 660 nm)</th>
<th>Absorbance . m². s⁻¹</th>
<th>VO2max</th>
<th>CSA (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type I</td>
<td>0.30</td>
<td>1.67 . 10⁻⁵</td>
<td>0.10</td>
</tr>
<tr>
<td>Type IIa</td>
<td>0.30</td>
<td>1.67 . 10⁻⁵</td>
<td>0.10</td>
</tr>
</tbody>
</table>
The type I and IIa fibres become more and the type IIId fibres less oxidative. Type IIId fibres occupy the largest relative area in the deep gluteus medius muscle (55 – 59 %), so their oxidative capacity contributes most to the results for the whole muscle tissue. The decrease of the earlier mentioned CS activity is in line with the decrease of the SDH activity in the type IIId fibres.

Van der Laarse et al. found a linear relationship between the SDH activity (expressed in absorbance units per m per second of incubation time) and the maximum velocity of oxygen consumption (VO$_{2\max}$) (van der Laarse et al. 1989). Furthermore, they described a hyperbolic relationship between VO$_{2\max}$ and the cross-sectional area of the muscle fibres (van der Laarse et al. 1998). We determined for our foals the VO$_{2\max}$ in relation to the cross-sectional area of the four different fibre types at 22 weeks of age (table 3) and concluded that the VO$_{2\max}$ is relatively low. This means that, at 22 weeks, the fibres are still immature and it can be expected that, in the course of age, the CSA and / or oxidative capacity will increase.

Exercise effect: Previous studies on the same group of animals have shown that the exercise did not change the muscle fibre type composition (Dingboom et al. in press). However, an effect of (the lack of) exercise on the development of the SDH activity from 0 to 22 weeks of age (further decrease in the low oxidative IIId fibres) was found in the population of type IIId fibres. Apparently, this fibre type is the most sensitive for exercise regimen. When movement was allowed (training and pasture group), the oxidative capacity in these fibres remained stable. In case of restricted movement, the oxidative capacity of type IIId fibres declined, possibly because they were not recruited sufficiently (Henneman, 1981).

We conclude that the oxidative capacity of the locomotory muscles of horses decreases during the first postnatal months and this decrease is stronger when movement is restricted. This subtle effect of (non) exercise could only be made visible with the method which analyses the muscle at the level of the muscle fibres, and not with biochemical assessment of CS activity of the muscle tissue.

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References


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